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THE FOSSIL RECORD OF TADPOLES

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Abstract: Anurans are characterized by a biphasic lifecyle, consisting of radically different larval ("tadpole") and adult ("frog") morphs. Although the fossil record for tadpoles is more limited compared to the record for frogs, it is more extensive and informative than generally appreciated. The tadpole fossil record consists exclusively of body fossils, often in the form of skeletons with associated soft tissues. Tadpole fossils are known from more than 40 localities of Early Cretaceous (late Berriasian – early Valanginian) to late Miocene age: 24 localities (Early Cretaceous and Cenozoic) in Europe, mostly from deposits of middle Eocene – Miocene age in central and southern Germany and northern Czech Republic; four or five localities (Miocene) in Asia; five localities (latest Cretaceous – Miocene) in continental Africa; and three localities each on the Arabian Plate (Early Cretaceous and Oligocene) and in North America (Eocene) and South America (Campanian and Paleogene). Fossil tadpoles are assignable to at least 16 species belonging to 13 genera and five (possibly as many as seven) families. The tadpole fossil record is dominated by pipoids (Pipidae, Palaeobatrachidae, Rhinophrynidae, and basal pipimorphs), but also includes representatives of Pelobatidae and Ranidae, and possibly Pelodytidae and ?Discoglossidae sensu lato. The tadpole fossil record is limited to lacustrine deposits, yet a significant number of localities in those deposits have yielded size series of tadpole body fossils that have proven informative for examining ontogenetic patterns. Other body fossils suggested at various times to be tadpoles are reviewed: the enigmatic Middle Devonian *Palaeospondylus* is a fish; the unique holotype specimen of the basal Triassic proto-frog *Triadobatrachus* is a fully transformed individual, not a metamorphic tadpole; a fossil from the Middle or Late Jurassic of China originally described as a tadpole is an insect; a small skeleton from the Early Cretaceous of Israel originally reported as a tadpole likely is not; and the identity of a fossil preserved within a piece of Miocene Dominican amber and said to be a tadpole hatching from an egg cannot be verified. Extant tadpoles are known to excavate shallow depressions (so-called tadpole nests or holes) in fine-grained sediments at the bottom of shallow, low energy water bodies; however, there is no convincing evidence for those structures or any other traces attributable to the activities of tadpoles in the fossil record.

Key words: Anura, fossils, ontogeny, Salientia, tadpoles, taphonomy

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Introduction

Anurans are unique among living tetrapods in primitively having a biphasic lifecycle characterized by radically different larval ("tadpole") and adult ("frog") body forms (e.g., Wassersug 1975, Duellman and Trueb 1986, Altig and McDiarmid 1999a, Reiss 2002, Handrigan and Wassersug 2007). Although there are numerous variations on the standard tadpole body plan (e.g., Orton 1953, 1957, Starrett 1973, Sokol 1975, Duellman and Trueb 1986, Altig and McDiarmid 1999a, 1999b: fig. 12.1), tadpoles generally can be described as free swimming organisms comprised of a body (head + trunk) that is short (no more than about one-third of the tadpole's total length), somewhat dorsoventrally depressed, and globular or ovoid in form and a tail that is elongate, laterally compressed, bears dorsal and ventral fins that lack internal hard tissue supports, and is supported by an axis of caudal musculature that typically lacks vertebrae. As tadpoles grow, certain bones begin to ossify from cartilaginous precursors in a more-or-less consistent sequence and small hindlimbs emerge, but the forelimbs remain concealed within the body until the start of metamorphosis. During metamorphosis, tadpoles undergo profound structural remodelling culminating in the distinctive frog body form consisting of a short trunk, no tail, elongate hindlimbs and relatively shorter forelimbs, and osteological novelties including a sacrum with expanded diapophyses, a urostyle, an anteriorly-directed and elongated iliac shaft, and fusion of the radius and ulna in the forelimb and of the tibia and fibula in the hindlimb. Although there are numerous exceptions (most notably, various kinds of direct development in which the larval stage is eliminated: e.g., Duellman 1985, 1989, Thibaudeau and Altig 1999), the stereotypical biphasic life cycle summarized above is widespread among living anurans (e.g., Duellman 1985, McDiarmid and Altig 1999a). About three-quarters of the known extant anuran species have a tadpole at some interval

in their development (McDiarmid and Altig 1999a) and tadpoles are widely regarded as being primitive for anurans (e.g., Noble 1925, Orton 1953, 1957, Szarski 1957, Tihen 1965, Lynch 1973, Sokol 1975, Wassersug 1975, Duellman 1985, Cannatella 1999, Roelants et al. 2011; but see Harris 1999).

Studies on extant species are responsible for much of what we know about the structure, development, diversity, ecology, and evolution of tadpoles (e.g., McDiarmid and Altig 1999b, Reiss 2002, Rose 2005, Wells 2007, Roelants et al. 2011). Additionally, morphological features of extant tadpoles have been employed alone or in combination with adult features to infer phylogenetic relationships among anurans (e.g., Orton 1953, 1957, Inger 1967, Kluge and Farris 1969, Lynch 1973, Maglia et al. 2001, Haas 2003, Pugener et al. 2003). Although fossil tadpoles have been known since the early part of the 19th Century (Bronn 1828, Goldfuss 1831), similar contributions from the fossil record have been more limited. This situation is reflected in statements such as: "Studies of tadpole morphology and the evolution of the tadpole as a life-history stage of a frog have been obscured by the paucity of paleontological material" (McDiarmid and Altig 1999a: 3) and "Insights in[to] the morphological diversification of the larval body plan are compromised by the paucity of the anuran fossil record" (Roelants et al. 2011: 8731). While I do not dispute the essence of such statements, the fossil record of tadpoles is more extensive and informative than generally appreciated. Here I provide the first comprehensive, global review of the tadpole fossil record and highlight some of the insights it has provided.

The Tadpole Fossil Record

Occurrences and taxonomic diversity

The fossil record of tadpoles is limited to body fossils; see Table 1 for an annotated summary of published occurrences. Compared to the global fossil record for metamorphosed anurans (see reviews by Sanchiz 1998, Báez 2000, Roček 2000, 2013, Roček and Rage 2000a, Gardner and Rage 2016), the record for tadpoles is more limited in terms of its temporal and geographic extent as well as the number of localities, specimens, and taxa. The fossil record for tadpoles is notably superior to that of frogs in several respects, namely that most tadpole fossils consist of skeletons, many of those preserve soft tissues, and a number of growth series are available (see below). Whereas the fossil record for frogs extends from the Early Jurassic (earliest Triassic for salientians) to Holocene and is founded on hundreds of localities distributed across most continents except Antarctica, the tadpole record is limited to the Early Cretaceous (late Berriasian – early Valanginian) to late Miocene (coincidentally, both the oldest and youngest occurrences are in Spain) and consists of over 40 localities: 24 localities (Early Cretaceous and Cenozoic) in Europe, mostly from deposits of middle Eocene – Miocene age in central and southern Germany and northern Czech Republic; four or five localities (Miocene) in Asia; five localities (latest Cretaceous – Miocene) in continental Africa; and three localities each on the Arabian Plate (Early Cretaceous and Oligocene) and in North America (Eocene) and South America (Campanian and Paleogene). Compared to the over 100 genera and species and several dozen families of anurans known by fossil bones and skeletons of metamorphosed individuals, fewer taxa can be recognized within the fossil tadpole record. As summarized in Table 1, at least 16 species belonging to 13 genera and five (possibly as many as seven) families are known from the tadpole fossil record.

The tadpole fossil record is dominated by pipoids, especially the aquatic families Palaeobatrachidae and Pipidae. The former is represented by tadpoles belonging to several species of *Palaeobatrachus* Cope, 1865, along with indeterminate palaeobatrachids, from the midde Eocene to early-middle Miocene boundary of Europe (one occurrence in Bulgaria, two occurrences in Italy, and multiple occurrences in Czech Republic and Germany). Pipid tadpoles have a more extensive distribution, as follows: Late Cretaceous – Paleogene of continental Africa (three taxa: *Xenopus* (*Libycus*) *hasaunus* Špinar, 1980a in the early Oligocene of Libya; *Eoxenopoides reuningi* Haughton, 1931 at a locality of uncertain Late Cretaceous or Paleogene age in South Africa; and *Vulcanobatrachus mandelai* Trueb, Ross et Smith, 2005 at probable Campanian locality in South Africa); late Oligocene on the Arabian Plate (Yemen: *Xenopus arabiensis* Henrici et Báez, 2001); and in South America (*Llankibatrachus truebae* Báez et Pugener, 2003 during the Eocene-Oligocene and *Saltenia ibanezi* Reig, 1959 during the Campanian, both in Argentina). Also known are: 1) a size series of tadpoles belonging to an undescribed pipid from the early Miocene of Ethiopia; 2) an indeterminate pipid tadpole from an unspecified locality, presumably of Late Cretaceous or Palaeogene age, in the Democratic Republic of Congo; and 3) tadpoles belonging to two monospecific genera of basal pipimorphs from the Early Cretaceous of Israel (Aptian: *Thoraciliacus rostriceps* Nevo, 1968; Hauterivian or Barremian: *Shomronella jordanica* Estes, Špinar et Nevo, 1978). *Shomronella jordanica* is the only fossil anuran species erected on the basis of tadpoles and currently considered diagnosable. An earlier named species, *Probatrachus vicentinus* Peters, 1877, which was erected on the basis of a late stage metamorphic skeleton from the Oligocene of Italy, is now considered a nomen vanum (Sanchiz 1998; see additional taxonomic notes in corresponding entry in Table 1). The third pipoid family, Rhinophrynidae, is documented by metamorphosing tadpoles of *Chelomophrynus bayi* Henrici, 1991 from the middle Eocene of the western USA.

For non-pipoids, tadpoles are known for both pelobatid genera: *Pelobates* Wagler, 1830 from the late Oligocene of Germany (*P.* cf. *decheni* Troschel, 1861) and the Oligocene-Miocene boundary or early Miocene of eastern Turkey (*Pelobates* sp.), whereas the temporally longer ranging *Eopelobates* Parker, 1929 (at least two species: *E. anthracinus* Parker, 1929 and *E. bayeri* Špinar, 1952) is known at a greater number of localities dating from the early Oligocene to middle Miocene in Germany and Czech Republic. Several Oligocene and Miocene localities in Germany also contain indeterminate pelobatid tadpoles. Two other non-pipoid families may also be represented by fossil tadpoles: ?Discoglossidae sensu lato (= Costata Lataste, 1879 comprised of families Alytidae Fitzinger, 1843 + Bombinatoridae Gray, 1825 in current usage; see Frost et al.

Table 1. Reported fossil occurrences of tadpole body fossils, arranged by continent and geologic age.

Age	Locality	Taxa, material, remarks, and selected references
EUROPE[1] (n = 24 localities)		
Late Miocene, Vallesian[2] (MN9–10[3])	Libros, Teruel Basin, northeastern Spain; Libros Gypsum Unit	Ranidae: *Pelophalyx pueyoi* (NAVÁS, 1922) – Size series of at least 72 premetamorphic tadpoles, described and figured in taphonomic study by McNamara et al. (2010); also one tadpole mentioned and figured by Piveteau (1955: 269, fig. 31).
Middle Miocene, Astracian (MN7[3])	Climbach, west-central Germany	Pelobatidae: *Eopelobates* sp. – Premetamorphic tadpole described in account for *Palaeobatrachus goldfussi* TSCHUDI, 1838 (= *Palaeobatrachus diluvianus* (GOLDFUSS, 1831)) and figured as "Frosch-Larven" by Meyer (1860: 165, pl. XX, fig. 6), subsequently re-identified by Špinar (1972: 109) as "eopelobatid" (= *Eopelobates* in current usage).
Early-middle Miocene boundary, Orleanian[4] or equivalent to Central Paratethys stages late Karpatian – early Badenian[5] (MN5[4, 5])	Randecker Maar, southwestern Germany	Palaeobatrachidae: *Palaeobatrachus hauffianus* (FRAAS, 1909) – Three large metamorphosing tadpoles: one reported by (Roček and Rage 2000a: 1344); all three described and figured by Roček et al. (2006); and specimens mentioned and one example figured by Rasser et al. (2013: 438, pl. V, fig. 5). Pelobatidae indet. – Undescribed tadpoles mentioned and one example figured by Rasser et al. (2013: 438, pl. V, fig. 7). Ranidae indet. – Two undescribed, almost completely metamorphosed skeletons mentioned and one example figured by Rasser et al. (2013: 438, pl. V, fig. 8).
Early Miocene, Orleanian[2] or equivalent to Burdigalian[6] (MN3[2])	Hrabák and Nástup mine, both in Most Basin[6, 7] (= North Bohemian Basin[8] or North Bohemian Browncoal Basin[7]), northern Bohemia, Czech Republic; Most Formation[6]	Pelobatidae: *Eopelobates* cf. *anthracinus* PARKER, 1929. – Isolated tadpole bones (parasphenoids, lesser numbers of frontoparietals and vertebrae) reported by Špinar (1972: 219–220).
Early Miocene, Agenian or Orleanian[2] (MN1–4[3] or MN3[4])	Kaltennordheim, central Germany	Pelobatidae: gen. et sp. not specified – Incomplete tadpole skeleton (originally identified as *Palaeobatrachus* ? *rarus* WOLTERSTORFF, 1887) and two isolated parasphenoids (both originally identified as *Palaeobatrachus* sp.) described and figured by Wolterstorff (1887: 127, pl. VII, figs 6 and 7, 8, respectively), all subsequently re-identified as Pelobatidae (genus and species not specified) by Špinar (1972: 37).
Late Oligocene or early Miocene[9] (MN zone not specified)	Trischberg bei [near] Herbon (= Herbon), central Germany	Pelobatidae: *Eopelobates* sp. – Premetamorphic tadpole described in account for *Palaeobatrachus goldfussi* TSCHUDI, 1838 (= *Palaeobatrachus diluvianus* (GOLDFUSS, 1831)) and figured as "Frosch-Larven" by Meyer (1860: 168, pl. XX, fig. 5), subsequently re-identified by Špinar (1972: 109) as "eopelobatid" (= *Eopelobates* in current usage).
Oligocene-Miocene boundary[2], late Agenian or early Orleanian (MN zone not specified)	Odeř, Sokolov Basin, northern Bohemia, Czech Republic	Palaeobatrachidae: *Palaeobatrachus* sp. – Two tadpoles mentioned as Palaeobatrachidae (genus and species not specified) by Špinar (1972: 24).

