

LATE PLIOCENE ALBANERPETONTIDAE (LISSAMPHIBIA) FROM ITALY

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After several decades of stability, a recent paper by Venczel and Gardner (2005) provided new insights into the last stage of the long evolutionary history of the Albanerpetontidae, which are an extinct clade of small-bodied, salamander-like lissamphibians (e.g., Fox and Naylor, 1982; Gardner, 2001; McGowan, 2002). As summarized by Gardner and Böhme (in press), albanerpetontid fossils currently are known from nearly 80 Middle Jurassic–Neogene localities, mostly in Europe and North America, but also in Africa (Morocco) and Asia (Uzbekistan). Until recently, the youngest known occurrences of albanerpetontids were in the Miocene of Western and Central Europe; many fossils from these localities pertain to the type species *Albanerpeton inexpectatum* Estes and Hoffstetter, 1976, which was first described from the middle Miocene of La Grive-Saint-Alban, France. In 2005, Venczel and Gardner announced the discovery of the first post-Miocene albanerpetontid fossils at Csarnóta 2, which is a fissure infill of early Pliocene age (late Ruscianian or MN 15) in south-central Hungary, and they named the new species *Albanerpeton pannonicus* Venczel and Gardner 2005 based on isolated and partly articulated bones from that site. *A. pannonicus* is characterized by a combination of primitive and derived characters, including reduced ornamentation on the jaws and smaller body size compared to the Miocene *A. inexpectatum*.

Here we report an even younger occurrence of *Albanerpeton pannonicus* from a fissure infill of late Pliocene age (late Villanyian or MN 17; Sala et al., 1994; Sala, 1996; Sala and Masini, 2007) at Rivoli Veronese, in northeastern Italy. These fossils represent the geologically youngest record for *Albanerpeton* and the Albanerpetontidae as a whole and they extend the geographical range of *Albanerpeton* south of the Alps. The co-occurrence at Rivoli Veronese of fossils of *Albanerpeton* and several extant taxa, in particular the plethodontid salamander *Speleomantes*, casts doubt on the suggestion (Böhme, 2003) that *Albanerpeton* preferred drier conditions.

Institutional Abbreviation—MCSNVR, Museo Civico di Storia Naturale di Verona, Verona, Italy.

SYSTEMATIC PALEONTOLOGY

LISSAMPHIBIA Haeckel, 1866
ALLOCAUDATA Fox and Naylor, 1982
ALBANERPETONTIDAE Fox and Naylor, 1982
ALBANERPETON Estes and Hoffstetter, 1976
ALBANERPETON PANNONICUS Venczel and Gardner, 2005
(Fig. 1)

Referred Material—Premaxilla: one right (MCSNVR-V.1002); maxillae: two right (MCSNVR-V.1003 and V.1004) and one left (MCSNVR-V.1005); dentaries: 10 right (MCSNVR-

V.1006–15), nine left (MCSNVR-V.1016–24), and one fragment from an indeterminate side (MCSNVR-V.1025); one fragmentary frontal (MCSNVR-V.1026); and one incomplete vertebra (MCSNVR-V.1027).

Locality and Age—Fissure infill, Rivoli Veronese, Verona Province, northeastern Italy; late Pliocene, late Villanyian European Land Mammal Age, MN 17, *Miomys pliocaenicus* zone.

Description

Premaxilla—The only available premaxilla (MCSNVR-V.1002; Fig. 1A–C) is a nearly complete right element that is missing the distal ends of the two lateralmost teeth. This specimen has a maximum height (excluding teeth) of about 2.0 mm and, considering its small size, is relatively robustly built. The pars dorsalis is moderately tall, but still low compared to some other albanerpetontid premaxillae of comparable size (cf. Gardner, 1999a:text-fig. 2A–C) and has a relatively broad laterodorsal notch that extends along about the dorsal third of the process. Adjacent to the laterodorsal notch, the labial surface of the pars dorsalis bears a low, dorsal boss that is ornamented with indistinct, irregularly-shaped ridges and is delimited ventrally by a weak groove (Fig. 1A, B). The rest of the labial surface of the premaxilla is nearly smooth, except for a few tiny foramina and weak ridges. The dorsal edge of the pars dorsalis is deeply concave, almost V-shaped, in labial or lingual outline; this concavity appears to be natural, rather than due to breakage. The medial edge of the bone bears flange-like protuberances and grooves of varying lengths, which indicate that in life this premaxilla was strongly sutured or, perhaps, weakly fused with the complementary left premaxilla. The suprapalatal pit in the lingual surface of the pars dorsalis (Fig. 1C) is moderately large, undivided, and ovoid in outline. The suprapalatal pit is connected through the pars palatinum with a relatively large palatal foramen. The size of the palatal foramen may have been exaggerated by breakage, because it appears to be confluent medially and labially with a smaller foramen (the so-called ‘unnamed foramen’ of Gardner, 1999b) that lies in the junction of the pars dentalis and pars palatinum; typically in albanerpetontids these two foramina are separated by bone (J. D. Gardner, pers. comm., 2007). As in other albanerpetontids, the pars palatinum is a lingually broad shelf. The vomerine process probably is incomplete, but it appears to have been well developed.

