Giant pelobatid fossil larva from the middle Miocene of Bulgaria

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Abstract: So far, in Bulgaria several fossils of extinct anuran species have been found, but all seem doubtful. Only two pelobatid remains have been found from the Balkans and the regions – younger species (Late Pleistocene) of the genus *Pelobates* from Serbia and Miocene *Pelobates* sp. from Turkey. The fossil in the current study represents a larva of the genus *Eopelobates*, the first discovery of this genus not only for Bulgaria but for the Balkans as well. This pelobatid larva is gigantic, more than 200 mm in total length. The fossil is found in a diatomitian complex from the middle Miocene.

Keywords: development, extinct, *Eopelobates*, frontoparietal complex, gigantism, skeleton

Introduction

Previously reported fossil anurans from Bulgaria have been discovered from the bituminous argillites (shales) near Brezhani Village, in the south-western part of the country (Stefanov, 1951). The earliest reported taxon was *Rana temporaria fossilis* Stefanov, 1951, which name later was stated by Martín et al. (2012) as nomenclaturally unavailable. From the same locality (Oligocene sediments of the Pirin Mine, in the Brezhani Graben), Gaudant & Vatshev (2012) reported several skeletons of adult anurans, as well as four tadpoles attributed to *Palaeobatrachus* cf. *grandipes* (Giebel, 1851). They also stated that the previously reported taxa (erroneously given by the authors as *Rana temporaria temporaria* Linnaeus, 1758) belonged to the genus *Palaeobatrachus* Tschudi, 1859, but did not provide any arguments about this. The specimen reported by Stefanov (1951) was not included in our study due to the fact that it was not available and virtually lost (personal communication with NT); it was only briefly discussed. Considering the data presented in the original paper (Stefanov, 1951; Fig. 1 and Fig. 2) and pending on the general habitus, including the pointed snout, the divided frontoparietal, elongated ilia and urostyle, shape of the sacral vertebra with posteriorly declined diapophyses, femur and tibiofibula ratio, the specimen

clearly showed its affiliation to the ranid frogs. A more precise taxonomic conclusion would be possible only if the material becomes available.

Previously, pelobatid fossils from the Balkans were reported only from Anatolian Turkey (larva; Rückert-Ülkümen et al., 2002) and Serbia (scapula from an adult specimen; Đurić, 2016). Fossilised species of *Eopelobates* from the region have not been reported to this day.

Material and methods

Locality: The material in this study was found in March–April 2014 near Satovcha Graben region, Western Rhodope Mts, SW Bulgaria, with coordinates N41.631295°, E24.016411° (Fig. 1). In some of its sediments, the richest local paleoflora in Bulgaria was found (Bozukov & Ivanova, 2015). Bozukov (2002) determined the age of the formation as middle Miocene (for more information on the locality see Nel et al., 2016). The composition of the sediment, that contains the fossil of the anuran larva, determines the origin from a diatomitian complex from that epoch. The site corresponds to a large, deep, eutrophic freshwater palaeolake, which also corresponds to the established diatomitian flora (Bozukov, 2002; Bozukov & Ivanova,

Fig. 1. Locality of the fossil anuran remain near Satovcha Village, SW Bulgaria (A); highly compressed diatomic clays of the locality (B).

2015; Simov et al., 2021a, b). This is the first vertebrate fossil found in any of the sediments of the studied locality.

Material: The studied material presents a fossilised skeleton (cranial bones and vertebrae) of a large pelobatid larva, surrounded by fossil leaves (Fig. 3). The fossil is assigned to the collection of the National Museum of Natural History at the Bulgarian Academy of Sciences, Sofia with catalogue number FR 33.

The developmental stages of anuran larvae were defined by Nieuwkoop & Faber (1956). They provided information about the skeletal formation, whereas the

table proposed by Gosner (1960) was mainly focused on external morphological traits. Trueb & Hanken (1992) provided a comparison between the two mentioned tables. For the current study, both schemes were used, but we mostly followed Gosner's stages.

The fossil was photographed with a stereomicroscope STEMI2000-c equipped with a Canon EOS-1300d DSLR camera. The coordinates of the species records were projected on a map with the LAEA Europe projection (ETRS89-extended) and the WGS 84 geographic coordinate system using QGIS 3.16.0 software.

