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THE GEOLOGICALLY YOUNGEST ALBANERPETONTID AMPHIBIAN, FROM THE LOWER PLIOCENE OF HUNGARY

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Abstract: The Albanerpetontidae are salamander-like, Middle Jurassic to Neogene lissamphibians from Laurasia and North Africa. Extensive series of albanerpetontid bones recently identified in collections from the Csarnóta 2 locality, south-central Hungary, extend the temporal range of the clade forward about seven million years from the middle Miocene to the early Pliocene. The Hungarian material is diagnostic for the Euramerican type genus *Albanerpeton* and pertains to a new species, *A. pannonicus* sp. nov., which differs from the seven previously reported congeners (Early Cretaceous–Miocene) in a distinctive combination of primitive and derived character states of the jaws and frontals, including a unique ventromedian keel on the azygous frontals. Some of the Hungarian specimens are articulated sets of skull bones, including ones containing the first three-dimensional examples of a nasal and jugals known for albanerpetontids, that help clarify some details of cranial osteology in these amphibians. Cladistic analysis nests *A. pannonicus* within the robust-snouted clade, as the sister taxon to an unnamed late Palaeocene species from Canada and *A. inexpectatum* from early–middle Miocene deposits in France, Austria and Germany. This phylogeny and recent reports of diagnostic *Albanerpeton* material from the Campanian of France and Maastrichtian of Romania suggest the evolutionary history of *Albanerpeton* was more complex than previously hypothesized, with Europe having played a larger role. The 25 fossiliferous layers at Csarnóta 2 record a shift from forest to grassland palaeoenvironments. Fossils of *A. pannonicus* are present in all layers, implying that this species was not adversely affected by the change in palaeoenvironments.

Key words: *Albanerpeton*, Albanerpetontidae, Europe, Hungary, Pannonian Basin, Pliocene.

THE Albanerpetontidae Fox and Naylor, 1982 are superficially salamander-like tetrapods known from the Middle Jurassic–Neogene of Laurasia and North Africa (e.g. Fox and Naylor 1982; Gardner and Averianov 1998; Gardner 2000*a*, 2002; McGowan 2002; Gardner *et al.* 2003). Recent cladistic analyses place albanerpetontids as the sister-taxon of either all other lissamphibians (i.e. caecilians, frogs and salamanders) or of only frogs + salamanders (Gardner 2001; McGowan 2002; Ruta *et al.* 2003). Currently three genera containing 11 species are recognized (Gardner *et al.* 2003). The exclusively European genus *Celtedens* McGowan and Evans, 1995 contains two Early Cretaceous species, one each from Spain and Italy (McGowan and Evans 1995; McGowan 2002), and may extend back into the Late Jurassic (Gardner *et al.* 2003). The Eurafrican genus *Anoualerpeton* Gardner *et al.*, 2003 contains two species, one each from the Middle Jurassic of England and the basal Cretaceous of Morocco (Gardner *et al.* 2003). The type genus *Albanerpeton* Estes and Hoffstetter, 1976 includes six Early Cretaceous–late Palaeocene species from the North American Western Interior and the type species *A. inexpectatum* Estes and Hoffstetter, 1976 from early–middle Miocene deposits in France, Austria and Germany (e.g. Estes and Hoffstetter 1976; Estes 1981; Fox and Naylor 1982; Gardner 1999*a*, *b*, *c*, 2000*a*, *b*, 2002). Until recently, *A. inexpectatum* was the geologically youngest known albanerpetontid and the osteologically best understood member of *Albanerpeton*, thanks to collections of isolated and rare articulated, three-dimensionally preserved bones from fissure infills of late middle Miocene age (de Bruijn *et al.* 1992; Steininger *et al.* 1996) near La Grive-Saint-Alban, south-eastern France (Estes and Hoffstetter 1976; Gardner 1999*a*, 2000*c*). In a pair of conference abstracts, recently we (Venczel 2003; Venczel and Gardner 2003) announced the discovery of abundant, well-preserved albanerpetontid fossils at the lower Pliocene Csarnóta 2 locality in Hungary, an occurrence that extends the temporal range of albanerpetontids forward about seven million years. Here we (1) formally name and describe a new species of *Albanerpeton* for the Hungarian material, (2) present additional information about cranial structure in albanerpetontids based on the new Hungarian species and (3) examine the phylogenetic relationships, palaeobiogeography and palaeoecological setting of this new species.

GEOLOGY AND MATERIALS

Csarnóta 2 is a richly fossiliferous, partly brecciated, red clay column that was formed by the infilling of a fissure in Middle Triassic limestone (Jánossy 1986). The column and some surrounding limestone were left standing by quarry workers in a now abandoned limestone quarry located about 1·5 km south of the village of Csarnóta in south-central Hungary (Jánossy 1986, fig. 5). Csarnóta 2 has yielded a taxonomically diverse assemblage of aquatic and terrestrial vertebrates (see Jánossy 1986, pp. 20–21). Mammalian fossils indicate that the Csarnóta 2 fissure infill is early Pliocene in age, equivalent to the Ruscinian European Land Mammal Age (e.g. Savage and Russell 1983; Jánossy 1986; de Bruijn *et al.* 1992; Fejfar *et al.* 1998). There is some disagreement about which 'Mammals Neogene' (MN) zone Csarnóta 2 lies within: most authors (e.g. Savage and Russell 1983; Jánossy 1986; de Bruijn *et al.* 1992) have favoured MN 15 (late Ruscinian), but Fejfar *et al.* (1998) favoured MN 14 (early Ruscinian). For this paper, we follow the majority view that Csarnóta 2 is MN 15 in age. Other abandoned quarries in the same area contain fissure infills (designated Csarnóta 1, 3 and 4) of approximately the same age, but these are not as richly fossiliferous as Csarnóta 2. To date, albanerpetontid fossils have been identified only at Csarnóta 2.

The Csarnóta localities were discovered by Móric Pálfy in the early part of the previous century. Tivadar Kormos made the first collections from Csarnóta 2 from 1910 into the 1930s. From about 1955 to 1958, Miklós Kretzoi and Dénes Jánossy made extensive collections at Csarnóta 2 by excavating a shaft about 1 × 1·5 m square and 3 m deep through 25 layers of fossiliferous, reddish brown to dark brown coloured sediments; these layers were numbered 1–25, from top to bottom (Jánossy 1979, 1986). Each layer was collected individually and the matrix was screened, washed and sorted to remove the fossils. Albanerpetontid fossils were found in all layers. The specimens reported here were identified and selected by one of us (MV) during the course of a larger study on the Csarnóta 2 herpetofauna; a comprehensive analysis of this herpetofauna will be published elsewhere.

Osteological terms and measurements for jaws and frontals used here generally follow Gardner (1999*a*–*c*, 2000*a*–*c*), with one exception. Based on its inferred contacts with one of the more posterior skull bones, the terms 'prefrontal notch' (Gardner 1999*a*) and 'lacrimal notch' (Gardner 2000*a*) have been used for the indentation in the laterodorsal edge of the pars dorsalis on the premaxilla in albanerpetontids. One specimen reported here from Csarnóta 2 suggests that the nasal contacted this notch in at least some individuals. Here we remove any reference to the presumed contact(s) of this notch by proposing the replacement term 'laterodorsal notch'. We also use the informal name 'Paskapoo species' (*sensu* Gardner 2002) for an undescribed late Palaeocene *Albanerpeton* species from the Paskapoo Formation of Alberta, Canada.

Comparative specimens. Collectively we have seen the following relevant albanerpetontid taxa and specimens. *Celtedens*: *C. megacephalus* (Costa, 1864), type species, holotype skeleton described by Costa (1864; see also Estes 1981; Gardner 2000*c*; McGowan 2002); *C. ibericus* McGowan and Evans, 1995, holotype and referred skeletons, including three specimens documented by McGowan (2002); and *Celtedens* sp., jaws and frontals from Purbeck (Berriasian), England, including specimens listed by McGowan and Ensom (1997) and Gardner (2000*a*). *Anoualerpeton* Gardner *et al.* 2003: *An. unicus* Gardner *et al.*, 2003, type species, and *An. priscus* Gardner *et al.*, 2003, skull and postcranial specimens described by Gardner *et al.* (2003). *Albanerpeton*: *A. inexpectatum* Estes and Hoffstetter, 1976, type species, skull and postcranial bones described by Estes and Hoffstetter (1976) and Gardner (1999*a*, 2000*c*); *A. arthridion* Fox and Naylor, 1982, jaws, frontals and humerus described by Gardner (1999*b*); *A. cifellii* Gardner, 1999*c*, holotype premaxilla described by Gardner (1999*c*); *A. galaktion* Fox and Naylor, 1982, *A. gracilis* Gardner, 2000 and *A. nexuosus* Estes, 1981, jaws and frontals described by Gardner (2000*b*). For *Albanerpeton*, we have also seen jaws, frontals and a parietal of the unnamed Paskapoo species from the upper Palaeocene of Alberta, Canada, and jaws, frontals, vertebrae and limb elements reported by Grigorescu *et al.* (1999) of an indeterminate *Albanerpeton* sp. from the Maastrichtian of Romania. Although we have not examined any of the *Albanerpeton* sp. material from the Upper Cretaceous of Romania and France reported by Duffaud (2000) in his unpublished PhD thesis, we have seen photographs from his thesis (Duffaud 2000, figs 1–12) depicting jaws from Pui (Maastrichtian), Romania, and jaws, vertebrae and a humerus from La Neuve (middle–late Campanian), France.

Institutional abbreviations. MÁFI, Magyar Állami Földtani Intézet (Geological Institute of Hungary), Budapest, Hungary;

MNHN.LGA, La Grive-Saint-Alban collection in the Museum National d'Histoire Naturelle, Paris, France.

SYSTEMATIC PALAEONTOLOGY

Subclass LISSAMPHIBIA Haeckel, 1866
Order ALLOCAUDATA Fox and Naylor, 1982
Family ALBANERPETONTIDAE Fox and Naylor, 1982

Genus ALBANERPETON Estes and Hoffstetter, 1976

Albanerpeton pannonicus sp. nov.
Text-figures 1–7, 8D

Derivation of name. From 'Pannonia', a province of the Roman Empire in the Carpathian Basin, in reference to the geographical area in present-day Hungary from which the new species is known.

Holotype. MÁFI V.22000, fused pair of nearly complete premaxillae, articulated with anterior end of right maxilla (Text-fig. 1A–B).

Holotype locality, horizon, and age. Csarnóta 2 locality, south-central Hungary; layer 3 in pit; early Pliocene, late Ruscinian (MN 15).

Referred specimens. All specimens are from Csarnóta 2. Fragmentary skulls (*n* = 24), each consisting of either a maxillary arcade comprising a maxilla articulated with some combination of a jugal, lacrimal, prefrontal and palatal bones or an incomplete skull roof comprising fused frontals articulated with some combination of a prefrontal, lacrimal and nasal: MÁFI V.22003/1, V.22011, V.22012/1–3, V.22015, V.22021/1–2, V.22033/2, V.22034, V.22039, V.22053, V.22055, V.22075, V.22076/1–2, V.22077, V.22093/1–3, V.22094/1, V.22100/1–2, V.22111; fused premaxillae (*n* = 6): MÁFI V.22017/1–2, V.22023, V.22026/1, V.22041/1, V.22072/1; isolated premaxillae (*n* = 38): MÁFI V.22006/1–5, V.22007, V.22018/1–3, V.22026/2, V.22030/1–2, V.22036/1–4, V.22041/2, V.22050, V.22057, V.22067, V.22072/2–3, V.22078/1–2, V.22083, V.22089/1–3, V.22095, V.22101/1–2, V.22105, V.22106/1–3, V.22113/1–3; isolated maxillae (*n* = 50): MÁFI V.22002/1–6, V.22013/1–10, V.22014/1–2, V.22028/1, V.22038/1–3, V.22043/1–2, V.22048, V.22056/5, V.22070/1–4, V.22087/1–2, V.22092/1–4, V.22099/1–4, V.22110/1–10; fused frontals, not articulated with other bones (*n* = 39): MÁFI V.22003/2–3; V.22004/1–3, V.22005/1–4, V.22016/1–7, V.22022, V.22025, V.22029, V.22035, V.22040, V.22045, V.22060, V.22063, V.22066/1–2, V.22071, V.22081, V.22082/1–2, V.22088, V.22094/2, V.22104/1–5, V.22112/1–2; mandibles (*n* = 20): MÁFI V.22009, V.22010/1–4, V.22020/1–4, V.22032/1–2, V.22047, V.22052, V.22059, V.22062, V.22065, V.22080, V.22097, V.22108/1–2; dentaries (*n* = 302): MÁFI V.22001/1–18, V.22008/1–38, V.22019/1–37, V.22024/1–2, V.22027/1–8, V.22031/1–10, V.22037/1–24, V.22042/1–3, V.22044/1–6, V.22046/1–10, V.22049, V.22051/1–4, V.22056/1–4, V.22058/1–3, V.22061/1–10, V.22064/1–3, V.22068/1–12, V.22073/1–4, V.22079, V.22084, V.22085/1–11, V.22090/1–17, V.22096/1–23, V.22102/1–11, V.22107/1–25, V.22114/1–16; presacral vertebrae (*n* = 10): MÁFI V.22028/2, V.22054, V.22074/1, V.22086/1–2, V.22098/1, V.22103/1, V.22109/1–2, V.22114/17; humeri (*n* = 16): MÁFI V.22033/1, V.22069, V.22074/2, V.22086/3, V.22091/1–5, V.22098/2–4, V.22103/2–3, V.22109/3–4.

Distribution. Known only from the holotype locality, in all 25 layers.

Differential diagnosis. Species of *Albanerpeton* differing from other albanerpetontid species in one putative autapomorphy: fused frontals ventrally bear a narrow, flattened median keel between the paired ventrolateral crests. Within *Albanerpeton*, differs from *A. arthridion* and resembles other congeners in two premaxillary synapomorphies: suprapalatal pit low in pars dorsalis, with ventral margin of pit approximately level with dorsal surface of pars palatinum, and suprapalatal pit larger, occupying at least 4 per cent of lingual surface area of pars dorsalis. Differs from *A. cifellii*, *A. galaktion* and *A. gracilis* and resembles other congeners in primitively having premaxilla with subcircular suprapalatal pit. Differs from *A. nexuosus*, *A. inexpectatum* and Paskapoo species and primitively resembles other congeners in having premaxilla with boss on labial surface occupying about upper one-third or less of pars dorsalis and with labial ornament confined to boss and consisting of irregular pits, grooves and ridges. Resembles *A. nexuosus*, *A. inexpectatum* and Paskapoo species and differs from other congeners in the following synapomorphies: premaxilla robustly constructed and variably fused medially; pars dorsalis on premaxilla relatively short, with ratio of height:width across suprapalatal pit less than about 1·55, and strongly sutured dorsally with nasal; premaxillary lateral process on maxilla relatively short, with length subequal to depth at base; and internasal process on fused frontals relatively narrow and acuminate or spike-like in dorsal or ventral outline. Compared to *A. nexuosus*, *A. inexpectatum* and Paskapoo species, resembles last two species (and differs from other congeners) in one premaxillary synapomorphy: two openings present for suprapalatal pit in about 30 per cent or more of specimens; further resembles *A. inexpectatum* (and differs from other congeners) in two frontal apomorphies: fused frontals approximately equilateral in dorsal or ventral outline (condition uncertain for Paskapoo species) and ventrolateral crests wide and triangular in transverse view, with ventral face deeply concave along orbit; primitively differs further from *A. nexuosus* (and resembles other congeners) in lacking tall dorsal flange on lingual edge of maxillary process on premaxilla, in having occlusal edges of maxilla and dentary straight to shallowly convex in lingual outline, and in having maxillary and dentary teeth weakly heterodont in size anteriorly;

primitively differs further from Paskapoo species (and resembles other congeners) in retaining well-developed vomerine process on premaxilla; and primitively differs further from *A. inexpectatum* (and resembles other congeners) in lacking external ornament on maxilla and dentary and in lacking coronoid process on dentary. Resembles *A. inexpectatum*, Paskapoo species and *A. gracilis* in one apomorphy: anterior end of maxillary tooth row approximately in line with point of maximum indentation along anterior margin of nasal process on maxilla. Resembles Paskapoo species and *A. arthridion* in one apomorphy: inferred snout-pelvic length less than about 45 mm.