Maxilla—The labial surface of the maxilla (Fig. 1D) is generally smooth, except for three or four tiny foramina located in the anterior part, below the area for connection with the lacrimal. The anterior region of the maxilla bears a triangular nasal process that projects dorsally, a relatively short premaxillary lateral process that projects anteriorly, and a shelf-like premaxillary dorsal process that extends lingually. More posteriorly, the dorsal surface along the posterior part of the pars dorsalis bears a shallow, elongate depression for contact with the jugal. The lingual edge of the pars palatinum is indented by a concave notch spanning about four tooth positions; in life, this notch formed part of the internal narial opening. The ventral or occlusal edge

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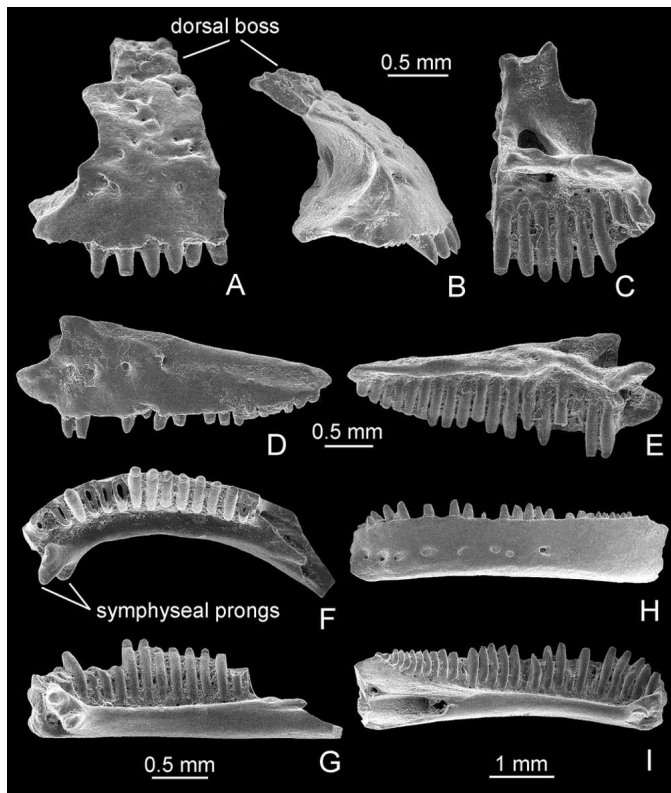


FIGURE 1. Jaws of *Albanerpeton pannonicus* Venczel and Gardner, 2005, from fissure infill at Rivoli Veronese, Italy; late Pliocene (late Villanyian, MN 17) in age. **A–C**, nearly complete, right premaxilla, MCSNVR-V.1002, in **(A)** labial, **(B)** lateral, and **(C)** lingual and slightly occlusal views. **D, E**, nearly complete left maxilla, MCSNVR-V.1005, in **(D)** labial and **(E)** lingual views. **F, G**, right dentary, MCSNVR-V.1006, preserving about anterior half of bone, in **(F)** occlusal and **(G)** lingual views. **H, I**, left dentary, MCSNVR-V.1016, preserving about anterior three-quarters of bone, in **(H)** labial and **(I)** lingual views. Specimens shown at different magnifications.

of the pars dentalis is relatively straight in labial or lingual outline. The tooth row extends along almost the entire length of the pars dentalis, almost to the posterior tip of the bone (Fig. 1E). The largest and best preserved specimen (MCSNVR-V.1005; Fig. 1D, E) is about 3.3 mm long and its tooth row is about 3.0 mm long.