Fig. 2. The fossil of *Eopelobates* cf. *bayeri* giant larva from Satovcha Vill., Bulgaria (catalogue number FR 33) (right) and its bone description scheme (left). Fr – frontals; Para – parasphenoid; PME – posterior median element; Pro – prooticums; Ex – exoccipitals; Ver – vertebrae; Sacr – sacrum.

Results

Description and identification

The fossil consists of several bones, such as parasphenoid, paired frontoparietal bones, posterior median element (behind the parasphenoid), paired prooticum, eight (first five presacral distinguishable) vertebrae and part of the sacrum (Fig. 2). The total length of the fossil is approximately 50 mm. The parasphenoid is 24 mm long and the frontoparietals are approximately 19 mm and 18.5 mm long. The frontoparietal is represented by two halves, which later, along with the posterior median element (Fig. 2), will form the frontoparietal complex during metamorphosis. This tripartite composition is characteristic for the larval *Pelobates* Wagler, 1830 and *Eopelobates* Parker, 1929 (Roček and Wuttke, 2010; Roček et al., 2014). Based on the presence of unpaired (unique trait for *Pelobates* and *Eopelobates*) ossified pars medialis of the parasphenoid, at least stage

40 could be assigned to the described larva (after Gosner, 1960). However, direct comparison of the larval development of some skeletal characters between fossil (Maus & Wuttke, 2004; Roček, 2013) and present pelobatids (Talavera, 1990) should be treated cautiously. A rounded process on the posterior margin of the parasphenoid occurs in all species of Pelobatidae (Roček and Wuttke, 2010). In ventral aspect, the presence of a not well developed, but still present keel on the parasphenoid bone (Fig. 2), is an evidence that this specimen belongs to the genus *Eopelobates*; a keel is present also in *Pelobates* cf. *decheni* Troschel, 1861, but is much more prominent (see Roček and Wuttke, 2010). The general morphology of the parasphenoid bone of our fossil is similar to *Eopelobates bayeri* Špinar, 1952 (see Špinar, 1972; Roček, 2013), a species described from the Hrabák mine near Most and Nástup and the Merkur mines near Kadaň, the Czech Republic (early Miocene). *Eopelobates bayeri* is also the pelobatid with the vastest range in Europe during the Mio-

cene, according to the fossil record. Some differences from *E. bayeri* can be detected as well. The cultriform process of the parasphenoid is wider and leaf-like, more similar to *Eopelobates anthracinus* Parker, 1929 (see Špinar, 1972). Although the caudal end of the parasphenoid bears two protuberances with a slight depression between them, as in *E. bayeri* (Špinar, 1972), in the Satovcha fossil the caudal end is wider. For this reason, the assignment of the current fossil tadpole remains questionable, until adult specimens are discovered. The tadpole could represent an undescribed species of *Eopelobates*. For the purpose of this study, we identify the current fossil larva as *Eopelobates* cf. *bayeri*.

The external structure of the bones of the fossil is very well preserved (Fig. 2). Several vertebrae of the vertebral column are present, the centra of the vertebrae are not fully ossified (Fig. 2). Only the first five presacral vertebrae are clearly distinguishable, the rest are more or less tentatively separated from each other. Most probably there are eight presacral vertebrae. A part of the sacrum is also present, after the eighth vertebra. Roček and Wuttke (2010) summarised that in premetamorphic pelobatid larvae eight presacral vertebrae are present. The authors note that V2, V3 and V4 are provided with perpendicular stout transverse processes, completed with cartilage at their ends. At that stage, the neural arches are not yet fused in the midline and the centra are incomplete. These statements correspond more or less to the vertebrae of the Bulgarian larva.

Systematics

Anura Fischer, 1813

Superfamily Pelobatoidea Bonaparte, 1850

Family Pelobatidae Bonaparte, 1850

Genus †*Eopelobates* Parker, 1929

Species †*Eopelobates* cf. *bayeri* Špinar, 1952

Remarks

During the larval development in *Pelobates fuscus* (Laurenti, 1768), the ossification begins with the frontoparietals (Luther, 1914; Roček, 1980) or parasphenoid in stage 31. However, according to the observations of Smirnov (1992), the paired frontoparietal appears in stage 33 and later, in stage 36, new ossifications (posterior median element, exoccipital and prootic) appear. The subsequent changes could not be observed as no