[1] European portion of table excludes reports of fossil tadpoles from unspecified Tertiary localities in "Rheinischen Braunkohle" (= "Rhine browncoal or lignite") or Rhön region of Germany (e.g., Meyer 1860, Wolterstorff 1886, 1887) and some papers that simply mentioned previous reported occurrences (e.g., Laube 1901). Maps presented by Vergnaud-Grazzini and Hoffstetter (1972: fig. 2), Mlíkovský (1992: figs 2, 3), and Wuttke et al. (2012: fig. 7) depict geographic locations for most of the listed Tertiary tadpole localities. Špinar (1972: text-fig. 1) and Walther and Kvaček (2007: text-fig. 1) provided more detailed maps depicting Tertiary frog and tadpole localities in the Czech Republic and adjacent portion of southeastern Germany.
[2] Sanchiz (1998).
[3] Mlíkovský (2002).
[4] Database of Vertebrates: Fossil Fish, Amphibians, Reptiles, Birds (fosFARbase) at www.wahre-staerke.com; accessed 15 May 2016.
[5] Rasser et al. (2013: fig. 1).
[6] Kvaček et al. (2004: table 1).
[7] Age and stratigraphy follows Kvaček and Walther (2004), Kvaček and Teodoridis (2007), and Kvaček et al. (2014). Historically, an Oligo-Miocene age was favored for many of the Czech fossil tadpole localities (e.g., Špinar 1972).
[8] Špinar (1972).
[9] Wuttke et al. (2012: fig. 7 caption).

Age	Locality	Taxa, material, remarks, and selected references
Late Oligocene, Chattian (MP30[2–4])	Rott, west-central Germany	Palaeobatrachidae: *Palaeobatrachus* sp. – Part and counterpart of premetamorphic tadpole[10] figured by Wuttke (1996a: fig. 8.5). That same specimen previously was figured as *Eopelobates* sp. by Wuttke (1989: fig. 6.5) and cited as such by Gaudant (1997: 441). Pelobatidae: *Eopelobates anthracinus* Parker, 1929 – Two tadpoles, one each reported and figured by Maus and Wuttke (2002: 132, fig. 4) and by Roček et al. (2014: 536, fig. 1e). Pelobatidae: *Eopelobates* sp. – Premetamorphic tadpole described in account for *Palaeobatrachus goldfussi* Tschudi, 1838 (= *Palaeobatrachus diluvianus* (Goldfuss, 1831)) and figured as "Frosch-Larven" by Meyer (1860: 167, pl. XXI; reproduced here in Text-fig. 1a), subsequently re-identified by Špinar (1972: 109) as "eopelobatid" (= *Eopelobates* in current usage). Pelobatidae: *Pelobates* cf. *decheni* Troschel, 1861 – Size series of 24 premetamorphic tadpoles described and figured by Maus and Wuttke (2002). Pelobatidae gen. et sp. unspecified. – Incomplete tadpole skeletons (skull and skull + vertebral column): three specimens[11] reported and figured by Bronn (1828: 381–383, pl. IIIa–c) and two specimens reported and figured by Gaudant (1997: 441–442, figs 5, 6E).
Late Oligocene, Chattian or Neochattium[12] (MP30[2])	Orsberg, west-central Germany	Palaeobatrachidae: *Palaeobatrachus* sp. – Metamorphic skeleton reported and figured by Goldfuss (1831: 123, pls. XII, fig. 6) in account for his new species *Rana diluviana* (= *Palaeobatrachus diluvianus* (Goldfuss, 1831)), also described and figured by Meyer (1860: 160, pl. XVIII, fig. 5) in account for *Palaeobatrachus goldfussi* Tschudi, 1838 (= *Palaeobatrachus diluvianus* (Goldfuss, 1831)); generic identification confirmed by Špinar (1972: 108). Premetamorphic tadpole described in account for *Palaeobatrachus goldfussi* Tschudi, 1838 (= *Palaeobatrachus diluvianus* (Goldfuss, 1831)) and figured as "Frosch-Larven" by Meyer (1860: 160–161, pl. XXI, fig. 10), subsequently re-identified as Palaeobatrachidae (genus and species not specified) by Špinar (1972: 109). Tadpole reported and figured by Wolterstorff (1886: 44, 48, pl. IV, fig. 4) as *Palaeobatrachus diluvianus*, subsequently accepted as a member of that genus but not assigned to species by Špinar (1972: 109). The identity of a second tadpole from Orsberg also reported by Wolterstorff (1886: 44, 48, pl. IV, fig. 3) as belonging to *P. diluvianus* and regarded by Špinar (1972: 109) as belonging to *Palaeobatrachus* seems questionable, because judging by Wolterstorff's lithograph the diagnostically important parts of the body are either missing (skull) or badly incomplete (vertebral column). Pelobatidae: *Eopelobates* sp. – Six premetamorphic tadpoles[13] reported and figured by Goldfuss (1831: 123, pls. XII, figs 7–9, XIII, figs 1–3) in account for his new species *Rana diluviana* (= *Palaeobatrachus diluvianus* (Goldfuss, 1831)), subsequently re-identified as *Eopelobates* sp. by Špinar (1972: 108). Remarks: Meyer (1860: 161) mentioned 36 tadpoles from Orsberg deposited in Bonn, but provided no further details.
Late Oligocene, Chattian (MP28[2, 4])	Enspel, west-central Germany	Pelobatidae: *Pelobates* cf. *decheni* Troschel, 1861 – Size series of 88 premetamorphic to late metamorphic tadpoles described and figured by Maus and Wuttke (2002, 2004) and Roček and Wuttke (2010). One tadpole preserving soft tissue included in large scale taphonomic study of diagenetically altered melanin by Colleary et al. (2015: fig. 1W, X). Pelobatidae indet. – One giant, premetamorphic tadpole mentioned and figured by Wuttke (1996b: 231, fig. 4), later described and figured by Roček and Wuttke (2010: 335, fig. 8h). Anura indet. – Two unidentified tadpoles preserving soft tissue, one each examined for taphonomic studies of bacterial biofilms by Toporski et al. (2002: fig. 1) and by Barden et al. (2015: fig. 1a, b).

[10] Figured by Wuttke (1989: fig. 6.5, 1996a: fig. 8.5) as specimen number LACM (Natural History Museum of Los Angeles County) 5770 and its locality was not explicitly stated. The correct specimen number is LACM 129704 (LACM 5770 is the locality number) and the specimen is part of the George Statz collections from Rott (S. McLeod, pers. comm. 2016).

[11] Bronn (1828) was uncertain about the identities of these three fossils and did not recognize them as tadpoles. He compared them both to vertebrates and scorpions, and concluded they could only be regarded as "Skorpionförmigen" (Bronn 1828: 383) or scorpion-shaped. His lithographs of the three specimens (Bronn 1828: pl. III, fig. 11a–c) depicted skeletons with body outlines of premetamorphic tadpoles, and at least the first two of those figured tadpoles were pelobatids.

[12] Mai (1995).

[13] According to Meyer (1860), at least four of these tadpoles also were figured in his "Frosch-Larven" plates, as follows: his pl. XXI, fig. 1 depicts same specimen as Goldfuss' pl. XIII, fig. 1 (Meyer 1860: 164); his pl. XXII, fig. 2 depicts same specimen as Goldfuss' pl. XII, fig. 8 (Meyer 1860: 165; note that his citation of Goldfuss' "Taf. XIII. Fig. 2" must refer to the tadpole drawing labelled with both a Roman numeral "II" and Arabic numeral "8", because the drawing in that same plate labelled with an Arabic numeral "2" is the skull of a metamorphosed palaeobatrachid); his pl. XX, fig. 4 depicts same specimen as Goldfuss' pl. XIII, fig. 2 (Meyer 1860: 166); and his pl. XX, fig. 3 depicts same specimen as Goldfuss' pl. XII, fig. 9 (Meyer 1860: 166). Neither of the remaining two premetamorphic tadpoles illustrated by Goldfuss appears to be depicted in Meyer's monograph.

Age	Locality	Taxa, material, remarks, and selected references
Middle or late Oligocene[14], Chattian[4] (MP zone not specified)	Ponte (= Laverdá), northeastern Italy	Palaeobatrachidae indet. – One late metamorphic skeleton, described and figured by Peters (1877; image reproduced here in Text-fig. 1c) as holotype and only known specimen of *Probatrachus vicentinus* PETERS, 1877. Remarks: Peters (1877) published two versions of the species name: "*Probatrachus* (*vicetinus*)" on p. 680 versus "*Probatrachus vicentinus*" in caption for fig. 1 on p. 682. Name later amended by Portis (1885) to *Palaeobatrachus vicentinus*, and now considered a nomen vanum (Sanchiz 1998: 138) within Palaeobatrachidae. See Martín et al. (2012: 170) for nomenclatural history and comments.
Early Oligocene, Rupelian – early Chattian[15] (MP zone not specified)	"Pirin" Mine, southwestern Bulgaria; Goreshtitsa Formation[15]	Palaeobatrachidae: *Palaeobatrachus* cf. *grandipes* (GIEBEL, 1850) – Four premetamorphic skeletons, described and one example figured by Gaudant and Vatsev (2012).
Early Oligocene, Rupelian[2, 4] (MP21–24[3])	Sieblos, Rhön Mountains, central Germany; "Sieblos-Schichten" or "Sieblos Beds"[16]	Pelobatidae: *Eopelobates* sp. – Premetamorphic tadpole described in account for *Palaeobatrachus gracilis* MEYER, 1857 (= *Palaeobatrachus grandipes* (GIEBEL, 1850)) and figured as "Frosch-Larven" by Meyer (1860: 179, pl. XX, fig. 2), subsequently re-identified by Špinar (1972: 109) as eopelobatid (= *Eopelobates* in current usage). Gaudant (1985) reported an unspecified number of *Eopelobates* sp. tadpoles, then later described and figured two examples[17] (Gaudant 1997: 436–438, fig. 2). Tadpoles mentioned by Schleich (1988: 165) and Martini and Rothe (1993: 47) refer to specimens reported by Meyer (1860) and Gaudant (1985).
Early Oligocene, Rupelian[2, 4] (MP21[4, 18])	Monteviale (= Monte Viale), northeastern Italy; Calcarenti di Castelgomberto Formation[17]	Palaeobatrachidae indet. – Two tadpoles, one early metamorph and one of uncertain relative age, described and figured by Portis (1885) and Pandolfi et al. (in press).
Early Oligocene[5], Rupelian[19] (MP zone may not be reliably known[20])	Varnsdorf, northeasternmost Bohemia, Czech Republic, and Seifhennersdorf, southeasternmost Germany, both in Zittau Basin; Loučeň Formation[4]	Palaeobatrachidae: *Palaeobatrachus* sp. – Tadpoles reported at both localities (Walther 1957, Špinar 1972, Gaudant 1997). From Seifhennersdorf: four examples, including one late stage metamorph, figured by Walther (1957: fig. 5a–c); many other undescribed tadpoles are present in collections of the Museum für Mineralogie und Geologie Dresden (Z. Roček, pers. comm. 2016). Pelobatidae: *Eopelobates* sp.[17] – From Varnsdorf: associated tadpole skull described and figured by Gaudant (1997: 438, figs 3A, 6C). From Seifhennersdorf: isolated parasphenoid described and figured by Gaudant (1997: 438, 440, figs 3B, 6A).

[14] Vergnaud-Grazzini and Hoffstetter (1972).
[15] Gaudant and Vatsev (2012).
[16] Sensu Martini and Rothe (1993).
[17] Identified as "*Eopelobates* ? sp." by Gaudant (1997).
[18] Pandolfi et al. (in press).
[19] Walther and Kvaček (2007).
[20] MP zones reported for Czech tadpole localities probably deserve to be re-evaluated in light of recent palaeobotanical studies in the region (e.g., Kvaček and Teodoridis 2007, Kvaček et al. 2014). From youngest to oldest, those reported MP zone values are: MP21 for Kundratice, Markvartice, and Suletice (Wuttke et al. 2012: fig. 7 caption); MP22 for Bechlejovice (Mlíkovský 2002); and MP23–24 for Varnsdorf and Seifhennersdorf (Mlíkovský 2002).

