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CHAPTER

12

Review of the Albanerpetontidae (Lissamphibia), with Comments on the Paleoecological Preferences of European Tertiary Albanerpetontids

The Albanerpetontidae are an extinct clade of Middle Jurassic–Pliocene and primarily Laurasian amphibians (e.g., Estes and Hoffstetter 1976; Fox and Naylor 1982; McGowan and Evans 1995; Gardner 2000a, 2001; McGowan 2002; Gardner et al. 2003). In life, albanerpetontids were small-bodied (total length less than about 100 mm), salamander-like animals with a tail and two pairs of similarly sized limbs (e.g., McGowan and Evans 1995). Albanerpetontids are characterized by numerous osteological features, including: fused frontals; an interdigitating intermandibular joint; nonpedicellate marginal teeth tipped with tricuspid, chisel-shaped crowns; and modified "cervical" vertebrae that superficially resemble the atlas-axis complex in mammals (e.g., Estes and Hoffstetter 1976; Fox and Naylor 1982; McGowan and Evans 1995; Gardner 2000a, 2001; McGowan 2002). Currently three genera and over a dozen species are recognized (Table 12.1).

Fossils of albanerpetontids have been known since the mid-19th century (Costa 1864) and for over a century were interpreted as belonging to salamanders (e.g., Costa 1864; D'Erasmo 1914; Estes 1964, 1969, 1981; Seiffert 1969; Estes and Hoffstetter 1976; Naylor 1979; Carroll and Holmes 1980; Duellman and Trueb 1986; Carroll 1988; Roček 1994). Albanerpetontids currently are widely regarded as a distinct clade of possible lissamphibians, separate from salamanders (Caudata), frogs (Salientia), and caecilians (Gymnophiona) (e.g., Fox and Naylor 1982; McGowan and Evans 1995; Gardner 2000a, 2001; McGowan 2002; Ruta et al. 2003a; Schoch and Milner 2004). Interest in albanerpetontids has increased substantially over the past few decades, with reports of new occurrences, characters, and taxa (e.g., Nessov 1981, 1988, 1997; Estes 1981; Fox and Naylor 1982; Evans and Milner 1994; McGowan and Evans 1995; McGowan 1996, 1998a, 2002; Gardner and Averianov 1998; Sanchíz 1998; Grigorescu et al. 1999; Gardner 1999a–c, 2000a–c; Gardner et al. 2003; Evans and McGowan 2002; Rees and Evans 2002; Böhme 2003; Wiechmann 2003; Folie

Table 12.1. Summary of albanerpetontid genera and species accepted here, nomen dubia albanerpetontid taxa, and nonalbanerpetontid taxa transferred to the Caudata. Cited references are limited to those containing relevant taxonomic and/or descriptive information.

(A) Genera and Species within the Albanerpetontidae

Genus *Albanerpeton* Estes and Hoffstetter 1976; type genus; ?late Barremian, latest Aptian or earliest Albian–early Pliocene; Europe and North America; seven named and one, possibly two, unnamed species.

- *A. inexpectatum* Estes and Hoffstetter 1976; type species; early and middle Miocene; France, Austria, Germany, Czech Republic. Material: articulated first trunk vertebra+axis (holotype), plus isolated and rare articulated skull bones (mandibles, premaxillae, maxillae, lacrimal, prefrontal, frontals, parietals, and neurocranium), isolated vertebrae, humeri, and femora. References: Estes and Hoffstetter (1976); Estes (1981); Sanchíz (1998); Gardner (1999a); Rage and Hossini (2000); Wiechmann (2003); this chapter.
- *A. nexuosum* (Estes 1981); late Santonian or early Campanian–late Maastrichtian, ?early Paleocene; Alberta, Canada, and Colorado, Montana, New Mexico, Texas, Utah, and Wyoming, USA. Material: dentary (holotype), plus fused premaxillae and isolated dentaries, premaxillae, maxillae, and frontals. References: Estes (1964, 1981); Gardner (2000b).
- *A. arthridion* Fox and Naylor 1982; latest Aptian or earliest Albian–middle Albian; Oklahoma and Texas, USA. Material: premaxilla (holotype), plus isolated dentaries, premaxillae, maxillae, frontals, atlantes, and humeri. References: Estes (1969, 1981); Fox and Naylor (1982); Gardner (1999b).
- *A. galaktion* Fox and Naylor 1982; late Santonian or early Campanian–late Maastrichtian; Alberta, Canada, and Utah and Wyoming, USA. Material: premaxilla (holotype), plus isolated dentaries, premaxillae, maxillae, and frontals. References: Fox and Naylor (1982); Gardner (2000b).
- *A. cifellii* Gardner 1999c; late Turonian; Utah, USA. Material: premaxilla (holotype). Reference: Gardner (1999c)
- *A. gracile* (Gardner 2000); middle Campanian; Alberta, Canada, and Utah and Texas, USA. Material: premaxilla (holotype), plus isolated dentaries, premaxillae, maxillae, and frontals. Reference: Gardner (2000b).
- *Albanerpeton pannonicus* Venczel and Gardner 2005; early Pliocene; Hungary. Material: fused premaxillae (holotype), plus isolated and rare articulated skull bones (mandibles, premaxillae, maxillae, lacrimals, prefrontals, frontals, jugals, nasal, and ?palatal bones) and isolated vertebrae and humeri. Reference: Venczel and Gardner 2005.
- *Albanerpeton* n. sp. (="Paskapoo species" of Gardner 2002); late Paleocene; Alberta, Canada. Material: fused premaxillae and isolated dentaries, maxillae, premaxillae, frontals, and parietal. References: Gardner (2000a, 2002); Gardner and Scott (unpubl. obs. 2001).
- ?*Albanerpeton* n. sp. (= *Albanerpeton* n. sp. sensu Wiechmann 2003); late Barremian; Uña, Spain. Material: premaxillae and frontals. Reference: Wiechmann (2003). Note: see text ("European Record") for comments on generic assignment of this species.

Genus *Celtedens* McGowan and Evans 1995; Kimmeridgian–early Albian; Europe; two named and one unnamed species.

- *C. megacephalus* (Costa 1864); type species; early Albian; Italy. Material: incomplete skeleton (holotype). References: Costa (1864); D'Erasmo (1914); Estes (1981); McGowan (2002).
- *C. ibericus* McGowan and Evans 1995; late Barremian; Spain. Material: incomplete skeleton (holotype) and three other incomplete skeletons. References: McGowan and Evans (1995); McGowan (2002); S. E. Evans (pers. comm. 2003).
- *Celtedens* n. sp. (sensu Wiechmann 2003); Kimmeridgian–early Tithonian; Guimarota Mine and Porto Dinheiro, Portugal. Material: dentaries, premaxillae, maxillae, frontals, parietals, and vertebrae. Reference: Wiechmann (2003).

Genus *Anoualerpeton* Gardner et al. 2003; late Bathonian–?Berriasian; Europe and Africa; two named species.

- *An. unicus* Gardner et al. 2003; type species; ?Berriasian; Morocco. Material: premaxilla (holotype), plus isolated dentaries, articular, premaxillae, maxillae, frontals, parietal, humeri, and vertebrae. Reference: Gardner et al. (2003).
- *An. priscus* Gardner et al. 2003; late Bathonian; England. Material: premaxilla (holotype), plus isolated dentaries, premaxillae, maxillae, frontals, parietals, quadrates, and vertebrae. References: McGowan (1996); Gardner et al. (2003).

(B) Nomina Dubia Taxa within the Albanerpetontidae

Genus *Nukusurus* nomen dubium (Nessov 1981); late Cenomanian–Coniacian; Uzbekistan; two named species. Note: Genus and both species all nomina dubia according to Gardner and Averianov 1998.

- *N. insuetus* nomen dubium (Nessov 1981); type species; early Cenomanian; Uzbekistan. Material: articulated dentary+angular (holotype) plus one articulated dentary+angular. References: Nessov (1981, 1988, 1997); Nessov and Udovichenko (1986); Gardner and Averianov (1998).
- *N. sodalis* nomen dubium (Nessov 1997); Coniacian; Uzbekistan. Material: dentary (holotype). References: Nessov and Udovichenko (1986); Nessov (1997); Gardner and Averianov (1998).

(C) Nonalbanerpetontid Taxa Transferred to the Caudata

- *Ramonellus longispinus* Nevo and Estes 1969; late Aptian; Israel. Material: multiple incomplete skeletons, including the holotype. References: Nevo and Estes (1969); Estes (1981); Milner (2000); Gardner et al. (2003).
- *Bishara backa* Nessov 1997; late Santonian or Campanian; Kazakhstan. Material: atlantal centrum (holotype). References: Nessov (1997); Gardner and Averianov (1998).

and Codrea 2005; Venczel and Gardner 2005), analyses of phylogenetic relationships (e.g., Trueb and Cloutier 1991; McGowan and Evans 1995; Gardner 2001, 2002; McGowan 2002; Gardner et al. 2003; Ruta and Coates 2003; Ruta et al. 2003a,b; Venczel and Gardner 2005; Anderson in press), and interpretations about functional anatomy (e.g., Fox and Naylor 1982; McGowan 1998b; Gardner 2001), paleobiogeography (e.g., Gardner and Averianov 1998; Gardner 2002; Gardner et al. 2003), and paleoecology (e.g., Gardner 2000a; Böhme 2003).

The Albanerpetontidae are of interest for at least two reasons. First, because they are widely regarded as a clade of possible lissamphibians (e.g., Fox and Naylor 1982; McGowan and Evans 1995; Gardner 2001; McGowan 2002; Ruta et al. 2003a; Schoch and Milner 2004), albanerpetontids are important for deciphering the evolutionary history of the Lissamphibia. Second, albanerpetontids are of interest in their own right because they were a moderately successful clade that contained at least three genera and a dozen species, with a known temporal range of about 160 million years and a geographic distribution that encompassed Europe, North America, Asia, and Africa (e.g., Estes and Hoffstetter 1976; Fox and Naylor 1982; McGowan and Evans 1995; Gardner and Averianov 1998; Gardner 2002; McGowan 2002; Gardner et al. 2003; Venczel and Gardner 2005; Table 12.2).

Considering the current level of interest in albanerpetontids and the potential significance of the group, a review of the Albanerpetontidae is timely. The inclusion of this paper in a volume on studies of microvertebrate assemblages is not out of place because much of what we know about albanerpetontids is founded on isolated and rare articulated bones recovered from dozens of microvertebrate localities. In this chapter, we do the following: (1) provide a historical overview of previous work on albanerpetontids; (2) summarize the fossil record and taxonomy of albanerpetontids; (3) discuss the systematics and some aspects of the evolutionary history of the group; (4) present new interpretations about the paleoecological preferences of European Tertiary albanerpetontids; and (5) briefly discuss the potential for future studies.

HISTORY OF PREVIOUS WORK

The first published account of an albanerpetontid specimen was by Costa (1864), who described a poorly preserved, anterior end of an articulated skeleton from the Lower Cretaceous (early Albian) "Calcari ad ittioliti," near Naples, Italy. Costa (1864) interpreted the fossil as a salamandrid salamander and erected it as the holotype of his new species, *Triton megacephalus*. Subsequently D'Erasmo (1914) redescribed this specimen as *Triton* (?) *megacaphalus*, and in a pair of papers, Kuhn (1938, 1960) questionably reassigned the species first to *Heteroclitotriton* and then to *Triturus*. The albanerpetontid affinities of the skeleton were formally recognized when it was redescribed by Estes (1981) as *Albanerpeton megacephalus*. Most recently, McGowan and Evans (1995) designated the skeleton as the genotype for their new genus *Celtedens*.

After the discovery of the Italian fossil, a century passed before additional albanerpetontid fossils were reported. In his monograph on microver-

Table 12.2. Summary of albanerpetontid occurrences.