other elements were preserved in the studied specimen, such as supratemporal on the dorsal roof of the otic capsule (stage 39), septomaxilla, premaxilla and nasal (stages 41–42) (Smirnov, 1992). In *Pelobates syriacus* Boettger, 1889, frontoparietals are also among the first bones to appear in the ontogeny and at least in stage 39 these ossifications are already present (Smirnov, 1992). In *Pelobates cultripes* (Cuvier, 1829), the stages follow a similar pattern (Maglia, 2003), but some species-specific peculiarities are observed. Pars medialis appears in stage 41. In this species, the neural arches of the first seven vertebrae begin to ossify in stage 31, those of vertebrae I–X begin to ossify in stage 35 and most of the neural arches of the presacral vertebrae (I–VIII) connect dorsally via a cartilaginous bridge. The ossification of the hypochord and vertebral centra begin in stage 39. The development of the current fossil corresponds to stage 42 (see Fig. 3 in Maglia, 2003), since the vertebral centra of the first vertebrae (I–V) were not fully ossified (Fig. 2). The incompletely ossified centra correspond to the Gosner's stages between 35 and 42 [after Banbury & Maglia, 2006 for *Spea multiplicata* (Cope, 1863)].

Discussion

Based on the available data, most probably the genus *Pelobates* originates from North America (Roček & Rage 2000). Roček et al. (2014) summarised the oldest records (in geological aspect) of Pelobatidae in Europe (all from the earliest Eocene; MP 7): at Dormaal, Belgium (Duffaud, 2000); at Le Quesnoy (formerly called Creil) and Rians, both in France (Nel et al., 1999; Duffaud, 2000; Rage & Roček, 2003); and at Silveirinha, Portugal (Antunes & Russell 1981; Rage & Augé 2003). Pelobatids are also reported from the MP 10 Prémontré sands. All fossil records are fragmentary bones and because of the fragmentary status, it is not possible to identify them clearly. However, at least some of these specimens probably belong to the genus *Eopelobates* (Roček et al., 2014). *Pelobates decheni* Troschel, 1861 is known from the latest Oligocene (MP 30) of Rott, Germany (Böhme et al., 1982). Two species have been described from the middle Miocene: *Pelobates sanchizi* Venczel, 2004 (MN 6, Hungary; Venczel 2004; MN 4, the Czech Republic; see Ivanov, 2008) and *Pelobates fahlbuschi* Böhme, 2010 (MN 5, Sandelzhausen; Böhme, 2010).

Lutetiobatrachus gracilis Wuttke in Sanchiz, 1998 from the middle Eocene, (lower Geiseltalium) Grube

Messel near Darmstadt, Hessen, Germany can be assigned to the family Pelobatidae based on the structure of the frontoparietal bone (Wuttke, 2012a), although it can be a member of a new, undescribed family (see Roček, 2013).

The genus *Eopelobates* was distributed in North America, Europe and Asia from the Late Cretaceous (Borsuk-Białynicka, 1978) to the Pliocene (Roček et al., 2014). The type species of the genus is *Eopelobates anthracinus* from the late Oligocene (MP 30) of Rott, Germany (Koenigswald et al. 1992). Six species are assigned to this genus: *E. anthracinus* (late Oligocene), *E. bayeri* (early Oligocene–middle Miocene; holotype skeleton from the late Oligocene, NMP Pb 412, described by Špinar (1952, 1972); *E. hinschei* (Kuhn, 1941) (lower Geiseltalian section “Oberes Hauptmittel”, MP 13, middle Eocene holotype skeleton, GMH 1312), and *E. wagneri* (Weitzel, 1938) from the Messel Formation (MP 11, middle Eocene holotype, HLMD-Me 1286; Wuttke, 2012b) (all four species from Europe), and *E. grandis* Zweifel, 1956 (Chadron Formation, Ahern Member; latest Eocene or Chadronian NALMA; South Dakota, USA; Zweifel, 1956) and *E. deani* Roček, Wuttke, Gardner & Bhullar, 2014 (middle Eocene; BHM-123 (original number BHI-123); Roček et al., 2014) (from North America). The two species *E. wagneri* and *E. hinschei* are very similar morphologically and share the same geographic and stratigraphic distribution (middle Eocene, Germany). Without a detailed study, they should/could be considered as valid species for the moment (Roček et al., 2014).

Eopelobates bayeri is the pelobatid species with the vastest range in Europe and is found in Belgium (Smith, 2003), the Czech Republic (Špinar, 1952, 1972), Slovakia (Hodrová, 1981, 1988), Bulgaria (this study) and Russia (Syromyatnikova, 2017). Besides Bulgaria (present study), tadpoles of *Eopelobates* from Europe are found also in the Czech Republic (Bechlejovice; Bellon et al. 1998; Špinar, 1972).