Age	Locality	Taxa, material, remarks, and selected references
Early Oligocene, Rupelian[7] (MP zones may not be reliably known[20])	Bechlejovice, Markvartice, Kundratice, and Suletice, all in České středohoří Mountains, northern Bohemia, Czech Republic; mostly in Ústí Formation[7]	Palaeobatrachidae: *Palaeobatrachus* sp.[21] – From Bechlejovice (earliest Rupelian[7]): size series ca. 100 premetamorphic to metamorphosing tadpoles, described and figured by Špinar (1963, 1972), Roček (2003), Roček and Van Dijk (2006), and Roček et al. (2006). Also present at Bechlejovice are greater numbers of transformed *Palaeobatrachus* skeletons, pertaining to one or more congeners (see Špinar 1972, Roček 2003). From Markersdorf (= Markvartice in contemporary usage; late Rupelian[7]), two published specimens: 1) a tadpole axial skeleton described in account for *Palaeobatrachus goldfussi* Tschudi, 1838 (= *Palaeobatrachus diluvianus* (Goldfuss, 1831)) and figured as "Frosch-Larven" by Meyer (1860: 161, pl. XIX, fig. 2; image reproduced here in Text-fig. 1b), subsequently re-identified as Palaeobatrachidae (genus and species not specified) by Špinar (1972: 37, 109) and 2) a tadpole reported and figured by Wolterstorff (1886: 44, pl. IV, fig. 10) as *Palaeobatrachus luedeckei* Wolterstorff, 1886 is reliably assignable to *Palaeobatrachus* on the basis of its pronounced otic capsules and its parasphenoid bearing an elongate processus cultriformis and lacking lateral wings, however, the tadpole is too immature to be reliably identified to species. Špinar (1972: 21) also mentioned the presence of numerous tadpoles at Markvartice. From Sulloditz (= Suletice in contemporary usage; late Rupelian[7]), two incomplete tadpole skeletons, both reported in "Froschlarven" account and figured as "Batrachierlarven" by Bieber (1880: 123 and pl. III, figs 3, 9), can be identified as palaeobatrachids on the basis of their free ribs (Z. Roček, pers. comm. 2016); however, the identities of the other five tadpoles from the same locality (Bieber 1880: 121–123, pl. III, figs 4–8) cannot be established from the published descriptions or drawings. Pelobatidae: *Eopelobates* spp. – From Bechlejovice (earliest Rupelian[7]): size series of more than 60 premetamorphic to metamorphosing tadpoles, described and figured by (Špinar 1963, 1972, Roček et al. 2014). Špinar (1972: 219, 222) recognized two tadpole morphs: most belong to his morph "B" and were referred to *E. bayeri* Špinar, 1952, whereas only two tadpoles belong to his morph "A" and were identified as *E.* cf. *anthracinus* Parker, 1929. Bechlejovice also yielded five skeletons and numerous bones of transformed individuals of *E. bayeri*, but none of *E.* cf. *anthracinus* (Špinar 1952, 1963, 1972). From Kundratice (early Rupelian[7]): one premetamorphic tadpole described and figured as "*Eopelobates* ? sp." by Gaudant (1997: 440, figs 3C, 6B). ?Discoglossidae[22] (sensu lato) indet.[23] – From Bechlejovice (earliest Rupelian[7]): one incomplete, early metamorphic tadpole reported and figured by Špinar (1972: 229–230, text-fig. 95B, pl. 182, fig. 3).
Middle Eocene, Lutetian [2] (MP 11[3])	Messel, central Germany; *Tetraedon* facies, Messel Formation[24]	Palaeobatrachidae: *Palaeobatrachus tobieni* (Sanchiz, 1998) – Undescribed tadpoles mentioned by Wuttke (2012b: 30) and one example figured by Wuttke (1988: fig. 156, as "*Messelbatrachus tobieni*").
?Tertiary	Unknown locality in vicinity of Česká Lípa, northern Bohemia, Czech Republic	Anura indet. – Tadpoles mentioned in a brief report by Reuss (1855: 54). It is unknown where this locality was located, if it still exists, or if any of its frog fossils (both tadpoles and adults) were deposited in an institutional collection (Z. Roček, pers. comm. 2016).
Early Cretaceous, late Berriasian – early Valanginian[25]	Santa María de Meir[26], northeastern Spain; La Pedrera de Rúbies Lithographic Limestones[25]	Anura indet. – Undescribed tadpole of unspecified relative age mentioned by Roček (2000: 1309; pers. comm. from B. Sanchiz; also pers. comm. to JDG from B. Sanchiz 2016). Remarks: Metamorphosed anuran skeletons known from the locality are assignable to *Eodiscoglossus santonjae* Villalta, 1954 and *Neusibatrachus wilferti* Seiffert, 1972, neither of which has been associated with the undescribed tadpole.

[21] Here I follow Roček (2003) in conservatively identifying palaeobatrachid tadpoles from Bechlejovic and other Czech localities only to genus, because features useful for differentiating congeners generally are not evident in tadpoles. Špinar (1972) took an even more conservative approach by identifying all palaeobatrachid tadpoles from those localities only to the family level.

[22] Questionably assigned by Špinar (1972) to "Bombinidae", which in the sense used by him included genera currently divided between Alytidae Fitzinger, 1843 and Bombinatoridae Gray, 1825 or equivalent to Discoglossidae sensu lato (e.g., Sanchiz 1998) or Costata Lataste, 1879 (e.g., Frost et al. 2006).

[23] In their review of previous work at Bechlejovice, Kvaček and Walther (2004: 13) erroneously implied that this tadpole fossil had been included by Špinar (1976) in his type description of *Opisthocoelellus hessi* Špinar, 1976. That species is known only by its holotype skeleton, which belongs to a subadult and also was collected at Bechlejovice. The status of *O. hessi* is contentious: Sanchiz (1998: 128) regarded it as a nomen dubium within the alytid genus *Latonia* Meyer, 1843, whereas Roček (2013: 413) considered it a distinct species of the alytid genus *Discoglossus* Otth, 1837. Although the co-occurrence at Bechlejovice of the unique tadpole reported by Špinar (1972) and the postmetamorphic holotype skeleton of *O. hessi* might indicate those specimens belong to the same species (see discussion of this approach in "Taxonomic identifications" section in text), that association has never been formally proposed.

[24] Wuttke (2012b).

[25] Báez and Sanchiz (2007).

[26] Alternate versions for the locality name, with different Spanish or Catalan spellings, include: Santa Maria de Meia (or Meià), Santa Maria de Meya (or Meyá), Pedrera de Rubies (or Rúbies), La Cabrúa, El Reguer, and Pedrera de Meià (B. Sanchiz, pers. comm. 2016).

Age	Locality	Taxa, material, remarks, and selected references
Asia (n = 4 or ?5 localities)		
Early Miocene, late Burdigalian[27]	Shanwang, Shandong Province, eastern China; Shanwang Formation[27]	Ranidae: *Rana* sensu lato indet. – Multiple tadpoles have long been known from the Shanwang biota (e.g., Young 1936, Yang and Yang 1994, Sanchiz 1998, Wang et al. 2008). Young (1936: 193, pl. 1, fig. 2) reported eight tadpoles (relative ages not specified) and depicted a premetamorphic example in his description of the new species *Rana basaltica* Young, 1936. Roček et al. (2011: 512, 514, figs 8, 9) described and figured a size series of 23 tadpoles (none of which appear to be specimens reported by Young (1936)), all conservatively identified as *Rana* sp. Among their 23 specimens, Roček et al. (2011: 514) recognized two tadpole morphs based on differences in outline of the trunk and details of the mouth and eyes, but concluded those differences likely were preservational artefacts. Ranidae: *Rana* cf. *basaltica* Young, 1936 – Late stage metamorphic skeleton of a "froglet" depicted by Roček et al. (2011: fig. 7D).
Oligocene-Miocene boundary or early Miocene[28]	Multiple localities (3 or ?4) in Gürcü Valley, central Anatolia, eastern Turkey[28]	Pelobatidae: *Pelobates* sp. – Size series of 40+ premetamorphic tadpoles described and figured by Paicheler et al. (1978), Wassersug and Wake (1995), Rückert-Ülkümen et al. (2002), and Dubois et al. (2010).
North America (n = 3 localities)		
Middle Eocene, Uintan[29] or early – middle Uintan[30]	Elko, Nevada, western USA; Elko Formation[29]	Anura indet. – Undescribed tadpoles mentioned by Henrici (1994: 157, as pers. comm. from T. Cavendar). Remarks: These undescribed tadpoles were collected from the type locality for the pelodytid (or stem pelodytid sensu Henrici and Haynes (2006)) *Miopelodytes gilmorei* Taylor, 1941 and, potentially, could belong to that species.
Middle Eocene, early Uintan[31]	Battle Mountain, Wyoming, western USA; Wagon Bed Formation[31]	Rhinophrynidae: *Chelomophrynus bayi* Henrici, 1991 – Size series of 18 metamorphosing tadpole skeletons, described and figured by Henrici (1991, 2016). Remarks: Stratigraphically higher in the same quarry is a bonebed that preserves hundreds of isolated bones from at least 19 young adults of *C. bayi* (Henrici and Fiorillo 1993).
Middle Eocene, Bridgerian-Uintan boundary[32]	University of Florida fossil vertebrate locality US068 (Watson II)[33], Fossil Lake Uinta, Uinta Basin, Utah, western USA; Parachute Creek Member[34], Green River Formation	Anura indet. – Part and counterpart of premetamorphic tadpole, part slab described and figured by Gardner (1999) and figured by McDiarmid and Altig (1999c: fig. 1.1); both slabs depicted here in Text-fig. 1e, f. Remarks: The sole tadpole reported from the Green River Formation cannot be associated with any of the rare metamorphosed anuran fossils or the two named species (e.g., see Grande 1984, Gardner 1999, Henrici et al. 2013, Roček et al. 2014) known from other localities in the formation.
Africa and Arabian Plate[35] (n = 8 localities)		
Early Miocene, Aquitanian-Burdigalian boundary[36]	Mush Valley, central Ethiopia[36]	Pipidae: unidentified xenopodine species – Size series of tadpoles, preliminarily reported by Clemens et al. (2015).

[27] Long considered middle Miocene in age (see Roček et al. 2011), radiometric dating by He et al. (2011) yielded a slightly older age of late early Miocene for the Shanwang biota, approximately correlative with MN4 in the middle Orleanian of the European Land Mammal age.

[28] Dubois et al. (2010 and references therein).

[29] Previously considered middle Miocene in age (e.g., Taylor 1941), the Elko Formation (= "Elko Shales") in earlier literature is now dated as middle Eocene and within the Uintan North American Land Mammal age (see detailed discussion by Henrici and Haynes (2006)).

[30] Regional correlation chart presented by Smith et al. (2008: fig. 4) suggests an early – middle Uintan age for the formation.

[31] Henrici (1991, 2016).

[32] Age based on placement of "Bonanza paleofloral site" in regional correlation chart provided by Smith et al. (2008: fig. 3).

[33] Equivalent to University of Florida fossil plant locality UF 18054 as originally reported by Gardner (1999: 457) and the "Bonanza paleofloral site" of Smith et al. (2008) (R. Hulbert and S. Manchester, pers. comm. 2016).

[34] Originally reported by Gardner (1999) as Evacuation Creek Member (sensu Bradley 1931), but better regarded as Parachute Creek Member (sensu Cashion and Donnell 1974) as per contemporary usage (e.g., Grande 1984, 2013).

[35] Except for Mush Valley, ages and locality details follow Gardner and Rage's (2016) recent review of the lissamphiban fossil record from the region.

[36] Pan et al, (2012). Those authors reported an absolute age of 21–22 million years for the fossil-bearing deposits, which equates to the Aquitanian-Burdigalian boundary.

Age	Locality	Taxa, material, remarks, and selected references
Probably late Oligocene, Chattian	Ar Rhyashia, southwestern Yemen; Yemen Volcanic Group	Pipidae: *Xenopus arabiensis* Henrici et Báez, 2001 – Tadpole mentioned by Henrici and Báez (2001: 872); depicted here in Text-fig. 1d.
Early Oligocene, Rupelian	Jabal al Hasawinah (= Jebel al Hasawnah), west-central Libya; Tarab (= Taráb) Formation	Pipidae: *Xenopus* (*Libycus*) *hasaunus* Špinar, 1980a – Several metamorphic tadpoles reported by Špinar (1980a: 344).
Late Cretaceous or Palaeogene (precise age uncertain)	Unspecified crater lake, Democratic Republic of Congo (formerly Zaire); unnamed clastic sequence overlying a kimberlite pipe	Pipidae indet. – One premetamorphic tadpole, mentioned by Báez (1996: 337), and described and figured by Roček and Van Dijk (2006: 119–120, fig. 4V).
Latest Cretaceous or earliest Palaeogene (precise age uncertain)	Banke, Northern Cape Province, western South Africa; unnamed clastic sequence overlying a kimberlite pipe	Pipidae: *Eoxenopoides reuningi* Haughton, 1931 – Unspecified number of undescribed, metamorphic tadpoles mentioned by Haughton (1931: 248). In his more detailed re-description of the species, Estes (1977: 57, 60, 77, figs. 6, 11C) remarked on a few features of the tadpoles and figured several examples. Remarks: The "morphological stages" employed by Haughton (1931: 240–244) document variation in the vertebral column and sacral region of metamorphosed adults (see also Estes 1977: 60–62), and should not be confused with "stages" of tadpole growth.
Late Cretaceous, probably Campanian	Stompoor (= Marydale), Northern Cape Province, west-central South Africa; unnamed clastic sequence overlying a kimberlite pipe	Pipidae: *Vulcanobatrachus mandelai* Trueb, Ross et Smith, 2005 – Size series of 15 premetamorphic to metamorphosing tadpoles, mentioned by Trueb et al. (2005: 535) and described and figured by Roček and Van Dijk (2006: 116, 119, fig. 4A, B, D–K, N, O).
Early Cretaceous, Aptian	Amphibian Hill, western Makhtesh Ramon, southern Israel; Hatira Formation	Basal Pipimorpha: *Thoraciliacus rostriceps* Nevo, 1968 – Size series of 12 premetamorphic to metamorphosing tadpoles, described and figured by Roček and Van Dijk (2006: 113–114, fig. 1A–F); one example depicted here in Text-fig. 1g. Remarks: The same locality yielded a problematic fossil reported as an indeterminate tadpole by Nevo (1956: 1192, fig. 2, 1964: 36, 37, pl. VII); see "Putative tadpole body and trace fossils" section in text.
Early Cretaceous, Hauterivian or Barremian	Wadi el Malih, Shomron or Samaria region, northern Israel (or Palestinian West Bank); Tuff Member, Tayasir Volcanics (= Tayasir Formation)	Basal Pipimorpha: *Shomronella jordanica* Estes, Špinar et Nevo, 1978 – Size series of ca. 270 premetamorphic to metamorphosing tadpoles, described and figured by Estes et al. (1978), Chipman and Tchernov (2002), and Roček and Van Dijk (2006: 114, 116, figs 2, 3A–M, 5); one example depicted here in Text-fig. 1h.
South America (n = 3 localities)		
Middle Eocene – early Oligocene or early Eocene[37]	Pampa de Jones and Confluencia localities, Nahuel Huapi Lake, Neuquén Province, southwestern Argentina; Huitrera Formation[38]	Pipidae: *Llankibatrachus truebae* Báez et Pugener, 2003 – Size series of 12 premetamorphic and metamorphic tadpoles, described and figured in type description by Báez and Pugener (2003: 449–453, figs 10–12). Previously reported in conference abstracts (Báez 1991, 1997) and review papers (Báez 1996: 342, 2000: 1392, fig. 4).
Late Cretaceous, Campanian[39]	Abra El Zunchal[40], Salta Province, northeastern Argentina; Morales Member, Las Curtiembres Formation[41]	Pipidae: *Saltenia ibanezi* Reig, 1959 – Several tadpoles of unspecified relative ages mentioned by Báez (1981: 131, 1996: 338) and Scanferla et al. (2011: 198), and one example (same specimen) figured by Báez (1981: pl. III, figs B, C) and Scanferla et al. (2011: fig. 2E).