Continent	Geological Age	Unit and Locality	Taxa	Inferred Depositional Environment	References
Europe	Early Bathonian (Kriwet et al. 1997; originally reported as late Bajocian by Seiffert 1969)	Unspecified unit, Gardies, Dépt. Aveyron, France	Albanerpetontidae indet.	Nearshore, shallow marine	Seiffert 1969; Estes 1981
Europe	Early Bathonian	Chipping Norton Mbr., Chipping Norton Fm., Hornsleasow Quarry, Gloustershire, England	Albanerpetontidae indet.	Freshwater to brackish coastal marsh	Evans and Milner 1994: table 18.2; Evans and Waldman 1996: table 1; S. E. Evans pers. comm. 2005
Europe	Late Bathonian	Forest Marble Fm., Kirtlington Cement Quarry (type locality of *Anoualerpeton priscus*) and Tarlton Clay Pit localities, both in Oxfordshire, and Swyre and Watton Cliff localities, both in Dorset, England	*Anoualerpeton priscus* (Kirtlington Cement Quarry); Albanerpetontidae indet. (other localities)	Freshwater to brackish coastal marsh: lagoonal deposits (Kirtlington Cement Quarry and Tarlton Clay Pit) and overbank deposits (Swyre and Watton Cliff)	Evans and Milner 1991, 1994; Evans 1992; Evans and Waldman 1996; McGowan 1996; Gardner et al. 2003
Europe	Kimmeridgian	Alcobaça Fm., Guimarota Mine, Leira District, Portugal	*Celtedens* n. sp. (sensu Wiechmann 2003)	Freshwater to brackish coastal lagoon	Estes 1981; McGowan 1998a, 2002; Schudack 2000*; Wiechmann 2000a,b, 2003
Europe	Late Kimmeridgian–early Tithonian	Sobral Unit (locally corresponding to Praia Azul member; Mateus 2004), Porto das Barcas locality, Lisboa District, Portugal	Albanerpetontidae indet.	Brackish to marine	Wiechmann 2003
Europe	Late Kimmeridgian–early Tithonian	Amoreira-Porto Novo Member, Lourinhã Fm., Porto Dinheiro locality (= Pinheiro), Lisboa District, Portugal	*Celtedens* n. sp. (sensu Wiechmann 2003)	Freshwater fluvial and floodplain	Estes 1981; Wiechmann 2003

TABLE 12.2. Summary of albanerpetontid occurrences. (continued)

Continent	Geological Age	Unit and Locality	Taxa	Inferred Depositional Environment	References
Europe	Berriasian	Cherty Freshwater Mbr., Lulworth Fm., Purbeck Limestone Gp., various localities, including Sunnydown Farm Quarry and Lovell's Quarry, Isle of Purbeck, Dorset, England	*Celtedens* sp. or spp.	Freshwater to brackish coastal lagoon and lacustrine	Ensom 1988; Ensom et al. 1991; McGowan and Ensom 1997; Gardner 2000a; Evans and McGowan 2002
Europe	Berriasian	Unio Beds and Upper "Cypris" Clays and Shales, Peveril Point Mbr., Durlston Fm., Purbeck Limestone Gp., various localities, Isle of Purbeck, Dorset, England	Albanerpetontidae indet.	Freshwater to weakly brackish coastal floodplain and fluvial	Underwood and Rees 2002: text-fig. 2; Evans and McGowan 2002
Europe	Barremian	Wessex Fm., various localities, Isle of Wight, England	Albanerpetontidae indet.	Coastal floodplain, fluvial, and lacustrine	Evans et al. 2003; Sweetman 2003, 2004, pers. comm. 2003
Europe	Early Barremian	Camarillas (and ?Castellar) Fm., Galve localities (including Yacimiento Herrero), Teruel Prov., Spain	Albanerpetontidae indet.	Freshwater fluvial and floodplain	Estes 1981; Estes and Sanchíz 1982; McGowan 1998a
Europe	Late Barremian	Unspecified unit, Pio Pajarón locality, Cuenca Prov., Spain	Albanerpetontidae indet.	Deltaic and freshwater fluvial	Wiechmann 2003
Europe	Late Barremian	La Huérguina Fm., Uña locality, Cuenca Prov., Spain	?*Albanerpeton* n. sp. (=*Albanerpeton* n. sp. sensu Wiechmann 2003); *Celtedens megacephalus*; Albanerpetontidae indet.	Marginal and freshwater lacustrine	McGowan 1998a, 2002; Wiechmann 2000b, 2003; Gomez et al. 2001*

Europe	Late Barremian	La Huérguina Fm., Las Hoyas locality (type locality of *Celtedens ibericus*), Cuenca Prov., Spain	*Celtedens ibericus*	Freshwater lacustrine	McGowan and Evans 1995; McGowan 1998a, 2002
Europe	Early Albian	"Calcari ad ittioliti," Pietraroia locality (type locality of *Celtedens megacephalus*), Benevento Prov., Italy	*Celtedens megacephalus*	Freshwater to brackish and intermittently dry lagoon	Costa 1864; D'Erasmo 1914; Estes 1981; Bravi 1994*; McGowan 1998a, 2002
Europe	Early Cretaceous (stage uncertain)	Vitabäck Clays, Annero Fm., excavation near Vitäback farmhouse, Scania, Sweden.	Albanerpetontidae indet	Freshwater floodplain lake	Rees and Evans 2002
Europe	Middle–late Campanian	"Begudien terminal" unit, La Neuve locality, Dépt. Var, France	*Albanerpeton* sp.	Lacustrine	Duffaud 2000; Garcia et al. 2000*
Europe	Late Campanian or early Maastrichtian	Unnamed unit ("unit B" sensu Baceta et al. 1999), Laño quarry, Basque-Cantabrian Region, Spain	Albanerpetontidae indet.	Freshwater fluvial and floodplain	Astibia et al. 1990; Duffaud and Rage 1999; Gomez-Alday 1999*
Europe	?Early Maastrichtian	Unspecified unit, Cruzy locality, Dépt. Hérault, France	Albanerpetontidae indet.	Floodplain	Buffetaut et al. 1999
Europe	Late Maastrichtian	Auzas Marls Formation, Cassagnau 1 locality, Dépt. Haute-Garonne, France	Albanerpetontidae indet.	Brackish coastal marsh	Laurent et al. 2002
Europe	Early–middle or late Maastrichtian (see Therrien 2005:19)	Sânpetru Fm. (="Pui beds" sensu Therrien 2005) and Densuş-Ciula Fm., various localities, Haţeg Basin, Romania†	*Albanerpeton* sp.	Freshwater fluvial and floodplain	Grigorescu et al. 1999; Duffaud 2000; Folie et al. 2002; Smith et al. 2002; Codrea et al. 2002; Folie and Codrea 2005
Europe	Early Oligocene (MP21)	Fissure infill, Möhren 12 locality, Bavaria, Germany	*Albanerpeton* sp.	Karst	Böhme and Ilg 2003
Europe	Early Oligocene (MP22)‡	Unspecified unit and fissure infill at Ehrenstein locality, Germany	Albanerpetontidae indet.	Karst	Wiechmann 2003

TABLE 12.2. Summary of albanerpetontid occurrences. (continued)

Continent	Geological Age	Unit and Locality	Taxa	Inferred Depositional Environment	References
Europe	Early Oligocene (MP22–23)	Fissure infill, Grafenmühle 11 locality, Bavaria, Germany	*Albanerpeton* sp.	Karst	Böhme and Ilg 2003
Europe	Early Oligocene (MP23)	Fissure infill, Ronheim 1, Bavaria, Germany	*Albanerpeton* sp.	Karst	Böhme and Ilg 2003
Europe	Late Oligocene (MP28)‡	Unspecified unit and fissure infill at Herrlingen locality, Germany	Albanerpetontidae indet.	Karst	Wiechmann 2003
Europe	Late Oligocene (MP30)	Doline infill, Oberleichtersbach locality, Bavaria, Germany	*Albanerpeton* sp.	Lacustrine	Böhme unpubl. obs. 2005
Europe	Early Miocene (MN1)	Fissure infill, Weißenburg 6 locality, Bavaria, Germany	*Albanerpeton* sp.	Karst	Böhme 2003: appendix; Böhme and Ilg 2003
Europe	Early Miocene (MN3)	Holešice Mbr., Most Fm., Ahnìkov locality , Merkur-North opencast mine, Bohemia, Czech Republic	*Albanerpeton inexpectatum*	Freshwater swamp	Böhme 2003: appendix; Kvaček et al. 2004
Europe	Early Miocene (MN3)	Fissure infills, Stubersheim 3 and Wintershof West localities, Bavaria, Germany	*Albanerpeton inexpectatum*	Karst	Böhme 2003: appendix; Böhme and Ilg 2003
Europe	Early Miocene (MN4a)	Fissure infills, Petersbuch 2, 7, 8, and 28 localities, Bavaria, Germany	*Albanerpeton inexpectatum*	Karst	Böhme 2003: appendix; Böhme and Ilg 2003
Europe	Early Miocene (MN4b)	Fissure infill, Erkertshofen 1 locality, Bavaria, Germany	*Albanerpeton inexpectatum*	Karst	Böhme 2003: appendix; Böhme and Ilg 2003
Europe	Early Miocene (MN4b)	Unspecified unit, Oberdorf O3 and O4, Steiermark, Austria	*Albanerpeton inexpectatum*	Freshwater swamp	Sanchíz 1998; Böhme 2003: appendix; Böhme and Ilg 2003

Europe	Early Miocene (MN4)	Fissure infills, Petersbuch 4, 5, 36 (Coll Rummel), and 38B localities, Bavaria, Germany	*Albanerpeton inexpectatum*	Karst	Böhme 2003: appendix; Böhme and Ilg 2003
Europe	Early Miocene (MN5)	Unspecified unit, Obergänserndorf 2 locality, Lower Austria, Austria	*Albanerpeton* sp.	Floodplain	Böhme 2002, 2003: appendix; Böhme and Ilg 2003
Europe	Early Miocene (MN5)	Unspecified unit, Teiritzberg T2/3 and T2/6 localities, Lower Austria, Austria	*Albanerpeton* sp.	Estuary	Böhme 2002, 2003: appendix; Böhme and Ilg 2003
Europe	Early Miocene (MN5)	Older Series of the Upper Freshwater Molasse, Puttenhausen 1 locality, Bavaria, Germany	*Albanerpeton inexpectatum*	Floodplain	Böhme 2003: appendix; Böhme and Ilg 2003
Europe	Early Miocene (MN5)	Maar Lake, Randecker Maar locality, Baden-Würtemberg, Germany	*Albanerpeton inexpectatum*	Lacustrine	Wiechmann 2001, 2003; Böhme and Ilg 2003
Europe	Early Miocene (MN5)	Older Series of the Upper Freshwater Molasse, Adelschlag, Eitensheim, and Undorf bei Regensburg (Bahnstrecke) localities, Bavaria, Germany	*Albanerpeton inexpectatum*	Floodplain	Böhme 2003: appendix; Böhme and Ilg 2003; Reichenbacher et al. 2004
Europe	Early Miocene (MN5)	Older Series of the Upper Freshwater Molasse, Arth 1a locality, Bavaria, Germany	*Albanerpeton inexpectatum*	Riparian pool and floodplain	Böhme 2003: appendix; Böhme and Ilg 2003
Europe	Middle Miocene (MN5)	Older Series of the Upper Freshwater Molasse, Maßendorf and Gisseltshausen 1a and 1b localities, Bavaria, Germany	*Albanerpeton inexpectatum*	Floodplain	Böhme 2003: appendix; Böhme and Ilg 2003

TABLE 12.2. Summary of albanerpetontid occurrences. (continued)

Continent	Geological Age	Unit and Locality	Taxa	Inferred Depositional Environment	References
Europe	Middle Miocene (MN5)	Older Series of the Upper Freshwater Molasse, Sandelzhausen unterer Geröllmergel C2 and C3/D1 localities, Bavaria, Germany	*Albanerpeton inexpectatum*	Riparian pool and floodplain	Böhme 1999, 2003: appendix; Böhme and Ilg 2003
Europe	Middle Miocene (MN6)	Unspecified unit, Sansan locality, Dépt. Gers, France	*Albanerpeton inexpectatum*	Marsh or marginal lacustrine	Rage and Hossini 2000
Europe	Middle Miocene (?MN5, ?MN6, and MN7/8)	Fissure infills, fissure M (MN7/8) in Milliet Quarry, fissure L7 (MN7/8) in Lechartier Quarry and unrecorded fissures (MN5–MN7/8) in Peyre and Beau quarries; all near La Grive- Saint- Alban, Dépt. Isère, France§	*Albanerpeton inexpectatum*	Karst	Estes and Hoffstetter 1976; Estes 1981; Gardner 1999a
Europe	Late Miocene (MN9)	Unspecified unit, Richardhof-Golfplatz locality, Lower Austria, Austria,	*Albanerpeton inexpectatum*	Lacustrine	Harzhauser and Tempfer 2004
Europe	Early Pliocene (MN15)	Fissure infill, Csarnóta 2 locality (type locality of *Albanerpeton pannonicus*), south-central Hungary	*Albanerpeton pannonicus*	Karst	Venczel and Gardner 2005
North America	Neocomian (stage uncertain)	Lakota Fm., OMNH locality V1423, South Dakota, USA	Albanerpetontidae indet.	Freshwater fluvial and floodplain	Gardner and Cifelli unpubl. obs. 2005
North America	Aptian–Albian	Lower part (Unit V) of Cloverly Fm., OMNH locality V62, Wyoming, USA	Albanerpetontidae indet.	Freshwater fluvial and floodplain	Gardner 1999b