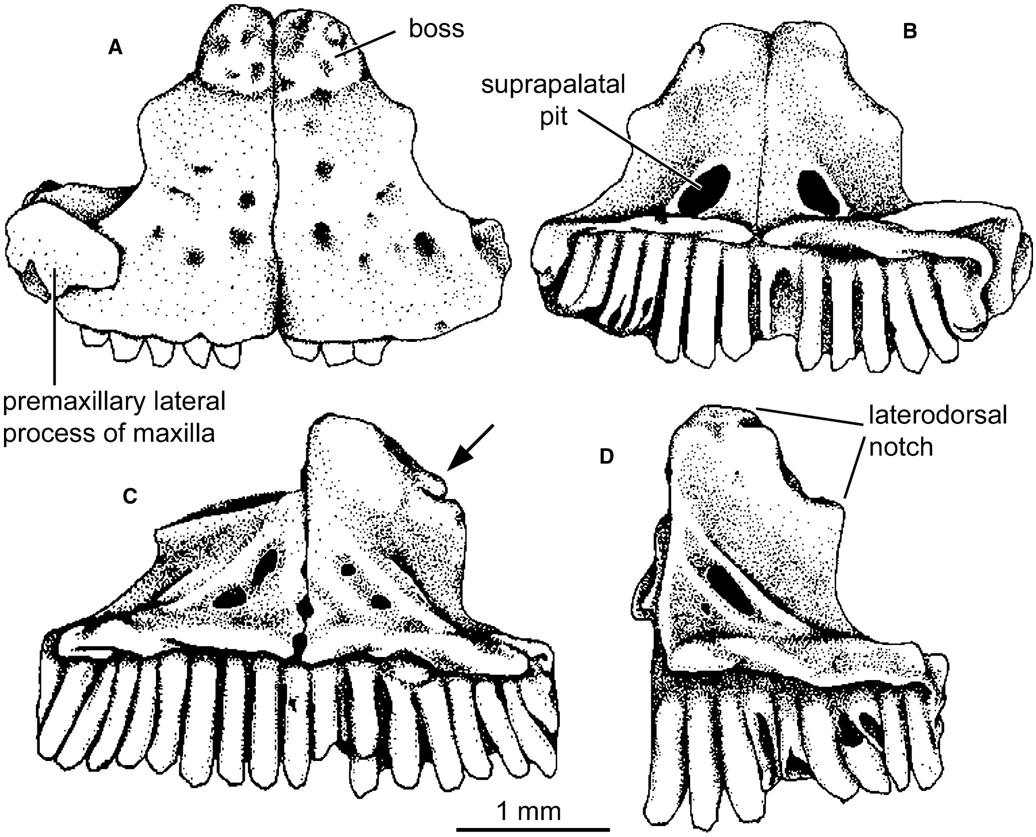
Description

Abundant isolated and lesser numbers of articulated elements are available from Csarnóta 2. Most specimens are incomplete, but generally these are available in sufficient numbers that the morphology and contacts of each element can be documented or inferred with confidence. As with specimens of *Albanerpeton inexpectatum* from karst deposits at La Grive-Saint-Alban, material of *A. pannonicus* from Csarnóta 2 varies in its quality of fossilization. Some specimens are well fossilized with solid bone and hard, glossy surfaces from which matrix can be removed relatively easily. In other specimens the bone is softer, with the external surfaces duller in appearance and encrusted in places with precipitates and matrix that are sometimes difficult to remove without damaging the underlying bone. Consequently, in the latter specimens details of surface ornament and suture patterns are often more difficult to interpret.

Premaxilla (Text-figs 1–2). The inventory of premaxillae includes seven fused pairs (e.g. Text-fig. 1A–C) and 38 isolated bones (e.g. Text-figs 1D, 2). Specimens range in height from *c.* 1·80 to 2·45 mm (Table 1). Despite their small size, these premaxillae are relatively robust in build when compared, for example, to equivalent-sized premaxillae of *Albanerpeton arthridion* (e.g. Gardner 1999*b*, text-fig. 2A–D). Grooves and flanges along the medial surface of isolated premaxillae indicate these bones were paired and sutured medially to one another in life. The seven pairs of articulated premaxillae are weakly fused. In these fused specimens, a median line of fusion is present labially and lingually between the pars dorsalis and pars dentalis portions of the left and right bones, whereas the medial edges of the pars palatinum on each bone simply abut one another. Absolute sizes of the largest isolated (i.e. sutured in life) and fused premaxillae are similar, which implies that if premaxillae fused ontogenetically, as has been suggested for *A. inexpectatum* (Gardner 1999*a*, 2002), the timing of fusion was more variable in *A. pannonicus*.

TABLE 1. Measurements (in mm) and ratios for premaxillae and fused frontals of *Albanerpeton pannonicus* sp. nov.; Csarnóta 2 locality, southern Hungary; early Pliocene (Ruscinian; MN 15) in age. Measurements follow Gardner (1999*a*, fig. 2). For fused premaxillae, left and right sides are measured and counted separately. Abbreviations in headings: N, number of specimens; x, mean; SD, standard deviation.

Measurement or ratio	N	Range	x and SD
Premaxillae			
Maximum height of premaxilla, excluding teeth	25	1·80–2·45	2·17 ± 0·14
PDH (height of pars dorsalis)	25	1·06–1·47	1·24 ± 0·09
PDW^1 (width of pars dorsalis across base of laterodorsal notch)	25	0·73–1·13	0·97 ± 0·11
PDW^2 (width of pars dorsalis across suprapalatal pit)	25	0·80–1·30	1·01 ± 0·12
LdND (depth of laterodorsal notch)	25	0·50–0·94	0·66 ± 0·10
LdNW (maximum width of laterodorsal notch)	25	0·20–0·71	0·48 ± 0·13
SPH (height of suprapalatal pit)	25	0·10–0·40	0·23 ± 0·07
SPW (maximum width of suprapalatal pit)	25	0·11–0·37	0·25 ± 0·07
PDH:PDW^2 (relative height of pars dorsalis)	25	1·08–1·50	1·25 ± 0·11
LdND:PDH (relative depth of laterodorsal notch)	25	0·38–0·76	0·53 ± 0·08
LdNW:PDW (relative width of laterodorsal notch)	25	0·27–0·71	0·49 ± 0·11
SPH:PDH (relative height of suprapalatal pit)	25	0·07–0·30	0·18 ± 0·06
SPW:PDW^2 (relative width of suprapalatal pit)	25	0·13–0·38	0·25 ± 0·07
Fused frontals			
FL (midline length)	15	2·89–4·12	3·61 ± 0·52
FW^1 (width across posterior end, between posterolateral corners of ventrolateral crests)	9	3·48–4·49	4·06 ± 0·35
FW^2 (width across posterior edge of frontal roof, between medial edges of ventrolateral crests)	11	1·57–2·07	1·90 ± 0·14
VCW (width of ventrolateral crest, just behind slot for receipt of prefrontal)	15	0·54–1·00	0·78 ± 0·15
FL:FW^1 (relative length of fused frontals)	9	0·88–0·95	0·91 ± 0·03
VCW:FW^2 (relative width of ventrolateral crests)	11	0·29–0·48	0·41 ± 0·06

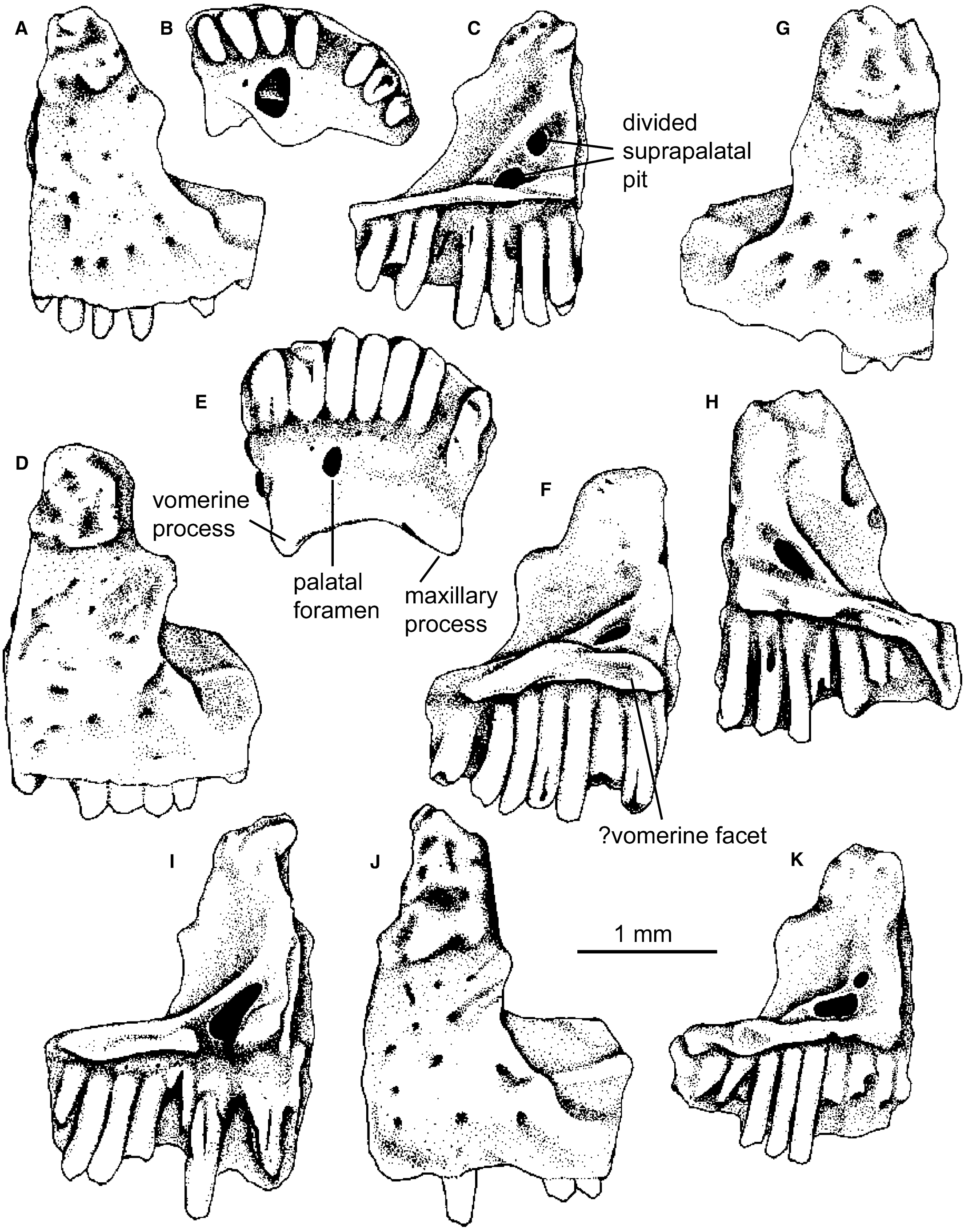


TEXT-FIG. 1. Premaxillae of *Albanerpeton pannonicus* sp. nov.; Csarnóta 2 locality, southern Hungary; early Pliocene (Ruscinian; MN 15) in age. A–B, MÁFI V.22000; holotype; fused pair of nearly complete premaxillae, articulated with anterior end of right maxilla; in labial and lingual views. C, MÁFI V.22072/1; fused pair of premaxillae, with left premaxilla lacking about dorsal one-third of pars dorsalis; arrow points to unnamed, knob-like process along lingual edge of laterodorsal notch; in lingual view. D, MÁFI V.22105; nearly complete right premaxilla; in lingual view.

The pars dorsalis is relatively low and broad, with the ratio of height:width across the suprapalatal pit ranging from *c.* 1·08 to 1·50 (Table 1). In labial or lingual profile the dorsal edge of the pars dorsalis varies from straight to broadly convex in outline and may extend horizontally or be inclined mediodorsally–lateroventrally. The laterodorsal notch varies considerably in depth and width (Table 1) and in profile varies from a distinctive, somewhat L-shaped notch to a less well-defined, shallow concavity. The dorsal and dorsolateral edges of the pars dorsalis typically bear low, indistinct ridges and grooves for sutured contact with the nasal. Some premaxillae also bear slightly larger knobs and prongs (e.g. MÁFI V.22072/1, Text-fig. 1C) or, less commonly, small facets (e.g. MÁFI V.22006/2, Text-fig. 2H) along the lingual margin of the laterodorsal notch, for even stronger contact with the nasal.

In labial aspect about the dorsal one-sixth to one-third of the pars dorsalis is covered by a low boss. On fused premaxillae the line of fusion remains between the left and right bosses, unlike in *Albanerpeton nexuosus* (cf. Text-fig. 1A vs. Gardner 2000*b*, fig. 5A). The boss is ornamented with an irregular arrangement of shallow pits and grooves, all enclosed by low ridges. The labial surface of the premaxilla below the boss typically is smooth, aside from scattered external nutritive foramina. However, in MÁFI V.22006/4 (Text-fig. 2J) the labial surface of the pars dorsalis below the boss is slightly roughened. Considering that MÁFI V.22006/4 is one of the largest premaxillae at hand, this roughened texture may be ontogenetic. A scoop-shaped facet in the lateroventral corner of the labial surface of the pars dentalis was overlapped, in life, by the premaxillary lateral process from the maxilla; this process is preserved in articulation on the right side of the holotype (Text-fig. 1A).

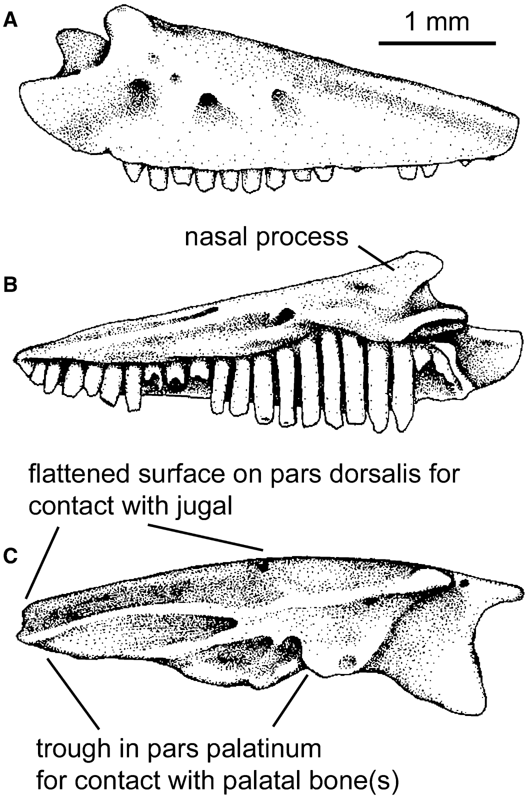
In lingual view the suprapalatal pit opens in the medial part of the pars dorsalis, just above the pars palatinum, and faces lingually. Typically the suprapalatal pit is a single opening of moderate size (i.e. occupies *c.* 5–15% of the lingual surface area of the pars dorsalis) and ovoid to elliptical in outline (e.g. Text-fig. 1B). In rare specimens the outline of the suprapalatal pit approaches the narrow, triangular or slit-like shape seen in the holotype premaxillae of *Albanerpeton cifellii* and some referred premaxillae of *A. gracilis* (Text-fig. 1D vs. Gardner 1999*c*, fig. 3G; Gardner 2000*b*, fig. 7B, F–G). In about one-third of the premaxillae from Csarnóta 2, two smaller openings are present for the suprapalatal pit. A subdivided suprapalatal pit also occurs in some premaxillae of the other two Tertiary congeners: *A. inexpectatum* (19 of 26 specimens; Gardner 1999*a*) and the



TEXT-FIG. 2. Premaxillae of *Albanerpeton pannonicus* sp. nov.; Csarnóta 2 locality, southern Hungary; early Pliocene (Ruscinian; MN 15) in age. A–C, MÁFI V.22006/1; nearly complete left premaxilla; in labial, occlusal and lingual views. D–F, MÁFI V.22006/3; nearly complete left premaxilla; in labial, occlusal and lingual views. G–H, MÁFI V.22006/2; nearly complete right premaxilla; in labial and lingual views. I–J, MÁFI V.22006/4; left premaxilla lacking medial part of pars palatinum; in lingual and labial views. K, MÁFI V.22030/1; nearly complete left premaxilla; in lingual view.

Paskapoo species (one of three specimens; JDG, pers. obs. 2003). In premaxillae of *A. pannonicus* having two openings for the suprapalatal pit, these two openings may be similar or different in size and shape (Text-fig. 1C vs. 2K). A weakly developed (i.e. labiolingually low) internal strut typically is present lateral to the suprapalatal pit and, less commonly, medial to the pit. Where present, the lateral internal strut may be perforated laterally by tiny foramina. As in other albanerpetontids, the pars palatinum is a lingually broad shelf. The lateral end of this shelf is developed into a flange-like maxillary process that, in life, was dorsally overlapped by the premaxillary dorsal process of the maxilla; the latter process is preserved in articulation on the right side of the holotype. Near its medial end, the pars palatinum bears a lingually projecting, prong-like vomerine process. A shallow concavity in the lingual face of the vomerine process (Text-fig. 2F) probably is a facet for contact with the vomer. The medial edge of the vomerine process typically is straight and extends anteroposteriorly, but in the fused premaxillae MÁFI V.22072/1 (Text-fig. 1C) the medial edges of both vomerine processes are concave and partially enclose between them a small median opening. The palatal foramen opens ventrally in about the labial one-half of the pars palatinum and opens dorsally in the floor of the suprapalatal pit. The canal connecting the dorsal and ventral openings of the palatal foramen extends dorsoventrally through the pars palatinum. In most specimens the diameter of the palatal foramen is subequal to or less than the diameter of the shaft of any of the more medial teeth, but in MÁFI V.22006/1 (Text-fig. 2B) the palatal foramen is larger than the diameter of any tooth shaft on that specimen. As in other albanerpetontids, in some premaxillae a second and much smaller foramen of unknown function opens more medially and labially in the junction between the pars palatinum and pars dentalis. The pars dentalis is moderately deep and becomes shallower laterally.