[37] Previously both localities were considered middle Eocene – early Oligocene in age (Báez and Pugener 2003). Radiometric dating of Pampa de Jones (type locality for *Llankibatrachus truebae*) supports an earliest Eocene age for that locality (Wilf et al. 2010). Confluencia (located 40 km to the northeast) does not seem to have been radiometrically dated, meaning its age is less well resolved.

[38] Báez and Pugener (2003).

[39] Previously considered Santonian – Campanian (e.g., Báez 1981), subsequent radiometric and palynological work supports a Campanian age (Scanferla et al. 2011 and references therein).

[40] Locality name "Abra El Zunchal" follows (Scanferla et al. 2011: 197); earlier works used the locality name "Alemania" (Báez 1996) or "Alemanía" (Sanchiz 1998).

[41] Scanferla et al. (2011 and references therein).

2006) is known by a single, anteriorly incomplete tadpole from Bechlejovice (early Oligocene), Czech Republic, and Pelodytidae may be represented by undescribed tadpoles from the middle Eocene type locality of *Miopelodytes gilmorei* TAYLOR, 1941 in the western USA. Although neobatrachians account for about 95 percent of the extant species of anurans (Frost et al. 2006), there are just three occurrences of unequivocal neobatrachian tadpole fossils, all dating from the Miocene and within the family Ranidae: late Miocene of Spain (*Pelophalyx pueyoi* (NAVÁS, 1922)); early-middle Miocene boundary of Germany (Ranidae indet.); and early Miocene of eastern China (*Rana* indet. and *Rana* cf. *basaltica* YOUNG, 1936). Finally, taxonomically indeterminate tadpoles are known from the middle Eocene of the western USA and the Early Cretaceous (late Berriasian – early Valanginian) of Spain.

Taxonomic identifications

Identifying extant tadpoles to family, genus, or species can be challenging (e.g., see summary of misidentifications provided by Altig and McDiarmid 1999b: table 12.2). That task is even more difficult for fossil specimens that are flattened into two dimensions and for which diagnostically important features such as coloration, the position of the spiracle, and details of the oral apparatus generally are not well preserved or visible. In this regard, it is historically interesting to note that although Bronn (1828) was the first to document and figure tadpole fossils, he did not recognize them as such (see Table 1, footnote 11). That oversight is understandable, considering that work on extant tadpoles was still in its infancy in the early 19th Century; e.g., see historical summary of extant tadpole research by McDiarmid and Altig (1999a). Credit for identifying the first fossil tadpoles in a scientific publication goes to Goldfuss (1831), who described premetamorphic tadpoles from the upper Oligocene locality of Orsberg, Germany.

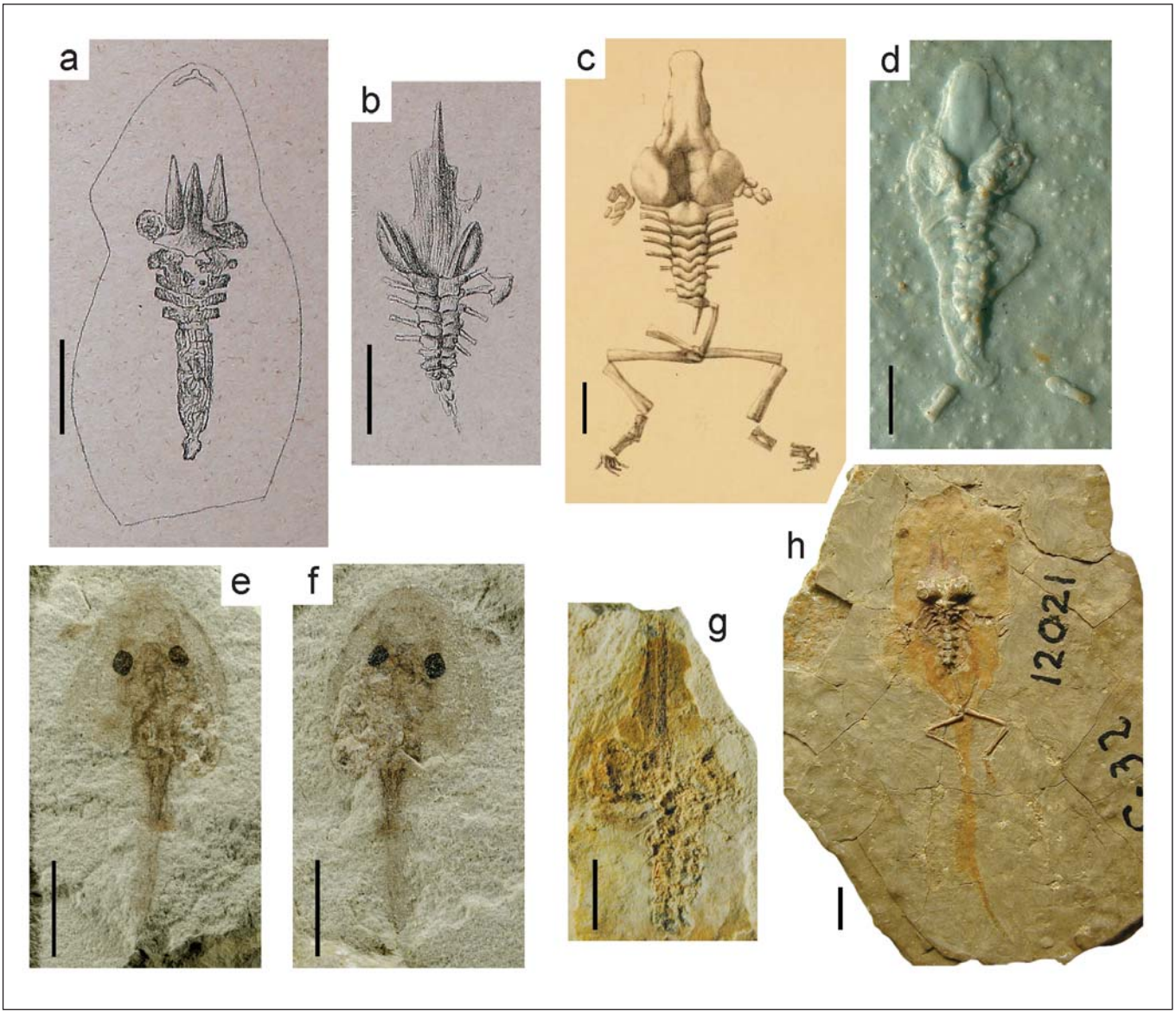
Taxonomic identifications of tadpole fossils generally have relied on three approaches, employed either alone or in combination. Historically, tadpoles routinely were identified on the basis of their co-occurrences with metamorphosed anurans of known taxonomic identities. Taxonomic associations that utilize co-occurrences of tadpoles and adults hinge on the assumption that tadpoles and adults preserved at the same locality belong to the same taxon. While that approach may seem straightforward for localities where one kind of frog and one kind of tadpole are present or where multiple kinds of adults and tadpoles occur at similar ratios (e.g., frog A and tadpole A are ten times more abundant than frog B and tadpole B), such associations potentially can be mis-leading. For example, in early treatments of anurans from Oligocene localities in Germany and Czech Republic, tadpoles often were identified as *Palaeobatrachus* on the basis that adults of that genus were well represented in the same localities (e.g., Goldfuss 1831, Meyer 1860, Wolterstorff 1886, 1887). Suspicions about those identifications were raised by Noble (1931: 496), who noted that two distinctive morphs were present among those "*Palaeobatrachus*" tadpoles. The subsequent discovery of metamorphosed skeletons of *Eopelobates* at some of those localities (Špinar 1952) resulted in a suite of features being recognized for differentiating tadpoles of *Palaeobatrachus* and *Eopelobates* (Špinar 1963: table on p. 203, 1972: table on p. 38); that same list of features can be extended to the familial level, for differentiating palaeobatrachid and pelobatid tadpoles. Using co-occurrences of tadpoles and adults to identify tadpoles does not work for the few localities that have not yielded any fossils of metamorphosed anurans. Those few exceptions are several of the Oligocene-Miocene boundary localities in Turkey that yielded only *Pelobates* sp. tadpoles (Dubois et al. 2010), two Oligocene localities in Italy (Ponte and Monteviale) that yielded rare palaeobatrachid tadpoles (Peters 1877, Portis 1885, Pandolfi et al. in press), and a middle Eocene locality in the Green River Formation of the western USA that yielded a single, indeterminate tadpole (Gardner 1999).

The second approach has been to identify tadpoles using features that are diagnostic for particular taxa (e.g., the suite of features provided by Špinar (1963, 1972) for differentiating palaeobatrachid and pelobatid tadpoles; frontoparietal and vertebral features provided by Maus and Wuttke (2002) for differentiating *Pelobates* and *Eopelobates* tadpoles). The third approach has been to use taxonomically identifiable individuals at the end of a growth series to identify less diagnostic tadpoles farther back in the series. With a sufficiently large or well-preserved sample, it may be possible to trace backwards through a size series and associate younger tadpoles with older, taxonomically identifiable individuals. This approach obviously is feasible only in situations where a growth series is available that culminates in metamorphosed individuals or, in the case of *Shomronella jordanica*, later stage tadpoles that are sufficiently diagnostic.

Regardless of which approach is used, taxonomic identifications are easiest for later stage tadpoles, especially metamorphic ones, because those are beginning to exhibit many of the osteological features that are diagnostic for metamorphosed individuals of the taxon. In lacking many or all of those diagnostically important features, earlier stage tadpoles are more challenging to identify to genus or species. In recognition of the difficulties inherent in identifying tadpoles to lower taxonomic levels, some authors have conservatively elected to identify tadpoles only to the familial or generic level. For example, in their respective studies of growth series of palaeobatrachid tadpoles from Bechlejovice (early Oligocene, Czech Republic), specimens were identified as Paleobatrachidae sp. by Špinar (1972) and as *Palaeobatrachus* sp. by Roček (2003). Similarly, most of the ranid tadpoles documented by Roček et al. (2011) from Shanwang (early Miocene, China) were identified as *Rana* indet.

Taphonomy and its paleoecological and evolutionary implications

All reliable reports of tadpole fossils are in fine-grained, freshwater lacustrine deposits. Unfortunately, lacustrine deposits are relatively uncommon in the geological record, and they become increasingly scarce farther back in the rock record. For example, Picard and High (1972: fig. 1) showed that about 85 percent of 242 lacustrine deposits known for the western USA were formed during the Cenozoic. Similarly, 12 of the 19 lacustrine Lagerstätten tabulated by



Text-fig. 1. Examples of tadpole body fossils. All specimens are oriented with head (anterior end) towards top of figure. Developmental stages estimated for most using the Nieuwkoop and Faber (1967) system (abbreviated as "NF"). Images at different magnifications; vertical scale bars are all 5 mm. a – *Eopelobates* sp. (Pelobatidae), institutional collection number not reported; early Oligocene, Rott, west-central Germany: early premetamorphic tadpole, ~ NF stage 52, axial skeleton plus body outline (tail portion not shown) and mouthparts, in ventral view. Image is lithograph reproduced from Meyer (1860: pl. XXI, fig. 5). Scale bar estimated from *Eopelobates* tadpoles at similar developmental stages depicted by Roček et al. (2014: fig. 1d, e). b – *Palaeobatrachus* sp. (Palaeobatrachidae), institutional collection number not reported; early Oligocene, Markvartice (= Markersdorf in older literature), northern Bohemia, Czech Republic: early metamorphic tadpole, ~ NF stage 60, axial and pectoral skeleton, in dorsal view. Image is lithograph reproduced from Meyer (1860: pl. XIX, fig. 2). Scale bar estimated from a *Palaeobatrachus* tadpole at similar developmental stage depicted by Roček (2003: fig. 2J). c – *Palaeobatrachus* sp. (Palaeobatrachidae), PMHU (Paläontologisches Museum, Humboldt University, Berlin, Germany) MB.I.107.22.1; middle or late Oligocene, Ponte (= Laverdá), northeastern Italy: late metamorphic tadpole, ~ NF stage 64, nearly complete skeleton (Z. Roček, pers. comm. 2016; but see Sanchiz 1998: 138) preserved as natural cast, in dorsal view. Image is lithograph reproduced from Peters (1877: fig. 1). This is the holotype and only known specimen of *Probatrachus vicentinus* Peters, 1877, now considered a nomen vanum (Sanchiz 1998; see additional taxonomic notes in corresponding entry in Table 1). d – *Xenopus arabiensis* Henrici et Báez, 2001 (Pipidae), CM (Carnegie Museum of Natural History, Pittsburgh, USA) 79029; late Oligocene, Ar Rhyashia, southwestern Yemen: mid premetamorphic tadpole, ~ NF stage 57, axial skeleton, in dorsal view. Image is photograph of rubber peel (i.e., showing bones in positive relief) made from original specimen preserved as a natural mold. Image is photograph courtesy of A. Henrici. e, f – Anura indet., UF (University of Florida, Gainesville, Florida, USA) 143200; middle Eocene, Fossil Lake Uinta, Utah, western USA: early premetamorphic tadpole, approximately Gosner (1960) stage 30, represented only by body outline and soft tissues, preserved on part (e) and counterpart (f) slabs, in dorsal view. Images are photographs, both courtesy of G. Housego. g – *Thoraciliacus rostriceps* Nevo, 1968 (basal Pipimorpha), HUJZ (Hebrew University, Jerusalem, Israel) Th04; Aptian, Amphibian Hill, western Makhtesh Ramon, southern Israel: mid metamorphic tadpole, NF stage 61, axial skeleton, in ventral view. Image is photograph courtesy of Z. Roček. h – *Shomronella jordanica* Estes, Špinar et Nevo, 1978 (basal Pipimorpha), HUJZ (Hebrew University, Jerusalem, Israel) 12021; Hauterivian or Barremian, Wadi el Malih, Shomron or Samaria region, northern Israel (or Palestinian West Bank): late metamorphic tadpole, NF stage 63, virtually complete specimen preserving skeleton, body outline, and soft tissues, in ventral view. Image is photograph courtesy of Z. Roček.