North America	Latest Aptian–earliest Albian	Middle unnamed unit in Antlers Fm., OMNH locality V706, Oklahoma, USA	*Albanerpeton arthridion*	Freshwater fluvial and floodplain	Cifelli et al. 1997; Gardner 1999b
North America	Early–middle Albian	Upper unnamed unit, Antlers Fm., Forestburg localities (including type locality of *Albanerpeton arthridion*) and Butler Farm locality, Texas, USA	*Albanerpeton arthridion*	Freshwater fluvial and floodplain	Estes 1969; Fox and Naylor 1982; Gardner 1999b
North America	Latest Albian–earliest Cenomanian	Mussentuchit Mbr., Cedar Mountain Fm., multiple localities, Utah, USA	*Albanerpeton* sp., cf. *A.nexuosum*; Albanerpetontidae indet.	Freshwater fluvial and floodplain	Cifelli et al. 1999; Gardner 1999c
North America	Cenomanian	Dakota Fm., multiple localities, Utah, USA	Albanerpetontidae indet.	Freshwater fluvial and floodplain; minor brackish	Eaton et al. 1999; Gardner unpubl. obs. 2005
North America	Late Turonian	Smoky Hollow Mbr., Straight Cliffs Fm., multiple localities (including type locality of *Albanerpeton cifellii*), Utah, USA	*Albanerpeton cifellii*; Albanerpetontidae indet.	Freshwater fluvial and floodplain	Eaton et al. 1999; Gardner 1999c, unpubl. obs. 2005
North America	Early or middle Coniacian–early Santonian	John Henry Mbr., Straight Cliffs Fm., multiple localities, Utah, USA	Albanerpetontidae indet.	Freshwater fluvial and floodplain; minor brackish	Eaton et al. 1999; Gardner 1999c, unpubl. obs. 2005
North America	Late Santonian or early Campanian (Aquilan NALMA)	Wahweap Fm., multiple localities, Utah, USA	Albanerpetontidae indet.	Freshwater fluvial and floodplain	Gardner 2000b
North America	Late Santonian or early Campanian (Aquilan NALMA)	Deadhorse Coulee Mbr., Milk River Fm., multiple localities (including type locality of *Albanerpeton galaktion*), Alberta, Canada	*Albanerpeton galaktion*; *Albanerpeton nexuosum*; Albanerpetontidae indet.	Freshwater fluvial and floodplain	Fox and Naylor 1982; Gardner 2000b
North America	Middle Campanian (Judithian NALMA)	Aguja Fm., multiple localities, Texas, USA	*Albanerpeton galaktion*; *Albanerpeton gracile*; Albanerpetontidae indet.	Freshwater fluvial and floodplain	Standhardt 1986; Rowe et al. 1992; Sankey 1998; Gardner 2000b

TABLE 12.2. Summary of albanerpetontid occurrences. (continued)

Continent	Geological Age	Unit and Locality	Taxa	Inferred Depositional Environment	References
North America	Middle Campanian (Judithian NALMA)	Kaiparowits Fm., multiple localities, Utah, USA	*Albanerpeton galaktion*; *Albanerpeton gracile*; *Albanerpeton nexuosum*; Albanerpetontidae indet.	Freshwater fluvial and floodplain	Eaton et al. 1999; Gardner 2000b
North America	Middle Campanian (Judithian NALMA)	Judith River Fm., Clambank Hollow locality, Montana, USA	Albanerpetontidae indet.	Freshwater fluvial and floodplain	Sahni 1972; Gardner 2000b
North America	Middle Campanian (Judithian NALMA)	Foremost Fm., multiple localities, Alberta, Canada	Albanerpetontidae indet.	Freshwater fluvial and floodplain; minor brackish	Gardner 2000b, 2005; Peng et al. 2001
North America	Middle Campanian (Judithian NALMA)	Oldman Fm., multiple localities, Alberta, Canada	*Albanerpeton galaktion*; *Albanerpeton gracile*; *Albanerpeton nexuosum*	Freshwater fluvial and floodplain	Gardner 2000b, 2005; Peng et al. 2001
North America	Middle Campanian (Judithian NALMA)	Dinosaur Park Fm., multiple localities (including type locality of *Albanerpeton gracile*), Alberta, Canada	*Albanerpeton gracile*; Albanerpetontidae indet.	Freshwater fluvial and floodplain	Gardner 2000b, 2005
North America	Middle Campanian (Judithian NALMA)	Oldman Fm. or Dinosaur Park Fm., Woodpile Creek locality, Saskatchewan, Canada	Albanerpetontidae indet.	Freshwater fluvial and floodplain	Gardner 2000b
North America	Late Campanian–early Maastrichtian (Edmontonian NALMA)	Upper part of Fruitland Fm. or lower part of Kirtland Fm., locality KUVP NM-37, New Mexico, USA	*Albanerpeton nexuosum*; Albanerpetontidae indet.	Freshwater fluvial and floodplain	Gardner 2000b
North America	Late Campanian–early Maastrichtian (Edmontonian NALMA)	Lower part of Kirtland Fm., locality KUVP NM-18, New Mexico, USA	Albanerpetontidae indet.	Freshwater fluvial and floodplain	Gardner 2000b

North America	Late Campanian–early Maastrichtian (Edmontonian NALMA)	St. Mary River Fm., Scabby Butte locality, Alberta, Canada	Albanerpetontidae indet.	Freshwater fluvial and floodplain	Gardner 2000b
North America	Late Maastrichtian (Lancian NALMA)	Laramie Fm., locality UCM 77062, Colorado, USA	*Albanerpeton nexuosum*	Freshwater fluvial and floodplain	Gardner 2000b
North America	Late Maastrichtian (Lancian NALMA)	Lance Fm., multiple localities (including type locality of *Albanerpeton nexuosum*), Wyoming, USA	*Albanerpeton nexuosum*; *Albanerpeton galaktion*; Albanerpetontidae indet.	Freshwater fluvial and floodplain	Estes 1964, 1981; Breithaupt 1982, 1985; Gardner 2000b
North America	Late Maastrichtian (Lancian NALMA)	Scollard Fm., KUA-1 locality, Alberta, Canada	Albanerpetontidae indet.	Freshwater fluvial and floodplain	Gardner 2000b
North America	Late Maastrichtian (Lancian NALMA)	Frenchman Fm., Gryde and Wounded Knee localities, Saskatchewan Canada	Albanerpetontidae indet.	Freshwater fluvial and floodplain	Fox 1989; Gardner 2000b
North America	Late Maastrichtian and/or early Paleocene (Lancian and/or Puercan NALMA)	Hell Creek Fm., Bug Creek Anthills locality, Montana, USA	*Albanerpeton nexuosum*; Albanerpetontidae indet.	Fluvial and floodplain (including reworked late Maastrichtian fossils and sediments)	Estes 1981; Gardner 2000b
North America	Middle Paleocene (Torrejonian NALMA)	Paskapoo Fm., ?Who Nose locality, Alberta, Canada	Albanerpetontidae indet.	Freshwater fluvial and floodplain	Gardner and Scott unpubl. obs. 2003
North America	Late Paleocene (Tiffanian NALMA)	Paskapoo Fm., Cochrane and DW localities, Alberta, Canada	*Albanerpeton* n. sp. (="Paskapoo species" of Gardner 2002)	Freshwater fluvial and floodplain	Gardner 2000a; Gardner and Scott unpubl. obs. 2001
Asia	Early Cenomanian	Upper part of Khodzhakul Fm., Chelpyk locality (type locality of *Nukusurus insuetus* nomen dubium) and Sheikdzheili locality (SSHD-8 and 8a), Kyzylkum Desert, Uzbekistan	Albanerpetontidae indet. (including *Nukusurus insuetus* nomen dubium)	Fluvial	Nessov 1981, 1988, 1997; Nessov and Udovichenko 1986; Gardner and Averianov 1998

TABLE 12.2. Summary of albanerpetontid occurrences. (continued)

Continent	Geological Age	Unit and Locality	Taxa	Inferred Depositional Environment	References
Asia	Coniacian	Bissekty Fm., Dzhyrakuduk (CB1-17) locality (type locality of *Nukusurus sodalis* nomen dubium), Kyzylkum Desert, Uzbekistan	Albanerpetontidae indet. (*Nukusurus sodalis* nomen dubium)	Fluvial	Nessov and Udovichenko 1986; Nessov 1997; Gardner and Averianov 1998; Archibald et al. 1998*
Africa	Neocomian, probably Berriasian	Couches Rouges ("red beds") sandstone, Anoual locality (type locality of *Anoualerpeton unicus*), Talsinnt Prov., Morocco	*Anoualerpeton unicus*	Freshwater to brackish coastal deltaic	Broschinski and Sigogneau-Russell 1996; Sigogneau-Russell et al. 1998; Gardner et al. 2003

Dépt., Départment; Fm., Formation; Gp., Group; Mbr., Member; NALMA, North American Land Mammal "Age"; Prov., province.

Most occurrences have been verified by one or both of us, either by firsthand examination of voucher specimens or from published descriptions and/or figures. Entries grouped by continent and then from geologically oldest to youngest occurrences. The position of the MN5 zone within the Miocene Epoch is contentious; we follow Steininger's (1999: fig. 1.1) interpretation that MN5 straddles the early–middle Miocene boundary. Here we accept a late early Miocene age for the following localities correlated with MN5: Obergänserndorf 2 and Teiritzberg T2/3 and T2/6 based on work by Scholger (1998) and Puttenhausen 1, Randecker Maar, Adelschlag, Eitensheim, Undorf bei Regensburg, and Arth 1a based on preliminary work by Zwing et al. (2005).

* These references do not mention albanerpetontids but contain relevant details about the geological age and/or depositional environment of localities not found in other papers cited in the same entry. For the most current overview of many of the Mesozoic localities mentioned in this table, see Kielan-Jaworowska et al. (2004: chap. 1 and references therein).

† Therrien (2005) suggested localities historically placed in the Sânpetru Formation instead belong to a new, as yet unnamed formation.

‡ MP zone reported by Wiechmann (2003:151) is tentatively accepted here, even though the locality contains several fissure infills of different ages and Wiechmann (2003) did not identify which fissure infills yielded albanerpetontid fossils.

§ Type locality for *Albanerpeton inexpectatum* was originally reported as Fissure M in Milliet Quarry (Estes and Hoffstetter 1976; Estes 1981), but this is uncertain (Gardner 1999a:63–64).

tebrates from the uppermost Cretaceous (late Maastrichtian) Lance Formation of Wyoming, USA, Estes (1964) erected the new salamander genus and species *Prodesmodon copei* for distinctive salamander vertebrae (including the holotype trunk vertebra) and albanerpetontid dentaries, premaxillae, and maxillae. *Prodesmodon* initially was regarded as a plethodontid salamander on the basis of vertebral features (Estes 1964; Wake 1966). Five years later, Estes (1969) associated Lower Cretaceous (Albian) albanerpetontid dentaries, a premaxilla, and a humerus from Texas, USA, with new and previously reported salamander vertebrae (including the holotype trunk vertebra) of *Prosiren elinorae*, a species that had been named previously by Goin and Auffenberg (1958). In the same paper, Estes (1969) allied *Prodesmodon* and *Prosiren* in his new salamander family Prosirenidae on the basis of their strikingly similar, referred jaws, and downplayed the substantial vertebral differences between the two genera. The same year, Nevo and Estes (1969) named the salamander *Ramonellus longispinus* for a collection of articulated but incomplete skeletons from the Lower Cretaceous of Israel, and they questionably assigned this taxon to the Prosirenidae on the basis of similarities in the humerus of *Ramonellus*, *Prosiren*, and a then-undescribed taxon from the Miocene of France. Also in 1969, Seiffert described from the Middle Jurassic of France a peculiar, isolated atlantal centrum that he interpreted as belonging to an indeterminate salamander.