Dentary—None of the available dentaries is complete; however, collectively they document all the relevant structures (Fig. 1F–I). The symphyseal area consists anteriorly of a vertically flat surface that is followed posteriorly by two symphyseal prongs, one dorsal and one ventral, that project lingually; in some specimens, one of these prongs is shorter than the other. Below the symphyseal prongs, the Meckelian canal opens anteriorly as a small pore inside the symphysis. In lingual view (Fig. 1G, I), the subdental shelf is a dorsoventrally low shelf with a rounded lingual surface that fully encloses the Meckelian canal. The subdental shelf deepens more posteriorly and the Meckelian canal opens under the posteriormost sixth to eighth tooth positions. The dorsal edge of the bone is relatively straight in lingual or labial view along the length of the dental parapet and behind the tooth row. Several dentaries preserve part of the bone behind the tooth row; these exhibit scars on the lingual surface for contact with the prearticular and angular. Along about the anterior two-thirds of the labial surface of the dentary is a row of up to seven foramina that usually lies closer to the ventral edge of the bone than to the dorsal edge. The tooth row follows the labially convex curvature of the dentary and does not reach the posterior

end of the bone. The largest specimen, MCSNVR-V.1007 (not figured), is about 5.2 mm long in preserved length and its tooth row is about 4.3 mm long.

Dentition—Based on the available specimens, it is possible to state that the maximum number of tooth positions is eight for the premaxilla, 18 for the maxilla, and 27 for the dentary (but one left dentary may have 28 tooth positions). Teeth are closely-spaced, pleurodont, non-pedicellate, and have cylindrical shafts. The crowns are labiolingually compressed and bear a triangular central cusp that, in the best-preserved teeth, is flanked mesially and distally by a much smaller cusp.

Frontal—A fragment of a left frontal (not figured) preserves part of the lateral side, including the anterolateral slot; according to Venczel and Gardner (2005:1236, text-fig. 7; contra McGowan, 2002), in albanerpetontids this slot articulated with the prefrontal. Unfortunately, the frontal fragment does not preserve the more medial part of the bone. Consequently, the presence of the keel seen along the ventral midline on fused frontals of *Albanerpeton pannonicus* from Csarnóta 2 (see Venczel and Gardner, 2005:text-figs. 6B, C, E, 7B) cannot be verified. The dorsal surface of the fragment is ornamented with the typical albanerpetontid arrangement of polygonal pits enclosed by low ridges.

Vertebra—One fragmentary vertebra (not figured) has a short (1 mm long), hourglass-shaped, amphicoelous centrum with a concave ventral surface. The vertebra bears robust transverse processes that extend perpendicular to the main vertebral axis and has no visible foramina in the lateral sides of the vertebra behind the transverse processes. The anterior edge of the neural arch is V-shaped in dorsal profile.

DISCUSSION

Taxonomic Remarks

Among known albanerpetontids, specimens from Rivoli Veronese most closely resemble jaws described for *Albanerpeton pannonicus* in the following combination of features: small size; premaxilla relatively robust, with a relatively low pars dorsalis bearing a dorsal boss ornamented with ridges and with suprapalatal pit moderate in size and ovoid in outline; maxilla and dentary lack labial ornament and have teeth that are weakly heterodont anteriorly and with the adjacent edge of the jaw relatively straight. Compared to the two recognized European albanerpetontid species, jaws from Rivoli resemble those of *A. pannonicus* in primitively lacking the following four apomorphies of *A. inexpectatum*: no dorsal boss on premaxilla; labial surface of premaxillary pars dorsalis ornamented with pustules; labial surface of larger dentaries and maxilla ornamented with ridges; and dorsally projecting, triangular process immediately behind tooth row on dentary (cf. Gardner, 1999b:pls. 1, 2 for *A. inexpectatum* versus Venczel and Gardner, 2005:text-figs. 1–5 for *A. pannonicus*). Although the one available frontal fragment is too incomplete to determine the presence of a ventromedian keel, which was the only autapomorphy recognized by Venczel and Gardner (2005) for *A. pannonicus*, the above list of preserved features allows the material from Rivoli Veronese to be assigned with confidence to *A. pannonicus*. An unusual feature seen in the one available premaxilla from Rivoli Veronese is the deeply concave dorsal edge of the pars dorsalis (Fig. 1A, C). Considering the amount of intraspecific variation reported in the outline of that process in other albanerpetontids (e.g., Gardner 1999a, b, 2000; Venczel and Gardner, 2005), that feature probably is not taxonomically significant.