Allison and Briggs (1991: table 4, fig. 3) are of Cenozoic age. It thus is hardly surprising that the tadpole fossil record is so heavily biased towards Cenozoic occurrences (ca. > 80 percent).

The taphonomic bias towards lacustrine deposits also means that the fossil tadpole record likely is heavily (if not exclusively) skewed towards so-called "pond-type" tadpoles adapted for living in quiet water. Consequently, the fossil record is missing the numerous tadpole ecomorphs adapted for other habitats, such ephemeral ponds, flowing water ("stream-type" tadpoles), and isolated pockets of water in more terrestrial or arboreal settings (for a summary of these ecomorphs, see McDiarmid and Altig (1999: table 2.2.)). The combined bias towards tadpole fossils being preserved only in lacustrine deposits and the diminishing number of such deposits from farther back in time means that the fossil record holds little promise for testing either (1) the suggestion that the hypothetical, ancestral tadpole was a pond-type, benthic tadpole similar to those of extant, archaic frogs such as extant alytids and bombinatorids (e.g., Cannatella 1999, Altig and McDiarmid 1999b) or (2) the hypothesis by Roelants et al. (2011) that tadpoles experienced explosive morphological radiations in the Triassic – Early Jurassic and around both the Late Jurassic-Early Cretaceous and Late Cretaceous-Paleogene boundaries.

Most tadpole fossils are articulated or associated skeletons (e.g., Text-fig. 1a–d, g, h), preserved either as permineralized skeletons or natural molds, and many of which also preserve body outlines and details of soft internal structures such as cranial nerves and blood vessels (e.g., Text-fig. 1h). Some specimens consist only of isolated bones (e.g., skull and vertebrae reported by Špinar (1972) from the lower Miocene Hrabák and Nástup mine localities in Czech Republic) or are body fossils that lack any bony tissue and, instead, preserve only soft tissues (e.g., Text-fig. 1e, f). Whereas fossil tadpoles generally are preserved in dorsal or ventral aspect (e.g., all examples depicted here in Text-fig. 1) owing to the dorsoventrally depressed body characteristic of pond-type tadpoles, some of the tadpoles reported by McNamara et al. (2010: see figs 1A–C, E, 2) at Libros are preserved in lateral or lateral-oblique orientations. The role played by biofilms and geochemical processes in preserving soft tissues of tadpoles is an active area of research (Toporski et al. 2002, McNamara et al. 2010, Barden et al. 2015, Colleary et al. 2015).

The numbers of tadpole fossils recovered from a given locality varies considerably, from just one to several hundred; the most extreme example being the Lower Cretaceous (Hauterivian or Barremian) locality of Wadi el Malih, Israel, which has yielded over 250 tadpoles of *Shomronella jordanica* and a single conspecific specimen interpreted as either a late metamorphic tadpole (Chipman and Tchernov 2002: 91) or an early postmetamorphic "froglet" (Roček and Van Dijk 2006: caption for fig. 3N). Chipman and Tchernov (2002) argued that the absence (or near absence) of metamorphosed individuals within the *Shomronella* assemblage was because adults were terrestrial; if correct, that would be the geologically oldest record for terrestriality within Pipimorpha. Conversely, several richly fossiliferous lacustrine deposits containing fossils of metamorphosed anurans are curiously deficient in tadpole fossils. For example, tadpoles have not been reported from the Eocene localities of Eckfeld and Geiseltal in Germany (e.g., Wuttke 2012a), whereas just one tadpole has been reported from the paracontemporaneous Green River Formation in the western USA (Gardner 1999). It is unknown why tadpole fossils are absent or scarce from such deposits.

Taphonomic interpretations for accumulations of tadpole fossils have been presented for several Cenozoic localities in Europe (Bechlejovice, Czech Republic: Špinar 1972; Enspel and Rott, Germany: Maus and Wuttke 2002, 2004; Libros, Spain: McNamara et al. 2010) and the Early Cretaceous of Israel (Nevo 1968, Estes et al. 1978, Chipman and Tchernov 2002). Not surprisingly, such studies emphasize that preservation of such small-bodied and delicate animals requires rapid burial in fine-grained sediments (e.g., silts and muds) and anoxic conditions. Nevo (1968: 261) and Špinar (1972: 188) postulated that mass accumulations of frog and lesser numbers of tadpole fossils at Makhtesh Ramon (Aptian, Israel) and Bechlejovice (early Oligocene, Czech Republic), respectively, were the result of volcanic gases poisoning the waters and resulting in mass kills. For *Shomronella jordanica* (Hauterivian or Barremian, Israel), Estes et al. (1978) interpreted the original collection of tadpoles as a mass death assemblage whose members died when their pond dried up. Mass deaths caused by disease have been reported for modern tadpole populations (e.g., Nyman 1986, Márquez et al. 1995, Tiberti 2011), and likely occurred in the past. Other biotic and abiotic phenomena (e.g., algal blooms, changes to water chemistry and oxygen levels) that have been implicated in the paleontological literature with mass deaths of fish (see review by Elder and Smith 1988) also can be expected to have deadly implications for fossil tadpole populations. Although the catastrophic, mass kill scenario is an appealing explanation for how large numbers of fossil tadpoles might come to be preserved in a locality, a pair of more recent studies serves as a good reminder that such assemblages may accumulate in other, less sensational ways. Studies of both the *Shomronella* locality (Chipman and Tchernov 2002) and the lower Miocene *Rana* locality of Libros in Spain (McNamara et al. 2010) demonstrated that tadpole fossils in those localities were not preserved in a single layer, as would expected for a catastrophic event, but instead were dispersed throughout the sequence and, thus, represent time-averaged, attritional assemblages. As pointed out by McNamara et al. (2010), mass death events may still have occurred and contributed some corpses to the depositional basin, but a single "big kill" event need not be the default explanation for every large accumulation of tadpole fossils.

Where tadpole fossils can be identified to genus or species, typically just one taxon is recognized at a given locality. However, six European Cenozoic localities (three each in Germany and Czech Republic) contain tadpoles referable to multiple taxa. Palaeobatrachids and pelobatids co-occur at all six localities: Randecker Maar (early-middle Miocene boundary); Rott and Orsberg (late Oligocene); and Seifhennersdorf, Varnsdorf, and Bechlejovice (early Oligocene). In addition, Randecker Maar also contains a few ranid tadpoles and Bechlejovice contains a single ?discoglossid sensu lato tadpole. Tadpoles belonging to different taxa typically occur at different relative abundances

within and among localities. For example, at Bechlejovice palaeobatrachid tadpoles are most abundant (n = 98: Roček 2003, counts on pp. 598, 600, 602), pelobatid tadpoles are about one-third to one-half as common (n = 32: Špinar 1972, counts on pp. 222–225 versus n = 45: Roček et al. 2014, counts on pp. 531–532), and the ?discoglossid sensu lato taxon is known by just one tadpole (Špinar 1972: 229). The two pelobatid species recognized at Rott and Bechlejovice exhibit different relative abundances: at Rott *E. anthracinus* is rare and *Pelobates* cf. *decheni* is abundant (n = 2 versus 24: Maus and Wuttke 2002, Roček et al. 2014), similarly at Bechlejovice *E.* cf. *anthracinus* is rare and *E. bayeri* is abundant (n = 2 versus 20: Špinar 1972, counts on pp. 222–224). Comparisons with modern tadpole communities, most of which contain multiple taxa and ecomorphs (e.g., Hoff et al. 1999: figs 9.1, 9.2), suggest that fossil tadpole localities preserving multiple taxa in different relative abundances more closely approximate the actual tadpole assemblages of the time within the depositional area, as compared to fossil localities that contain (or are interpreted to contain) just one species.

Growth series and ontogenetic studies

Despite the limited number of fossil tadpole localities, it is striking that a significant percentage of those preserve multiple specimens of varying sizes and at different stages of ontogenetic development. In addition to being useful for making taxonomic identifications of younger tadpoles (see above "Taxonomic identifications" section), growth series of fossil tadpoles also can be informative for documenting patterns and timing of ontogenetic development and for establishing character state polarities and distributions (e.g., Roček 2003).

Because growth and metamorphosis occur along a continuum, tadpole development typically is described using stages based on the sequential and predictable appearance of morphological or osteological landmarks. The two most widely used staging systems for neontological and paleontological studies are by Gosner (1960: based on extant *Incilius valliceps* Wiegmann, 1833 and relies largely on external features) and by Nieuwkoop and Faber (1967: based on extant *Xenopus laevis* Daudin, 1802, relies on both internal and external features, and often abbreviated as "NF"). McDiarmid and Altid (1999c: table 2.1) provided a helpful table correlating stages of the Gosner (1960) and Nieuwkoop and Faber (1967) developmental systems. Over 40 other staging systems have been created by neontologists for specific anuran taxa (see Duellman and Trueb 1986: table 5-6). Not to be outdone, some paleontologists developed their own staging systems to better describe development for particular fossil series. Those include Meyer's (1860) six-stage system for "palaeobatrachids" (i.e. a combination of palaeobatrachids and then-unrecognized pelobatids), Špinar's (1972) separate eight-stage systems (not precisely equivalent to one another) for palaeobatrachids and *Eopelobates*, Henrici's (1991) six-stage system (not equivalent to that of Meyer (1860)) for *Chelomophrynus*, and Chipman and Tchernov's (2002) use of 10 size classes based on femora length for *Shomronella*. In his study of *Palaeobatrachus* development, Roček (2003) used a modified version of the NF system by adding some intermediate stages to better describe developmental changes in that genus. Developmental series described to date for fossil anurans (see summary below) conform well to patterns seen in extant anurans, suggesting the pattern and sequence of those ontogenetic changes are deeply rooted in anuran history.

It is important to emphasize that no fossil tadpole growth series yet reported contains a complete and unbroken sequence of individuals represented every stage of development – instead, they record intervals along the continuum from smaller, posthatchling and premetamorphic individuals, through to almost completely metamorphosed "froglets", and on to fully mature adults. Whereas premetamorphic tadpoles belonging to Gosner's (1960) stages 31–41 are commonly encountered as fossils, both early stage tadpoles (i.e., hatchlings and young larvae or equivalent to Gosner's (1960) stages 20–25 and 26–30, respectively) and, to a lesser extent, metamorphic individuals (Gosner's (1960) stages 42–46) are less common. In their study of growth series of *Pelobates* tadpoles from two Oligocene localities in Germany, Maus and Wuttke (2002: 135, 137) postulated that earlier growth stages were absent because those tadpoles still had cartilaginous (not yet ossified) skeletons that did not readily fossilize. Those authors further postulated that different ecological niches and habitat preferences for early stage tadpoles and metamorphs – they specifically mentioned metamorphs moving into nearshore, shallow waters where their carcasses might become trapped in vegetation and not carried into deeper parts of the lake basin for burial – also acted as ecological and taphonomic filters against those stages being preserved. It also is worth noting that earlier stage tadpoles tend to be small, which is another factor working against them being preserved.

Reported growth series of fossil tadpoles are summarized below. Although not necessarily indicated, many of these series also contain conspecific or congeneric adults.

1) Palaeobatrachidae: *Palaeobatrachus* sp. (early Oligocene, Bechlejovice, Czech Republic) – Eggs + late premetamorphic tadpoles through metamorphosed froglets, n = 171 post-hatchlings, including 98 tadpoles (Roček 2003); Špinar (1972) assigned tadpoles to his stages I (i.e., limbs not distinct) through to VI–VIII (i.e., froglet and adults), whereas Roček (2003) assigned tadpoles to NF stages 58–65+.
2) Pelobatidae: i) *Pelobates* sp. (Oligocene-Miocene boundary or early Miocene, Gürcü Valley, Turkey) – Late premetamorphic to early metamorphic tadpoles, n = 21, Gosner stages 37–42 (Ruckert-Ülkümen et al. 2002). From nearby, paracontemporaneous localities in the Gürcü Valley, Dubois et al. (2010) reported 19 tadpoles of *Pelobates* sp. at comparable stages of development (Gosner stages 36–42), but did not describe those as a growth series. ii) *Pelobates* cf. *decheni* (late Oligocene, Rott, Germany) – Late premetamorphic to early metamorphic tadpoles, n = 24, Gosner stages 38–42 (Maus and Wuttke 2002). iii) *Pelobates* cf. *decheni* (late Oligocene, Enspel, Germany) – Late premetamorphic to early metamorphic tadpoles, n = about 70, Gosner stages 39–42 (Maus and Wuttke 2002). A follow up study by Roček and Wuttke (2010) provided additional details based on a larger sample of 88 specimens from Enspel. iv) *Eopelobates* spp., combined *E.* cf *anthracinus* + *E. bayeri*

(early Oligocene, Bechlejovice, Czech Republic) – Early premetamorphic through metamorphosed froglets; Špinar (1972) assigned 32 tadpoles to his growth stages II (i.e., limbs not distinct) to V (i.e., late stage, premetamorphics) and VIII (i.e., adults), whereas Roček et al. (2014) assigned 45 tadpoles to NF stages 51–66. Note that Špinar's (1972) original sample did not include any metamorphic individuals (his stages VI and VII), whereas Roček et al.'s (2014) study included several metamorphs.