The approximate maximal length of the tadpoles of *Eopelobates* was about 100 mm (Fig. 1j in Roček et al., 2014). A well-preserved giant fossil pelobatid larva (163 mm, stage 41) from the late Miocene was described by Bustillo et al. (2017). The authors stated that this gigantic larva of *Pelobates* was preserved in a diatomite, which was associated with shore vegetation. Data presented in Rückert-Ülkümen et al. (2002) from the Miocene of Turkey give maximal snout-vent length of 44 mm, vs. caudal length of 33 mm (not the same

specimen) for larvae of *Pelobates* sp. Under controlled laboratory conditions, metamorphosis is usually completed within 2–2.5 months after hatching in *P. fuscus*, but some individuals do not metamorphose at all within two years (between 5 and 25 months), being between stages 34 and 43 and having snout-vent length of 28.5 mm (21–34 mm, $n = 23$) (Smirnov, 1992). For *P. syriacus*, tadpoles ($n = 4$) with snout-vent length of 42 mm in Gosner's stage 39 were reported by the same author. Thus, retention of the larval development in *P. fuscus* in the laboratory may be attained under natural conditions in *P. syriacus* (Smirnov, 1992). Even in recent species of *Pelobates*, gigantic tadpoles occur exceptionally and the maximal reported length greatly overpass the commonly attained, e.g. based on a large sampling ($n = 209$), the largest reported tadpole by Siderovska et al. (2001) (stages 34 to 45) was respectively 110.8 mm for *P. fuscus* (stage 39–40) and 104 mm for *P. syriacus* (stage 41). Respectively, the maximal reported lengths for both species were 185 mm and 145 mm (Kuzmin, 2012). For *P. fuscus*, Nöllert (1990) has summarised larval lengths from several localities and gives length from 105 mm to 220 mm. The same author explained that larvae of *Pelobates fuscus insubricus* Cornalia, 1873 can reach maximal length of 140–150 mm. Another exceptional length of 200 mm was reported in Grillitsch et al. (1983) for three-years old, multiple overwintering larvae. The largest ever cited length was 226 mm (Hirschfeld, 1970). Present day larval gigantism has been reported only in few anuran taxa, e.g. *Pelophylax* spp. (Borkin et al., 1984; Covaciu-Marcov et al., 2003; Milto, 2009). Hirschfeld et al. (1970) reported a giant larva (226 mm) of *Lithobates pipiens* (Schreber, 1782) (as *Rana pipiens*), but grown in laboratory conditions. The giant larvae of *Xenopus laevis* Daudin, 1802 lacked thyroid glands and the thyroid hormone that stimulates tail resorption and metamorphosis (Rot-Nikčević & Wassersug, 2003). That is why our fossil (with length of more than 200 mm with the tail; Fig. 3) falls into the concept of giant anuran larvae, with length similar to giant larvae of *P. fuscus* described by Grillitsch et al. (1983). This is one of the largest amphibian larvae ever found.

Environmental conditions could influence and facilitate the prolonged larval development as in the case of *Pelophylax ridibundus* (Pallas, 1771) that inhabit thermal waters where it has been reported to surpass the reported maximal dimensions (Covaciu-Marcov et al., 2003). The largest tadpole of *Pseudis paradoxa* (Linnaeus, 1758) ever reported has a length of 220.5

Fig. 3. Reconstruction of the size and shape of *Eopelobates* cf. *bayeri* giant larva from Satovcha Vill., Bulgaria (catalogue number FR 33). Scale = 5 cm.

mm (Emerson, 1988), coming from a region with little seasonal variation in temperature and day length, with expressed equatorial climate. There are three environmental conditions that make possible for tadpoles to grow large: long-lasting large ponds, warm and wet climate, and the formation of soil rich in clay during the rainy season (creating shelters) (Roček et al., 2006; Fabrezi et al., 2009). These authors describe the favourable conditions for giant tadpoles of the extinct *Palaeobatrachus* and the recent species of *Pseudis* Wagler, 1830.