A major advance in our understanding of albanerpetontid structure and the proper association of their skeletal elements occurred when Estes and Hoffstetter (1976) described the new prosirenid genus and species *Albanerpeton inexpectatum* on the basis of abundant isolated and rare articulated skull and postcranial bones from middle Miocene fissure infills near La Grive-Saint-Alban, France. In addition to jaws and vertebrae, the Miocene collections included distinctive skull roof bones (lacrimal, prefrontal, parietals, and fused frontals), a neurocranium, humeri, and femora. Although the referred jaws of *A. inexpectatum* closely resembled those then referred to *Prodesmodon* and *Prosiren* and the referred humeri resembled those described for *Prosiren* and *Ramonellus*, the vertebrae of *A. inexpectatum* differed from vertebrae in the other three genera. Atlantes assigned to *A. inexpectatum* did, however, closely resemble the Middle Jurassic atlas reported by Seiffert (1969).

Estes and Hoffstetter's (1976) paper set the stage for two studies that challenged previous associations of some prosirenid jaws and vertebrae. On the basis of morphological evidence and on stratigraphical occurrences of relevant Cretaceous specimens in the North American Western Interior, Naylor (1979) convincingly argued that jaws originally assigned by Estes (1964) to *Prodesmodon* instead pertained to *Albanerpeton*, the latter of which he retained in the Prosirenidae. Fox and Naylor (1982) extended this argument to *Prosiren elinorae* by arguing that Estes's (1969) association of jaws and vertebrae for that species was incorrect. Instead, Fox and Naylor (1982) retained the holotype and referred vertebrae in *Prosiren elinorae* and transferred the jaws to their new species *A. arthridion*. In the same paper, these authors also erected a second new species, *A. galaktion*, for jaws, frontals, parietals, and atlantes from the Upper Cretaceous Milk River Formation of Alberta, Canada. The most significant and enduring aspect of Fox and Naylor's (1982) paper was their proposal that *Albanerpeton* was not a salamander, but instead represented a distinct group ("lineage" in their terminology) of possible lissamphibians, for which they erected the new family Albanerpetontidae and new order Allocaudata. Despite some initial skepticism (e.g., Estes and Sanchíz 1982; Duellman and Trueb 1986; Milner 1988), Fox and Naylor's (1982) proposal that albanerpetontids are not salamanders has not been effectively challenged, and the group is now widely accepted as a separate clade of possible lissamphibians.

Two papers from 1981 appeared too late to be included in Fox and Naylor's (1982) study. In the *Handbook of Paleoherpetology* volume dealing with caudates, Estes (1981) continued to recognize a Prosirenidae sensu lato comprising a monotypic *Prosiren* (sensu Estes 1969), a monotypic *Ramonellus*, and the following three species of *Albanerpeton: A. inexpectatum; A. megacephalus*, which included the skeleton first reported by Costa (1864); and his new species *A. nexuosus* (amended to *A. nexuosum* by Folie and Codrea 2005), which was founded on jaws formerly assigned by Estes (1964) to *Prodesmodon* and on jaws, skull roof bones, and atlantes from the Milk River Formation that were assigned by Fox and Naylor (1982) to *A. galaktion*. The same year, Nessov (1981) reported the first Asian albanerpetontid fossils and erected the new genus *Nukusurus*.

The history of albanerpetontid research since the early 1980s is more straightforward and has consisted largely of descriptive, taxonomic, and phylogenetic studies. Highlights from this interval include the first report of a well-preserved, articulated albanerpetontid skeleton with traces of skin and soft tissue (McGowan and Evans 1995); discoveries of albanerpetontid fossils in Africa (Sigogneau-Russell et al. 1998) and the Upper Cretaceous of Europe (e.g., Astibia et al. 1990; Grigorescu et al. 1999; Duffaud 2000); revisions of previously named taxa and descriptions of new taxa (e.g., McGowan and Evans 1995; Gardner and Averianov 1998; Gardner 1999a–c, 2000a,b; McGowan 2002; Gardner et al. 2003; Wiechmann 2003; Venczel and Gardner 2005); and character-based cladistic analyses (e.g., Trueb and Cloutier 1991; McGowan and Evans 1995; Gardner 2001, 2002; McGowan 2002; Gardner et al. 2003; Ruta et al. 2003a; Venczel and Gardner 2005). New occurrences and fossils continue to be identified, and descriptions of several new taxa are in preparation.

FOSSIL RECORD AND TAXONOMY OF ALBANERPETONTIDS

Albanerpetontid fossils are known from the Middle Jurassic (Bathonian) to early Pliocene—an interval of approximately 160 million years according to the timescales of Steininger et al. (1996) and Gradstein et al. (2004)—and from the continents of Europe, North America, Asia, and Africa. Currently three genera are recognized: the Euramerican Early Cretaceous–Neogene type genus *Albanerpeton*; the Eurafrican Middle Jurassic–Early Cretaceous *Anoualerpeton*; and the exclusively European Late Jurassic–Early Cretaceous *Celtedens*. Species and genera of albanerpetontids are differentiated by features of the frontals and jaws (Fox and Naylor 1982; McGowan and Evans 1995; Gardner and Averianov 1998; Gardner 1999a–c, 2000a,b, 2002; McGowan 2002; Wiechmann 2003; Venczel and Gardner 2005).

Tables 12.1 and 12.2 summarize, respectively, the taxonomy and known occurrences of albanerpetontids accepted by us.

European Record

The longest temporal record of albanerpetontids is in Europe, where fossils are known from the early Bathonian–early Pliocene and from 11 countries, as follows (Table 12.2): England (early Bathonian–Barremian); France (early Bathonian–middle Miocene); Portugal (Kimmeridgian–early Tithonian); Spain (Barremian–late Campanian or early Maastrichtian); Italy (early Albian); Sweden (Early Cretaceous; stage unknown); Romania (Maastrichtian); Germany (early Oligocene–middle Miocene); Czech Republic (early Miocene); Austria (early–late Miocene); and Hungary (early Pliocene). Both the geologically oldest (early Bathonian, England and France) and youngest (early Pliocene, Hungary) occurrences of albanerpetontids are in Europe. Most European localities have produced isolated and, less commonly, articulated skull and postcranial bones. Fissure infills of middle Miocene age at La Grive-Saint-Alban, France, and of early Pliocene age at Csarnóta 2, Hungary, are especially important for having yielded hundreds of three-dimensionally preserved skull and postcranial bones that have proven informative for determining associations of isolated bones and for documenting the structure and contacts of these elements (Estes and Hoffstetter 1976; Venczel and Gardner 2005). The only articulated albanerpetontid skeletons yet discovered come from two European Lower Cretaceous sites: one skeleton from Pietraroia (early Albian), Italy, and four skeletons from Las Hoyas (late Barremian), Spain (Costa 1864; McGowan and Evans 1995; McGowan 2002; S. E. Evans pers. comm. 2003). All three albanerpetontid genera and five named species within those genera are recognized from Europe (Table 12.1): *Anoualerpeton* (one species), *Albanerpeton* (two species), and *Celtedens* (two species).

The geologically oldest albanerpetontid fossils are of early Bathonian age. Both records consist of a single, taxonomically indeterminate specimen: an atlantal centrum described by Seiffert (1969; see also Estes 1981) from "sapropelitic rock" near Gardies, south-central France, and an undescribed articular (S. E. Evans pers. comm. 2005) from Hornsleasow Quarry, south-central England. Seiffert (1969) originally reported a slightly older age of late Bajocian for the atlas, but more recent geological and paleontological work in the Gardies area (see Kriwet et al. 1997) indicates that the locality is early Bathonian. The undescribed articular from Hornsleasow Quarry is the basis for Evans and Milner (1994: table 18.2) and Evans and Waldman (1996: table 1) having recorded an albanerpetontid in their faunal list for that locality. The next oldest albanerpetontid fossils come from four late Bathonian localities in the Forest Marble Formation of southern England (e.g., Evans and Milner 1991, 1994). The most productive of these localities is the Kirtlington Cement Quarry, which has yielded several hundred skull and postcranial bones (e.g., McGowan 1996; Gardner et al. 2003) that currently are interpreted as belonging to *Anoualerpeton priscus* (Gardner et al. 2003). The Late Jurassic record is restricted to three Kimmeridgian and early Tithonian localities in Portugal: Porto das Barcas, Guimarota Mine, and Porto Dinheiro. According to Wiechmann's (2003) Ph.D. dissertation, the last two localities have produced jaws, frontals, parietals, and vertebrae of an unnamed new species of *Celtedens*. Judging from Wiechmann's (2003) figures, we concur that frontals from both localities are reliably diagnostic for *Celtedens* in being relatively elongate and in having a bluntly rounded internasal process.

For the Early Cretaceous, the oldest occurrences anywhere in the world are in the Berriasian-age Purbeck Limestone Group in south-central England. Abundant skull and postcranial bones have been recovered from localities in the Cherty Water Member of the Lulworth Formation, including frontals that are diagnostic for *Celtedens* (McGowan and Ensom 1997; Gardner 2000a; Evans and McGowan 2002). On the basis of previously published accounts, Wiechmann (2003) regarded material from the Lulworth Formation as belonging to one indeterminate *Celtedens* species; however, preliminary examination by one of us (Gardner unpubl. obs. 2003) of jaws and frontals from this formation indicates that several morphs may be present, which raises the possibility that more than one species may be represented in the unit. The overlying Durlston Formation has produced taxonomically indeterminate jaw fragments (Underwood and Rees 2002; Evans and McGowan 2002). The last record of albanerpetontids in the British Isles occurs on the Isle of Wight, off the south-central coast of England, in the Barremian-age Wessex Formation. Evans et al. (2003) described a taxonomically indeterminate articular from the unit. Additional cranial and postcranial bones have been recovered from several microsites in the Wessex Formation; this material appears to be from a previously unrecognized albanerpetontid taxon (S.C. Sweetman pers. comm. 2003).

Elsewhere in Europe, Barremian albanerpetontids are known from localities in Spain. Galve (early Barremian) and Pio Pajarón and Uña (both late Barremian) have produced isolated albanerpetontid bones. Material from Galve has been assigned to the species now called *Celtedens megacephalus* (Estes and Sanchíz 1982; McGowan 1998b), but because the diagnostically important frontals from this locality have not been examined by us or adequately figured, we conservatively list this occurrence as "Albanerpetontidae indet." in Table 12.2. According to Wiechmann (2003), Uña has yielded jaws and frontals of *C. megacephalus* (McGowan 2002 also referred frontals from Uña to this species), frontals and premaxillae of an unnamed new species of *Albanerpeton*, and taxonomically indeterminate skull bones. If Wiechmann's (2003) taxonomic identifications are correct, Uña contains the oldest multispecific albanerpetontid assemblage and the oldest occurrence of *Albanerpeton*. Although we have not seen the material (four frontals and four premaxillae) of the putative new *Albanerpeton* species, judging from descriptions and figures in Wiechmann's (2003) dissertation, it appears that the assigned frontals more closely resemble those of *Anoualerpeton* (a genus that was not formally described at the time of Wiechmann's study) than *Albanerpeton* in being relatively more elongate. Because we question Wiechmann's (2003) generic identification, here we record the Uña species as "?*Albanerpeton* n. sp."

The most famous of the Spanish localities is the late Barremian Las Hoyas quarry, which has yielded slab-style albanerpetontid skeletons, including one (the holotype of *Celtedens ibericus*) that preserves details of soft tissue. Two skeletons from Las Hoyas have been described and figured in detail (McGowan and Evans 1995; McGowan 2002), and a third skeleton was briefly mentioned by McGowan (2002). All three of these were assigned by McGowan (2002) to *C. ibericus*. A fourth, undescribed skeleton also has been collected from Las Hoyas (S. E. Evans pers. comm. 2003). The two skeletons first reported by McGowan and Evans (1995) have been extremely informative for showing the body form and certain osteological details (e.g., presence of a jugal), but some features are difficult to interpret because both specimens are small and flattened, and some bones are crushed or broken. All four skeletons from Las Hoyas are currently being studied by S. E. Evans and J. D. Gardner. The only other albanerpetontid skeleton known to us is the holotype of *C. megacephalus* from Pietraroia (early Albian), southern Italy. This specimen is the anterior end of a poorly preserved, slab-style skeleton (Costa 1864; D'Erasmo 1914; Gardner 2000c; McGowan 2002), and it documents the last occurrence of *Celtedens*. The final Early Cretaceous (stage uncertain) and most northerly occurrence of albanerpetontids in Europe consists of taxonomically indeterminate, fragmentary skull bones from southernmost Sweden (Rees and Evans 2002).