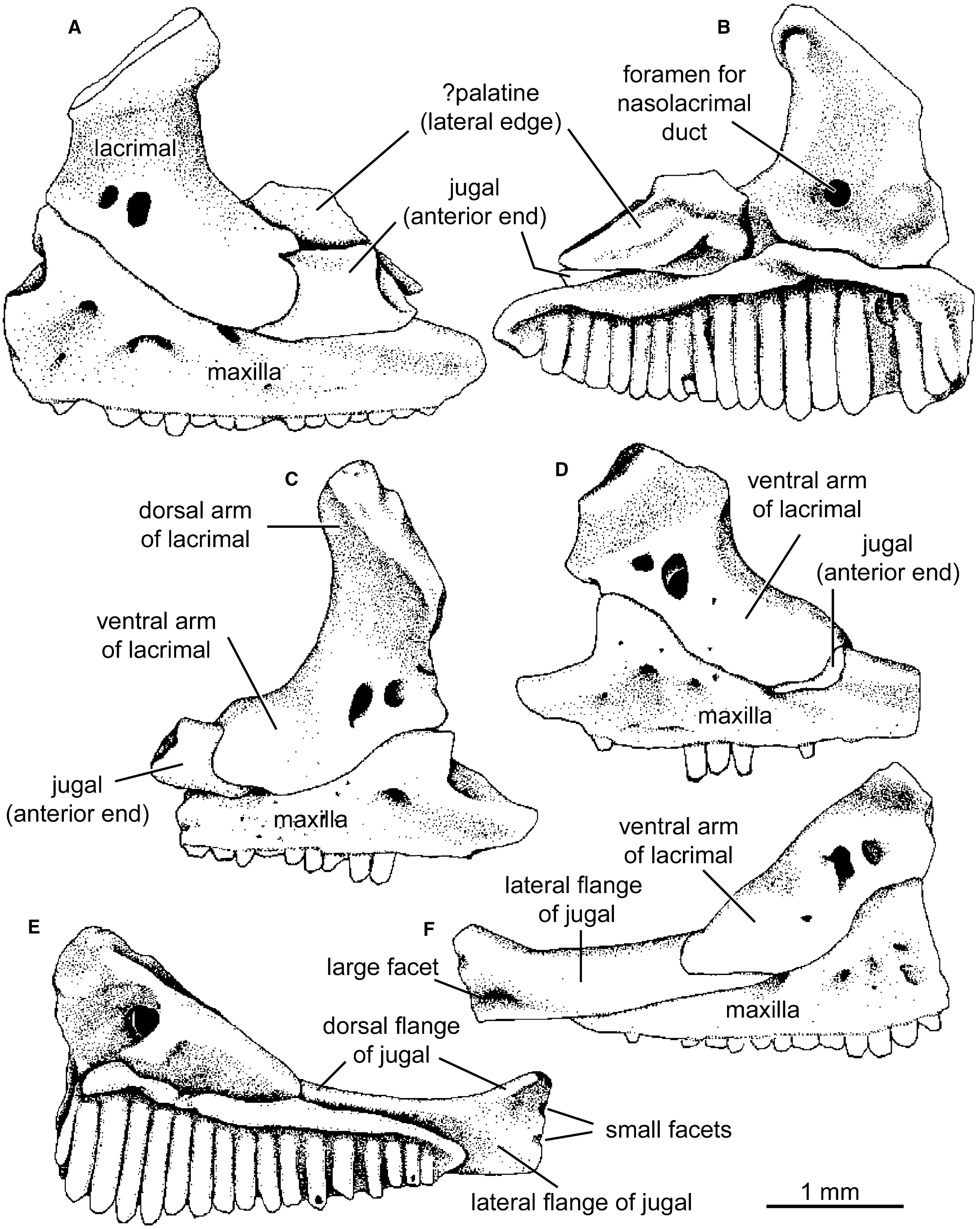
Maxilla (Text-figs 3–4). Maxillae are preserved both as isolated bones (e.g. Text-fig. 3) and in maxillary arcades where the maxilla is articulated with a lacrimal, jugal and, rarely, one or more palatal bones (e.g. Text-fig. 4). As in other albanerpetontids, the maxilla is a moderately elongate, low bone (Text-fig. 3A–B). Near its anterior limit, the pars dorsalis bears a dorsally projecting nasal process with a posteriorly concave leading margin that, in life, formed the posterior margin of the external narial opening. The pars dorsalis becomes shallower posteriorly and its dorsal surface, from the base of the nasal process back almost to the posterior end of the bone, is flattened (Text-fig. 3C) for contact with the jugal (Text-fig. 4; see also jugal account, below). Aside from external nutritive foramen scattered across about the anterior one-third to one-half of the bone, the labial face of the maxilla is smooth. In labial or lingual view the anteriorly projecting premaxillary lateral process is relatively short (i.e. length subequal to depth at base) and its anterior end ranges from blunt to acute in outline. The pars palatinum is a lingually broad shelf that anteriorly bears the flange-like premaxillary dorsal process. Just behind the premaxillary dorsal process, the medial edge of the pars palatinum is indented by a concavity that, in life, formed the lateral margin of the internal narial opening. The more posterior part of the pars palatinum narrows labially and its dorsal surface is indented by several pits and an anteroposteriorly elongate trough for articulation with palatal bones (see palatal bones account, below). The pars dentalis is deepest anteriorly and becomes shallower posteriorly. The ventral margin of the pars dentalis is nearly straight to shallowly convex in labial or lingual outline. The anterior end of the tooth row is approximately in line with the leading edge of the nasal processes and extends back to the posterior end of the bone.



TEXT-FIG. 3. Maxilla of *Albanerpeton pannonicus* sp. nov.; Csarnóta 2 locality, southern Hungary; early Pliocene (Ruscinian; MN 15) in age. A–C, MÁFI V.22099/1; nearly complete left maxilla; in labial, lingual and dorsal views.

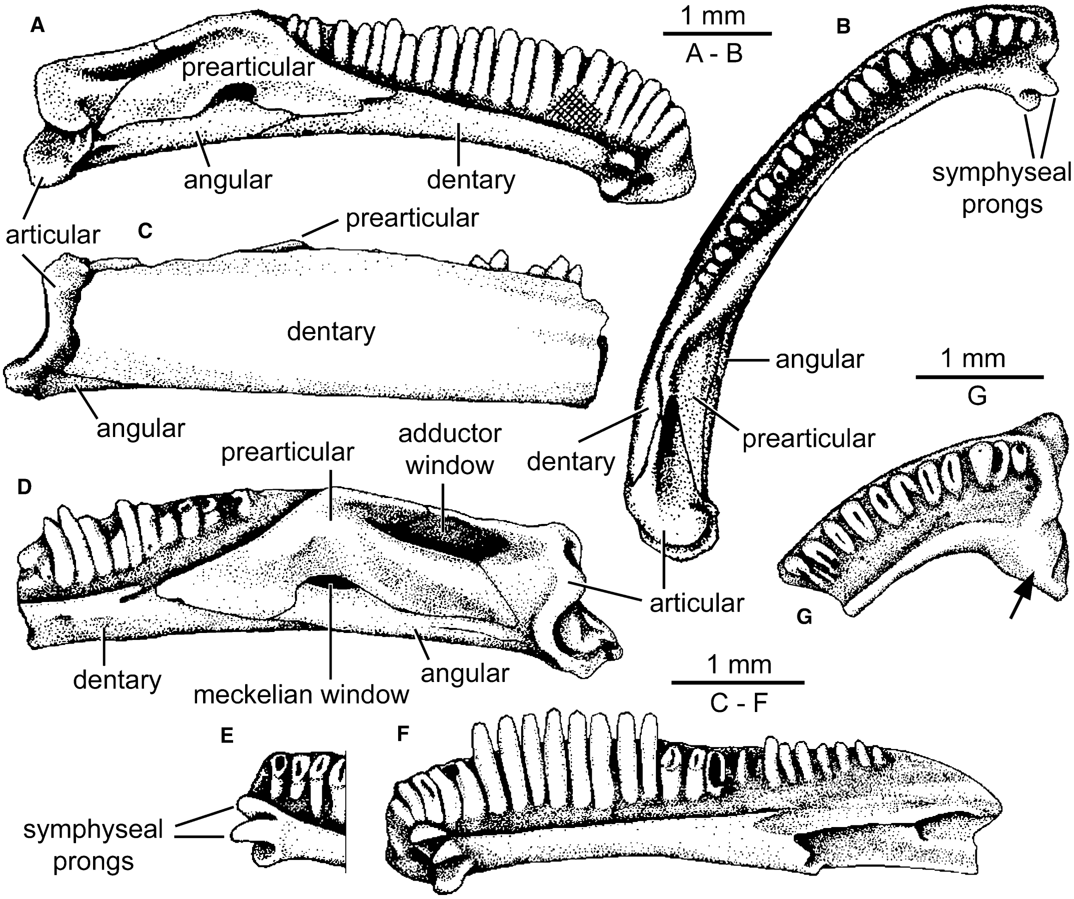
Mandible (Text-fig. 5). Twenty mandibles with articulated dentaries and post-dentary bones (e.g. Text-fig. 5A–D) and just over 300 isolated dentaries (e.g. Text-fig. 5E–G) are available. The largest mandibles are *c.* 6·6 mm long. The mandible is broadly curved labially in dorsal or ventral view, especially along about the anterior one-half of the dentary, indicating that the head was broadly rounded.

The dentary is an elongate bone that is slightly tapered anteriorly in labial or lingual view. The symphyseal surface is vertical and flattened anteriorly and, more posteriorly, bears one or two symphyseal prongs (Text-fig. 5B, E) that project medially and slightly posteriorly to interlock, in life, with complementary prongs on the opposite dentary. MÁFI V.22031/1 (Text-fig. 5G) is unusual because the posterior part of the symphysis is swollen posteriorly and expanded lingually, more so than is typical for albanerpetontids, and in place of the well-developed symphyseal prongs are low, bulge-like processes and shallow indentations. Other features of MÁFI V.22031/1 are typical for albanerpetontids (e.g. teeth closely packed, with mesiodistally compressed bases and highly pleurodont attachment; dental parapet relatively tall; anterior portion of subdental shelf relatively shallow and trough-like; and symphyseal end swollen labially), so the identification of this specimen as an albanerpetonid dentary seems secure. Considering that symphyseal prongs are



TEXT-FIG. 4. Maxillary arcades of *Albanerpeton pannonicus* sp. nov.; Csarnóta 2 locality, southern Hungary; early Pliocene (Ruscinian; MN 15) in age. A–B, MÁFI V.22012/1; left maxilla lacking anteriormost end, articulated with incomplete lacrimal, jugal and ?palatine; in labial and lingual views. C, MÁFI V.22034; right maxilla lacking posterior end, articulated with nearly complete lacrimal and incomplete jugal; in labial view. D, MÁFI V.22077; left maxilla lacking posterior end, articulated with incomplete lacrimal and jugal; in labial view. E–F, MÁFI V.22076/1; right maxilla lacking anterior end, articulated with incomplete lacrimal and nearly complete jugal; in lingual and labial views.

autapomorphic for albanerpetontids (e.g. Fox and Naylor 1982; Gardner 2001), the unusual condition in MÁFI V.22031/1 appears to be an anomaly. The labial surface of the dentary is unornamented, except for a loose row of up to about six external nutritive foramina extending along the anterior one-third to one-half of the bone. Below these foramina, the ventral surface of the dentary bears a shallow, anteroposteriorly elongate scar that is bounded labially by a low ridge. The tooth row extends

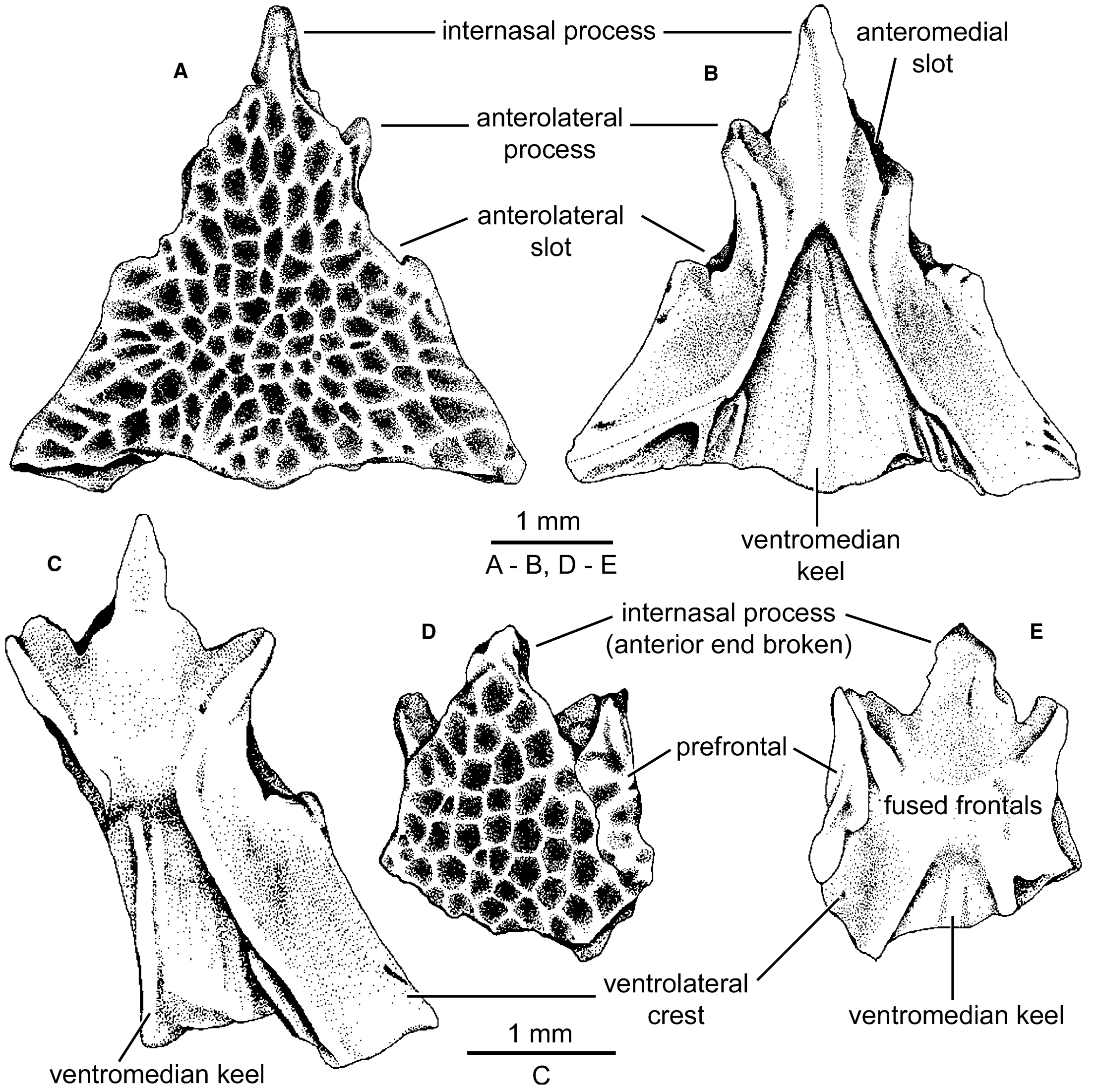


TEXT-FIG. 5. Mandibles of *Albanerpeton pannonicus* sp. nov.; Csarnóta 2 locality, southern Hungary; early Pliocene (Ruscinian; MN 15) in age. A–B, MÁFI V.22009; complete left mandible; in lingual and occlusal views; cross-hatching denotes matrix adhering to bone. C–D, MÁFI V.22097; incomplete right mandible, preserving about posterior three-fifths of dentary and complete post-dentary bones; in labial and lingual views. E–F, MÁFI V.22084; nearly complete right dentary, lacking posteriormost end; anterior end only in lingual, slightly posterior view and complete specimen in lingual view. G, MÁFI V.22031/1; incomplete left dentary, preserving about anterior one-quarter of ramus and having anomalous bulge (denoted by arrow) in place of symphyseal prongs; in occlusal view.

along about the anterior three-quarters of the dentary. The Meckelian canal is closed lingually below most of the tooth row, but opens anteriorly through a small foramen in the underside of the symphyseal end of the bone. The subdental shelf is shallow, lingually narrow and gutter-shaped in transverse profile anteriorly and, more posteriorly, becomes deeper and narrower. The dental parapet is relatively deep anteriorly and becomes shallower posteriorly. The dorsal margin of the parapet is straight to shallowly convex dorsally in labial or lingual profile. In contrast to *Albanerpeton inexpectatum*, the dentary of *A. pannonicus* lacks a dorsally projecting process immediately behind the tooth row (cf. Gardner 1999*a*, pl. 2, figs A–B, E vs. Text-fig. 5C, F).

