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# A NEW SALAMANDRID AMPHIBIAN FROM THE MIDDLE MIocene OF HUNGARY AND ITS PHYLOGENETIC RELATIONSHIPS

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**SYNOPSIS** A fossil salamandrid, *Carpathotriton matraensis* gen. et sp. nov., from the Astaracian (Middle Miocene, MN 7) localities of Mátraszólós 1 and 2 (Northern Hungary, Nógrád County) is described. Within newts, *Carpathotriton* is diagnosed by a combination of primitive and derived characters including a premaxillary-frontal contact, a well-developed fronto-squamosal arch, low supraorbital crest and weak sculpture on the frontal surface. Referred material comprises abundant cranial, vertebral and appendicular skeletal elements that exhibit limited morphological variation of mainly allometric nature. The dentary of *Carpathotriton* is unique in displaying a prominent dental parapet with an extremely short tooth row and a relatively long toothless posterior ramus. The quadrate is provided with an exuberant anterolateral process that may be a homoplasy with some members of the *Tylototriton* group. Trunk vertebrae of *Carpathotriton* have extremely high neural spines with some enlargement on their dorsal margin similar to some Recent Eastern Asiatic salamandrads and the Oligocene newt *Archaeotriton*. The available fossil record suggests that *Carpathotriton* never extended into the western Paratethys area, but might have had a wider distribution in the central and eastern Paratethys region, surviving up to late Astaracian times (MN 7 + 8). Taphonomic setting of the Mátraszólós localities indicates that *Carpathotriton matraensis* was closely associated with aquatic environments.

**KEY WORDS** Astaracian, Paratethys, Palaeobiogeography, Palaeoenvironment, Salamandridae, Taxonomy

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## INTRODUCTION

The family Salamandridae, comprising 20 genera and more than 60 living species, represents one of the most diverse groups of caudate amphibians distributed across Europe, North Africa, Asia and North America but with most fossil

and Recent representatives found within Europe. Thus one may conclude that the European continent and adjacent territories were important in the evolutionary history of this salamander family.

Traditionally, within Salamandridae two major groups are distinguished, the ‘true’ salamanders (*Chioglossa*,

*Mertensiella* and *Salamandra*), and the newts (*Cynops*, *Echinotriton*, *Euproctus*, *Neurergus*, *Notophtalmus*, *Pachytriton*, *Paramesotriton*, *Pleurodeles*, *Salamandrina*, *Taricha*, *Triturus* and *Tylototriton*). This arrangement is supported by numerous studies that indicate the monophyly of 'true' salamanders and newts, excluding *Salamandrina* (e.g. Titus & Larson 1995; Larson *et al.* 2003; Montori & Herrero 2004; Weisrock *et al.* 2006). The latter genus was seen as a newt by Naylor (1978), but it was placed in the *Salamandra*-group by Wake & Özeti (1969). Estes (1981) grouped *Salamandrina* in his most primitive salamandrid group ('group I') together with *Chioglossa*, *Mertensiella*, *Megalotriton* and *Salamandra*. Nevertheless, several recent morphological and molecular contributions have considerably changed the taxonomy of salamandrids. The generic name *Lyciasalamandra* Veith & Steinfartz, 2004 is used to accommodate *L.* (= *Mertensiella*) *luchani* and a further six related species (Veith & Steinfartz 2004). The genus *Calotriton* Gray, 1858 was resurrected to include the Pyrenean brook newts, *C.* (= *Euproctus*) *asper* and *C. arnoldi*, while the name *Euproctus* is retained for the Tyrrhenian brook newts only (*E. montanus* and *E. platycephalus*) (Carranza & Amat 2005). Furthermore, the large European genus *Triturus* appears not to be monophyletic (Caccone *et al.* 1994; Titus & Larson 1995; Larson *et al.* 2003; Montori & Herrero 2004; Litvinchuk *et al.* 2005). The first person to address the taxonomic subdivision of *Triturus* was Bolkay (1928), who established three groups within the genus *Triturus* based on cranial osteological characters: the subgenera *Palaeotriton* (*Triturus boscai*, *T. italicus*, *T. helveticus*, *T. montandoni*, *T. vulgaris* and *T. vittatus*), *Mesotriton* (*T. alpestris*) and *Neotriton* (actually a synonym of *Triturus*) with *T. cristatus* and *T. marmoratus*. However, more recently, the large-bodied *T. vittatus* has been placed in the subgenus *Triturus* (see Arntzen & Olgun 2000 and references therein). Montori & Herrero (2004), beside *Triturus* (= *Neotriton* of Bolkay), resurrected the generic names *Lissotriton* (= *Palaeotriton* of Bolkay, excluding *T. vittatus*) and *Mesotriton*. Finally, Litvinchuk *et al.* (2005) split *Triturus* into four monophyletic genera: *Triturus* Rafinesque, 1815; *Lophinus* Rafinesque in Gray, 1850 (due to priority, this name is a synonym of *Lissotriton* Bell, 1839); *Mesotriton* Bolkay, 1928 and *Ommatotriton* Gray, 1850, to accommodate *O. ophryticus* and *O. vittatus*.