The European Late Cretaceous record of albanerpetontids is limited to the Campanian and Maastrichtian. Diagnostic *Albanerpeton* bones have been reported from La Neuve (middle–late Campanian) in southeastern France (Duffaud 2000) and from several Maastrichtian localities in the Haţeg Basin of west-central Romania (e.g., Grigorescu et al. 1999; Duffaud 2000; Folie and Codrea 2005). The precise age of the Romanian localities is uncertain. Originally they were considered late Maastrichtian, but more recent work suggests a slightly older age of early–middle Maastrichtian (see Therrien 2005:19). Duffaud (2000) stated that specimens available to him from France and Romania were most similar to *A. nexuosum*, whereas Folie and Codrea (2005) stated that the Romanian specimens available to them were most similar to *A. inexpectatum*. Considering their provenance and the fact that no other species of *Albanerpeton* have been identified from the Late Cretaceous–Eocene of Europe, we suggest that the French and Romanian specimens probably pertain to one or more previously unrecognized species in the genus. From one of the localities in the Haţeg Basin, Grigorescu et al. (1999) also briefly described, but did not figure, a specimen that they interpreted as a pair of fused frontals belonging to *Celtedens*. Although we have not examined this specimen firsthand, one of us (J.D.G.) has seen an unpublished drawing that appears to depict fused, incomplete frontals from a squamate, not an albanerpetontid. Rare, taxonomically indeterminate albanerpetontid bones also have been reported from Laño quarry (late Campanian or early Maastrichtian) in the Basque region of Spain and from Cruzy (?early Maastrichtian) and Cassagnau 1 (late Maastrichtian) in southern France (Table 12.2).

Until the late 1990s, the only post-Mesozoic records for albanerpetontids in Europe were collections of isolated and rare articulated skull and postcranial bones of *Albanerpeton inexpectatum* from middle Miocene fissure infills in quarries near La Grive-Saint-Alban, east-central France (Estes and Hoffstetter 1976; Estes 1981; Gardner 1999a). The precise age of many of these specimens is uncertain, because fissure infills in the La Grive-Saint-Alban quarries range in age from MN5 to MN7/8, and in many cases, the fissures from which particular specimens were collected is not reliably known (Gardner 1999a). Beginning in the late 1990s, numerous new occurrences have been identified that extend the Tertiary record for albanerpetontids in Europe from the early Oligocene (MP21) to the early Pliocene (MN15) and eastward into Germany, Austria, the Czech Republic, and Hungary. Except for material described from Oberdorf O3 and O4, Obergänserndorf 2, and Teiritzberg T2/3 and T2/6 (all early Miocene) in Austria (Sanchíz 1998; Böhme 2002), Sansan (middle Miocene) in France (Rage and Hossini 2000), Randecker Maar (early Miocene) in Germany (Wiechmann 2003), and Csarnóta 2 (early Pliocene) in Hungary (Venczel and Gardner 2005), specimens from other localities in Germany, Austria, and the Czech Republic have not been studied in any detail. For the time being, most of these specimens appear to be referable to *Albanerpeton* and, in some cases, to *A. inexpectatum*. The unnamed new species of *Albanerpeton* mentioned by Böhme (2002:340) from the Merkur-North locality (early Miocene) of the Czech Republic can be disregarded because subsequent examinations of undescribed frontals and jaws from the locality indicate that these specimens pertain to *A. inexpectatum* (M. F. Wiechmann pers. comm. 2003 to M.B.; Gardner unpubl. obs. 2005). The geologically youngest record of albanerpetontids comes from a fissure infill at Csarnóta 2 (early Pliocene or MN15), south-central Hungary. Several hundred isolated and articulated skull bones and isolated vertebrae and limb bones, which were collected in the early 1950s from this fissure infill, recently were described as belonging to the new species *A. pannonicus* (Venczel and Gardner 2005).

North American Record

Albanerpetontids are reliably known in North America from the Early Cretaceous to late Paleocene by isolated elements recovered from microsites. Occurrences are restricted to the Western Interior of southern Alberta and Saskatchewan, Canada, southward into the United States from Montana to Texas. Five named and one unnamed species of *Albanerpeton* have been recognized from the continent.

The geologically oldest, unequivocal albanerpetontid fossils from North America are taxonomically indeterminate, fragmentary jaws recently identified (Gardner and Cifelli unpubl. obs. 2005) from the Neocomian age (stage unknown) Lakota Formation of South Dakota, USA. The next oldest albanerpetontid fossils are taxonomically indeterminate jaws from the lower part of the Cloverly Formation in Wyoming, USA (Gardner 1999b). The Cloverly Formation is considered to be of Aptian–Albian age (Ostrom 1970; Jacobs et al. 1991) and perhaps slightly younger than fossiliferous horizons in the Antlers and Paluxy formations of Texas and Oklahoma, USA (Jacobs et al. 1991). Several localities in the middle and upper parts (latest Aptian–middle Albian) of the Antlers Formation in Texas and Oklahoma have yielded isolated jaws, frontals, atlantes, and humeri of *Albanerpeton arthridion* (Estes 1969; Fox and Naylor 1982; Cifelli et al. 1997; Gardner 1999b). An atlantal centrum from the base of the Paluxy Formation (early–middle Albian), Texas, that originally was reported as being from an albanerpetontid (Winkler et al. 1990) is probably from a salamander (Gardner 1999b). Microsites straddling the Albian–Cenomanian boundary in the Mussentuchit Member of the Cedar Mountain Formation in Utah, USA, have yielded albanerpetontid jaws belonging to two species (Cifelli et al. 1999; Gardner 1999c): an indeterminate genus and species represented by small jaws that primitively resemble those of A. *arthridion* and an indeterminate species of *Albanerpeton*, cf. A. *nexuosum*, represented by a larger dentary and pair of larger, fused premaxillae. Microsites spanning the Cenomanian–early Santonian in the Dakota and Straight Cliffs formations in Utah have produced incomplete albanerpetontid jaws, atlantes, and frontals. Most of these specimens are not identifiable below family level (Gardner 1999c; Gardner unpubl. obs. 2005), but one distinctive premaxilla from the Smoky Hollow Member (late Turonian) of the Straight Cliffs Formation was described as the holotype and only known specimen of A. *cifellii* (Gardner 1999c).

In terms of the number of specimens, localities, and taxa, the richest record of albanerpetontids in the North American Western Interior occurs from the late Santonian or early Campanian to the end of the Cretaceous. Microsites in at least 14 formations from this interval have produced abundant jaws and lesser numbers of skull roof bones and atlantes. In the most recent treatment of latest Cretaceous North American albanerpetontids, Gardner (2000c) recognized three species of *Albanerpeton* on the basis of diagnostic jaws and frontals: A. *nexuosum* from the late Santonian or early Campanian–late Maastrichtian of Alberta, Colorado, Montana, New Mexico, Texas, Utah, and Wyoming; A. *galaktion* from the late Santonian or early Campanian–late Maastrichtian of Alberta, Utah, and Wyoming; and a then-new species, A. *gracilis* (amended to A. *gracile* by Folie and Codrea 2005), from the middle Campanian of Alberta, Utah, and Texas. Five formations in the Western Interior are known to contain fossils of more than one species: A. *nexuosum* and A. *galaktion* in the Milk River Formation (late Santonian or early Campanian) of Alberta and the Lance Formation (late Maastrichtian) of Wyoming; A. *galaktion* and A. *gracile* in the middle Campanian Aguja Formation of Texas; and all three congeners in the middle Campanian Oldman Formation of Alberta and Kaiparowits Formation of Utah. Rare jaws of A. *nexuosum* have been reported from the Bug Creek Anthills in the Hell Creek Formation of Montana, and these previously were considered to be late Maastrichtian in age (Estes 1981; Gardner 2000b). These fossils are better regarded as late Maastrichtian or earliest Paleocene in age because the Bug Creek Anthills is now interpreted as a mixed assemblage of early Paleocene and reworked late Maastrichtian fossils (Lofgren 1995; Cifelli et al. 2004). The only unequivocal, post-Cretaceous occurrences of albanerpetontids in North America are undescribed skull bones (currently being described by J. D. Gardner and C. S. Scott) from the Paskapoo Formation of southern Alberta. These specimens include fragmentary, taxonomically indeterminate jaws from a middle Paleocene quarry in Calgary and slightly younger jaws and skull roof bones belonging to a new, unnamed species of *Albanerpeton* from several upper Paleocene quarries near Calgary and Red Deer.

Although there are no verified records of Jurassic albanerpetontids in North America, two sets of researchers (Gardner unpubl. obs. 2003; A. O. Averianov et al. unpubl. obs. 2005) have independently raised suspicions about the identity of a pair of isolated atlantal centra described by Curtis and Padian (1999) from the Lower Jurassic (?Sinemurian–Pliensbachian) Kayenta Formation of Arizona. Curtis and Padian (1999) interpreted these atlantes as being from an indeterminate salamander. However, judging by published photographs (Curtis and Padian 1999: figs 11, 12), certain features of these specimens—particularly the form of the odontoid process and anterior cotyles—compare more favorably with albanerpetontid atlantes. Another possibility is that these atlantes may be from the stem caecilian *Eocaecilia micropodia*, which was described by Jenkins and Walsh (1993) from the same formation.

Asian Record

The fossil record of albanerpetontids in Asia is limited to the central part of the continent. The late Russian paleontologist Lev Nessov reported albanerpetontid fossils from the Middle Jurassic of Kirghizia and the Upper Cretaceous of Uzbekistan and Kazakhstan (Nessov 1981, 1988, 1997; Nessov and Udovichenko 1986), and he named two Late Cretaceous genera and three species (Nessov 1981, 1997). In a detailed review of Asian albanerpetontids, Gardner and Averianov (1998) concluded that the record was more limited than previously thought. The main findings of their review were: (1) Nessov's (1981) report of an albanerpetontid frontal from the Middle Jurassic (Callovian) Balabansay Formation in Kirghizia was unproven, because the specimen had not been described or figured and it could not be relocated in any institutional collection; (2) the names *Nukusurus* Nessov 1981, *N. insuetus* Nessov 1981 (type species), and *N. sodalis* Nessov 1997 were nomina dubia within the Albanerpetontidae because the respective holotype dentaries of the two species are not distinctive below the family level; and (3) the holotype atlas and only specimen of *Bishara backa* Nessov 1997, from the Bostobe Formation (late Santonian or Campanian) of Kazakhstan, belongs to an indeterminate salamander, not an albanerpetontid. Gardner and Averianov (1998) concluded that no albanerpetontid genera or species could be recognized from Asia, and that the fossil record of unequivocal albanerpetontids on the continent was limited to five Upper Cretaceous dentaries from Uzbekistan–one from the Bissekty Formation (Coniacian) and four from the Khodzhakul Formation (early Cenomanian). We are not aware of any further reports of albanerpetontid fossils from Asia. As an aside, it should be noted that Shishkin (2000:307) erroneously attributed (A. O. Averianov pers. comm. 2005) the holotype dentary of *N. insuetus* nomen dubium to either the upper part of the Khodzhakul Formation or the basal part of the Beshtyube Formation and listed its age as either Cenomanian or ?early Turonian.

African Record

The fossil record of albanerpetontids in Africa is limited to a collection of isolated and rare articulated skull bones, vertebrae, and humeri from the Anoual microvertebrate locality in east-central Morocco. This locality is a fossiliferous lens in the Couches Rouges ("red beds") and is dated as Early Cretaceous, probably Berriasian (Sigogneau-Russell et al. 1998). Albanerpetontid fossils from the Anoual locality were mentioned by Broschinski and Sigogneau-Russell (1996) and Sigogneau-Russell et al. (1998) and, most recently, were described by Gardner et al. (2003) as belonging to the new species *Anoualerpeton unicus*.

A relationship between the salamander *Ramonellus longispinus* from the Early Cretaceous (late Aptian) of Israel and taxa that are now regarded as albanerpetontids has been proposed by several authors (Estes 1969, 1981; Nevo and Estes 1969; Estes and Hoffstetter 1976; Milner 2000). Gardner et al. (2003) reviewed the evidence for such a relationship and concluded that *Ramonellus* exhibits a suite of primitive and derived character states of the jaws, limbs, and vertebrae that indicate it is a salamander, not an albanerpetontid.