Post-dentary bones appear virtually identical to those described for *Albanerpeton inexpectatum* (Estes and Hoffstetter 1976; Estes 1981; Gardner 1999*a*). The angular and articular are fused, with no line of fusion evident between the two bones. The angular forms the ventromedial portion of the post-dentary area and the articular forms the posterior end. As is typical for albanerpetontids (e.g. Fox and Naylor 1982; Gardner 2001), the facet on the articular for contact with the quadrate on the skull faces posteriorly and is concave. The prearticular is a labiolingually compressed, triradiate bone that forms the dorsoanterior portion and much of the lingual portion of the mandibular post-dentary region. The dorsal apex of the prearticular rises just slightly above the adjacent, dorsal edge of the dentary to form a low, coronoid process-like projection. The prearticular and the fused angular + articular enclose between them a large dorsal opening and a smaller lingual opening; following Schoch and Milner's (2000, fig. 9) terminology for stereospondyls, we regard these openings as, respectively, the adductor and meckelian windows.

Marginal teeth (Text-figs 1–3B, 4–5). Teeth on the premaxilla, maxilla and dentary are characteristic for albanerpetontids in being highly pleurodont, non-pedicellate, relatively straight and closely spaced and in having labiolingually compressed crowns that bear three mesiodistally aligned cuspules. The cuspules are weakly developed, with the median cuspule being slightly longer than the adjacent mesial and distal cuspules. As a result, the



TEXT-FIG. 6. Skull roof bones of *Albanerpeton pannonicus* sp. nov.; Csarnóta 2 locality, southern Hungary; early Pliocene (Ruscinian; MN 15) in age. A–B, MÁFI V.22081; fused, nearly complete frontals lacking left anterolateral process; in dorsal and ventral views. C, MÁFI V.22082/1; fused, incomplete frontals lacking about posterior two-thirds of right side; in ventral view. D–E, MÁFI V.22003/1; fused, incomplete frontals preserving about anterior one-half of bone (except for distal end of internasal process), articulated with complete right prefrontal; in dorsal and ventral views.

occlusal surface of the crown appears shallowly convex to slightly wedge-shaped in labial or lingual outline. Maxillary and dentary teeth are weakly heterodont in size anteriorly, with teeth about one-third of the distance posteriorly along the tooth row being only slightly longer than adjacent teeth. The number of tooth positions ranges from 7 to 10 ($x = 8$; $n = 25$) on the premaxilla, 15–21 ($x = 18$; $n = 16$) on the maxilla and 22–29 ($x = 25$; $n = 27$) on the dentary. Occasional specimens have one or more empty tooth slots for replacement teeth (e.g. Text-fig. 1B) and rare specimens preserve an incompletely developed, non-functional replacement tooth.

Frontals (Text-figs 6–7). The structure of the frontals is documented by 39 isolated, fused pairs of frontals (e.g. Text-fig. 6A–C) and a lesser number of fused frontals articulated with other skull bones. Three examples of the latter specimens are figured here: MÁFI V.22003/1 (Text-fig. 6D–E) is the anterior end of a fused pair of frontals articulated with a right prefrontal; MÁFI V.22094/1 (Text-fig. 7A–B) is an incomplete, fused pair of frontals articulated on the right side with a prefrontal and dorsal end of a lacrimal; and MÁFI V.22015 (Text-fig. 7C–D) is an incomplete, fused pair of frontals articulated on the left side with a prefrontal, dorsal end of a lacrimal and a complete nasal. Regardless of overall size, each pair of frontals is solidly fused along the midline; some specimens preserve a faint line of fusion ventrally along about the anterior one-third of the bone. Midline length varies from *c.* 2·89 to 4·12 mm and is consistently less than the width across the posterior edge of the bone (Table 1).

Intact, fused frontals resemble an equilateral triangle in dorsal or ventral outline.

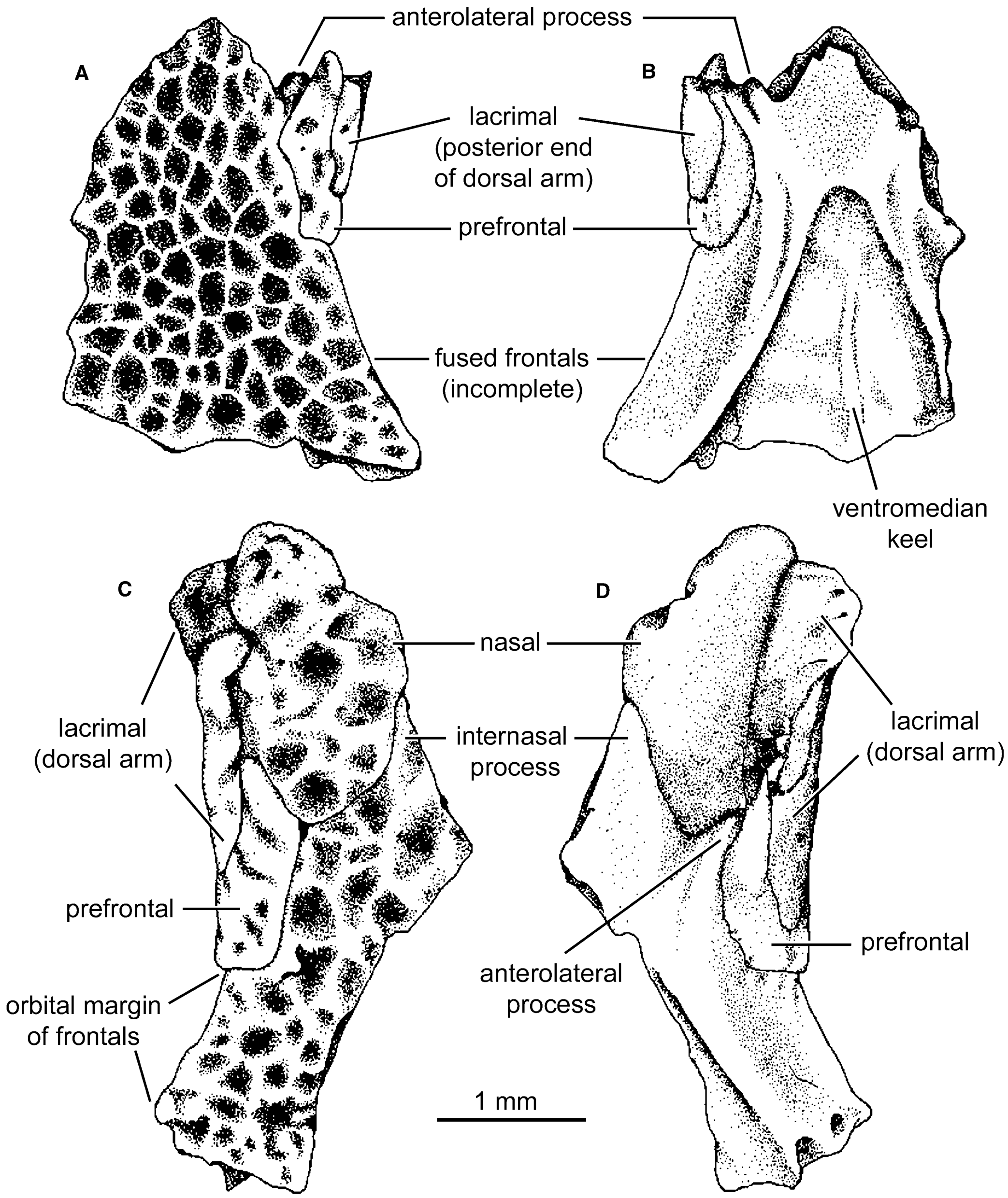
The internasal process projects anteriorly and is elongate, narrow and spike-like in dorsal or ventral outline. To either side and slightly more posteriorly, the anterolateral process is developed as a shorter, prong-like process. In the anterior part of the frontals, the edge of the bone to either side of the midline is excavated by two slots. The anteromedial slot lies between the internasal and anterolateral processes, whereas the anterolateral slot, which has deeply excavated dorsal and ventral margins, lies more laterally and posteriorly just behind the anterolateral process. MÁFI V.22003/1, V.22094/1 and, especially, V.22015 are informative for showing contacts between the fused frontals and more anterior skull roof bones, as follows: (1) the anteromedial slot in the frontal receives the posterior end of the nasal in a mortise and tenon fashion, with the medioposterior edge of the nasal also fitting into the complementary groove in the lateral face of the internasal process and the lateroposterior edge of the nasal also fitting into the complementary groove in the anterior face of the anterolateral process; (2) the nasal slightly overlaps medially onto the dorsal surface of the internasal process; (3) the anterolateral slot in the frontal receives the posterior end of the prefrontal in a mortise and tenon fashion, with the medial edge of the prefrontal also fitting into the complementary groove along the posterior face of the anterolateral process; (4) dorsal edges of the lateroposterior margin of the nasal and of the anteromedial margin of the prefrontal overlap onto, and broadly contact one another across, the dorsal surface of the anterolateral process, thereby preventing the process from being exposed dorsally in life; and (5) the prefrontal excludes the lacrimal from contacting the frontal. The remainder of the lateral edge of the frontals lies behind the anterolateral slot and contributes to the orbital margin; in this region, the lateral edge of the bone is nearly straight to shallowly concave in dorsal or ventral outline and extends posterolaterally. The posterior edge of the frontal roof is slightly concave to either side of the midline. Dorsal ornament consists of the usual albanerpetontid arrangement of moderately broad and shallow, polygonal pits enclosed by narrower, low ridges. Ornament covers most of the dorsal surface of the frontals, but is restricted to the median and proximal portions of the internasal process.

The ventrolateral crest on the underside of the fused frontals arises at the base of the anterolateral process, runs posterolaterally along the lateral margin and extends slightly past the posterior edge of the frontal roof. The crest is relatively broad in ventral view, with the ratio of crest width, as measured just behind the more posterior slot, vs. width across the posterior edge of the frontal roof, as measured between the medial edges of both crests (see Gardner 1999*a*, fig. 2B), ranging from *c.* 0·29 to 0·48 (Table 1). The crest becomes absolutely and relatively broader with increased frontal size. Along the orbital margin the ventrolateral crest is somewhat triangular in cross-section, with the medial edge deeper than the lateral edge, and, especially in larger specimens, the ventral face is deeply concave. Near its posterior end, the medial face of the ventrolateral crest bears a shallow facet for articulation with a complementary tab from the parietal. On the ventral surface of the frontals, a ridge that we call the 'ventromedian keel' (Text-figs 6B–C, E, 7B) extends anteroposteriorly along the midline between the ventrolateral crests. The ventromedian keel is narrow and shallow, with its ventral surface ranging from flat to shallowly convex in transverse profile.

Nasal (Text-fig. 7C–D). One specimen, MÁFI V.22015 (Text-fig. 7C–D), preserves a complete left nasal that is partially articulated with adjacent skull bones. In dorsal view the nasal in MÁFI V.22015 is somewhat pear-shaped, with the narrower end projecting anterolaterally. By contrast, in ventral view the nasal appears more crescent-shaped, with a convex medial margin and a concave lateral margin. The entire dorsal surface of the nasal is covered with the same pattern of ornament seen on the frontals. Posterior contacts of the nasal with the frontals and prefrontal were detailed in the frontal account, above. As for the remaining contacts, about the anterior two-thirds of the lateral margin of the nasal in MÁFI V.22015 is tightly sutured with the left lacrimal. No other bones are preserved articulated with the nasal in this specimen, but the presence of suture marks on the exposed anterior and anteromedial edges of the nasal indicate that these surfaces did articulate with other skull bones. The nasal in MÁFI V.22015 lies to the left of the skull midline (as demarcated by the internasal process on the fused frontals) and the anteromedial edge of the nasal runs along the inferred skull midline, forward from the internasal process. These features indicate that, in life, the nasals were paired and broadly contacted one another across the skull midline, in front of the frontals. Judging by the asymmetrically, bilobate and obliquely orientated anterior margin of the nasal in MÁFI V.22015 and the complementary shapes of the dorsal and dorsolateral edges of the pars dorsalis in most of the figured premaxillae, the nasal articulated anteromedially along the dorsal edge of the premaxillary pars dorsalis and more anterolaterally along the laterodorsal notch in the premaxillary pars dorsalis. Shallow notches and depressions along the anteroventral surface of the nasal in MÁFI V.22015 presumably articulated with complementary structures along the dorsolingual margin of the premaxillary pars dorsalis (see premaxilla account, above).

Prefrontal (Text-figs 6D–E, 7). No isolated prefrontals have been identified, but several specimens preserve a prefrontal articulated with one or more other skull bones. The structure and contacts of the prefrontal are unambiguously documented by three specimens figured here: MÁFI V.22003/1 (Text-fig. 6D–E) consists of a right prefrontal articulated with an incomplete, fused pair of frontals; MÁFI V.22094/1 (Text-fig. 7A–B) consists of a right prefrontal articulated with a ventrally incomplete lacrimal and an incomplete, fused pair of frontals; and MÁFI V.22015 (Text-fig. 7C–D) consists of a left prefrontal articulated with a ventrally incomplete lacrimal, a complete nasal and an incomplete, fused pair of frontals.

The prefrontal is anteroposteriorly elongate and irregular in dorsal or ventral outline, with a pointed anterior end that is directed slightly laterally. The bone is relatively small; for example, in MÁFI V.22015 the prefrontal is about one-third the size of the nasal. The dorsal surface is covered with low ridges and shallow pits and grooves similar to those on the frontals and



TEXT-FIG. 7. Skull roof bones of *Albanerpeton pannonicus* sp. nov.; Csarnóta 2 locality, southern Hungary; early Pliocene (Ruscinian; MN 15) in age. A–B, MÁFI V.22094/1; fused, incomplete frontals lacking anterior end and posterior part of left margin, articulated with complete right prefrontal and posterior end of dorsal arm of right lacrimal; in dorsal and ventral views. C–D, MÁFI V.22015; fused, incomplete frontals preserving internasal process and lateral part of left side of bone, articulated with complete left prefrontal, complete left nasal and dorsal arm of left lacrimal; in dorsal and ventral views.

nasals, but less regular in outline. As detailed in the two preceeding sections, above, MÁFI V.22015 (Text-fig. 7C–D) shows that the prefrontal articulates posteriorly and posteromedially with the frontals, anteromedially with the nasal, and anterolaterally with the lacrimal. In both MÁFI V.22003/1 and V.22094/1, the relatively smooth edge on the prefrontal where it would have contacted the nasal suggests these two bones were, at best, weakly sutured together in life. By contrast, MÁFI V.22015 and V.22094/1 show that the prefrontal is tightly bound anterolaterally with the dorsoposterior end of the lacrimal. The line of contact between these two bones can be traced across all visible surfaces on both specimens. MÁFI V.22003/1 lacks any trace of the lacrimal, yet on this specimen the prominent ridges and grooves on the exposed anterolateral face of the prefrontal also imply a strong contact between this bone and the lacrimal. More posteriorly, the rest of the lateral edge of the prefrontal is free of bony contacts and contributed, in life, to the dorsal margin of the orbit.

Lacrimal (Text-figs 4, 7). All available lacrimals are incomplete and are articulated either with skull roof bones or more commonly with a maxilla, jugal and, sometimes, palatal bones. The most nearly complete lacrimal, which is part of MÁFI V.22034 (Text-fig. 4C), shows that the lacrimal is a U- or V-shaped bone tilted on its side, with the apex directed anteriorly. A broad trough extending horizontally along the labial face of the lacrimal separates the dorsal and ventral arms of the bone. Along the ventral margin of this trough, the bone is perforated by a canal that presumably carried the nasolabial duct (Gardner 1999*a*). The medial opening of this canal is consistently single and, in most specimens, the canal bifurcates within the bone to open laterally through two foramina. In life, the lower surface of the dorsal arm and the upper surface of the ventral arm collectively formed the anterior rim of the orbit. The anterior end of the lacrimal, where the dorsal and ventral arms meet, appears to be reasonably intact in MÁFI V.22034 (Text-fig. 4C). Judging by this specimen, the anterior end of the lacrimal is blunt, shallowly concave in labial or lingual outline and, in life, formed the posterior margin of the external narial opening. The shape of the anterior end of the lacrimal is similar in two other figured lacrimals (Text-fig. 4A–B, D), but it is unclear whether the preserved margin is intact or damaged in those specimens.