The climate during the middle Miocene was comparable to the present day in the tropic regions. The analyses of the diatomaceous flora reveal that during that epoch, Satovcha area was a large and deep, eutrophic freshwater paleolake, surrounded by mountain

slopes, where the paleorivers were depositing coenobiotic flora. The richness of the flora suggests humid and warm-temperate to subtropical climate (mean annual temperatures above 15–16°C and rainfalls over 1000 mm). The mixed mesophytic forest of the area was close to the mixed semi-evergreen forests of South-East Asia. That rich flora (containing many different insects along with the frog of *Eopelobates* from this study) was discovered in diatomic clays that had been strongly compressed during the diagenesis (see Nel et al., 2016). Similar to our study, the giant fossil pelobatid larva from Tresjuncos, Spain (Bustillo et al., 2017) was also found in a diatomic clay layer. The authors stated that the location, where the larva was found, was a marshy border of shallow, littoral environment. Apparently, the environmental conditions and the habitat

Fig. 4. Review of the fossil pelobatid records of Europe (see Appendix I). The Bulgarian record is from the present study.

(shallow freshwaters with clay) of Tresjuncos, Spain during the late Miocene were very similar with the environmental conditions of Satovcha Vill., Bulgaria during the middle Miocene. The coexisting ecological complexes (warm and wet climate, large freshwater wetland and rich diatomic clay) correspond to the conditions that would have been suitable for tadpole gigantism, as described by Roček et al. (2006) and Fabrizio et al. (2009). The thermophilic elements, survived from the Paleogene, are one of the characteristics of the Satovcha paleoflora that confirms the refugium role of that area for some European Paleogene relicts (Bozukov, 2002; Bozukov & Ivanova, 2015; Simov et al., 2021a, b; Nel et al., 2016).

Both *Eopelobates* and *Pelobates* co-occurred in Europe throughout the Oligocene (Roček, 2013), but have been rarely found at the same localities (Fig. 4). The presence of *Eopelobates* together with *Pelobates* has been reported from the late Oligocene (Rott;

Böhme et al., 1982) and early/middle Miocene (Sandelzhausen; Böhme, 2010) of Germany, Pliocene of Poland (Weże 1 and Rębielice Królewskie 1; Młynarski, 1977; Młynarski, 1984; Sanchiz and Młynarski, 1979), Slovakia (Ivanovce; Hodrová, 1981) and Ukraine (Dolinskoe; Ratnikov, 2002).

The genus *Eopelobates* became extinct during the middle/late Miocene (Rage & Roček, 2003; Syromyatnikova, 2017). Some authors (Sanchiz & Młynarski, 1979; Hodrová, 1981; K.A. Tatarinov in Chkhikvadze, 1981, 1984; Sanchiz, 1998), however, reported representatives from the Pliocene of Poland, Hungary, Slovakia and Ukraine, but most of the material from these localities are postcranial bones or just fragments of cranial bones, all features that are not reliable basis for distinguishing between these two genera which are very similar in many skeletal aspects. That is why it is highly doubtful that *Eopelobates* survived until the Pliocene (Rage & Roček, 2003; Roček, 2013). In addi-

tion, the Miocene was the epoch when *Eopelobates* began to be replaced by species of *Pelobates*, even *P. fuscus* (Roček, 2013).

Acknowledgments

We are grateful to Michail Simov and Dr Nikolay Simov (Sofia, Bulgaria) for the information about Satovcha locality and the photo of the locality; to Ilya Acosta (Sofia, Bulgaria) for the maps of the European localities of the fossil pelobatid remains and the locality near Satovcha Vill.; to Dr Boyan Zlatkov (Sofia, Bulgaria) for the help with the figures editing and the valuable suggestions during the manuscript preparation. We appreciate very much the valuable comments and recommendations by Dr Andrea Villa (Barcelona, Spain) on the manuscript.

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Appendix I

Pelobatid fossils in Europe.

*Not included on the map of the distribution (Fig. 4)