3) Pipidae: i) Undescribed xenopodine species (early Miocene, Mush Valley, Ethiopia) – Early premetamorphic tadpoles to metamorphosed froglets, unspecified number, NF stages ~ 46 onwards (Clemens et al. 2015; M. Clemens, pers. comm. 2016). ii) *Vulcanobatrachus mandelai* (probably Campanian, Marydale, South Africa) – Mid premetamorphic tadpoles to metamorphosed froglets, n = 13, NF stages 54/55–66 (Roček and Van Dijk 2006). iii) *Llankibatrachus truebae* (middle Eocene – early Oligocene or early Eocene, Pampa de Jones and Confluencia, Argentina) – Early premetamorphic tadpoles to a nearly metamorphosed froglet, n = 12, NF stages 51 to 65–66 (Báez and Pugener 2003).
4) Basal Pipimorpha: i) *Thoraciliacus rostriceps* (Aptian, Israel) – Mid premetamorphic to late metamorphic tadpoles, n = 12, NF stages 54 to 63 (Roček and Van Dijk 2006). ii) *Shomronella jordanica* (Hauterivian or Barremian, Israel) – This species is documented by about 270 specimens, ranging from late hatchlings/early premetamorphic tadpoles to late stage metamorphs and, possibly, one early postmetamorph. Studies by Estes et al. (1978) and Roček and Van Dijk (2006) used the NF staging system and broadly agreed in the stages they recognized: Estes et al. (1978) assigned tadpoles to NF stages 46 through to perhaps as old as NF stage 65, whereas Roček and Van Dijk (2006) assigned tadpoles to NF stages 47–50 through to NF stages 63–64 and also recognized one possible early postmetamorphic specimen which, although not explicitly stated by those authors, would correspond to NF stage 65 or 66+. Comparisons of those studies with the intervening one by Chipman and Tchernov (2002) are difficult, because the latter authors used size classes based on femora length. Their study did, however, document an even earlier stage tadpole notable for being tiny (4 mm total length) and not exhibiting any ossified bones.
5) Rhinophrynidae: *Chelomophrynus bayi* (middle Eocene, Wyoming, USA) – Metamorphic tadpoles to metamorphosed froglets, n = 18 tadpoles, tadpoles approximately Gosner stage 42 (= Henrici's stage I) to Gosner stage 44 (= Henrici's stage IV) (Henrici 1991, 2016).
6) Ranidae: *Pelophalyx pueyoi* (late Miocene, Libros, Spain) – i) Early to late stage premetamorphic tadpoles, n = 72, Gosner stages 30 to 41, with tadpoles assigned to groups of stages rather than to individual stages (McNamara et al. 2010). ii) *Rana* sensu lato indet. (early Miocene, Shanwang, China) – Late hatchlings to early metamorphic tadpoles, n = 23, NF stages 43 to 57 (Roček et al. 2011). From the same locality, those authors also figured a nearly metamorphosed froglet as *Rana* cf. *basaltica* (Roček et al. 2011: fig. 7D).

There are several other reports of notable tadpole fossils in the literature. Cenozoic crater lakes in Europe have yielded rare examples of gigantic tadpoles. From Randecker Maar (Miocene, Germany) Roček et al. (2006) reported three metamorphic tadpoles (NF stages 60 to 64) of *Palaeobatrachus hauffianus* (Fraas, 1909) that ranged in total lengths from 100–150 mm; by contrast, normal *Palaeobatrachus* tadpoles at the same developmental stage are about 60 mm in total length. From Enspel (Oligocene, Germany), Wuttke (1996b) and Roček and Wuttke (2010) reported an early or mid premetamorphic tadpole (age estimated based on its poorly developed limbs) of an indeterminate pelobatid that measured 147 mm in total body length or about 1.5 times larger than *Eopelobates* tadpoles of comparable age in the same deposit. For the Randecker Maar tadpoles, Roček et al. (2006) suggested the tadpoles were able to grow to such large sizes because they lived under exceptionally favorable conditions, namely in a permanent, semitropical lake with few predators. That same explanation might also explain the large size for the Enspel tadpole.

A collection of smaller-sized, premetamorphic *Pelobates* sp. tadpoles (Oligocene-Miocene boundary or early Miocene, Turkey) reported by Dubois et al. (2010) included two specimens that each preserved a cluster of enigmatic black dots in the abdomen region. Dubois et al. (2010) considered various explanations for those dots – including whether they might be eggs produced by the tadpoles (see Wassersug's (1975) compelling arguments against paedomorphic tadpoles) – but ultimately, and despite what was implied by the title of their paper, Dubois et al. (2010) concluded that those dot-like structures were unidentifiable.

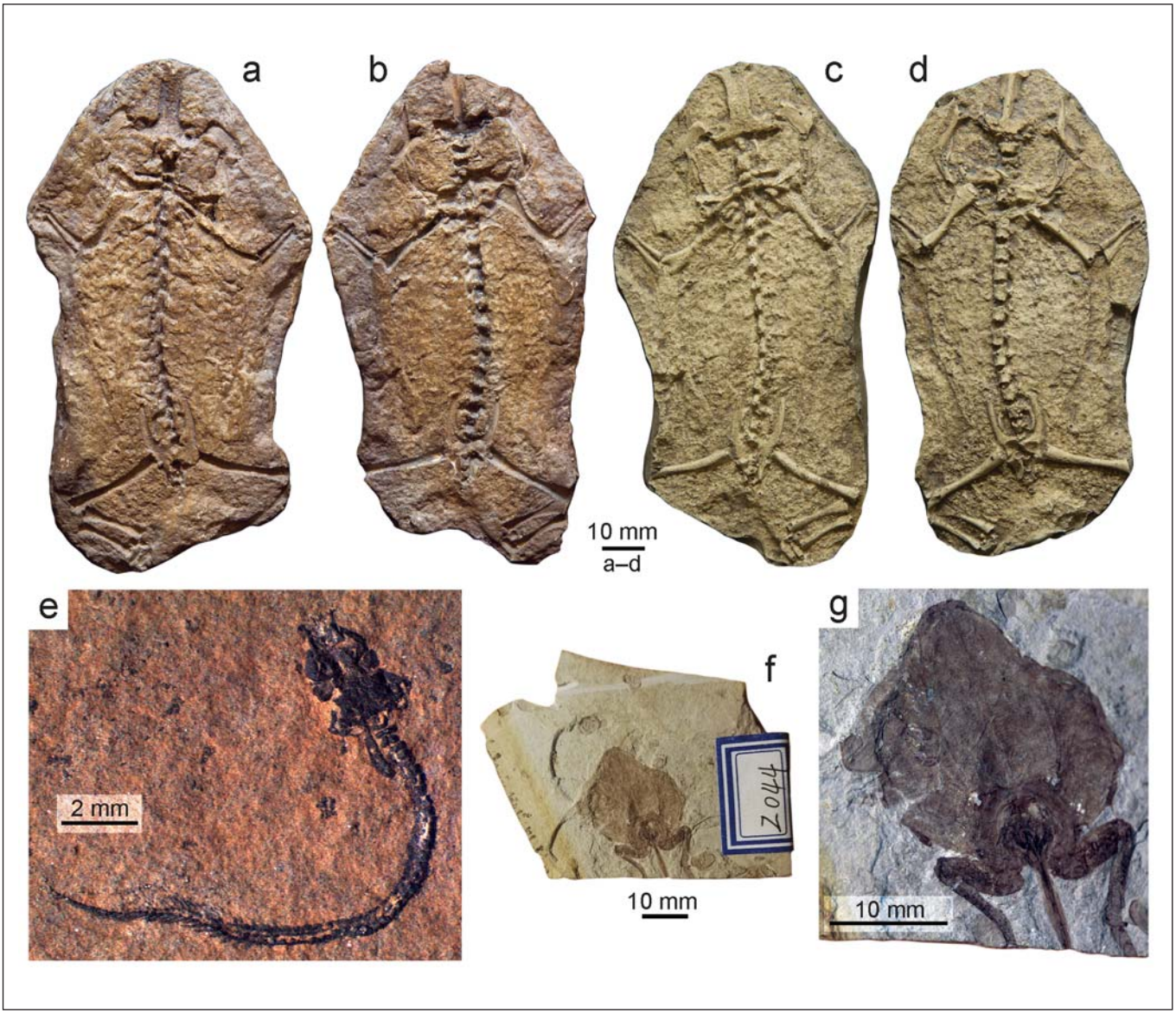
There are several reports of fossil anuran eggs from the Cenozoic of Europe. Those eggs are associated with several adult palaeobatrachids from the early Oligocene of Bechlejovice, Czech Republic (Špinar 1972), several adult pelobatids from the middle Eocene of Messel, Germany (Wuttke 2012a), and one adult ranid from the Pliocene of Willershausen, Germany (Strauss 1967, Špinar 1980b). Dubois et al. (2010: 49) suggested the structures reported as eggs by Špinar (1972) instead might be bubble-like traces caused by gas vesicles. Anuran eggs also have been reported in Miocene amber from the Dominican Republic (see below).

Putative Tadpole Body and Trace Fossils

In addition to occurrences discussed above and summarized in Table 1, additional body fossils and taxa of Middle Devonian to Miocene age have been interpreted as tadpoles and sedimentary structures of Silurian to Jurassic age have been interpreted as trace fossils formed by tadpoles.

Triadobatrachus massinoti (Piveteau, 1936a) from the Early Triassic of Madagascar

The most iconic of the purported tadpole fossils is the holotype and only known specimen of the basal salientian *Triadobatrachus massinoti*; note the original generic name "*Protobatrachus*" was amended by Kuhn (1962). *Triadobatrachus* is from the Early Triassic of Madagascar and it is the geologically oldest lissamphibian fossil. The holotype is challenging to interpret because (1) it consists of an



Text-fig. 2. Examples of putative tadpole body fossils. Photographs are at different magnifications; see corresponding scale bars. a–d – *Triadobatrachus massinoti* (Piveteau, 1936a) (Salientia); basal Triassic, Betsieka, northern Madagascar. Two copies of original holotype specimen, MNHN (Museum National d'Historie Naturelle, Paris, France) F.MAE.126, a split nodule exposing dorsal and ventral surfaces of a nearly complete skeleton preserved as a natural mold; all copies are oriented with head towards top of figure: first pair is replica (epoxy cast) of original fossil showing bones as impressions, in dorsal (a) and ventral (b) views; second pair is negative cast (also epoxy) showing bones in positive relief, in dorsal (c) and ventral (d) views. Interpreted as a metamorphic tadpole by Griffiths (1956, 1963), the unique holotype of *T. massinoti* now is regarded as being from a young post metamorphic individual (e.g., Rage and Roček 1986, 1989). See Rage and Roček (1989), Roček and Rage (2000), and Ascarrunz et al. (2016) for labelled interpretive drawings and other images. Replicas provided by MNHN and deposited in collections of the Royal Tyrrell Museum of Palaeontology (Drumheller, Canada) as TMP 2008.003.0009 (first pair) and TMP 2008.003.0008 (second pair). Photographs courtesy of G. Housego. e – *Palaeospondylus gunni* Traquair, 1890, NHMUK (Natural History Museum, London, England) PV P61846; Middle Devonian, Achanarras Quarry, northern Scotland. Complete skeleton preserved in typical pose and orientation, in this case with body curved, head (directed towards top of figure) and body exposed in dorsal view, and tail twisted such that its left side is exposed and the deeper, ventral portion of tail faces towards top of figure. Note continuous sequence of ring-like vertebrae along central axis of body and tail, and elongate and asymmetric tail fin supported internally by well-developed, bifurcating radials. Suggested to be a tadpole by Dawson (1893) and Jarvik (1980), *Palaeospondylus* is widely regarded as a larval fish, although its affinities remain controversial (e.g., Johanson et al. 2010 and references therein). See Moy-Thomas (1940) and Forey and Gardiner (1981) for labelled interpretive drawings of other specimens. Photograph courtesy of Z. Johanson. f, g – The Daohugou "tadpole", CAGS (Chinese Academy of Geological Sciences, Beijing, China) IG01-705; late Middle or early Late Jurassic, Daohugou, Inner Mongolia. Entire slab (f) and close up (g) of fossil; differences in matrix color are because photographs were taken using different lighting. This soft-bodied fossil lacks any indication of internal skeletal tissue. Originally interpreted by Yuan et al. (2004) as a tadpole body fossil (in dorsal or ventral view, with anterior towards top of figure), consisting of a head and body with prominent hind limbs and a thin, straight tail. Reinterpreted by Huang (2013: see his interpretive line drawing on p. 143) as an incomplete, cicadomorph insect (also in dorsal or ventral view, but with anterior towards bottom of figure), consisting of anteriorly projecting rostrum (= "tail" of tadpole), pro- and mid-thorax portion of body (= "head and body" of tadpole), and forelegs (= "hind legs" of tadpole). Photographs courtesy of Wang X. R and Yuan C. X., and their inclusion here arranged by Wang Y.

incomplete skeleton, missing the anterior end of the snout and most of the hands and feet, and is of moderate size (preserved midline length of about 9 cm), (2) the skeleton is preserved as natural molds or impressions exposed in dorsal and ventral aspect on two halves of a split nodule (Text-fig. 2a–d), and (3) it exhibits a mixture of primitive and derived characters. Although its relevance to the evolutionary history of anurans once was a source of debate (e.g., see historical summaries and discussions by Hecht 1962, Griffiths 1963, Estes and Reig 1973, Roček and Rage 2000b, Rage 2006, and references therein), *Triadobatrachus* now is widely regarded as the sister to all other salientians (e.g., Ford and Cannatella 1993, Báez and Basso 1996, Evans and Borsuk-Białynicka 1998, Rage 2006, Anderson 2007, Marjanović and Laurin 2014, Ascarrunz et al. 2016). The ontogenetic age of the holotype of *Triadobatrachus* also has been debated.