The dorsal arm of the lacrimal projects dorsally and slightly posteriorly. As shown by MÁFI V.22034 and, especially, MÁFI V.22015 (Text-figs 4C, 7C–D, respectively), the more distal part of the dorsal arm contributes to the anterolateral region of the skull roof. This part of the lacrimal is dorsoventrally flattened, anteroposteriorly elongate and, as shown by MÁFI V.22015, articulates along its medial margin with the nasal anteriorly and the prefrontal posteriorly. The dorsal surface on the dorsoposterior part of the lacrimal bears ornament similar to that on the prefrontal. Aside from this limited dorsal ornament, the rest of the external surface of the lacrimal is unornamented. The ventral arm of the lacrimal extends posteriorly and slightly ventrally. The underside of the ventral arm of the lacrimal articulates along much of its length with the dorsal margin of the maxillary pars dorsalis, from the distal end of the nasal process posteriorly to a point about two-thirds of the distance along the maxilla, and wraps ventrally onto the labial surface of the maxilla and extends lingually onto the maxilla across the dorsal surface of the pars palatinum. The posterior end and medioposterior edge of the ventral arm of the lacrimal do not contact the maxilla. Instead, the posteriorly open gap between the posterior end of the ventral arm of the lacrimal and the maxilla receives the anterior end of the jugal, whereas the lingually open gap between the medioposterior edge of the ventral arm of the lacrimal and the maxilla receives the medial edge of at least one palatal bone.

Jugal (Text-fig. 4). No complete or isolated jugals are available, but several specimens preserve the anterior part of a jugal in articulation with a maxilla and lacrimal (e.g. Text-fig. 4). The most informative specimen, MÁFI V.22076/1 (Text-fig. 4E–F), has a right jugal that is *c.* 2·0 mm long and appears to be missing only the posteriormost end of the bone. The jugal in this specimen is the basis for most of the description presented here. As preserved, the jugal in MÁFI V.22076/1 is an elongate and low bone, about three times longer than its maximum height, and lacks ornament. The bone consists of two flanges set at right angles to each other. In lateral or medial outline, the 'lateral flange' is uniformly low along the anterior three-quarters of its length, whereas the posterior part is expanded dorsally and slightly ventrally. The mediodorsal surface of the lateral flange bears the 'dorsal flange'. About the anterior three-quarters of the dorsal flange is developed as a lingually expanded, horizontal shelf. Behind this shelf, the dorsal flange narrows abruptly into a ridge that follows the mediodorsal edge of the lateral flange, to the broken posterior end of the bone.

MÁFI V.22076/1 shows that about the anterior two-thirds of the jugal (possibly slightly less when the bone was complete) extends anteriorly and slightly dorsally to broadly overlap onto the dorsal surface of about the posterior one-third of the maxilla. This and other specimens depicted in Text-fig. 4 further show that, in life, the anteriormost end of the jugal was solidly wedged between the underlying maxillary pars dorsalis and the overlying posterior end of the ventral arm of the lacrimal. In specimens preserving fragments of presumed palatal bones, such as MÁFI V.22012/1 (Text-fig. 4A–B), it appears that the anteromedial corner of the jugal may have contacted at least one of the palatal bones. Near its posterior end, the jugal in MÁFI V.22076/1 bears three shallow, posteriorly open, V-shaped facets: two tiny facets medially and one larger facet laterally.

Palatal bones (Text-fig. 4A–B). Two maxillary arcades, MÁFI V.22012/1 (Text-fig. 4A–B) and V.22076/2 (not figured), each have at least one piece of flat bone preserved along the dorsal surface of the pars palatinum on the maxilla. These pieces are small, obviously incomplete and appear to have been rotated dorsolaterally out of their original orientation. MÁFI V.22012/1 preserves a small, rhomboidal piece of flat bone, the lateral edge of which is sandwiched between the underlying maxillary pars palatinum and the overlying ventral arm of the lacrimal. MÁFI V.22076/2 preserves a piece of flat bone in approximately the same position and, immediately behind it, what appears to be a second piece of flat bone. In the latter specimen, both pieces of bone are crushed and the more anterior piece ventrally bears a tiny knob that may be a tooth, but this identification is not certain.

We interpret the pieces of flat bone described above as remnants of paired palatal bones, based on their form (dorsoventrally flattened) and position (lateral margin contacts pars palatinum on maxilla). Incomplete palates are known for several Lower Cretaceous *Celtedens* skeletons, but because the palatal bones in these skeletons are not well preserved, described or figured (see McGowan 2002), these skeletons are not especially helpful for resolving the identities of the palatal bones in MÁFI V.22012/1 and V.22076/2. Three observations suggest that the piece of palatal bone in MÁFI V.22012/1 and the presumed, more anterior piece of palatal bone in MÁFI V.22076/2 are remnants of the palatines: (1) each piece contacts along the posterior part of the maxilla or, in life, about midway along the palatal region; (2) their respective anterior ends are approximately in line with the indentation formed by the internal narial margin in the medial edge of the maxillary pars palatinum; and (3) assuming the preserved anterior end of each piece is reasonably intact, which appears to be the case in at least MÁFI V.22012/1, the posteriorly concave shape of the anterior edge suggests the bone contributed to the posterior margin of the internal narial opening. These conditions compare favourably with the typical temnospondyl pattern in which the palatine, where present, articulates laterally with the maxilla and its anterior end contributes to the posterior margin of the internal narial opening. The identity of the more posterior piece of bone in MÁFI V.22076/2 is more problematic: it may simply be part of the more anterior piece and therefore probably part of the palatine, or it may be from a separate bone. In the latter case, the piece of bone more probably is part of the pterygoid than the ectopterygoid, because the latter bone is not reliably known to occur in lissamphibians (Gardner 2001).

Postcranial bones. Csarnóta 2 has produced a small number of albanerpetontid presacral vertebrae and humeri. These resemble homologous elements reported elsewhere for albanerpetontids (e.g. Estes and Hoffstetter 1976; Estes 1981; McGowan 1996, 2002; Gardner 1999*b*).

Remarks. Albanerpetontid genera and species are differentiated largely by character states of the frontals and jaws (e.g. McGowan and Evans 1995; McGowan 1998, 2002; Gardner 2000*a*, 2002; Gardner *et al.* 2003). Albanerpetontid frontals, premaxillae, maxillae and dentaries from Csarnóta 2 appear to belong to one species, because each element is represented by a single morph. Where differences are evident among homologous specimens (e.g. premaxillae variably fused, suprapalatal pit subdivided in some premaxillae), these differences are within the range of intraspecific variation documented for other albanerpetontids (e.g. Gardner 1999*a*, *b*, 2000*b*; Gardner *et al.* 2003). The species from Csarnóta 2 can be assigned to *Albanerpeton* based on synapomorphies of the frontals (triangular in outline and moderately elongate) that are diagnostic for the genus and on nested sets of frontal and premaxillary synapomorphies (see below, 'Phylogenetic relationships') that diagnose less inclusive clades within the genus. Jaws and frontals from Csarnóta 2 differ in a unique suite of primitive and derived character states from homologous elements of all seven previously recognized species of *Albanerpeton*. We thus erect a new species, *A. pannonicus*, to accommodate the albanerpetontid material from Csarnóta 2. Most of the character states given in the specific diagnosis, above, for *A. pannonicus* are shared with one or more congeners; however, the ventromedian keel on the fused frontals is potentially autapomorphic. Frontals are available for all known albanerpetontid species, except *A. cifellii* (Gardner 1999*c*), and in all of these species the frontals lack a ventromedian keel.

Because of the temporal and geographical proximity of *Albanerpeton pannonicus* (early Pliocene; Hungary) and *A. inexpectatum* (early–middle Miocene; France, Austria and Germany) and because frontals and jaws of these species resemble one another in many respects, it is appropriate to review how the two species differ. *A. pannonicus* differs from *A. inexpectatum* in the following seven character states: (1) smaller body size, with estimated maximum snout–pelvic length less than *c.* 45 mm (vs. *c.* 1·2 times larger in *A. inexpectatum*); (2) ventromedian keel on frontals (vs. keel absent); (3) boss present on dorsal part of pars dorsalis on premaxilla (vs. boss absent); (4) labial ornament on premaxilla restricted dorsally to the boss (vs. ornament covers entire labial surface of pars dorsalis); (5) labial ornament on premaxilla consists of irregular ridges and grooves (vs. pustulate ornament); (6) labial surface of maxilla and dentary unornamented (vs. weakly developed, ridge-like labial ornament on large maxillae and dentaries); and (7) no dorsally directed, coronoid process on dentary immediately behind tooth row (vs. coronoid process present). For characters 5–7, states for *A. inexpectatum* can still be considered autapomorphic for that species, as previously suggested (Gardner 1999*a*, 2002; Gardner *et al.* 2003), because none of these character states is known in other albanerpetontids. The same studies identified another two autapomorphies for *A. inexpectatum*: (1) frontals relatively short and resemble an equilateral triangle in dorsal or ventral outline and (2) frontals bear ventrolateral crests that are relatively wide and triangular in transverse view, with the ventral face deeply concave along orbital margin. Neither of these character states can still be considered autapomorphic for *A. inexpectatum*, because both conditions also occur in *A. pannonicus*.

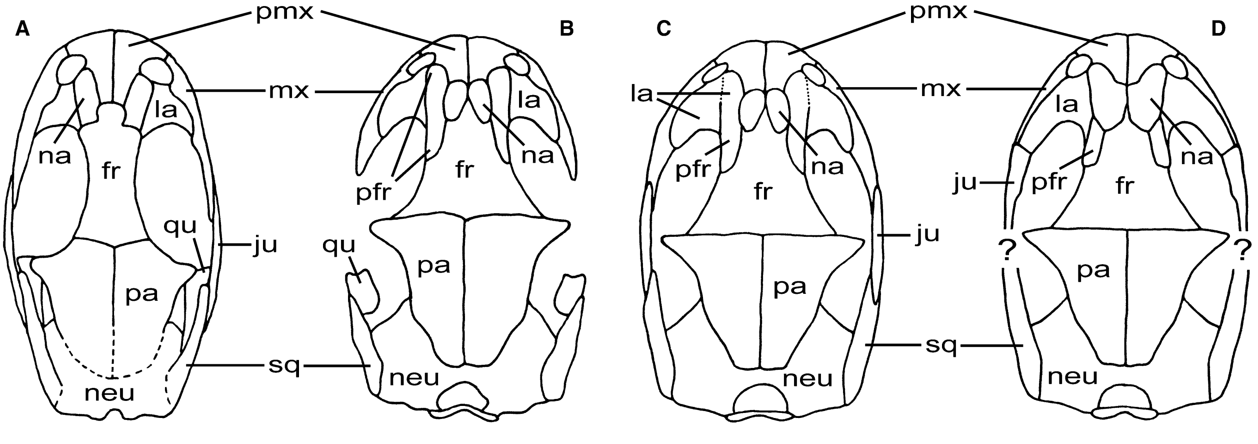
Albanerpeton pannonicus and *A. inexpectatum* are the only species in the genus for which lacrimals are available: approximately a dozen incomplete lacrimals are known for *A. pannonicus* (this study) and only one intact lacrimal (part of MNHN.LGA 1226; Estes and Hoffstetter 1976, pl. 5, figs 1–2; Gardner 2000*c*, figs 4–5) is known for *A. inexpectatum*. In most respects, lacrimals of the two congeners are similar. However, lacrimals available for *A. pannonicus* differ from the one lacrimal available for *A. inexpectatum*, as follows: (1) labial surface of the ventral arm is unornamented (vs. ornamented with short, irregular ridges and pustules); (2) line of contact between the lacrimal and prefrontal is visible on all surfaces, which implies the two bones are sutured or, at most, weakly fused to one another (vs. line of contact not visible dorsally, which implies the lacrimal and prefrontal are more solidly fused to one another); and (3) anterior margin of lacrimal appears to be posteriorly concave in labial or lingual outline (vs. anterior end of bone bears a prominent, anteriorly projecting process). Some of these differences may be taxonomically significant, but until lacrimals can be evaluated from additional taxa we consider it premature to use lacrimal characters to differentiate albanerpetontid species.

DISCUSSION

New information on cranial osteology

Prior to this study, our understanding of albanerpetontid cranial osteology relied on two sources of information: (1) rare, two-dimensional skeletons with skulls of *Celtedens* spp. preserved on slabs and (2) isolated and occasionally articulated, three-dimensionally preserved skull bones (mainly jaws and frontals) from species of all three genera, but especially from *Albanerpeton inexpectatum*. Published cranial reconstructions for *Celtedens* (McGowan and Evans 1995, fig. 2A; McGowan 1998, fig. 2; 2002, fig. 5B; Text-fig. 8A) are founded largely on the holotype skeleton of *C. ibericus*, the skull of which is articulated and largely complete, but has been dorsoventrally flattened, badly crushed anteriorly and split horizontally through the level of the palate, with the upper and lower portions of the skull preserved as part and counterpart (JDG, pers. obs. 2003). McGowan's (2002, fig. 5B) reconstruction of the skull in dorsal view evidently involves some extrapolation, because no known *Celtedens* skull exposes any significant amount of the dorsal surface (JDG, pers. obs. 1997, 2003). Previous cranial reconstructions for *Albanerpeton* (Estes and Hoffstetter 1976, fig. 4; see also Estes 1981, fig. 4D; Fox and Naylor 1982, fig. 5; Gardner 2000*c*, fig. 2A; Text-fig. 8B–C) are based largely on isolated and articulated bones (upper and lower jaws, frontals, parietals and a neurocranium, lacrimal and prefrontal) of *A. inexpectatum*; examples of other skull bones (i.e. nasal, jugal, quadrate and squamosal) depicted in those reconstructions were unknown for albanerpetontids at the time. Although previous interpretations about albanerpetontid cranial structure were based on different kinds of material from different taxa, they broadly agree. Nevertheless, some details are contentious (e.g. pattern of bones in the snout region; cf. Gardner 2000*c* vs. McGowan 2002) and other details remain poorly known (e.g. structure of the palatal, basicranial and occipital regions). *A. pannonicus* is represented by a larger sample of isolated and articulated sets of skull bones than any other congener. Contacts between articulated bones are readily discernible and two of the elements represented, the nasal and jugal, are the only three-dimensional examples of these bones available for albanerpetontids. For these reasons, *A. pannonicus* provides additional information about the structure of the snout and anterior part of the skull roof, cheek region and palate in albanerpetontids. These new insights are detailed below and incorporated into our revised cranial reconstruction for *Albanerpeton* in Text-figure 8D.

Details of the snout and anterior part of the skull roof in *Albanerpeton pannonicus* are provided by isolated and fused premaxillae and by articulated combinations of the



TEXT-FIG. 8. Albanerpetontid skull reconstructions, excluding ornament and mandibles, in dorsal view. A, *Celtedens ibericus* (Barremian; Spain); redrawn from McGowan (2002, fig. 5B); dashed lines are contacts of bones as inferred by McGowan (2002); ×3·8. B, *Albanerpeton inexpectatum* (early–middle Miocene; France, Austria and Germany); redrawn from Estes and Hoffstetter (1976, fig. 4B); ×3. C, *Albanerpeton inexpectatum*; redrawn from Gardner (2000*c*, fig. 2A); ×3. D, *Albanerpeton pannonicus* sp. nov. (early Pliocene; Hungary); reconstruction based on material reported here, with details of parietals and neurocranium adapted from specimens of *A. inexpectatum* (e.g. Estes and Hoffstetter 1976, pl. 8, figs 2–3; pl. 9, figs 1–4) and details of squamosals and overall shape of skull adapted from specimens of *C. ibericus* (e.g. McGowan and Evans 1995, fig. 1b; McGowan 2002, figs 4–5A) and *C. megacephalus* (e.g. Gardner 2000*c*, fig. 1; McGowan 2002; fig. 13); question mark (?) indicates uncertainty about nature of contact between jugal and squamosal; ×4. Quadrates not shown in last two figures for clarity. Abbreviations: fr, fused frontals; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; neu, neurocranium; pa, parietal; pfr, prefrontal; pmx, premaxilla; qu, quadrate; sq, squamosal.

nasal, prefrontal, lacrimal, maxilla and frontals. Previous interpretations about the structure of the anterior part of the skull in *Albanerpeton*, which were founded on more limited material of *A. inexpectatum* and, to a lesser extent, jaws and frontals of other congeners, are largely corroborated, but some unexpected differences are seen in the form and contacts of the nasal, prefrontal and lacrimal.