Species	Locality and publication	Epoch	Country
<i>Eopelobates anthracinus</i> Parker, 1929	(MP 30) Rott, Germany (Koenigswald et al., 1992)	late Oligocene	Germany
<i>Eopelobates bayeri</i> Špinar, 1952	(MP 21) Hoogbutsel, Belgium (Smith, 2003)	early Eocene	Belgium
<i>Eopelobates bayeri</i> Špinar, 1952	(MP 21) Boutersem, Belgium (Smith, 2003)	early Eocene	Belgium
<i>Eopelobates bayeri</i> Špinar, 1952	(MP 21) Hoeleden, Belgium (Smith, 2003)	early Eocene	Belgium
<i>Eopelobates bayeri</i> Špinar, 1952	Bechlejovice Czech Republic (Bellon et al. 1998; Špinar, 1972)	late Oligocene	Czech Republic
<i>Eopelobates bayeri</i> Špinar, 1952	Merkur mines near Kadaň, Czech Republic (Špinar, 1972)	early Miocene	Czech Republic
<i>Eopelobates bayeri</i> Špinar, 1952	Hrabák mine near Most and Nástup (Špinar, 1972)	early Miocene	Czech Republic
<i>Eopelobates bayeri</i> Špinar, 1952	(Badenian) Devínska Nová Ves–Bonanza, Slovakia (Hodrová, 1988)	middle Miocene	Slovakia
<i>Eopelobates</i> cf. <i>E. bayeri</i> Špinar, 1952	(Csarnotan) Ivanovce, Slovakia (Hodrová, 1981)	Pliocene	Slovakia
<i>Eopelobates hinschei</i> (Kuhn, 1941)	(Lower Geiseltalium) Geiseltal near Halle, Germany (Franzen & Haubold, 1986)	middle Eocene	Germany
<i>Eopelobates wagneri</i> (Weitzel, 1938)	Grube Messel near Darmstadt, Hessen, Germany (Wuttke, 2012b)	middle Eocene	Germany
<i>Eopelobates</i> sp., cf. <i>Eopelobates</i>	Headon Hill in UK (Rage & Ford, 1980)	late Eocene	England
<i>Eopelobates</i> cf. <i>E. hinschei</i> (Kuhn, 1941)	Hordle Cliff, England, (Milner et al., 1982)	late Eocene	England
<i>Eopelobates</i> sp.	(MP30) Oberleichtersbach, Germany (Böhme, 2008)	late Oligocene	Germany
<i>Eopelobates</i> sp.	Sandelzhausen, Germany (Böhme, 2010)	early Miocene	Germany
<i>Eopelobates</i> sp.	(Orleanian, MN4) Dolnice, Czech Republic (Hodrová, 1987)	early Miocene	Czech Republic
<i>Eopelobates</i> sp.	(MN14) Osztramos 1, Hungary (Venczel, 2001)	Pliocene	Hungary
<i>Eopelobates</i> aff. <i>bayeri</i> Špinar, 1952	Volchaya Balka (= Fortepianka) (Syromyatnikova, 2017)	late Miocene	Russia
<i>Eopelobates</i> cf. <i>bayeri</i> Špinar, 1952	Satovcha Village, this study	middle Miocene	Bulgaria

<i>Lutetiobatrachus gracilis</i> Wuttke in Sanchiz, 1998	(Lower Geiseltalium) Grube Messel near Darmstadt, Hessen, Germany (Wuttke, 2012a)	middle Eocene	Germany
<i>Pelobates decheni</i> Troschel, 1861	(MP 30) Rott, Germany (Koenigswald et al. 1992)	late Oligocene	Germany
<i>Pelobates</i> cf. <i>decheni</i> Troschel, 1861	Enspel, Germany (Roček & Wuttke, 2010)	late Oligocene	Germany
<i>Pelobates fahlbuschi</i> Böhme, 2010	Sandelzhausen, Germany (Böhme, 2010)	early Miocene	Germany
<i>Pelobates sanchizi</i> Venczel, 2004	(MN4) Mokrá-Western Quarry, Czech Republic (Ivanov, 2008)	early Miocene	Czech Republic
<i>Pelobates sanchizi</i> Venczel, 2004	(Badenian, MN6) Mátraszőlös 1, Hungary (Venczel, 2004)	middle Miocene	Hungary
<i>Pelobates sanchizi</i> Venczel, 2004	(Badenian, MN6) Mátraszőlös 2, Hungary (Venczel, 2004)	middle Miocene	Hungary
<i>Pelobates sanchizi</i> Venczel, 2004	(Badenian, MN6) Sámsonháza 3, Hungary (Venczel, 2004)	middle Miocene	Hungary
<i>Pelobates syriacus</i> Boettger, 1889	Pirro Nord P13 (Apulia, southeastern Italy) (Blain et al., 2016)	Early Pleistocene	Italy
<i>Pelobates fuscus</i> (Laurenti, 1768)	Russel-Tiglia-Egypte pit near the village of Tegelen (Early Pleistocene, The Netherlands) (Villa et al., 2018)	Early Pleistocene	Netherlands
<i>Pelobates cultripes</i> (Cuvier, 1829)	Almenara-Casablanca-3 (near the city of Almenara, Spain) (Blain et al., 2007)	Early Pleistocene	Spain
<i>Pelobates cultripes</i> (Cuvier, 1829)	Sierra de Atapuerca (Sima del Elefante, Burgos, North-Western Spain) (Blain et al., 2011)	Middle Pleistocene	Spain
<i>Pelobates cultripes</i> (Cuvier, 1829)	(MmQ3) Almenara (Castellón), Valencian Community, Almenara-Casablanca-3 (ACB-3) (Blain, 2009)	Early Pleistocene	Spain
<i>Pelobates cultripes</i> (Cuvier, 1829)	(MmQ3) Guadix-Baza Depression (Granada), Andalusia Community, Barranco-León (Blain, 2009)	Early Pleistocene	Spain
<i>Pelobates cultripes</i> (Cuvier, 1829)	(MmQ3-MmQ4) Atapuerca (Burgos), Castile and León Community, Gran Dolina (= Trinchera Dolina) (Blain, 2009)	Early Pleistocene	Spain
<i>Pelobates</i> cf. <i>cultripes</i> (Cuvier, 1829)	Begur (Girona), Catalonia Community, Bagur-1 (B-1) (Blain, 2009)	Middle Pleistocene	Spain
<i>Pelobates</i> cf. <i>cultripes</i> (Cuvier, 1829)	(MmQ3) Begur (Girona), Catalonia Community, Bagur-2 (B-2) (Blain, 2009)	Early Pleistocene	Spain