In his treatments of *Triadobatrachus* (as "*Protobatrachus*"), Pivetaeau (1936a, b, 1937, 1955) regarded the holotype skeleton as being from an adult animal. That remained the conventional wisdom until challenged by Griffiths (1956, 1963), who proposed that the holotype was "a tadpole in the later stages of metamorphosis" (Griffiths 1956: 343). In support of that larval interpretation, Griffiths (1963: 275–276) listed the following postcranial and cranial features: tail present, consisting of small vertebrae; no anuran-style sacrum (i.e., lacks diapophyses that are laterally directed, expanded, and incorporate fused sacral ribs); iliac shaft only moderately elongate anteriorly; radius and ulna in forelimbs and tibia and fibula in hindlimbs unfused; femur considerably longer than tibia and fibula; upper jaw elements absent; lower jaw bones weakly sutured; and parietal recess present along midline of the paired frontoparietals. In the latter paper, Griffiths (1963: 276–277) also argued for an aquatic origin for salientians and, under that scenario, softened his stance on the ontogenetic age of the holotype of *T. massinoti* by admitting it could be either a larva or an adult. Orton (1957: 80) quickly embraced Griffiths' (1956) larval interpretation, calling it "an illuminating idea which can account for virtually all of the peculiarities of the specimen". Hecht (1962: 43) disagreed by saying "the interpretation of *Protobatrachus* as a tadpole, is considered unlikely due to the well-ossified nature of the fossil." Perplexingly, but perhaps understandable given his staunch view that *Triadobatrachus* had nothing to do with the evolution of anurans, Tihen (1965: 309–310) dismissed the debate about the ontogenetic age of the holotype by stating "Whether it is a late stage larval or metamorphic individual … or an adult … is not of major import". Despite their detailed examination and reconsideration of the holotype of *T. massinoti*, Estes and Reig (1973) could offer only vague comments about its ontogenetic age, such as "[it was] probably a young stage" (p. 42) and "It may represent a young stage but is probably not far from adult" (p. 49). Their statement that its "interpretation as adult or larva … has not been satisfactorily resolved" (Estes and Reig 1973: 49) was a fair assessment of the situation at the time and remained so for over a decade to come.

Rage and Roček (1986: 257, 1989: 13) argued that the holotype of *T. massinoti* was from a postmetamorphic individual because it has fully developed dermal skull bones, a columella of adult size, ossified carpal and tarsal elements, and presumably both an ossified parahyoid and thyrohyals; note the presence of those hyoid bones recently was corroborated by a micro-CT study of the holotype by Ascarrunz et al. (2016: fig. 4). Rage and Roček (1986: 257, 1989: 13) also disputed the cranial features listed by Griffiths (1956, 1963) by (1) dismissing the weakly sutured lower jaw bones as equivocal evidence for *Triadobatrachus* being a larva, (2) identifying the posterior ends of both maxillae, thereby showing that at least some upper jaw bones were present (Rage and Roček 1989: fig. 2; see also Ascarrunz et al. 2016: fig. 4), and (3) re-interpreting the "parietal recess" of Griffiths (1963: 276) simply as part of the indistinct, dorsal ornament on the frontoparietals. As for the suite of postcranial features listed by Griffiths (1956, 1963), Rage and Roček (1989: 13) countered that those only need be considered larval features if one assumes – as Griffiths implicitly appeared to have done – that *Triadobatrachus* was a primitive anuran. In that interpretation, had the holotype individual lived longer it would have undergone metamorphosis, during which its "larval" features would have transformed into features characteristic of adult or fully metamorphosed anurans. For example, the tail would be lost as the caudal vertebrae fused to form a urostyle, the iliac shaft would grow farther anteriorly, and the radius and ulna would fuse to form a composite radioulna. The alternate interpretation, favored by Rage and Roček (1986, 1989) and tacitly accepted since, is that the postcranial features listed by Griffiths (1956, 1963) are not larval features, but instead are plesiomorphies indicative of *Triadobatrachus* being a basal salientian. Rage and Roček (1989: 13) concluded that the holotype of *T. massinoti* was a postmetamorphic individual, although they noted that the unossified epiphyses of its long bones indicated it likely died before reaching full maturity. The recent micro-CT study by Ascarrunz et al. (2016) revealed no features at odds with the interpretation that the holotype skeleton *T. massinoti* is from a postmetamorphic individual.

Palaeospondylus gunni Traquair, 1890 from the Middle Devonian of Scotland and a "tadpole" from the Early Cretaceous of Israel

Two kinds of small-bodied, moderately elongate, aquatic, and larval-like fossils have been regarded as possible tadpoles. The first of these is *Palaeospondylus gunni* Traquair, 1890, an enigmatic fish-like vertebrate known from hundreds of articulated skeletons, none longer than about 60 mm (Text-fig. 2e). Most examples of this fossil originate from the Achanarras Quarry in the Highlands of Scotland, a Middle Devonian locality that has yielded abundant specimens belonging to about 16 species of jawless and jawed fish (e.g., Trewin 1986, Johanson et al. 2011). Despite being known by hundreds of articulated skeletons, *Palaeospondylus* has proven challenging to study and interpret because all the specimens are small and most are flattened or crushed. Since its discovery, the identity of *Palaeospondylus* has been controversial: at various times it has been regarded either as a larva or an adult, and it has been referred to most major groups of fish (see historical summaries by Moy-Thomas 1940, Forey and Gardiner 1981,

Thomson 1992, 2004, Johanson et al. 2010, Janvier and Sanson 2016).

Palaeospondylus twice has been interpreted as a tadpole-like organism. In their brief treatments of *Palaeospondylus*, Dawson (1893: 186) stated "I should not be surprised if it should come to be regarded either as a forerunner of the Batrachians or as a primitive tadpole", while nearly a century later Jarvik (1980: 218) suggested "*Palaeospondylus* may be related to the anurans". Although Jarvik (1980: 218) went on to suggest that *Palaeospondylus* might also be a larval osteolepiform fish, most of his short discussion on the identity of *Palaeospondylus* focused on comparing it to extant and fossil tadpoles, and also to a problematic fossil discussed below from the Early Cretaceous of Israel. Jarvik (1980: 218) cited two morphological similarities between *Palaeospondylus* and bonafide tadpoles: 1) ring-shaped vertebrae and 2) the external shape of the tail. He bolstered that comparison by including side-by-side drawings of a *Palaeospondylus* skeleton and a Recent anuran tadpole depicted at the same size and in virtually identical poses (Jarvik 1980: fig. 153). Forey and Gardiner (1981: 136) countered that neither of the features cited by Jarvik (1980) are unique to tadpoles and, thus, are hardly convincing for regarding *Palaeospondylus* as a tadpole. There also are significant osteological differences between *Palaeospondylus* and tadpoles. For example, the cranium and branchial skeleton in *Palaeospondylus* are unlike those of tadpoles (cf. Forey and Gardiner 1981: fig. 1 versus Duellman and Trueb 1986: figs 6-6D, E, 6-7B). Further, as was alluded to by Moy-Thomas (1940: 407), whereas the caudal fin in *Palaeospondylus* is supported internally by a series of well-developed, bifurcating radials (see Text-fig. 2e), the caudal fin in tadpoles is a soft structure that lacks any internal supports (cf. Moy-Thomas 1940: text-fig. 6, pl. 25 versus Wassersug 1989: fig. 1). The only resemblances between *Palaeospondylus* and tadpoles are those common to aquatic, larval vertebrates in general: small size; elongate form; tail present and bearing dorsal and ventral fins; simple axial skeleton; and rudimentary girdles and appendages.

Although clearly not a tadpole, the affinities of *Palaespondylus* remain elusive. Work from the 1980s onwards has viewed *Palaespondylus* as a larval fish. Forey and Gardiner (1981) revived the idea that *Palaespondylus* was a larval lungfish, an idea that later received support from Thomson et al. (2003; see also Thomson 2004), who proposed that the co-occuring lungfish *Dipterus valenciennesi* Sedgwick et Murchison, 1829 likely was the adult form. The larval lungfish hypothesis has been contradicted by the subsequent discovery of a small *Dipterus* fossil at the Achanarras Quarry that falls within the size range of *Palaespondylus*, but is morphologically distinct in possessing well-developed tooth plates (Newman and Blaauwen 2008), and by developmental work that showed *Palaespondylus* possesses a suite of features not seen in larval lungfish and also lacks features expected for larval lungfish (Joss and Johanson 2007). Recent histological studies revealed a novel skeletal tissue unique to *Palaespondylus* and suggest its affinities lie within the osteichthyians or bony fishes (Johanson et al. 2010, 2011). Most recently, Janvier and Sanson (2016) revived the idea that *Palaespondylus* might be related to hagfishes by noting general resemblances between the two taxa, although they admitted there are no obvious synapomorphies to support that relationship.

A superficially *Palaespondylus*-like fossil from the Early Cretaceous (Aptian) of Israel also has been interpreted as a tadpole. The fossil was collected from the same locality (Amphibian Hill, at Makhtesh Ramon) that yielded over 200 metamorphosed anuran skeletons of the basal pipimorphs *Thoraciliacus rostriceps* and *Cordicephalus gracilis* (e.g., Nevo 1968, Trueb 1999, Roček 2000, Trueb and Báez 2006, Gardner and Rage 2016) and a dozen tadpole body fossils referable to *Thoraciliacus* (Roček and Van Dijk 2006). The fossil was described and figured twice as a tadpole by Eviatar Nevo: first briefly in his short paper announcing the discovery of frog fossils at Makhtesh Ramon (Nevo 1956: 1192, fig. 2) and then in more detail in his unpublished PhD thesis (Nevo 1964: 36–37, 106–108, pl. VII). Nevo (1964: 36) also mentioned that Makhtesh Ramon had yielded three additional tadpole fossils (all larger and presumably representing later ontogenetic stages), but he did not describe or discuss those further; presumably those three larger specimens were among the 12 bonafide tadpoles described by Roček and Van Dijk (2006) in their ontogenetic study of Cretaceous pipimorphs. Curiously, in his subsequent monographic treatment of anurans from Makhtesh Ramon, Nevo (1968: 258) only mentioned "one tadpole". Based on Nevo's (1956) paper, later workers generally accepted his tadpole identification (e.g., Hecht 1963: 22, Griffiths 1963: 282, Špinar 1972: 164, Jarvik 1980: 218, Metz 1983: 63) and, until the description of the older (Hauterivian or Barremian) size series of *Shomronella* tadpoles by Estes et al. (1978), the Makhtesh Ramon fossil was regarded as the geologically oldest tadpole fossil. Only Estes et al. (1978: 375) questioned whether the fossil was a tadpole, but they did not discuss it further. This *Palaespondylus*-like specimen was not among the 12 bonafide tadpole fossils from Makhtesh Ramon that were available for Roček and Van Dijk's (2006) ontogenetic study (Z. Roček, pers. comm. 2016).

Based on Nevo's (1964) more detailed description, the purported tadpole fossil from Makhtesh Ramon is about 33 mm long. According to Nevo (1964: 36) the specimen "is preserved as a brown limonitic cast and imprint. It consists of a well demarcated head and a long body and tail." Nevo (1964) described the head as roughly rectangular in outline and interpreted in it a number of tadpole-like cranial features, most notably azygous frontoparietals and a sword-like parasphenoid, large otic capsules, a possible spiracle, and possible imprints of a slightly detached beak. A series of small vertebrae extends along the axial column to the end of the tail, and the tail bears what appears to be an anteroposteriorly short, heterocercal caudal fin without any obvious indication of internal supports. No traces of limbs or girdles were reported. Nevo (1964: 107) tentatively suggested the fossil might be a tadpole of the co-occuring anuran *Thoraciliacus*. Jarvik (1980: 218) explicitly compared the Makhtesh Ramon fossil to *Palaespondylus*, and used that comparison to bolster his suggestion that the latter was tadpole. Based on figures published by Nevo (1956, 1964) and setting aside his interpretations of its structure, on the basis of its general structure and proportions the Makhtesh Ramon fossil seems more reminiscent of *Palaespondylus*

than of tadpoles, including tadpoles of *Thoraciliacus* described from Makhtesh Ramon by Roček and Van Dijk (2003). Intriguingly, however, no fish fossils have been reported from Makhtesh Ramon (see Database of Verte-brates: Fossil Fish, Amphibians, Reptiles, Birds (fosFARbase) at www.wahre-staerke.com; accessed 15 May 2016). Another possibility is that the Israeli specimen might be a young larval individual of the salamander *Ramonellus longispinus* Nevo et Estes, 1969, which is known at Makhtesh Ramon by about 16 presumably adult skeletons (e.g., Nevo and Estes 1969, Estes 1981, Gardner et al. 2003, Gardner and Rage 2016). More detailed study of this intriguing Early Cretaceous, tadpole-like fossil is needed to resolve its identity.

The Daohugou "tadpole" from the Middle or Late Jurassic of Inner Mongolia

Over the past few decades, lacustrine deposits of Middle Jurassic to Early Cretaceous age in northern China have produced numerous and often exquisitely-preserved salamander fossils (both larvae and adults) and lesser numbers of metamorphosed anuran fossils that collectively belong to about a dozen species (e.g., Wang 2004, Dong et al. 2013, Gao et al. 2013). Two vertebrate assemblages containing lissamphibians are recognized from those deposits: the Jehol Biota in northeastern China and the slightly older Daohugou Biota in southern Inner Mongolia (e.g., Wang et al. 2010, Pan et al. 2013, Sullivan et al. 2014). Age estimates for the Daohugou deposits have ranged from the Middle Jurassic to Early Cretaceous, but a consensus is emerging that the biota straddles the Middle-Late Jurassic boundary, spanning a restricted interval from the latter part of the Middle Jurassic (Bathonian or Callovian) to the early part of the Late Jurassic (Oxfordian) (e.g., see Wang et al. 2007, Gao et al. 2013, Sullivan et al. 2014, Wang et al. 2016). In contrast to the younger (Early Cretaceous) Jehol Biota, which contains both salamanders and anurans (e.g., Wang 2004, Wang et al. 2010, Dong et al. 2013, Sweetman 2016), fossils of anurans are curiously absent from the Daohugou Biota, although salamander fossils are abundant (see summaries by Gao et al. 2013, Wang et al. 2016).