Temporal and Paleobiogeographical Significance

The *Albanerpeton* fossils reported here extend the chronological range of the genus and the Albanerpetontidae as a whole

forward into the late Pliocene and the geographical range of *Albanerpeton* south of the Alps. The Rivoli Veronese fissure infill has yielded a taxonomically diverse small mammal assemblage (Sala et al., 1994; Sala, 1996; Fanfani and Masini, 1997; Kotsakis et al., 2003; Masini and Sala, 2007; Sala and Masini, 2007) that allows the site to be precisely correlated with the *Miomys pliocaenicus* zone in MN 17 (late Pliocene, late Villanyian European Land Mammal Age). The specimens from Rivoli Veronese thus demonstrate that *A. pannonicus* had a broader geographic distribution and survived at least a few million years past its only previously known occurrence in the early Pliocene (MN 15 or late Ruscinian European Land Mammal Age) at Csarnóta 2, Hungary. The presence of *Albanerpeton* in the Rivoli Veronese assemblage is perhaps not surprising because at the time of deposition the site lay in a favorable area close to a sea that occupied a large portion of what is now the Po Plain and during a temperate interval that probably preceded the latest Pliocene cooling.

Prior to this report, the only albanerpetontid fossil known from Italy was the poorly preserved holotype skeleton of *Cel- tedens megacephalus* (Costa, 1864) from the Lower Cretaceous (Albian) of Pietrarroia, in Benevento Province (McGowan, 2002; and literature therein). According to Venczel and Gardner's (2005) cladistic analysis, *C. megacephalus* is not closely related to *Albanerpeton pannonicus*, which means that the former species had nothing to do with the much later occurrence of *A. pannonicus* at Rivoli Veronese. The fossils from Rivoli Veronese extend the geographical range of *Albanerpeton* southwards in Europe and indicate that the Alpine chain, which was already in place by Pliocene time, was not an insurmountable barrier to the dispersal of that genus. In this context it is worth noting that Sala and Marchetti (2004) reported affinities between mammalian assemblages in northern Italy with those in eastern Europe and the Balkans, from the middle Pliocene onwards. Mammalian taxa with eastern affinities in the Pliocene of the Po valley are represented by *Petenya hungarica*, a soricid insectivore typical of Ruscinian and early Villanyian faunas from middle-eastern Europe, and also by more Oriental taxa at Rivoli Veronese (see also Kotsakis et al., 2003). It seems likely that different taxa could have followed the same dispersal route and probably penetrated south of the Alps through what is now central Slovenia (Sala, 2003).

A moderately diverse herpetofauna is known from Rivoli Veronese. Besides *Albanerpeton pannonicus*, the herpetofauna includes: the caudates *Triturus* sp. and *Speleomantes* sp.; the anurans *Bufo bufo* and *Rana* sp.; the lizards *Lacerta* gr. *L. viridis*, *Anguis fragilis*, and *Pseudopus* sp.; and the snakes *Natrix natrix*, *Vipera* gr. *V. aspis*, and Colubrinae indet. With the exception of *A. pannonicus*, all the above-listed taxa are still extant. *Speleomantes* and *Pseudopus* are no longer present in the Rivoli Veronese area, but living representatives of both genera occur only few hundreds of kilometers farther away (Sindaco et al., 2006).

Paleoecological Remarks

The sympatry of *Albanerpeton* and *Speleomantes* and certain components of the mammalian fauna at Rivoli Veronese invite reflections about the paleoecology of *Albanerpeton*. The functional morphology and paleoecology of *Albanerpeton* have been discussed by Gardner (1999b) and Venczel and Gardner (2005). The first stated that the "skull form is typical of terrestrial salamander taxa that burrow (eg. ambystomatids) or inhabit rocky crevices (eg. some plethodontids). Such crevices would have been common on the karst landscape inhabited by *A. inexpectatum*" (Gardner, 1999b:77) at La Grive-Saint-Alban, France. A similar karstic environment was available for *A. pannonicus* at Csarnóta 2, Hungary, where remains of known burrowing taxa

such as *Bufo* and *Pelobates* also have been identified (Venczel and Gardner, 2005).