The existence, form and contacts of nasals in albanerpetontids have been debated (Gardner 2000*c*; McGowan 2002). Although no examples of nasals are known for *Albanerpeton inexpectatum*, based on the complementary margins of adjacent bones (i.e. premaxillae, frontals and lacrimal: = 'prefrontal' of some authors; see next paragraph) Estes and Hoffstetter (1976; see also Estes 1981; Gardner 2000*c*) inferred that nasals were present as paired, relatively small and oval bones that contacted one another across the skull midline and separated the premaxillae and frontals. In contrast, McGowan (2002, fig. 5A–B) interpreted the nasals in the holotype skull of *Celtedens ibericus* as larger, more elongate bones that lay further laterally and did not separate the premaxillae and frontals. In reference to *Albanerpeton*, McGowan (2002, pp. 6 and 8, respectively) stated 'the small oval nasals described by previous authors do not appear to exist' and 'there appears to be no logical reason for their [nasals] presence'. One referred specimen (MÁFI V.22015) of *A. pannonicus* is decisive for resolving these differences of opinion, at least in *Albanerpeton*, because it preserves a complete left nasal that is articulated posteriorly with an incomplete pair of frontals, posterolaterally with a prefrontal and anterolaterally with the dorsal end of a lacrimal. We identify this bone as a nasal, because its position and preserved contacts are consistent with the primitive temnospondyl condition for the nasal. MÁFI V.22015 corroborates many aspects of previous interpretations about the nasal in *Albanerpeton* (e.g. Estes and Hoffstetter 1976; Estes 1981; Fox and Naylor 1982; Gardner 2000*c*), as follows: (1) paired nasals are present; (2) nasals lie immediately to either side of the midline, where they broadly contact one another anteromedially, are separated posteromedially by the internasal process on the frontals and separate the premaxillae from the fused frontals; and (3) each nasal posteriorly fits into the anteromedial slot in the frontals in a mortise and tenon fashion and, to either side, articulates medioposteriorly with the internasal process and lateroposteriorly with the anterolateral process on the frontals. However, in contrast to these same reconstructions, the nasal in MÁFI V.22015 differs in being relatively larger and less oval in outline. Further, the more bilobate anterior edge of the nasal in MÁFI V.22015, as compared to the smoothly convex edge inferred by Estes and Hoffstetter (1976), indicates that premaxillary–nasal contact was not limited to the dorsal edge of the premaxillary pars dorsalis and the leading edge of the nasal, but that the nasal probably also contacted the premaxilla more laterally along the laterodorsal notch. Considering that profiles of the dorsal and laterodorsal margins of the premaxillary pars dorsalis vary considerably in *A. pannonicus* and in all other congeners for which adequate series of premaxillae are available (Gardner 1999*a*, *b*, 2000*b*), the relative contribution of the laterodorsal notch to the premaxillary–nasal contact probably differed among conspecific individuals.

Three different interpretations previously have been presented about the nature of the prefrontal in albanerpetontids. Estes and Hoffstetter (1976) and Estes (1981) identified a large prefrontal in *Albanerpeton inexpectatum*. Although the prefrontal was not labelled in their cranial reconstruction for the species, from their respective descriptions it seems evident that they (Estes and Hoffstetter 1976, pp. 312–313; Estes 1981, p. 21) interpreted the prefrontal as an elongate bone that formed the anterolateral portion of the skull roof, where the bone contributed to the dorsoanterior margin of the orbit and contacted the premaxilla anteriorly, the nasal medially and the frontal posteriorly. Gardner (1999*a*, 2000*c*) agreed that *A. inexpectatum* had a prefrontal, but differed from the previous authors in noting that the bone was 'relatively small' (Gardner 2000*c*, p. 8). The above-cited interpretations were founded on the same referred specimen of *A. inexpectatum* (MNHN.LGA 1226), which consists of a three-dimensionally preserved right maxilla articulated with a solidly fused lacrimal + prefrontal (Estes and Hoffstetter 1976, pl. 5, figs 1–2; Gardner 2000*c*, figs 4–5). The precise limits of the prefrontal in MNHN.LGA 1226 are difficult to interpret, because the line of fusion with the lacrimal is not visible dorsally, although it can be traced across the other surfaces (Gardner 2000*c*). McGowan (2002) did not identify a prefrontal in any of the two-dimensionally preserved *Celtedens* skeletons he examined. In that same paper, he re-interpreted the elongate 'prefrontal' identified by Estes and Hoffstetter (1976) and Estes (1981) in *A. inexpectatum* as an elongate nasal (McGowan 2002, p. 6) and suggested 'Prefrontals may exist in albanerpetontids but not as separate bones' (McGowan 2002, p. 8). Three specimens reported here for *A. pannonicus* (MÁFI V.22003/1, V.22015 and V.22094/1) are informative for clarifying the nature of the prefrontal, at least in *Albanerpeton*, because each preserves a prefrontal. The identity of this bone as the prefrontal in these specimens seems secure, because the bone lies in approximately the same position and has the same contacts as do undisputed prefrontals in other temnospondyls; specifically, the prefrontal forms the anterodorsal margin of the orbital margin and articulates posteriorly and medioposteriorly with the frontal, anteromedially with the nasal and anterolaterally with the lacrimal. In MÁFI V.22015 and V.22094/1 the prefrontal and lacrimal are articulated. The lacrimal is missing from MÁFI V.22003/1, but the articular surface for contact with that bone is preserved intact on the prefrontal. The above observations show that the prefrontal does exist as a separate element in at least some albanerpetontids, although as seen in the referred specimen MNHN.LGA 1226 of *A. inexpectatum*, the prefrontal may fuse to some extent with the lacrimal in some individuals of at least that species. Contrary to Estes and Hoffstetter's (1976) reconstruction for *A. inexpectatum*, specimens reported here for *A. pannonicus* show that the prefrontal is an anteroposteriorly shorter bone that is excluded from contacting the premaxilla by the nasal and lacrimal. The *A. pannonicus* specimens also clarify that the area in the skull of *A. inexpectatum* interpreted by some previous authors as being formed by an elongate bone, either the 'prefrontal' (Estes and Hoffstetter 1976; Estes 1981) or the 'nasal' (McGowan 2002), is formed by two bones: anteriorly by the dorsal arm of the lacrimal and posteriorly by the entire prefrontal. Finally, the three specimens of *A. pannonicus* show that the prefrontal articulates posteriorly with the frontals in a mortise and tenon fashion, by fitting into the slot in the latter bone behind the anterolateral process, thereby excluding the lacrimal from contacting the frontals. This pattern of prefrontal–frontal contact is consistent with prior interpretations (Estes and Hoffstetter 1976; Estes 1981; Gardner 1999*a*, 2000*c*) based on specimens of *A. inexpectatum*. McGowan (1998, 2002) maintained that the lacrimal, not the prefrontal, fits into the more posterior slot in the frontals in *Celtedens*. Lacrimal–frontal contact may well occur in *Celtedens*, but this is difficult to verify because the relevant area of the skull is not well preserved in any available *Celtedens* specimens (JDG, pers. obs. 2003).

The existence of a relatively large, somewhat crescent-shaped lacrimal lying between the anterior part of the skull roof and the maxilla in albanerpetontids has never been disputed. The only lacrimal previously reported for *Albanerpeton* is a complete bone that is part of a referred specimen (MNHN.LGA 1226) of *A. inexpectatum*. Lacrimals available for *A. pannonicus* demonstrate that this bone is similar overall in both species, but suggest that two details of previous cranial reconstructions for the genus based on material of *A. inexpectatum* are probably incorrect. First, in contrast to Estes and Hoffstetter's (1976) original reconstruction, in which the lacrimal was capped by the prefrontal and, thus, excluded from the skull roof, specimens of *A. pannonicus* demonstrate that the dorsal arm of the lacrimal contributed to the anterolateral part of the skull roof. Second, more recently one of us (Gardner 2000*c*, fig. 5) identified an articular surface along the medial face of the anterodorsal end of the lacrimal in MNHN.LGA 1226 and suggested this surface contacted the premaxilla. This interpretation was based, in part, on the anterior position of the articular surface on the lacrimal and, in part, on the assumption that the nasals were small, as in Estes and Hoffstetter's (1976) reconstruction. The presence in MÁFI V.22015 of a larger and more irregular shaped nasal that probably articulated along the premaxillary laterodorsal notch (see nasal account, above) argues against Gardner's (2000*c*) suggestion that the lacrimal contacted the lateral edge of the premaxilla. Instead, it appears more likely that the medial articular surface on the lacrimal in MNHN.LGA 1226 contacted the lateroanterior edge of the nasal. In retrospect, exclusion by the nasal of lacrimal–premaxillary contact was implied by the large gap left by the absent nasals in Gardner's (2000*c*, fig. 4) drawing of a composite skull of *A. inexpectatum*.

Prior to the discovery of *Albanerpeton pannonicus*, no examples of jugals were known for *Albanerpeton*. Estes and Hoffstetter (1976, fig. 4) reconstructed the skull of *A. inexpectatum* as salamander-like in lacking a jugal and, thus, in having the maxillary arcade or cheek region open posteriorly (i.e. posterior end of maxilla free of bony contacts). This interpretation was accepted by most researchers up to the mid-1990s (e.g. Carroll and Holmes 1980; Trueb and Cloutier 1991; Milner 1994). During this interval, however, Fox and Naylor (1982, pp. 124, 127) suggested that *Albanerpeton* probably had a jugal and, thus, a closed maxillary arcade, because in Upper Cretaceous maxillae available to them the dorsoposterior surface was roughened in approximately the place where a jugal might be expected to articulate. The first report of a jugal in albanerpetontids was by McGowan and Evans (1995), who noted the presence of this bone in *Celtedens ibericus*. McGowan (2002, pp. 8–9, figs 5, 6B) interpreted the jugal in *C. ibericus* as a thin, splint-like bone that articulated along the labial surface of the squamosal posteriorly and of the maxilla anteriorly, thereby forming a closed maxillary arcade. The precise shape and contacts of the jugal cannot be established with confidence in *C. ibericus*, because the holotype skull has been crushed flat and both jugals are split through lengthwise along the horizontal plane, meaning that for each jugal only the outline of the broken surfaces of the bone and its contacts along the same fracture plane are visible on the surfaces of the part and counterpart slabs (JDG, pers. obs. 2003). Although the holotype skeleton of *C. ibericus* clearly is important for confirming the presence in albanerpetontids of a jugal that forms a closed maxillary arcade, it is less informative for showing the three-dimensional form and contacts of the jugal. Articulated, three-dimensional jugals now available for *A. pannonicus* help clarify some of these details. These new specimens support some aspects of Fox and Naylor's (1982) and McGowan's (2002) interpretations, but show two important differences. First, rather than being the simple, splint-like bone that McGowan (2002) interpreted for *C. ibericus*, the jugal in *A. pannonicus* is a more complex bone consisting of two flanges: a low and elongate lateral flange that mediodorsally bears a dorsal flange, the latter of which is developed anteriorly into a horizontal shelf. Second, the pattern of anterior contacts is more extensive and complex than previously suspected. Anteriorly, the jugal overlaps both labially and dorsally onto the maxilla and extends further forward, with the anterior end of the dorsal flange on the jugal being wedged into the gap between the dorsal surface of the maxilla below and the posterior end of the lacrimal above. The anterolingual corner of the jugal also may have contacted a palatal bone, but this is less certain. Considering that maxillary structure is fairly uniform among albanerpetontid genera and species, regardless of geological age (cf. Bathonian maxilla figured by Gardner *et al.* 2003, fig. 3D vs. Pliocene maxillae figured here, Text-figs 3–4), we predict that the pattern of maxillary–jugal contact documented here for *A. pannonicus* was similar in other albanerpetontid taxa. The observation that the jugal in MÁFI V.22076/1 expands, rather than tapers, towards its broken posterior end implies that the jugal articulated posteriorly with one or more bones. In temnospondyls having a jugal, this bone articulates posteriorly and medially with the squamosal and, where present, posterolaterally with the quadratojugal. Intriguingly, the posteriormost end of the jugal in MÁFI V.22076/1 bears a pair of small, shallow indentations medially and a larger, but still shallow indentation laterally; we interpret these indentations as articular facets. The positions of these facets may indicate a more complex articulation with the squamosal than was inferred by McGowan (2002) or that the posterior end of the jugal was also braced against another bone, presumably the quadratojugal, although no examples of the latter bone have been reported for albanerpetontids.

Specimens of *Albanerpeton pannonicus* provide no concrete information on the identities or shapes of palatal bones in albanerpetontids. Nevertheless, the inferred palatal bone fragments reported above in MÁFI V.22012/1 and V.22076/2 help clarify the pattern of contact between the more posterior palatal bone(s) and the maxillary arcade in albanerpetontids. The lateral margin of these palatal bone(s) articulates with the maxilla along the unnamed trough that extends along the dorsolingual surface of the pars palatinum on the latter bone, as Fox and Naylor (1982) and Gardner (2000*a*) had suggested previously based on isolated maxillae from other albanerpetontid species. In addition, the lateral edge of the palatal bones(s) also articulates dorsally with the base of the lacrimal and, perhaps, lateroposteriorly with the anteromedial corner of the jugal.

Phylogenetic relationships

Relationships among the seven previously recognized species of *Albanerpeton* were examined in two recent cladistic analyses (Gardner 2002; Gardner *et al.* 2003). Both studies corroborated monophyly of the genus and identified the same pattern of intrageneric relationships. The geologically oldest congener, *A. arthridion* (late Aptian–middle Albian; USA), was placed as the basalmost species and the sister-taxon of the 'post-middle Albian clade'. This clade, in turn, comprised two less inclusive sister-clades: the 'gracile-snouted clade' of *A. cifellii* (late Turonian; USA), *A. galaktion* (Campanian–Maastrichtian; Canada and USA) and *A. gracilis* (middle Campanian; Canada and USA) and the 'robust-snouted clade' of *A. nexuosus* (Campanian–Maastrichtian; Canada and USA), the Paskapoo species (late Palaeocene; Canada) and *A. inexpectatum* (early–middle Miocene; France, Austria and Germany). Within the robust-snouted clade, *A. nexuosus* was identified as the sister-taxon of the 'Tertiary clade', which contained the Paskapoo species and *A. inexpectatum* as sister-taxa. The only lack of resolution in both studies was an unresolved trichotomy among congeners in the gracile-snouted clade.

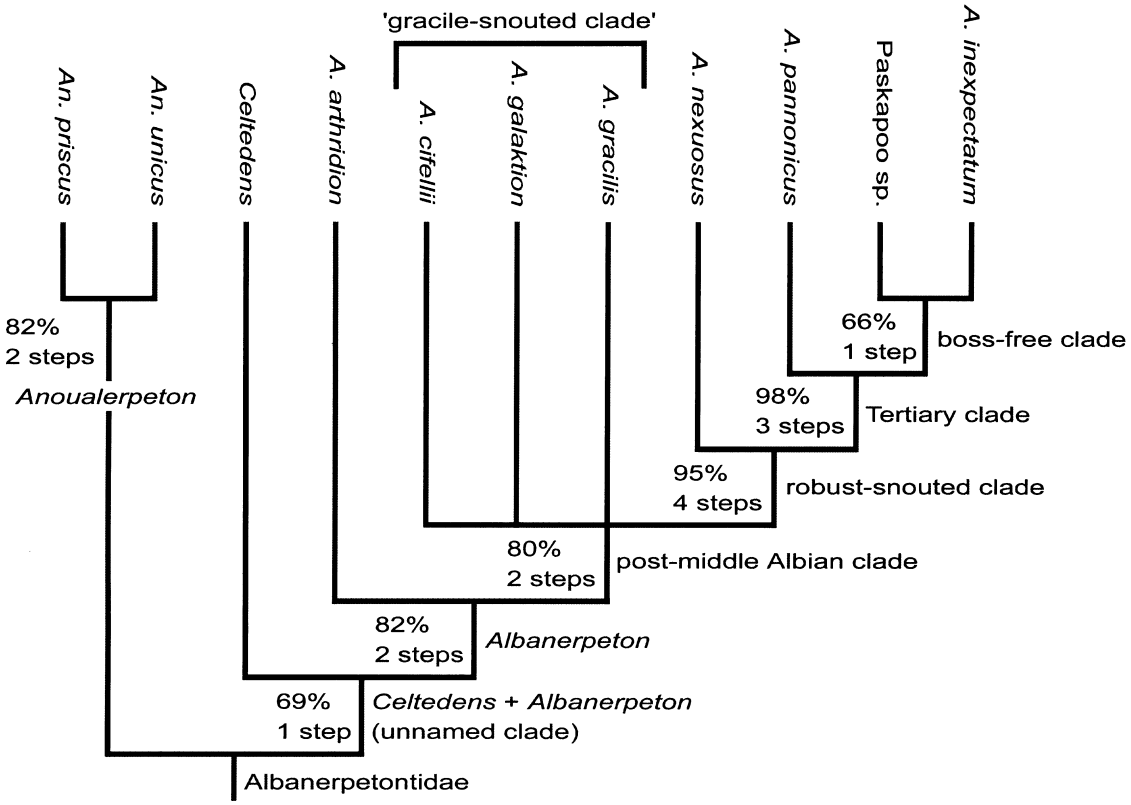
Our expanded analysis (see Appendix for details), which includes *Albanerpeton pannonicus* and some new characters, yields eight equally parsimonious trees, as compared to just three trees in previous analyses (Gardner 2002; Gardner *et al.* 2003). The strict consensus tree for the new analysis is depicted in Text-figure 9 and levels of support for clades are reported in Table 2. The new analysis yields two interesting results.