PHYLOGENY OF THE ALBANERPETONTIDAE

Evidence for Monophyly

Monophyly of the Albanerpetontidae has never been questioned (e.g., Fox and Naylor 1982; Milner 1988, 2000; McGowan and Evans 1995; Gardner 2000a, 2001; McGowan 2002; Ruta and Coates 2003; Ruta et al. 2003a,b; Schoch and Milner 2004). Two cladistic analyses (Gardner 2001; Ruta et al. 2003b) have found strong support for a monophyletic Albanerpetontidae composed of *Albanerpeton* + *Celtedens*. *Anoualerpeton* has not yet been included in a larger-scale cladistic analysis with the other two albanerpetontid genera and a representative selection of nonalbanerpetontids that could test its inclusion within the Albanerpetontidae. Nevertheless, because elements available for *Anoualerpeton* exhibit the full suite of albanerpetontid apomorphies (see below), we are confident that all three genera form a monophyletic Albanerpetontidae.

Drawing on work by Fox and Naylor (1982), Milner (1988), Gardner (2001), McGowan (2002), and Gardner et al. (2003), monophyly of the Albanerpetontidae is supported by at least the following apomorphies: (1) frontals solidly fused; (2) anteromedian edge of frontals bears a prominent, anteriorly projecting internasal process with a deep groove extending along both lateral faces; (3) posterior ends of paired nasals and prefrontals fit into complementary slots in the fused frontals; (4) symphyseal prongs on dentaries form an interdigitating symphyseal or intermandibular joint; (5) facet on articular bone in mandible for contact with quadrate faces posteriorly; (6) marginal teeth nonpedicellate; (7) crowns on marginal teeth labiolingually compressed and bear three mesiodistally aligned cuspules; and (8) anteriormost three vertebrae highly modified, consisting of an atlas lacking postzygapophyses and having a notch in the posteromedian edge of the neural arch roof, second vertebra (so-called axis) consisting only of a centrum and having a tripartite joint anteriorly with atlantal centrum, and third vertebra having its neural arch expanded anteriorly to fit into the complementary notch in the posterior edge of the atlantal neural arch roof and having its centrum variably fused anteriorly with the axis. Gardner (2001) suggested that apomorphies of the teeth were associated with a shearing bite and that other cranial and cervical apomorphies were involved in strengthening and increasing the mobility of the skull, mandibles, and cervical region for feeding and burrowing.

Higher Level Relationships of the Albanerpetontidae

All cladistic analyses that have included albanerpetontids, regardless of whether lepospondyls were also included, have consistently nested albanerpetontids within the Temnospondyli, close to caudates, salientians, ± gymnophionans (Trueb and Cloutier 1991; McGowan and Evans 1995;

McCord 1999; Gardner 2001; McGowan 2002; Ruta et al. 2003a,b; Anderson in press). Although there is widespread agreement from both cladistic and noncladistic studies that albanerpetontids are possible lissamphibians (e.g., Estes and Hoffstetter 1976; Estes 1981; Estes and Sanchíz 1982; Fox and Naylor 1982; Milner 1988, 2000; Trueb and Cloutier 1991; McGowan and Evans 1995; McCord 1999; Gardner 2000a, 2001; McGowan 2002; Ruta and Coates 2003; Ruta et al. 2003a,b; Schoch and Milner 2004; Anderson in press), the position of albanerpetontids with respect to gymnophionans, caudates, and salientians is not firmly established. Two alternatives have been proposed.

The first and more traditional interpretation is that albanerpetontids are most closely related to caudates. Among advocates of this hypothesis, albanerpetontids generally are placed as a clade within the Caudata (Estes and Hoffstetter 1976; Estes 1981; Estes and Sanchíz 1982; Trueb and Cloutier 1991: figs 6, 7; McCord 1999) and often allied with the Prosirenidae sensu Estes (1981). The strict consensus of the 12 trees found in Trueb and Cloutier's (1991: fig. 4) analysis differed slightly in placing albanerpetontids in an unresolved trichotomy with Urodela and the stem salamander *Karaurus*, which left open the possibility that albanerpetontids and caudates could be sister taxa. The strict consenus of three shortest trees generated in a recent morphological character-based analysis by Anderson (in press: fig. 5) recovered a sister pair of albanerpetontids + Urodela. In the discussion portion of a molecular study of relationships among extant, basal lissamphibians, Feller and Hedges (1998:511) stated that they favored a caudate-albanerpetontid relationship (the precise nature of this inferred relationship was never explicitly stated) on biogeographical grounds, because they regarded both groups as primarily Laurasian. A total of 17 morphological synapomorphies have been proposed for uniting albanerpetontids and caudates (Estes and Sanchíz 1982; Trueb and Cloutier 1991; McCord 1999; summarized by Gardner 2001: table 2), and three morphological character-based cladistic analyses have found support for an albanerpetontid-caudate relationship (Trueb and Cloutier 1991; McCord 1999; Anderson in press). In a review of papers published up to 2001, Gardner (2001): (1) argued that none of the 17 character states were convincing synapomorphies for uniting albanerpetontids and caudates to the exclusion of other groups; (2) noted numerous problems with the analyses by Trueb and Cloutier (1991) and McCord (1999); and (3) demonstrated that the albanerpetontid-caudate clades recovered in those two analyses were weakly supported. The albanerpetontid-urodele pairing recovered in Anderson's (in press) more recent study is difficult to evaluate because synapomorphies and levels of support were not reported. Also, as Anderson (in press) acknowledged, it in unclear from his analysis whether albanerpetontids could be the sister group to just the Urodela (i.e., crown clade salamanders) or to the more inclusive Caudata (i.e., stem + crown clade salamanders), because his analysis did not include any stem salamanders.

The second interpretation is that albanerpetontids are no more closely related to caudates than they are to salientians and, possibly, gymnophionians. All other morphological character-based cladistic analyses that have included albanerpetontids have consistently identified caudates and salientians (="Batrachia") as each other's closest relatives, to the exclusion of albanerpetontids (McGowan and Evans 1995; Gardner 2001; McGowan 2002; Ruta et al. 2003a,b). In these analyses, the Batrachia is supported by a small number of osteological synapomorphies, such as maxillary arcade open posteriorly and dermal scales absent, that do not occur in albanerpetontids. Consequently, exclusion of the Albanerpetontidae from the Batrachia appears justified. With regards to the Batrachia, it is important to note that although earlier molecular studies (e.g., Larson and Wilson 1989; Hay et al. 1995; Feller and Hedges 1998) generally identified a Caudata-Gymnophiona clade (="Procera" sensu Feller and Hedges 1998), more recent molecular analyses have found stronger support for the Batrachia (Zardoya and Meyer 2001; San Mauro et al. 2004, 2005). Schoch and Milner (2004) recently suggested that the Procera hypothesis may be better supported by morphological evidence than previously thought, but they did not present a cladistic analysis to test this possibility.

Relative to the Batrachia, three different positions have been identified for albanerpetontids: (1) albanerpetontids are the sister group of the Batrachia (McGowan and Evans 1995; Gardner 2001; McGowan 2002; Ruta et al. 2003b); (2) albanerpetontids are the sister group of Gymnophiona + Batrachia (Ruta et al. 2003a: fig. 5, their majority rule tree; see also Ruta and Coates 2003); or (3) albanerpetontids form an unresolved trichotomy with gymnophionans and batrachians (Ruta et al. 2003a: fig. 4, their strict consensus tree). Neither of the first two arrangements is overwhelmingly robust, because reversing the positions of albanerpetontids and gymnophionans requires three extra steps in the analysis by Gardner (2001), two extra steps in the analysis by McGowan and Evans (1995; reported by Gardner 2001:312), and just one extra step in the analyses by McGowan (2002) and Ruta et al. (2003a). Ruta et al. (2003a) further noted that some of their minimum + 1 step trees also recovered a sister-pair relationship between albanerpetontids and gymnophionans. Although these analyses did not find strong support for any particular placement of albanerpetontids outside of the Batrachia, placing albanerpetontids within the Batrachia or pairing them with either caudates or salientians was found to be less parsimonious because those alternatives required even more steps and character state conflicts. On balance, current evidence best supports placing albanerpetontids outside of and close to the Batrachia, but the exact position of albanerpetontids relative to batrachians and gymnophionans remains unresolved.

Relationships within the Albanerpetontidae

Four cladistic analyses have examined relationships within the Albanerpetontidae (Gardner 2002; Gardner et al. 2003; Wiechmann 2003; Venczel and Gardner 2005). These analyses are broadly comparable because they used many of the same jaw and frontal characters and included many of the same taxa.

The first analysis (Gardner 2002) focused on relationships among the seven species then recognized for *Albanerpeton* and used three non-*Albanerpeton* albanerpetontid taxa as outgroups, namely the genus *Celtedens* and two unnamed species, the "Kirtlington species" and "Anoual species," which correspond to the species now known as *Anoualerpeton priscus* and *An. unicus*. The key findings of that analysis were: (1) the three non-*Albanerpeton* taxa formed an unresolved polychotomy with *Albanerpeton;* (2) monophyly of *Albanerpeton* was corroborated; and (3) within *Albanerpeton,* the North American Early Cretaceous A. *arthridion* was the basalmost congener and sister taxon of the "post-middle Albian clade" which, in turn, was composed of two sister clades—the North American Late Cretaceous "gracile-snouted clade" containing A. *cifellii,* A. *galaktion,* and A. *gracile* in an unresolved trichotomy, and the Euramerican Late Cretaceous–Neogene "robust-snouted clade" containing A. *nexuosum* as the sister taxon of A. *inexpectatum* + the unnamed Paleocene species from Alberta, Canada.

In addition to consistently recovering a monophyletic *Albanerpeton,* later analyses also found a monophyletic *Anoualerpeton* consisting of *An. unicus* + *An. priscus* (Gardner et al. 2003; Venczel and Gardner 2005) and a monophyletic *Celtedens* (Wiechmann 2003) consisting of an unnamed new species from the Kimmeridgian–early Tithonian of Portugal and an indeterminate species from the Berriasian of England (the latter based on material from the Purbeck Group that may pertain to more than one species; Gardner unpubl. obs. 2003) as successively more distant sister species to C. *megacephalus* + C. *ibericus.* These analyses also consistently identified *Anoualerpeton* (represented by the "Kirtlington-Taxon" in Wiechmann's 2003 analysis) as the sister to *Albanerpeton* + *Celtedens.* Depending on the analysis, the sister pair of *Albanerpeton* + *Celtedens* was founded on one premaxillary apomorphy (Gardner et al. 2003; Venczel and Gardner 2005) or two frontal apomorphies (Wiechmann 2003). Reported indices of support for this sister pair were modest, with bootstrap values of 69% to 87% and decay indices of 1 or 2 steps.

Although all four analyses corroborated monophyly of *Albanerpeton,* patterns within the genus have proven less stable. The first two analyses (Gardner 2002; Gardner et al. 2003) included the same seven species of *Albanerpeton* and used the same subset of characters for resolving relationships within the genus. Both analyses identified A. *arthridion* as the sister to a less inclusive clade comprising the "gracile-snouted clade" + "robust-snouted clade," and they found relatively weak support for the "gracile-snouted clade" (decay index of 1 step and bootstrap values of 62% or 63%). Later analyses recovered the same basic patterns, except that the "gracile-snouted clade" collapsed. In Wiechmann's (2003) analysis, A. *cifellii,* A. *galaktion,* and A. *gracile* were placed along the stem of the "robust-snouted clade," whereas in Venczel and Gardner's (2005) analysis, their strict consensus tree placed the three "gracile-snouted" congeners in an unresolved polychotomy with the "robust-snouted clade." Each of the two most recent analyses also included a different, eighth species of *Albanerpeton:* the unnamed, putative *Albanerpeton* sp. in Wiechmann's (2003) analysis was placed immediately stemward of A. *arthridion* as the basalmost member of the clade, whereas in Venczel and Gardner's (2005) analysis, their new early Pliocene species, A. *pannonicus,* was nested within the "robust-snouted clade" as the sister of A. *inexpectatum* + the unnamed Paleocene species.