That situation appeared to change when a tadpole fossil was reported by Yuan et al. (2004) from the Daohugou beds in Ningeng County, Inner Mongolia. The tadpole identification for that fossil initially was accepted without comment by several workers (e.g., Roček et al. 2006: 666, Boucot and Poinar 2010: 169). Sullivan et al. (2014: 253) questionably accepted the tadpole identification, then later in the same paper (p. 280, "note added at press") they concurred with Huang (2013) that the specimen was not a tadpole.

The fossil reported by Yuan et al. (2004) is a small (30 mm in maximum preserved midline length) and flattened body fossil that is preserved as an organic film and lacks any indication of internal hard tissue (Text-fig. 2f, g). The fossil consists of a large portion whose outline resembles a bloated and somewhat lopsided teardrop, the broader end of which bears a pair of considerably smaller, L-shaped projections and between those a narrow, spike-like projection. One side of the teardrop-shaped region appears to be ruptured or torn, and the free ends of all three projections are truncated by one edge of the slab. Yuan et al. (2004) interpreted the fossil as a nearly complete tadpole consisting of a head (the narrow end) and large body, a posteriorly incomplete tail, and distally incomplete hindlimbs. Huang (2013: see his interpretive line drawing on p. 143) reinterpreted the specimen as the anterior portion of a cidacomorph insect that preserves the pro- and mid-thorax portions of the body (= "head and body" of tadpole), the distally incomplete forelegs (= "hind legs" of tadpole), and the anteriorly incomplete rostrum (= "tail" of tadpole) that had been forced anteriorward postmortem. In an unrelated descriptive paper about cicadomorphs from the Daohugou beds, Wang et al. (2007: fig. 1c) provided a close up photograph of the anterior end of a complete specimen that convincingly shows its forelegs and rostrum are indeed similar to the structures that Yuan et al. (2004) interpreted as the hindlegs and tail, respectively, of their "tadpole". The cicadomorph interpretation is attractive because it explains several peculiar aspects of the Daohugou "tadpole" (see Huang 2013, Sullivan et al. 2014), such as the absence of skeletal elements, the unusually broad or bloated "body", the oddly proportioned and jointed "hind limbs, and the narrow and evidently stiff "tail". Rejection of the original tadpole identification for this Jurassic fossil means an undescribed specimen from the Early Cretaceous (late Berriasian – early Valanginian) of Spain currently stands as the geologically oldest tadpole (see Table 1).

A Miocene tadpole and eggs preserved in Dominican amber?

Small-sized tetrapods occasionally are preserved in amber inclusions. Such specimens may be exquisitely preserved and are highly prized for the insights they can provide into taxa living in settings (i.e. subtropical and tropical forests) that otherwise are poorly represented in the fossil record (e.g., Grimaldi 1996, Boucot and Poinar 2010, Penney 2010a). For a fascinating review of forgeries involving extant vertebrates (including metamorphosed anurans) purposely embedded in amber and other materials, see Grimaldi et al. (1994).

At least three authentic lissamphibian fossils have been described from Dominican amber (early-middle Miocene boundary: see review by Penney 2010b). Those are two metamorphosed eleutherodactylid anurans (body of one individual and legs of a second, all preserved in one piece of amber: Poinar and Cannatella 1987) and the body of a metamorphosed plethodontid salamander (Poinar and Wake 2015). Also from Dominican amber, Boucot and Poinar (2010: 157, fig. 211) reported and figured, but did not describe, a tiny fossil identified as a tadpole emerging from an egg. Their small, black and white photograph shows a capsule-like structure (diameter of 1.3 mm, according to the caption) with an opening from which projects a whip-like structure. Although the photograph is suggestive of a tadpole tail emerging from an egg, that identification is impossible to verify solely from the published photograph. Pending a detailed description and comparison of this intriguing fossil, its identification as a tadpole emerging from an egg is best regarded as unproven.

A variety of arboreal frog species lay their eggs and have their tadpoles grow and metamorphose in small pools of water that accumulate in bromeliads, leaf axils, tree holes,

and other parts of plants (e.g., Wells 2007: 576). It is not inconceivable, as Boucot and Poinar (2010: 157) speculated, that some kind of disturbance to one of those arboreal water pools might cause its contents, including eggs or tadpoles, to empty out and become mired in resin. Equally intriguing is another piece of Dominican amber containing a small, egg-like fossil that Boucot and Poinar (2010: 158, fig. 218) figured as the trophic egg of an unidentified anuran. Trophic eggs are unfertilized eggs that females of certain anuran species lay to feed their tadpoles; that kind of parental care is characteristic for some anuran species whose tadpoles live in arboreal water pools (e.g., Wells 2007: 536–540).

Putative trace fossils – tadpole nests or holes

In fine-grained sediments at the bottom of shallow and low energy water bodies, such as in the backwaters of streams and near the margins of ponds, extant tadpoles sometimes excavate small (up to 55 mm in diameter and 15 mm deep), dish-like depressions that have concave bottoms, are subcircular to polygonal in outline, and are bordered by low, convex- or sharp-topped ridges or berms (e.g., Hitchcock 1858, Kindle 1914, Maher 1962, Boekschoten 1964, Bragg 1965, Dionne 1969, Ford and Breed 1970, Cameron and Estes 1971, Opatrny 1973, Black 1974, Willmann 1976, Metz 1983, Hoff et al. 1999; see also on-line article "Tadpole nests, past and present" at http://blogs.scientificamerican.com/tetrapod-zoology/tadpole-nests-past-and-present/; accessed 24 June 2016). These so-called "tadpole nests"[1] or "tadpole holes" (sensu Hitchcock 1858 and Dionne 1969, respectively) are excavated by one or more tadpoles thrashing their tails back and forth immediately above or through loose sediments, presumably while either foraging for food (Kindle 1914, Cameron and Estes 1971, Hoff et al. 1999) or excavating water-filled refuges for themselves as their ponds dry out (Bragg 1965, Ford and Breed 1970). As noted by Black (1974) and Hoff et al. (1999: 221), these structures are not commonly encountered, but appear to be more prevalent in temporary sites, such as ephemeral pools, ditches, and stretches of shallow water along the margins of ponds. Tadpole nests occur in aggregations that may cover several square meters or more, with nests either densely packed together in a honeycomb-like arrangement or more broadly separated in a less regular or seemingly random manner (e.g., Kindle 1914: pl. VIII, fig. 2, Maher 1962: fig. 1, Dionne 1969: fig. 1, Cameron and Estes 1971: fig. 1, Willmann 1976: fig. 1). The construction of tadpole nests appears to be widespread among modern anurans: tadpoles belonging to at least three families (bufonids, hylids, and scaphiopodids) have been observed excavating or in direct association with tadpole nests in both Europe and North America (e.g., Bragg 1965, Ford and Breed 1970, Black 1971, 1974, Cameron and Estes 1971 and references therein, Opatrny 1973, Willmann 1976, Hoff et al. 1999).

Structures interpreted as fossil tadpole nests have been reported since the mid-1800s, from rocks ranging in age from the Silurian to the Jurassic (see historical reviews by Vialov 1964, Cameron and Estes 1971, Metz 1983). In their detailed review and critique of fossil tadpole nests reported in the sedimentological literature up to the early 1970s, Cameron and Estes (1971) concluded that none of those could reliably be attributed to tadpoles. Instead, they re-interpreted those structures either as interference ripple marks formed by waves or currents intersecting at different angles or as natural molds of unknown origin(s) preserved on the underside of bedding planes.

To my knowledge, there has been only one subsequent report of fossil tadpole nests in the literature. Bhargava (1972) described a congregation of small (0.7–1.1 cm diameter, 0.5 cm tall), subcircular, and convex bulges exposed on the undersurface of an Upper Jurassic sandstone slab from India as molds of tadpole nests. Sarjeant (1975) agreed that those secondary structures resembled tadpole nests, but he doubted they had been formed by tadpoles because according to Bhargava (1972: 238) those structures occurred in sediments deposited in "a shallow marine environment". Although extant lissamphibians generally are intolerant of high salt concentrations, the possibility of encountering tadpole nests in brackish sediments cannot be completely dismissed because populations of some extant anuran species routinely breed in brackish waters (e.g., Ruibal 1959, Gordon and Tucker 1965, Beebee et al. 1993, Wells 2007:114–116). In support of his tadpole nest interpretation, Bhargava (1972: 238) quoted an interesting passage from Lull (1958: 61): "we have reports of little frogs of the genus *Rana* [probably a species of *Fejervarya* Bolkay, 1915] hopping about on the flats of a tidal creek opening into Manila Bay, and **two holes made by a crab were seen to full of wriggling tadpoles newly hatched** [my emphasis]. The tadpoles were developing in only slightly diluted sea water." The example cited by Bhargava (1972) does not describe "tadpole nests" in the sense that term had been used since the mid-1800s (i.e., for shallow depressions made by tadpoles in the bottoms of larger water bodies in which they can freely swim about), but instead describes small excavations originally made by other animals and secondarily occupied by tadpoles.

The apparent lack of tadpole nests in the fossil record is hardly surprising, considering that their fossilization potential appears to be minimal. Because those structures are excavated by the fluttering action of tadpole tails, the fine-grained sediments forming the floors and walls are not compacted unlike, for example, fossil tracks formed by feet pressing into and compacting sediments. Modern tadpole nests are ephemeral structures that are readily altered or destroyed by waves, currents, and activities of tadpoles and other aquatic organisms (Black 1971, 1974, Cameron and Estes 1972, Opatrny 1973). Tadpole nests would seem to have little chance of being preserved in an aqueous setting.

[1] I follow the recommendation of Cameron and Estes (1971) in using "tadpole nests" as the term that is both valid by definition and has priority over "tadpole holes". Although not noted by Cameron and Estes (1971), the term "tadpole nests" as used here is not to be confused with other kinds of "nests" made by adults of some extant anuran species for protecting their eggs and tadpoles; such structures include small, water-filled pools excavated in mud and "foam nests" (e.g., Kluge 1981, Duellman and Trueb 1986: 75–77, Wells 2007: table 11.1).

Cameron and Estes (1971) observed that in modern settings, the fine-grained and uncompacted sediments supporting tadpole nests are easily resuspended by the slightest water movement. Any influx of water-borne sediments could be expected to erode away or rework tadpole nests before those structures could be blanketed by a protective cap of sediments. Potentially an ash fall might be able to settle through the water column and cover tadpole nests without unduly altering their structure. Tadpole nests exposed by receding waters also are unlikely to be preserved. Ford and Breed (1970) and Cameron and Estes (1971) observed that the fine-grained sediments supporting modern tadpole nests dry and contract relatively quickly when exposed (see Bragg 1965: fig. 17), quickly distorting or destroying the three-dimensional structure of each nest. Additionally, Metz (1986) showed how exposed tadpole nests can promote the growth of mudcracks, which if left unchecked can contribute further to the rapid deterioration of exposed nests.

On the other hand, we should not entirely discount the possibility of tadpole nests being preserved in the fossil record. Metz (1983: 63, fig. 4) documented an instance of modern tadpole nests surviving "a month of wetting and drying, including a two-week period of being completely covered with water". Metz (1986) suggested that the distinctive pattern of radiating mudcracks formed in drying tadpole nests (e.g., Metz 1983: fig. 4, 1986: fig. 2) might be useful for recognizing fossil tadpole nests. The presence of in situ tadpole fossils also could be suggestive for recognizing fossil tadpole nests. Ford and Breed (1970) observed and both Bragg (1965: fig. 17) and Metz (1986: figs 1, 3) depicted modern tadpole carcasses in recently desiccated tadpole nests. To date, no such association has been reported in the fossil record. A final complication in identifying fossil tadpole nests is that other aquatic organisms, such as freshwater shrimp (Black 1974), can create similar depressions in bottom sediments.

Swimming and resting traces comparable to those described for fish (e.g., Stanley 1971, Higgs 1988) conceivably could be made by tadpoles, especially larger- and heavier-bodied individuals such as the gigantic palaeobatrachid and pelobatid tadpoles reported from the Oligocene and Miocene of Germany (Wuttke 1996b, Roček et al. 2003, Roček and Wuttke 2010). I am unaware of any such traces that have been attributed to the activities of tadpoles, either modern or fossil.

Concluding Remarks

"Anuran fossils are rare in the fossil record. Their small size, minimal ossification, and transient existence make their fossilization unlikely." (Chipman and Tchernov 2002: 86)

The above-quoted, opening statement in Chipman and Tchernov's (2002) ontogenetic study of Early Cretaceous tadpoles of *Shomronella jordanica*, nicely summarizes the general impression about the nature of the tadpole fossil record. That trio of limitations can be expanded further by adding the following inter-related points: the fossil record for tadpoles is (1) largely or exclusively (depending on the identity of the possible hatching tadpole in Dominican amber reported by Boucot and Poinar (2010)) restricted to lacustrine deposits, (2) geographically patchy (slightly more than half of the currently known localities are in Europe), (3) temporally constrained (currently reliably known from the basal Cretaceous – Miocene), and (4) samples only one major tadpole ecomorph (i.e., pond-type tadpoles); (5) tadpoles are known for only a fraction (five and possibly as many as seven) of the recognized anuran families; and (6) tadpole fossils are challenging to study. Despite these limitations, here I have documented and attempted to show the tadpole fossil record is better than generally appreciated, in terms of the number of localities and specimens, the quality of specimens, and the information that can be gleaned from those. Although the tadpole fossil record and our understanding of it will continue to be hampered by the limitations noted above, those fossils are critical for being the only direct evidence for the evolution of the highly specialized larval stage of anurans. Future discoveries and descriptions of tadpole fossils, applications of new approaches and techniques for studying those fossils, and integration with neontological studies undoubtedly will provide new insights into fossil tadpoles and their role in the evolutionary history of anurans.

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