First, monophyly of *Albanerpeton* and most of its less inclusive clades is corroborated, and these clades continue to be relatively well supported; however, monophyly of the gracile-snouted clade collapses (Text-fig. 9, Table 2). Just three of the eight shortest trees recover a monophyletic gracile-snouted clade. Text-figure 10 depicts one of these trees, which most closely matches the strict consensus trees from previous analyses (Gardner 2002, fig. 2A; Gardner *et al.* 2003, fig. 5) in leaving relationships among the three gracile-snouted species unresolved. In the other five trees recovered in the new analysis, *A. cifellii*, *A. galaktion* and *A. gracilis* form various paraphyletic arrangements along the branch between *A. arthridion* and the robust-snouted clade. Considering that the gracile-snouted clade was the weakest supported clade in both earlier analyses (Gardner 2002; Gardner *et al.* 2003), collapse of that clade in the new analysis is not overly surprising.

Second, our analysis places *Albanerpeton pannonicus* in the robust-snouted clade, as we expected, but not in the position we anticipated. In the new analysis, the robust-snouted clade is supported by up to seven apomorphies.

TABLE 2. Bootstrap and decay values for less inclusive clades within the Albanerpetontidae in branch-and-bound searches, for trees up to four steps longer than the minimum of 35 steps. The strict consensus of the eight shortest trees is shown in Text-figure 9. Monophyly of the 'gracile-snouted clade' is not supported in this analysis (contra Gardner 2002; Gardner *et al.* 2003), but the clade is included here for comparison.

Clade	Bootstrap value (% for 2000 runs)	Percentage of trees recovering clade				
		minimum length 35 steps (8 trees)	min +1 ≤ 36 steps (34 trees)	min +2 ≤ 37 steps (96 trees)	min +3 ≤ 38 steps (313 trees)	min +4 ≤ 39 steps (893 trees)
Anoualerpeton	82	100	100	92	75	73
Celtedens + *Albanerpeton*	69	100	76	73	65	56
Albanerpeton	82	100	100	92	89	80
post-middle Albian clade	80	100	100	91	71	60
'gracile-snouted clade'	49	38	35	31	33	29
robust-snouted clade	95	100	100	100	100	< 100
Tertiary clade	98	100	100	100	90	86
A. inexpectatum + Paskapoo species	66	100	68	57	64	56



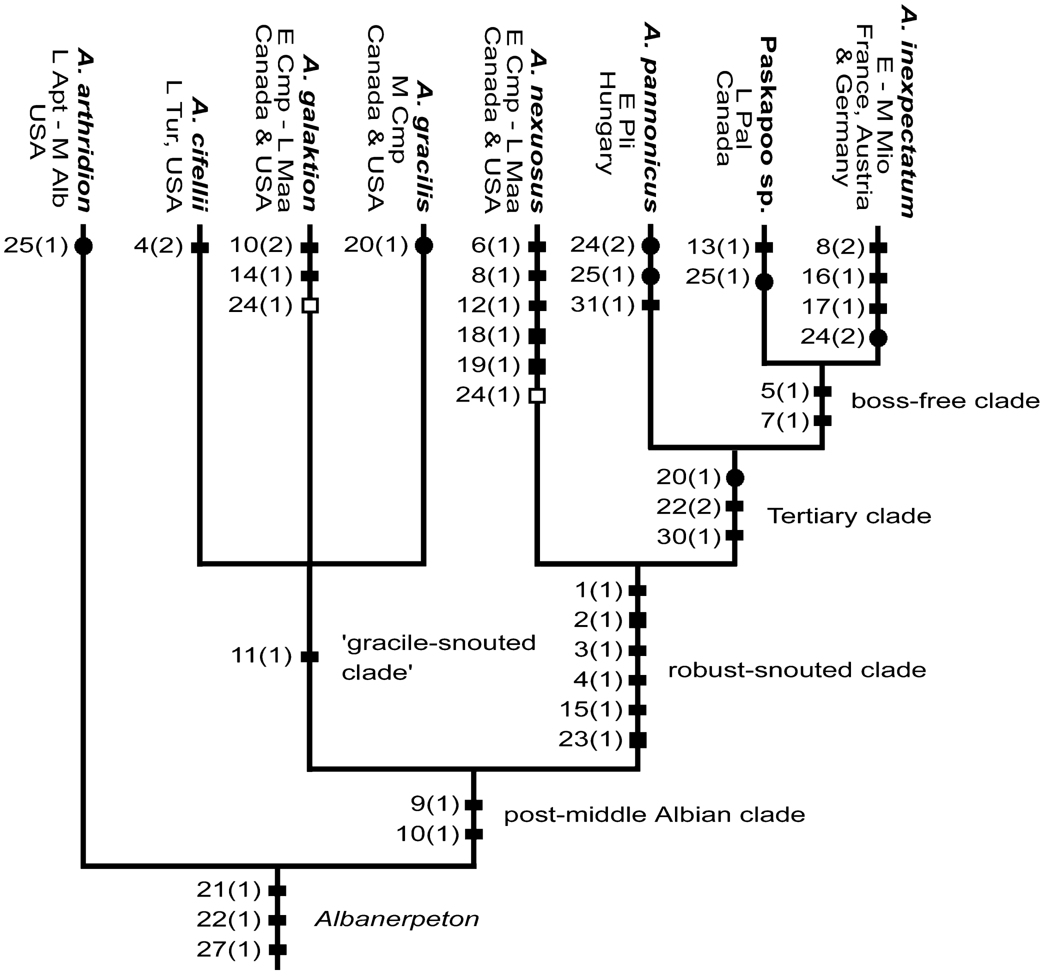
TEXT-FIG. 9. Strict consensus of eight shortest trees based on 21 informative characters scored for 11 albanerpetontid terminal taxon and a hypothetical 'all zero' ancestor, showing no support for monophyly of the 'gracile-snouted clade' (*sensu* Gardner 2002) and nesting *Albanerpeton pannonicus* sp. nov. within the robust-snouted clade as the sister of the other two Tertiary albanerpetontid species. Indices of support for clades are to left of each node: upper value is bootstrap value (%) for 2000 replicates and lower value is decay index (steps). Tree statistics (uninformative characters excluded): tree length = 35 steps; CI = 0·714, HI = 0·286, and RI = 0·825.

Three apomorphies support the clade in all eight trees under both ACCTRAN and DELTRAN optimizations: 1(1), premaxillae robust; 2(1), low pars dorsalis on premaxilla (convergent with *Anoualerpeton unicus*); and 3(1), premaxillae variably fused medially. The next three apomorphies are found in seven trees under both optimizations and in the eighth tree under the DELTRAN optimization: 4(1), premaxilla minimally overlaps and strongly sutured dorsally with nasal; 15(1), short premaxillary lateral process on maxilla; and 23(1), long internasal process on fused frontals (convergent with *An. priscus*). The ACCTRAN optimization in the eighth tree shifts character states 4(1), 15(1) and 23(1) stemward to the node supporting *A. cifellii* + robust-snouted clade; this arrangement is suspect, because the first apomorphy would need to change immediately to 4(2) in *A. cifellii* and, more importantly, because the last two apomorphies describe characters that cannot be scored for *A. cifellii* because the relevant bones (maxilla and frontals, respectively) are unknown for that species (Gardner 1999*c*). The last putative apomorphy occurs in the five trees having a paraphyletic arrangement of gracile-snouted species, where both optimizations for these trees postulate a reversal to an oval-shaped suprapalatal pit in the premaxilla [11(0)] at the node for the robust-snouted clade. By contrast, in previous studies (Gardner 2002; Gardner *et al.* 2003) all shortest trees under both optimizations consistently identified character states 1(1)–4(1), 15(1) and 23(1) as the only six synapomorphies for the robust-snouted clade and character state 11(0) as a symplesiomorphy for the robust-snouted clade, with character state 11(1) being the only synapomorphy for the 'gracile-snouted clade'. As in previous analyses, the robust-snouted clade is one of the two most strongly supported clades, with the highest decay (four steps) and second highest bootstrap (95 per cent) values.

Within the robust-snouted clade, *Albanerpeton pannonicus* is placed crownward of *A. nexuosus* as the sister-taxon of the Paskapoo species + *A. inexpectatum*. Here we use the name 'Tertiary clade' in an expanded sense for the clade of *A. pannonicus* (Paskapoo species + *A. inexpectatum*); previously the name 'Tertiary clade' was used for the last two species, which were the only Tertiary congeners then recognized (Gardner 2002; Gardner *et al.* 2003). As recognized here, the Tertiary clade is supported by up to five apomorphies. Three of these support the clade in all eight trees under both ACCTRAN and DELTRAN optimizations: 20(1), anterior end of tooth row on maxilla approximately in line with point of maximum indentation along leading edge of nasal process (convergent with *A. gracilis*); 22(2), frontals short; and 30(1), suprapalatal pit in premaxilla divided in about one-third or more of specimens. The reliability of character state 22(2) as a synapomorphy for this clade is suspect, because the relative length of the fused frontals cannot be determined accurately from the one set of posteriorly incomplete frontals available for the Paskapoo species (see Gardner 2000*a*, fig. 1C). Character state 30(1) is admittedly problematic, because it varies intraspecifically. Nevertheless, because this condition (suprapalatal pit variably divided) is seen in some individuals of *A. inexpectatum*, *A. pannonicus* and the Paskapoo species, but not in any other albanerpetontid species known to us, we believe that division of the suprapalatal pit is potentially informative for inferring relationships within the genus. Both optimizations in the five trees recovering a paraphyletic arrangement of gracile-snouted species and the ACCTRAN optimization in the three trees recovering a monophyletic 'gracile-snouted clade' also identify ventrolateral crests that are broad, triangular and have a deeply concave ventral surface [24(2)] as a synapomorphy for the Tertiary clade; this arrangement requires a reversal to narrower, convex ventrolateral crests [24(0)] in the Paskapoo species. By contrast, the DELTRAN optimization in the three trees recovering a monophyletic 'gracile-snouted clade' regards ventrolateral crests that are broad, triangular and have a deeply concave ventral surface as being convergent in *A. pannonicus* and *A. inexpectatum*. Finally, the ACCTRAN optimization in all eight trees identifies small body size [25(1)] as a homoplasy for both the Tertiary clade and *A. arthridion*; this arrangement requires a reversal to larger body size in *A. inexpectatum*. By contrast, the DELTRAN optimization in all eight trees regards small body size as having evolved independently in *A. arthridion* and twice within the Tertiary clade, once in *A. pannonicus* and once in the Paskapoo species. In having the highest bootstrap (98%) and second highest decay (three steps) values, the Tertiary clade is one of the two most strongly supported clades in our analysis.

As in previous analyses (Gardner 2002; Gardner *et al.* 2003), *Albanerpeton inexpectatum* and the Paskapoo species are identified as sister-species. Here we coin the name 'boss-free clade' for this clade. Both optimizations in all eight trees consistently identify only two synapomorphies for the clade: 5(1), premaxillary boss absent and 7(1), labial ornament on larger premaxillae covers entire pars dorsalis. Despite being supported by two unambiguous synapomorphies, the boss-free clade is one of the most poorly supported clades in our analysis, with the lowest bootstrap value (66%) and one of the lowest decay values (one step; tied with *Celtedens* + *Albanerpeton*). In previous analyses the sister-pair of *A. inexpectatum* + Paskapoo species was united by the same two synapomorphies identified here, but in terms of bootstrap and decay values, the clade was relatively better supported in earlier analyses.

Our prediction before running the cladistic analysis presented here was that *Albanerpeton pannonicus* and *A. inexpectatum* were sister-taxa. This prediction was based largely on the fact that both species exhibit two derived frontal character states, namely frontals relatively short [22(2)] and ventrolateral crests broad, triangular and with a concave ventral surface [24(2)] and, to a lesser extent, on the geographical and temporal proximity of both species in the European Neogene. Our cladistic



TEXT-FIG. 10. One of the eight shortest trees recovered in this analysis, which most closely resembles previously published strict cladograms (Gardner 2002, fig. 2; Gardner *et al.* 2003, fig. 5) of hypothesized relationships within *Albanerpeton* in depicting an unresolved, monophyletic 'gracile-snouted clade'. Note that the strict consensus cladogram generated in this analysis (Text-fig. 9) does not support monophyly of the 'gracile-snouted clade', because that clade was recovered in only three trees. Non-*Albanerpeton* terminal taxa depicted in Text-figure 9 are deleted for clarity. Distributions within *Albanerpeton* of apomorphies for all 31 characters used in this analysis are mapped onto tree using the DELTRAN character state optimization; see text for distributions using the ACCTRAN optimization. Abbreviations for time units are: Alb, Albian; Apt, Aptian; Cmp, Campanian; E, early; L, late; M, middle; Maa, Maastrichtian; Mio, Miocene; Pal, Palaeocene; Pli, Pliocene; Tur, Turonian. Tree statistics as for Text-figure 9. Apomorphy symbols are: solid bar, autapomorphy; solid circle, convergent within *Albanerpeton*; solid square, convergent with one or more non-*Albanerpeton* albanerpetontids; open square, convergent within *Albanerpeton* and with one non-*Albanerpeton* albanerpetontid.

analysis, however, corroborated the sister-pairing of *A. inexpectatum* and the Paskapoo species identified in previous analyses (Gardner 2002; Gardner *et al.* 2003) and, instead, placed *A. pannonicus* more stemward as the sister-taxon of the first two species. Two factors appear to have minimized the significance of the two frontal apomorphies that we initially thought would link *A. pannonicus* and *A. inexpectatum*. First, because the three Tertiary congeners are closely related, yet the character describing relative frontal length cannot be scored for the Paskapoo species, the node at which character state 22(2) lies is equivocal. Short frontals could be restricted to *A. pannonicus* and *A. inexpectatum* or, as suggested by our study (but see our cautionary comments, above) short frontals could be synapomorphic for the entire Tertiary clade. Second, the Paskapoo species and *A. inexpectatum* exhibit two premaxillary apomorphies (boss absent and labial ornament covers entire labial face of pars dorsalis) that are unique among albanerpetontids.

Although the most parsimonious arrangement identified in our analysis for the three Tertiary species is *Albanerpeton pannonicus* (Paskapoo species + *A. inexpectatum*), due to character state conflicts and unscored characters this pattern is not especially stable. Alternative arrangements within the Tertiary clade require just one additional step. In the 34 trees ≤ 36 steps long (i.e. minimum length plus one step), the arrangement of *A. pannonicus* (Paskapoo species + *A. inexpectatum*) is maintained in 23 trees and has a bootstrap value of 67 per cent. The next most common arrangement is *A. inexpectatum* (Paskapoo species + *A. pannonicus*), which occurs in eight of the 34 trees and has a bootstrap value of 25 per cent; in these trees the Paskapoo species and *A. pannonicus* are united by small body size [25(1)]. The least common arrangement (and the one we initially predicted) places the Paskapoo species as the sister-taxon of *A. inexpectatum* + *A. pannonicus*; this arrangement occurs in the remaining three trees and has a bootstrap value of 8 per cent. In this trio of trees, the sister-pairing of *A. inexpectatum* and *A. pannonicus* is supported in both optimizations by ventrolateral crests that are broad, triangular and have a deeply concave ventral surface [24(2)] and in DELTRAN by short frontals [22(2)]; the latter apomorphy shifts stemward to the node for the Tertiary clade under ACCTRAN.

Palaeobiogeography and palaeoecology

Previous attempts at interpreting the palaeobiogeographical history of *Albanerpeton* (Gardner 1999*a*, *b*, 2002) considered the seven congeners then recognized: the six Early Cretaceous–late Palaeocene species from the North American Western Interior and the European Miocene species *A. inexpectatum*. Based on a cladistic analysis (Gardner 2002) that placed the only Tertiary congeners then recognized, namely the Paskapoo species (late Palaeocene; Canada) and *A. inexpectatum* (early–middle Miocene; France, Austria and Germany), as sister-taxa and the most derived members of the genus, one of us (Gardner 1999*a*, *b*, 2002) suggested that the early history of *Albanerpeton* was centred in North America and that the presence of *A. inexpectatum* in Western Europe was best explained by a latest Cretaceous or early Palaeocene immigration of an unknown ancestral species from North America, prior to the extinction of the genus in North America.

Two developments suggest this ‘North American origin and diversification’ hypothesis is too simplistic. First, if Gardner’s (1999*a*, 2002) scenario of a single emigration event around the K/T boundary from North America to Europe followed by a minor Tertiary radiation in Europe was correct, we would expect the two European Neogene congeners, *Albanerpeton pannonicus* and *A. inexpectatum*, to be each other’s closest relatives and the most derived members of the genus. Instead, our cladistic analysis separates the two species by placing *A. pannonicus* further down the stem as the sister-taxon of two geologically older congeners from different continents, namely the Paskapoo species (late Palaeocene; North America) and *A. inexpectatum* (early–middle Miocene; Europe). The temporal and geographical inconsistencies in this phylogenetic arrangement are less easily accommodated within Gardner’s (2002) ‘North American origin and diversification’ hypothesis, without invoking more elaborate biogeographical scenarios, such as two independent immigrations to Europe from North America or an initial immigration to Europe, followed by a back immigration to North America.