<i>Pelobates</i> cf. <i>cultripes</i> (Cuvier, 1829)	(MmQ 2-3) Castelldefels, Massif de Garraf (Barcelona), Catalonia Community, Can Altisench (Blain, 2009)	Early Pleistocene	Spain
<i>Pelobates</i> sp.	(MP30) Oberleichtersbach, Germany (Böhme, 2008)	late Oligocene	Germany
<i>Pelobates</i> sp.	(Astaracian, MN6) Sansan, France (Rage & Hossini, 2000)	middle Miocene	France
<i>Pelobates</i> sp.	(Sarmatian) Tauț, Romania (Venczel & Știucă, 2008)	middle Miocene	Romania
<i>Pelobates</i> sp.	(Villanyian) Včeláre, Slovakia (Hodrová, 1985)	Pliocene	Slovakia
Pelobatidae indet. larvae	Enspel, Germany (Maus & Wuttke, 2002, 2004; Roček & Wuttke, 2010)	late Oligocene	Germany
Pelobatidae indet. adults	(MP 7) Le Quesnoy, France (Nel et al., 1999)	early Eocene	France
Pelobatidae indet. adults	(MP7) Silveirinha, Portugal (Rage & Auge, 2003)	early Eocene	Portugal
Pelobatidae indet. adults	(Sarmatian) Karpov Yar, Moldova (Skutschas & Bannikov, 2009)	middle Miocene	Moldova
Pelobatidae indet. adults	(Vallesian, MN9) Rudabánya, Hungary (Roček, 2005)	late Miocene	Hungary
<i>Pelobates</i> sp.	Gaverdovsky (Syromyatnikova, 2017)	late Miocene	Russia
<i>Pelobates</i> sp.	Volchaya Balka (= Fortepianka) (Syromyatnikova, 2017)	late Miocene	Russia
<i>Pelobates</i> sp.	Beşkonak Köyü, Anatolia (Rückert-Ülkümen, 2002)	Miocene	Turkey
<i>Pelobates</i> sp.	Baranica Cave near Knjaževac (Eastern Serbia) (Đurić et al., 2016)	late Pleistocene	Serbia
<i>Pelobates</i> sp.	Tresjuncos (Cuenca, Spain) (Bustillo et al., 2017)	late Miocene	Spain
<i>Pelobates</i> sp.	Monticino Quarry (latest Miocene, Italy) (Villa et al., 2021)	late Miocene	Italy
* <i>Eopelobates</i> cf. <i>E. bayeri</i> Špinar, 1952	Gorishnaya Vyganka, Ukraine (K.A. Tatarinov in Chkhikvadze 1981, 1984)	Pliocene	Ukraine
* <i>Pelobates fuscus</i> (Laurenti, 1768)	(Ruscinian) Europe (Sanchiz 1998)	Pliocene	Europe