On the basis of analyses conducted to date, and given our concerns about Wiechmann's (2003) indeterminate *Celtedens* species from Purbeck and his putative new *Albanerpeton* species from Uña, the following is our preferred, conservative arrangement of relationships within the Albanerpetontidae (Fig. 12.1): (1) *Anoualerpeton* is the sister to *Celtedens*+*Albanerpeton*; (2) within *Anoualerpeton*, *An. unicus*+*An. priscus* are sister taxa; (3) within *Celtedens*, the unnamed Kimmeridgian–early Tithonian congener is the sister to *C. megacephalus*+*C. ibericus*; (4) within *Albanerpeton*, *A. arthridion* is the basalmost congener and sister to a clade of post-middle Albian congeners; (5) the "post-middle Albian clade" consists of an unresolved polychotomy among *A. cifellii*, *A. galaktion*, and *A. gracile* and the "robust-snouted clade"; and (6) relationships within the "robust-snouted clade" are: *A. nexuosum* (*A. pannonicus* (*A. inexpectatum*+ unnamed Paleocene species)). As noted earlier in this chapter, in our opinion, the affinities of the unnamed late Barremian species from Uña that Wiechmann (2003) assigned to *Albanerpeton* are problematic. If Wiechmann's (2003) placement of this species immediately stemward of *A. arthridion* proves stable and depending on where the node for *Albanerpeton* is placed, the Barremian species may be either the basalmost member of *Albanerpeton* or the sister taxon of the genus. Alternatively, further analysis may show that the affinities of the Barremian taxon lie elsewhere within the Albanerpetontidae, perhaps closer to *Anoualerpeton*.

We are still in the early stages of understanding relationships within the Albanerpetontidae. Character-based cladistic analyses have been presented only recently (Gardner 2002; Gardner et al. 2003; Wiechmann 2003; Venczel and Gardner 2005), and we can expect that the phylogenetic framework presented here will continue to change as new analyses are performed.

TIMES OF DIVERGENCE AND PALEOBIOGEOGRAPHY

Phylogenetic frameworks presented in the previous section and fossil occurrences can be used to estimate minimum times of divergence for clades and to make constrained speculations about the paleobiogeographic history of albanerpetontids.

Fossil occurrences demonstrate that all four lissamphibian clades were present by the Middle Jurassic (Bathonian) and thus must have differentiated by that time (e.g., Milner 1993). A minimum date for the origin of the Lissamphibia is provided by the geologically oldest known members of the clade—the stem frogs *Triadobatrachus* and *Czatkobatrachus* from the earliest Triassic of, respectively, Madagascar and Poland (e.g., Rage and Roček 1989; Evans and Borsuk-Białynicka 1998). These occurrences indicate that the origins of the Lissamphibia and, probably, the Albanerpetontidae must have occurred earlier during the Permian or even Pennsylvanian (e.g., Milner 1988, 1994; McGowan 2002; Gardner et al. 2003; Ruta et al. 2003a; Schoch and Milner 2004). If this estimate is correct, a gap of at least 80 million years, according to the timescale of Gradstein et al. (2004), separates the inferred origin of the Albanerpetontidae from their first appearance in the fossil record in the early Bathonian. The duration of that gap means that at least the first one-third of the evolutionary history of albanerpetontids remains undocumented.

Cladistic analyses provide estimated minimum ages of late Bathonian for the split between *Anoualerpeton* and *Celtedens*+*Albanerpeton* on

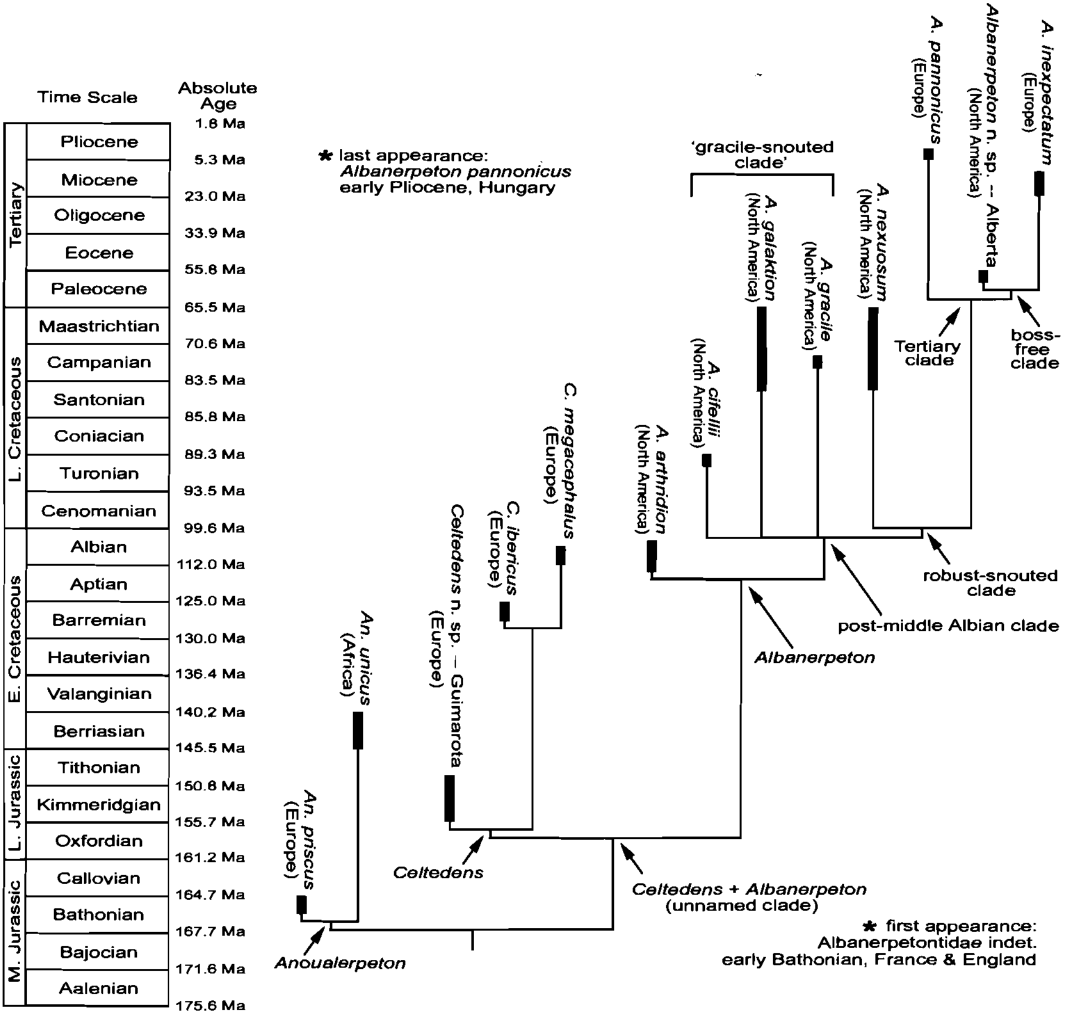

FIGURE 12.1. Hand-drawn cladogram showing our conservative, preferred pattern of relationships within the Albanerpetontidae, constrained against the geological timescale to show ranges of terminal taxa and estimated divergence times. Asterisks denote first and last unequivocal appearances of albanerpetontids in the fossil record. Tree topology is based on cladograms generated by character-based analyses by Wiechmann (2003: abb. 8.1) and Venczel and Gardner (2005: text-fig. 9). The putative new species that we list in the text and tables as "?*Albanerpeton* n. sp." (=*Albanerpeton* n. sp. sensu Wiechmann 2003) from the late Barremian of Uña, Spain, is not shown because we consider the generic affinities of that species unresolved; Wiechmann's (2003) analysis placed that species at the next node stemward below *A. arthridion*. Wiechmann's (2003:113) "*Celtedens* sp. indet." from the Berriasian of the Isle of Purbeck, England, also is not shown because it is based on specimens that may pertain to more than one species (Gardner unpubl. obs. 2003); Wiechmann's (2003) analysis placed "*Celtedens* sp. indet." as the sister of the three species of *Celtedens* shown here. First and last appearances of the Albanerpetontidae and the geographic and temporal ranges of terminal taxa follow Tables 12.1 and 12.2. The estimated minimum age for the node supporting the robust-snouted clade is constrained by jaws of *Albanerpeton* sp., cf. *A. nexuosum* from the Albian–Cenomanian boundary in Utah, USA (Gardner 1999c, 2002). Durations of intervals depicted in the geological timescale are not proportional. Absolute ages (Ma) for boundaries are from Gradstein et al. (2004: fig. 23.1).

the basis of the earliest record of *Anoualerpeton* in the late Bathonian of England (Gardner et al. 2003), and of Kimmeridgian for the split between *Celtedens* and *Albanerpeton* on the basis of the occurrence of Wiechmann's (2003) unnamed, new *Celtedens* species at Guimarota Mine and Porto Dinheiro in Portugal. The earliest verified appearance of *Albanerpeton* is much later in the latest Aptian or earliest Albian of Oklahoma (Gardner 1999b), which implies that about the first 40 million years (according to the timescale of Gradstein et al. 2004) of the history of *Albanerpeton* is missing (Gardner et al. 2003). If Wiechmann (2003) is correct that the unnamed late Barremian species from Portugal belongs to *Albanerpeton,* that species would narrow the gap between the inferred origin of the genus and its first appearance in the fossil record to about 30 million years.

Attempts to interpret the paleobiogeographic history of albanerpetontids (Feller and Hedges 1998; Gardner and Averianov 1998; Gardner 2002; Gardner et al. 2003; Wiechmann 2003; Folie and Codrea 2005; Venczel and Gardner 2005) are complicated by the group's temporally and geographically patchy fossil record. Except for one occurrence in the Berriasian of northern Africa, albanerpetontid fossils are known only from Laurasia (Table 12.2). Although this pattern has been taken as evidence that albanerpetontids originated in Laurasia (e.g., Feller and Hedges 1998; Gardner and Averianov 1998), this interpretation needs to be balanced against the realization that the Mesozoic record of small-bodied, nonmarine vertebrates in Gondwana is even poorer than in Laurasia (e.g., Sigogneau-Russell et al. 1998). Assuming that albanerpetontids originated in the Late Paleozoic and regardless of where the group arose, they may have had a much broader geographic distribution than what is implied by their known, primarily Laurasian, fossil record.

Even the Laurasian record of albanerpetontids contains some curious gaps. In the Mesozoic, albanerpetontid fossils have not been identified from either the Upper Jurassic Morrison Formation in Utah, USA, or the Lower Cretaceous Jehol Group in China. The apparent lack of albanerpetontid remains from these units is perplexing because both units preserve modest numbers of salamander and frog fossils (e.g., Evans and Milner 1993; Henrici 1998; Wang 2004; Evans et al. 2005) that were deposited under conditions (mainly freshwater lacustrine) that sampled appropriate environments and were suitable for preserving albanerpetontid fossils. Also, from a paleobiogeographic perspective, there is no obvious reason why albanerpetontids could not have been present during the Late Jurassic in Utah or the Early Cretaceous in China. During the Tertiary, albanerpetontids are entirely unknown from the Eocene, despite the fact that many richly fossiliferous amphibian localities from this epoch are known in Europe and North America. Albanerpetontids are last recorded in North America during the late Paleocene, so the lack of Eocene fossils there could indicate that albanerpetontids were extinct in North America by the Eocene. A similar interpretation cannot easily be made for Europe, however, because on that continent, albanerpetontids are known from earlier (Maastrichtian) and younger (Oligocene) intervals.

The presence of *Anoualerpeton unicus* in the basal Cretaceous (Berriasian) of Morocco and of indeterminate albanerpetontids in the early Late Cretaceous (Cenomanian and Coniacian) of Uzbekistan (Table 12.2) demonstrates that albanerpetontids were present on the African and Asian continents at those times. The occurrence of a second species of *Anoualerpeton* (*An. priscus*) in England indicates a broader Eurafrican distribution for the genus, and on the basis of the late Bathonian age of the European congener, the genus may have been present on the African continent by at least that time. Further insights into when and how albanerpetontids became established in Africa and Asia, how long they survived there, and whether they radiated on their respective continents must await discoveries of additional albanerpetontid fossils from those continents.