Second, in recent years disarticulated albanerpetontid material has been reported from several uppermost Cretaceous (middle Campanian–Maastrichtian) localities in Europe (Table 3). Although specimens from these localities have not been described, figured or interpreted in detail, preliminary work on material from the middle–late Campanian La Neuve locality in France (Duffaud 2000) and from various late Maastrichtian localities in the Haţeg Basin of Romania (Grigorescu *et al.* 1999; Duffaud 2000; Folie *et al.* 2002) strongly suggests that at least some of these specimens can be assigned to *Albanerpeton*. If these identifications are correct, the Romanian and French occurrences push the record for *Albanerpeton* in Europe back about 50 or 60 million years, respectively, according to relevant time scales (e.g. Gradstein *et al.* 1995; Berggren *et al.* 1995; Steininger *et al.* 1996), from the early Miocene into the Late Cretaceous (Table 3). If *Albanerpeton* immigrated just once into Europe from North America, as Gardner (2002) suggested, the Romanian and French fossils indicate that this event must have occurred earlier, by at least the Campanian.

Taken together, the phylogenetic arrangement proposed here for *Albanerpeton* and recent reports of purportedly diagnostic *Albanerpeton* remains from the Upper Cretaceous of France and Romania indicate that, contrary to Gardner’s (2002) ‘North American origin and diversification’ hypothesis, the biogeographical history of *Albanerpeton* was more complex, with Europe having played a more important role. Once the new European Cretaceous specimens are adequately described and assigned to one or more species that can be placed in a phylogenetic framework, it may be possible to interpret better the interplay between North America and Europe in the biogeographical history of *Albanerpeton*.

The Carpathian Basin of Central Europe contains a series of fossil localities, most notably Kohfidisch (MN 11) in Austria and Tardosbánya (MN 12), Polgárdi (MN 13) and Osztramos 1 (MN 14) in Hungary, that are informative for tracing the late Miocene–early Pliocene history of herpetofaunas in the region (Venczel 1999, 2001), leading up to the Csarnóta 2 (MN 15) herpetofauna. Among all

TABLE 3. Late Cretaceous and Cenozoic occurrences of albanerpetontids in Europe. References are: 1, Venczel (2003); 2, Venczel and Gardner (2003); 3, this paper; 4, Estes and Hoffstetter (1976); 5, Estes (1981); 6, Gardner (1999*a*); 7, Rage and Hossini (2000); 8, Böhme (1999); 9, Wiechmann (2001); 10, Sanchíz (1998); 11, Grigorescu *et al.* (1999); 12, Duffaud (2000); 13, Folie *et al.* (2002); 14, Smith *et al.* (2002); 15, Codrea *et al.* (2002); 16, Laurent *et al.* (2002); 17, Buffetaut *et al.* (1999); 18, Astibia *et al.* (1990); 19, Duffaud and Rage (1999); 20, Garcia *et al.* (2000).

Geological age	Unit, locality and country	Taxon	References
early Pliocene (MN 15)	fissure infill Csarnóta 2, Hungary [Hiatus *c.* 7 myr]	*Albanerpeton pannonicus*	1–3
middle Miocene (MN 7/8)	fissure infills La Grive-Saint-Alban, France	*Albanerpeton inexpectatum*	4–6
middle Miocene (MN 6)	unidentified unit Sansan, France	*Albanerpeton inexpectatum*	7
early Miocene (MN 5)	Upper Freshwater Molasse Sandelzhausen, Germany	*Albanerpeton inexpectatum*	8
early Miocene (MN 5)	Randecker Maar, Germany	*Albanerpeton inexpectatum*	9
early Miocene (MN 4)	unidentified unit Oberdorf O3 and O4, Austria [Hiatus *c.* 50 myr]	*Albanerpeton inexpectatum*	10
late Maastrichtian	Sânpetru and Densuş-Ciula formations, various localities, Haţeg Basin, Romania	*Albanerpeton* sp. Albanerpetontidae indet.	11–13 14–15
late Maastrichtian	Auzas Marls Formation Cassagnau, France	Albanerpetontidae indet.	16
?early Maastrichtian	unidentified unit Cruzy, France	Albanerpetontidae indet.	17
late Campanian	unidentified unit Laño, Spain	Albanerpetontidae indet.	18–19
middle–late Campanian	unidentified unit La Neuve, France	*Albanerpeton* sp.	12, 20

these localities, albanerpetontid remains have been identified only at Csarnóta 2. During this interval, other components of these herpetofaunas show strong Asiatic affinities and, during the late Miocene, two minor faunal changes across the boundaries between MN 10–MN 11 and MN 12–MN 13 (Venczel 1999). Changes within the non-albanerpetontid components of these herpetofaunas in the late Miocene–early Pliocene seem to be related to the opening of land connections with Asia during the 'Messinian Crisis' in the late Miocene and a climatic shift towards drier conditions (Venczel 1999). One of us (Venczel 2003) suggested that the presence of *Albanerpeton pannonicus* in the Csarnóta 2 assemblage may be due to the opening of land bridges to the south or east following the Messinian Crisis, which allowed albanerpetontids to enter present-day Hungary. If so, this begs the question as to whether the ancestors of *A. pannonicus* existed elsewhere in Europe or even Asia.

Regardless of how *Albanerpeton pannonicus* came to be in present-day Hungary, abundant remains of this species at Csarnóta 2 demonstrate it was at least locally abundant in the area during the early Pliocene. Sedimentological and fossil evidence indicate that the palaeoenvironment of *A. pannonicus* consisted of a karstic terrain, partially covered by a forested landscape that changed over time to a more open grassland or steppe landscape. Lithologies and inferred depositional histories of the partially brecciated, clay-rich sediments infilling the Csarnóta 2 fissure differ between the upper and lower layers. According to Kretzoi and Pécsi (1982), the chocolate-brown colour of the kaolinite-type 'terra-rossa' sediments in the lower layers (25–5) resulted from decaying deciduous leaves, whereas the red clays with calcite impregnation in the uppermost layers (4–1) are indicative of denudation. Differences are also evident among the micromammals: the lower layers are dominated by remains of murids, glirids, petauristids and microtids, whereas the upper layers are dominated by the remains of arvicolids, mole-rats, cricetids and mice (Kretzoi 1956, 1959, 1962; Jánossy 1979, 1986). Taken together, the sedimentological and fossil evidence indicate 'a very slow and gradual change through time from a forest animal community to a grassland-steppe faunal assemblage' (Jánossy 1986, p. 22). Rare bones of bony fish and cryptobranchid salamanders at

Csarnóta 2 indicate that a body of freshwater was located nearby (Jánossy 1979, 1986).

Preliminary analysis of the herpetofauna at Csarnóta 2 (MV, in prep.) reveals some interesting patterns. The lizard *Lacerta* is the most commonly represented reptile taxon and bones of this genus are found in all layers. By contrast, elements of geckonid lizards are most frequent in the lower half of the section (layers 25–12), whereas elements of the glass lizard *Ophisaurus* are restricted to layers 10–4. Among snakes, colubrids and viperids are most abundant in the uppermost three layers. Bones of turtles and salamanders are rare. For frogs, bones of the toad *Bufo* and the spadefoot *Pelobates* are present in all layers, with those of the former genus being relatively more common. Bones of *Albanerpeton pannonicus* are also present throughout the section, and are most abundant in the bottom two and top three layers. The presence of *Bufo*, *Pelobates* and *A. pannonicus* bones in all layers implies that these lissamphibian taxa were not adversely affected by the change from a forested to more open, grassland landscape, unlike many other components of the Csarnóta 2 assemblage. Considering that some extant species of the first two genera are accomplished burrowers (Duellman and Trueb 1986) and that a burrowing habit has been postulated for albanerpetontids (e.g. Estes and Hoffstetter 1976; Fox and Naylor 1982; Gardner 1999*a*), a burrowing lifestyle may have made these amphibians more resilient to the palaeoenvironmental changes that occurred at Csarnóta 2.

CONCLUSIONS

Collections made during the 1950s from the lower Pliocene (late Ruscinian or MN 15 in age) fissure infill at Csarnóta 2, south-central Hungary, have yielded hundreds of isolated and articulated albanerpetontid bones. These fossils are of interest for the following reasons: (1) they extend the temporal range of this extinct lissamphibian clade forward some seven million years, from their next youngest occurrence in the middle Miocene of France; (2) they document the existence of a previously unrecognized species, *Albanerpeton pannonicus* sp. nov., which is diagnosed by a unique combination of symplesiomorphies and synapomorphies of the jaws and frontals and by an autapomorphic, ventromedian keel on the fused frontals; and (3) articulated upper jaws, maxillary arcades and anterior skull roof bones of *A. pannonicus* help clarify some details of cranial structure in these regions for albanerpetontids. An expanded cladistic analysis that includes *A. pannonicus* and some new characters nests *A. pannonicus* crownward in the genus, as the sister-taxon of the unnamed Paskapoo species (late Palaeocene; Alberta, Canada) + *A. inexpectatum* (early–middle Miocene; France, Austria and Germany). This arrangement and recent reports of purportedly diagnostic *Albanerpeton* material from the Campanian of France and Maastrichtian of Romania suggest, contrary to previous interpretations, that (1) Europe played a larger role in at least the latter part of the history of *Albanerpeton* and (2) if the genus originated in North America, then it evidently arrived in Europe well before the K/T boundary, by at least the Campanian. Further insights into the role played by Europe in the history of *Albanerpeton* must await the description and phylogenetic analysis of Cretaceous fossils from France and Romania. The presence of *A. pannonicus* bones in all layers at Csarnóta 2 implies that this species was not adversely affected by the transition from forest to grassland, which occurred in the area during the early Pliocene.

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APPENDIX

1. General methodology and assumptions for the phylogenetic analysis

The analysis presented here is expanded from Gardner (2002) and Gardner *et al.* (2003). The current analysis relies on 21 informative characters (17 binary and four multistate) scored for 11 albanerpetontid terminal taxon and a hypothetical 'all zero' ancestor used to root the tree (see data matrix, below). Another ten characters (6, 8, 12–14, 16–17, 28–29 and 31; nine binary and one multistate) are not informative for assessing relationships and were excluded from searches, but are mapped onto the tree depicted in Text-figure 10. Other details and assumptions follow Gardner (2002) and Gardner *et al.* (2003).

2. Characters used in the phylogenetic analysis

More detailed treatments of characters were presented by Gardner (2002) for characters 1–25, by Gardner *et al.* (2003) for characters 26 and 27 and by Gardner (2000*a*) for characters 28 and 29. Characters 30 and 31 are new; these are discussed in the text. Anatomical breakdown of characters is as follows: premaxilla (n = 17), characters 1–14, 26–27 and 30; maxilla and dentary (n = 6), characters 15–20; frontals (n = 7), characters 21–24, 28–29 and 31; and body size (n = 1), character 25.

1. Build of premaxilla: 0, gracile; 1, robust.
2. Ratio of height of premaxillary pars dorsalis vs. width across suprapalatal pit: 0, 'high', ratio greater than about 1·55; 1, 'low', ratio less than about 1·55.
3. Inter-premaxillary contact: 0, sutured medially (i.e. paired); 1, fused medially in some individuals.
4. Premaxillary–nasal contact: 0, premaxillary pars dorsalis minimally overlaps and abuts against or weakly sutured with anterior end of nasal; 1, premaxillary pars dorsalis minimally overlaps and strongly sutured with anterior end of nasal; 2, anterior end of nasal fits into lingual facet on premaxillary pars dorsalis and braced ventrolaterally by expanded dorsal end of lateral internal strut.
5. Boss on premaxilla: 0, present; 1, absent.
6. Relative size of premaxillary boss, if present: 0, covers about dorsal one-quarter to one-third of pars dorsalis; 1, covers about dorsal one-half of pars dorsalis.
7. Distribution of labial ornament on large premaxillae: 0, restricted to dorsal part of pars dorsalis; 1, covers entire face of pars dorsalis.
8. Pattern of premaxillary labial ornament: 0, discontinuous, anastomosing ridges and irregular pits; 1, continuous ridges defining polygonal pits; 2, pustulate.
9. Vertical position of suprapalatal pit on pars dorsalis: 0, 'high', with ventral edge of pit well above dorsal face of pars palatinum; 1, 'low', with ventral edge of pit just above or, more typically, continuous with dorsal face of pars palatinum.
10. Size of suprapalatal pit relative to lingual surface area of pars dorsalis: 0, 'small', about 1 per cent; 1, 'moderate', about 4–15 per cent; 2, 'large', about 20–25 per cent.
11. Outline of suprapalatal pit: 0, oval; 1, triangular or slit-like.
12. Form of dorsal process on lingual edge of maxillary process: 0, low, isolated ridge; 1, high flange, continuous labially with base of lateral internal strut.
13. Form of vomerine process on premaxilla: 0, prominent; 1, weak.
14. Diameter of palatal foramen in premaxilla relative to diameter of base of medial teeth on bone: 0, 'small', foramen diameter ≤ tooth diameter; 1, 'large', foramen diameter > about one and one-third tooth diameter.
15. Length of premaxillary lateral process on maxilla relative to height of process at base: 0, 'long', length > height; 1, 'short', length ≤ height.
16. Dorsally projecting process on dentary immediately behind tooth row: 0, absent; 1, present.
17. Labial ornament on large maxilla and dentary: 0, absent; 1, present.
18. Labial or lingual profile of occlusal margin of maxilla and dentary: 0, essentially straight; 1, strongly convex or angular, with apex adjacent to tallest teeth.
19. Size heterodonty of teeth on maxilla and dentary: 0, weakly heterodont anteriorly; 1, strongly heterodont anteriorly.
20. Position of anterior end of maxillary tooth row relative to point of maximum indentation along leading edge of nasal process: 0, anterior to; 1, approximately in line.
21. Dorsal or ventral outline of fused frontals: 0, approximately rectangular- or bell-shaped; 1, approximately triangular.
22. Ratio of midline length of fused frontals vs. width across posterior edge of bone, between lateral edges of ventrolateral crests, in large specimens: 0, 'long', ratio more than about 1·2; 1, 'moderate', ratio between about 1·2 and 1·1; 2, 'short', ratio equal to or less than about 1·0.
23. Proportions of internasal process on fused frontals: 0, 'short', length ≈ width; 1, 'long', length > width.
24. Form of ventrolateral crest on large, fused frontals: 0, narrow and convex ventrally to bevelled ventrolaterally in transverse view; 1, narrow and triangular in transverse view, with ventral face flat to shallowly concave; 2, wide and triangular in transverse view, with ventral face deeply concave.
25. Estimated maximum snout–pelvic length: 0, 'large', > about 50 mm; 1, 'small', < about 45 mm.
26. Direction faced by suprapalatal pit in pars dorsalis of premaxilla: (0) laterolingually; (1) lingually.
27. Path followed by canal through pars palatinum in premaxilla, between dorsal and ventral openings of palatal foramen: (0) dorsolaterally–ventromedially; (1) vertically.
28. Frontal–nasal contact: (0) groove along lateral face of internasal process on frontals receives medial edge of nasal; (1) internasal process dorsally overlaps onto medial edge of nasal.
29. Dorsal or ventral outline of internasal process on frontals: (0) tapered anteriorly; (1) bulbous.
30. Suprapalatal pit variably divided: (0) undivided; (1) divided in about about one-third or more of specimens.
31. Flattened ventromedial keel extending along posterior two-thirds of fused frontals: (0) absent; (1) present.

3. Data matrix used in the phylogenetic analysis

Matrix expanded from previous analyses (Gardner 2002, table 1; Gardner *et al.* 2003, appendix) by the addition of characters 30 and 31 and *Albanerpeton pannonicus* sp. nov. Symbols: ?, unknown; 9, inapplicable.

Terminal taxa	Characters							% missing or inapplicable
	00000 12345	00001 67890	11111 12345	11112 67890	22222 12345	22223 67890	3 1	
Hypothetical ancestor	00000	00000	00000	00000	00000	00000	0	0
Anoualerpeton priscus	0?0??	?0?00	00000	00110	00110	00000	0	16
Anoualerpeton unicus	01000	00000	00?00	??110	00000	00000	0	10
Celtedens	000??	?0?00	0????	0000?	00000	1?110	0	32
Albanerpeton arthridion	00000	00000	0000?	00000	11001	11000	0	3
Albanerpeton gracilis	00000	00011	10000	00001	11000	11000	0	0
Albanerpeton galaktion	00000	00012	10010	?0000	11010	11000	0	3
Albanerpeton cifellii	00020	00011	1000?	?????	?????	11??0	0	42
Albanerpeton nexuosus	11110	10111	01001	00110	11110	11000	0	0
Albanerpeton inexpectatum	11111	91211	00001	11001	12120	11001	0	3
Albanerpeton pannonicus sp. nov.	11110	00011	00001	00001	12121	11001	1	0
Paskapoo species	11111	91011	00101	00001	1?101	11001	0	6