The fossiliferous deposit of Rivoli Veronese also is developed in a karstic area (Sala et al., 1994; Sala, 1996). The herpetofauna from this site suggests the presence, at least temporarily, of water bodies and some degree of environmental humidity. In the mammalian fauna, the presence of hygrophilous insectivores and flying squirrels indicates a rather humid and forested environment. The presence of *Speleomantes* is strong evidence that a burrowing life style was possible for small-bodied amphibians at Rivoli Veronese, although some minor ecological differences between *Speleomantes* and *Albanerpeton* presumably were present in order to avoid niche overlap. Obvious differences in dentition and anatomical structures related to prey manipulation (and therefore prey preferences), clearly betray different feeding specializations: hard-bodied or otherwise resilient preys have been proposed for *A. inexpectatum* (Gardner, 1999b), whereas extant *Speleomantes* species use their 'ballistic tongue' to capture a wide range of invertebrates (see individual species entries in Sindaco et al., 2006). Moreover, the robust structure of the head and neck, along with the variably developed cranial ornamentation in *Albanerpeton*—the latter of which is more prominent in *A. inexpectatum* than *A. pannonicus*—suggests that *Albanerpeton* may have been able to actively burrow deep beneath talus-covered slopes, rather than simply having exploited existing crevices.

Böhme's (2003) interpretation that *Albanerpeton inexpectatum* and, by implication, other European Neogene members of the genus, was a 'dry adapted' taxon (Böhme, 2003) is here considered too simplistic and probably influenced too much by a biased fossil record. Paradoxically, we could also include *Speleomantes* in the same category of 'dry adapted' animals if we relied only on its fossil occurrences to interpret its ecological preferences. All known *Speleomantes* fossils come from karstic sites, where they sometimes are associated with fossils of unequivocal 'dry adapted' taxa, such as agamid lizards at the Plio-Pleistocene site of Monte Tuttavista in Sardinia, Italy (Abbazzi et al., 2004). Such occurrences could suggest a much higher resistance to dryness for *Speleomantes* if we did not know that the ranges of extant species, despite embracing superficially dry karstic areas, consist largely of humid, forested, Apennine valleys with substrates formed on marls, schists, ophiolites, and even gypsum (Sindaco et al., 2006). It is remarkable that the fossil record of *Speleomantes* does not sample this wide ecological plasticity—instead, fossils are found only in fissure infills deposited in carbonate rocks (Delfino et al., 2005). The case study of *Speleomantes* suggests that *Albanerpeton* may have inhabited a broader range of habits in the European Neogene than is suggested by its fossil occurrences at karstic sites such as La Grive-Saint-Alban, Csarnóta 2, and Rivoli Veronese. Interestingly, a recent analysis of the paleoecological preferences of European Tertiary albanerpetontids (Gardner and Böhme, in press) suggested that stable, moist, and shaded conditions were preferred. Those authors further showed that although many of the most productive localities are in karstic settings, albanerpetontids clearly inhabited a broader range of habitats because their fossils are also known from numerous localities in floodplain, coastal deltaic, and lacustrine deposits.

CONCLUSIONS

Fossils from Rivoli Veronese referred here to *Albanerpeton pannonicus* represent the first late Pliocene record for the species and are the geologically youngest occurrence of the Albanerpetontidae. If the extended survival of *Albanerpeton* south of the Alps can be linked to favorable environmental conditions, the absence of this taxon in localities younger than late Pliocene may be due to environmental changes during that interval. As-

suming that the absence of *Albanerpeton* remains from the latest Pliocene onward is not due to taphonomic bias—a bias that probably did contribute to the limited fossil record of *Speleomantes* during that interval (Delfino et al., 2005)—extinction of albanerpetontids in southern Europe during the late Pliocene likely coincided with or slightly followed the first xeric phase, which began about 2.3 My according to Suc (1984), in the development of Mediterranean-type of vegetation. This proposed extinction scenario is consistent with the idea that the latest Pliocene, which is characterized by the first Arctic glaciations and the onset of glacial-interglacial cycles that predominated during the Quaternary, was a time of major changes in the European herpetofauna (see discussion and references in Delfino et al., 2003).

Acknowledgments—R. Zorzini and A. Vaccari (Verona) loaned the material. A. Bertini (Firenze) suggested pertinent literature. L. Rook (Firenze), J. Lutherbacher and E. Xoplaki (Bern) critically commented on an earlier draft of the manuscript. Reviews of the submitted manuscript were provided by A. Folie (Bruxelles), J.-C. Rage (Paris), and one anonymous referee. The editor, J. D. Gardner (Drumheller), carefully revised the manuscript and greatly improved it. The SEM pictures were taken by L. Tormo at Museo Nacional de Ciencias Naturales, Madrid, thanks to the courtesy of B. Sanchiz (Madrid), as part of a larger project supported by a Synthesys grant ES-TAF-1746 to M. Delfino.

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Submitted September 26, 2006; accepted February 27, 2007.