The comparatively richer European and North American records suggest that *Celtedens* was an exclusively European genus whose history was limited to that continent, whereas *Albanerpeton* was more broadly distributed and had a more complex history. Earlier speculations (Gardner 1999a, 2002) on the evolutionary history of *Albanerpeton* favored the idea that the genus originated and radiated in North America. According to this interpretation, the presence of *A. inexpectatum* in the Miocene of Western Europe was due to an emigration around the K/T boundary from North America into Europe. This "North American origin and diversification" hypothesis (sensu Venczel and Gardner 2005) has been seriously weakened by discoveries of diagnostic *Albanerpeton* fossils from numerous uppermost Cretaceous and Oligocene–early Pliocene localities in Europe (e.g., Folie and Codrea 2005; Venczel and Gardner 2005; Table 12.2) and of an early Pliocene species, *A. pannonicus*, from Hungary that appears to be more primitive than its geologically older Tertiary congeners (Venczel and Gardner 2005). Although the number of species that may be represented by the new European Cretaceous and Oligocene fossils is unknown and no phylogenetic analysis has considered these new finds, it is evident that the history of *Albanerpeton* was more complex than previously thought, with Europe having played a larger role (Wiechmann 2003; Folie and Codrea 2005; Venczel and Gardner 2005). If the late Barremian albanerpetontid from Spain proves to be a member of *Albanerpeton*, as Wiechmann (2003) proposed, the history of the genus will be even more complex and will extend back even further in Europe than in North America.

PALEOECOLOGICAL PREFERENCES OF EUROPEAN TERTIARY ALBANERPETONTIDS

Albanerpetontids are widely interpreted as having been fossorial on the basis of such features as their robustly constructed skull, specialized intermandibular and mandibular-skull joints, and modified cervical vertebrae (Estes and Hoffstetter 1976; Fox and Naylor 1982; McGowan 1998a, 2002; Gardner 1999a, 2001). Other aspects of the paleoecology of albanerpetontids have received less attention. Previous work generally has been limited to attempts to explain occurrences at one locality or at multiple localities in a narrow temporal range. Estes and Hoffstetter (1976; see also Estes 1981 and Gardner 1999a) interpreted the presence of abundant fossils of *Albanerpeton inexpectatum* in fissure infills near La Grive-Saint-Alban as evidence that this species thrived in karstic landscapes. Gardner (2000b) suggested that sympatry among *A. galaktion*, *A. gracile*, and *A. nexuosum* across parts of the North American Western Interior during the middle

Campanian was possible because differences in their snout and jaw structure and body size allowed them to exploit different ecological niches. In a study of middle Campanian microvertebrate assemblages in southeastern Alberta, Canada, Brinkman et al. (2004) regarded albanerpetontids as a characteristic member of their "inland," as opposed to "coastal," paleocommunity. Venczel and Gardner (2005) reported that the new early Pliocene *Albanerpeton* species at Csarnóta 2, Hungary, was not adversely affected by a change in the area from a forested to more open, grassland landscape and suggested that the apparent resiliency of this species may have been due to its burrowing lifestyle.

As part of a long-term research program by one of us (M.B.) on the distribution and paleoecology of lower vertebrates and their responses to climatic change during the Tertiary in Central Europe, many new occurrences of albanerpetontids have been identified in this region (Table 12.2). A particularly dense record occurs in the State of Bavaria, in southern Germany. In this region, fossils of *Albanerpeton* sp. and *A. inexpectatum* are known from 26 localities that span about 19 million years, according to the timescales of Steininger et al. (1996), Luterbacher et al. (2004), and Gradstein et al. (2004), from the basal Oligocene (MP21 or ≈34 Ma) to the earliest middle Miocene (MN5 or ≈15 Ma). Here we use these occurrences to interpret the paleoecological preferences of Oligocene and Miocene albanerpetontids in Europe.

In Bavaria, albanerpetontid fossils ~~generally~~ occur in two different depositional settings and geographical areas: (1) in fissure infills (16 localities) within Upper Jurassic limestones that form karstic plateaus of the Swabian and Franconian Alb, and (2) in floodplain deposits (9 localities) of the Older Series of the Upper Freshwater Molasse, located farther to the south in the North Alpine Foreland Basin. Within the study area and interval, just one locality occurs in a different depositional setting: Oberleichtersbach is a lacustrine deposit. The absolute and relative abundances of albanerpetontid fossils differ between the Bavarian fissure infills and floodplain deposits. The fissure infills have yielded multiple albanerpetontid bones (numbering over 150 specimens at Petersbuch 2), and in some of these localities, albanerpetontid bones are among the most common vertebrate remains. In contrast, localities in floodplain deposits have yielded far fewer specimens (in some cases only one), and albanerpetontid bones are consistently among the rarest vertebrate remains. A similar pattern occurs in Miocene deposits in France, where fissure infills in the La Grive-Saint-Alban area have produced hundreds of bones of *Albanerpeton inexpectatum* (Estes and Hoffstetter 1976), yet the marsh or marginal lacustrine beds at the Sansan locality have yielded just 32 bones of the same species (Rage and Hossini 2000). Patterns observed in Bavaria and France indicate that albanerpetontids in these areas during the Oligocene–Miocene evidently preferred karstified limestone plateaus over floodplains, although they obviously tolerated the latter. Further inferences about the paleoecology of these albanerpetontids may be made by considering other contemporaneous members of the karst and floodplain herpetofaunas, particularly those with living relatives whose ecological requirements can be used to infer paleoecological requirements for their fossil relatives.

Ongoing work by one of us (M.B.; see faunal list in Böhme and Ilg 2003) on fissure fill assemblages of late early Miocene or MN4 age in the study area indicates that besides *Albanerpeton inexpectatum*, these assemblages are characterized by fully aquatic taxa such as the crocodile *Diplocynodon* and palaeobatrachid frogs; by semiaquatic taxa such as the salamander *Triturus*, the pelobatid frog *Eopelobates*, and green frogs of the *Rana ridibunda* group (=*Rana* (*ridibunda*) sp. sensu Sanchíz 1998:92); and by taxa that were primarily terrestrial, but also heliophobe and hygrophilic (i.e., requiring shade and moisture), such as the salamanders *Chioglossa*, *Mertensiella*, *Salamandra*, and *Salamandrina*. As with many extant amphibians, the fossil amphibian taxa may also have been psychrophilic (i.e., preferring lower or more moderate temperatures). The crocodile and amphibians argue for permanent water bodies, such as streams or ponds, and the amphibians further argue for moist, cool, and shaded conditions. Fossils of the large-bodied (total length ≈50 cm) and, presumably, arboreal chamaeleonid *Chamaeleo caroliquarti* suggest stands of trees or forested areas, perhaps with multiple canopy layers, that would have reduced the amount of light and heat reaching the ground during the day, thereby keeping the forest floor relatively cool and humid. The presence of forests is also supported by the lateritic paleosols that typically infill the fissures, because such paleosols are formed in warm temperate to tropical forests. Another line of evidence suggests that *A. inexpectatum* preferred moist conditions: by the methodology of Böhme et al. (2006), there is a positive correlation between estimated annual precipitation and relative abundance of this species in fissures in the Petersbuch Quarry (Fig. 12.2). The suggestion here that the Miocene karstic ecosystem in Bavaria inhabited by *Albanerpeton* was characterized by relative stable, modest temperatures and moist conditions and by permanent water bodies is at odds with an earlier suggestion by one of us (Böhme 2003) that *A. inexpectatum* was a "dry adapted" taxon that preferred areas with a lower groundwater table and seasonally dry conditions.

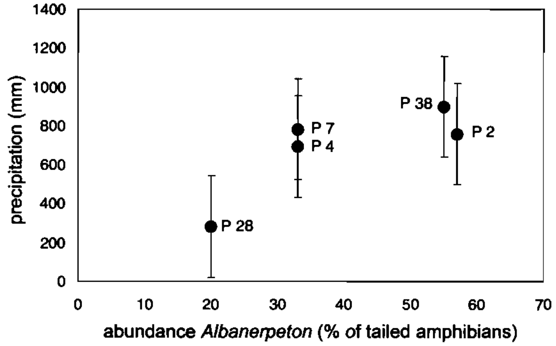

FIGURE 12.2. Relative abundance of *Albanerpeton* in the total tailed amphibian assemblage (i.e., *Albanerpeton* + Urodela) versus annual precipitation for fissure infills (MN4 in age) in the Petersbuch quarry, Bavaria, Germany. Relative abundance of *Albanerpeton* calculated from Böhme and Ilg (2003). Precipitation estimated by method of Böhme et al. (2006). Abbreviations correspond to fissures 2, 4, 7, 28, and 38 in the quarry.

Several lines of evidence indicate that a different set of conditions prevailed during the same interval on the floodplains in the North Alpine Foreland Basin, where remains of albanerpetontids are less abundant. The floodplain rocks are characterized by paleosols and temporary riparian pool deposits that indicate low or seasonally fluctuating ground water tables. Herpetofaunas of the floodplain localities are characterized by a near absence of heliophobe taxa (except *Salamandra*) and the presence of more light- and dry-tolerant taxa (squamates and non-*Eopelobates* pelobatid frogs) and of small-bodied chamaeleonids (total length <15 cm) such as *Chamaeleo bavaricus* and *C. sulcodentatus*. The land snail *Pomatias* is also abundant. Collectively, these taxa indicate scarce, probably lower vegetation that allowed light to reach the ground, thereby causing higher daytime temperatures and drier conditions at ground level and greater daily fluctuations in those conditions.

The above interpretations suggest that *Albanerpeton inexpectatum* preferred the more stable, moist, and shaded conditions and nearby permanent water bodies of the forested karstic environment, versus the more fluctuating, sunnier, and drier conditions and more ephemeral water bodies of the floodplain environment. Mesozoic and Paleocene occurrences of albanerpetontids are limited to lowland areas (Table 12.2), primarily fluvial floodplains (e.g., North American Western Interior), and coastal lagoonal and swamp environments (e.g., some European Jurassic localities and the basal Cretaceous Anoual locality in Morocco). Although the lack of albanerpetontid-bearing karstic localities may well be an artifact of erosion of more elevated plateaus, it is nonetheless clear that Mesozoic and Paleocene albanerpetontids were able to thrive in lowland areas, providing that their temperature and moisture requirements were met. Some Mesozoic localities, such as Upper Cretaceous (late Santonian or early Campanian) microsites in the Milk River Formation of Alberta, Canada, and the Upper Jurassic (Kimmeridgian) Guimarota Mine in Portugal, contain hundreds of albanerpetontid bones (e.g., Gardner pers. obs. 1998; Wiechmann 2000a). The abundance of fossils in these localities indicates that in some places and at some times, conditions in Mesozoic lowland environments were as favorable, if not more so, for albanerpetontids than were conditions favored by *A. inexpectatum* during the Miocene in upland karstic environments.

FUTURE WORK

Recent discoveries of fossils from the Upper Cretaceous and Oligocene–Pliocene of Europe and from the basal Cretaceous of the United States are filling gaps in the albanerpetontid fossil record. We hope that this trend will continue. Discoveries of additional fossils from the Paleogene of Europe, from the pre-Aptian of North America, and from any intervals in Asia and Africa would be particularly welcome. Although the basic body form of albanerpetontids and details of their jaws and skull roof seem to be relatively well understood, other aspects of their osteology (e.g., palate, braincase, and vertebrae) are less well known. Discoveries of pre–Middle Jurassic albanerpetontids or, ideally, stem albanerpetontids could help document the sequence in which albanerpetontid novelties were acquired. All albanerpetontid specimens reported to date appear to be from metamorphosed individuals, so discoveries of larval material could provide valuable ontogenetic information. We can expect continued refinements to the taxonomy of albanerpetontids as previously named taxa are revised and new ones are named. Optimistically, future cladistic studies will help establish the higher-level relationships of the Albanerpetontidae and provide a relatively robust framework of internal relationships that can be used to interpret character state transformations, paleobiogeography, and other aspects of the clade's evolutionary history.

ADDENDUM

After this chapter was accepted for publication, the following three new Cretaceous albanerpetontid occurrences were reported:

1. Early–middle Berriasian; upper part of unspecified unit; Champblanc Quarry, near Cherves-de-Cognac, Dépt. Charente, France; Albanerpetontidae indet. (Mazin et al. 2006; Pouech et al. 2006).
2. Late Barremian; La Huérguina Formation; Buenache de la Sierra locality, Cuenca Province, Spain; Albanerpetontidae indet. (Buscalioni and Fregenal-Martinez 2006).
3. Late Maastrichtian (Lancian North American Land Mammal "Age"); Hell Creek Formation; multiple localities, North Dakota, USA; *Albanerpeton nexuosum* and *Albanerpeton* sp. (Gardner unpubl. obs. 2006).

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