The earliest known fossil salamandrid is *Koalliella genzeli* Herre, 1950, from the Upper Palaeocene (MP 6) of Walbeck, Germany and Cernay, France (Estes *et al.* 1967; Estes 1981). *Koalliella genzeli* has also been recorded from the Lower Eocene (MP 7) of Dormaal, Belgium (Godinot *et al.* 1978) and probably from the Lower Eocene (MP 7) of Le Quesnoy, France (Nel *et al.* 1999). Further fossil representatives of salamandrids, have been described (e.g. Estes & Hoffstetter 1976; Sanchiz & Mlynarski 1979; Westphal 1980; Estes 1981; Hodrova 1984; Bailon 1989, 1991; Roček 1988, 1994, 1996a,b, 2005; Böhme 1998; Sanchiz 1998; Rage & Hossini 2000; Böhme & Rössler 2002; Böhme & Ilg 2003) including: *Archaeotriton* von Meyer, 1860 (Early–Late Oligocene), *Brachycormus* von Meyer, 1860 (Late Oligocene), *Chelotriton* Pomel, 1853 (Middle Eocene–Late Pliocene), *Chioglossa* Bocage, 1864 (Late Eocene–Recent), *Megalotriton* Zittel, 1890 (Upper Eocene or Lower Oligocene–Early Miocene), *Mertensiella* Wolterstorff, 1925 (Early Miocene–Recent), *Oligosomia* Navás, 1922 (Upper Miocene), *Palaeopleurodeles* Herre, 1941 (Upper Oligocene–Middle Mi-

cene), *Salamandra* Laurenti, 1768 (Late Eocene–Recent), *Salamandrina* Fitzinger, 1826 (Early Miocene–Recent), *Triturus* Rafinesque 1815 (?Eocene–Recent) and *Tylototriton* Anderson, 1871 (Middle Eocene–Recent). The fossil record of salamandrids also contains several genera and species with uncertain taxonomic status (taxon name usually preceded with 'cf' or 'aff') while a number of taxon names are synonyms of other taxa or are considered to be *nomina dubia* (e.g. *Salamandra goussardiana*, *Triturus sansaniense*, *T. minimus*, *T. lacasianum*: Estes 1981; Rage & Hossini 2000). Most salamandrid fossils are known from squashed skeletons or from dissociated three-dimensional material, which usually consists of vertebrae, appendicular skeleton and, very rarely, of cranial bones.

Until now only a few salamander taxa have been reported from the Middle Miocene (MN 6–8) of the Carpathian Basin, mostly from Děvínska Nová Ves (= Neudorf, Dévényújfalu) (Bratislava district), Slovakia. The fossil salamanders described from this locality include: *Bargmannia wettsteini*, *Salamandra broili*, *Voigtella ludwigi* and *Lissotriton* (= *Triturus*) *roehrsi* (Herre 1955). The taxonomic position of *Bargmannia wettsteini* has not yet been precisely established, since it is considered either a fossil dicamptodontid (Estes 1981) or a caudate *incertae sedis* (Milner 2000), while *Salamandra broili* and *Voigtella ludwigi* are synonyms of *Salamandra sansaniensis* (Estes 1981).

In the last three decades a number of Astaracian vertebrate localities in Hungary (Szentendre, Hasznos, Sámsonháza, Mátraszólós, Felsőtárkány, Felnémet), have been described (Kordos 1981, 1986; Hír 2003, 2004a; Hír & Kókay 2004; Hír *et al.* 1998, 2001; Gál *et al.* 1999a,b, 2000). Reports on fossil vertebrates, including salamandrids, were made by Hír *et al.* (1998, 2001) and Gál *et al.* (1999a,b, 2000). The taxa described briefly in these contributions consist of *Archaeotriton* sp. (Mátraszólós 2), *Lissotriton* (= *Triturus*) *roehrsi* (Felsőtárkány 3/2), *Lissotriton* cf. *roehrsi* (Mátraszólós 2), *Lissotriton* sp. (Mátraszólós 1) and Salamandridae indet. (Sámsonháza). In fact, *Archaeotriton* sp. was identified erroneously on the basis of a frontal bone and trunk vertebrae (Venczel, p. 45 in Gál *et al.* 2000), due to their apparent similarity with those of the Oligocene newt *Archaeotriton basalticus* (Böhme 1998; Böhme & Rössler 2002). A more detailed evaluation of the fossil material from Mátraszólós shows that the caudate remains appear to represent two distinct taxa: one a new salamandrid amphibian with some unique cranial and post-cranial skeletal features, the other, less frequent, closely related to *Lissotriton roehrsi*, as indicated by a combination of skull, vertebral and appendicular skeletal features.

This paper will (1) provide a detailed morphological description of the new salamandrid from Mátraszólós, (2) assess its taxonomic status and ascertain its phylogenetic relationships within Salamandridae and (3) discuss the palaeoenvironmental and palaeobiogeographical implications of the new taxon.

## Material, osteological terms and conventions

The fossils were collected after repeated intensive washing and sieving of the sediments using screens with meshes of 0.8 and 0.5 mm (Hír 2004b). The material includes a series of disarticulated cranial bones (premaxilla, frontal, parietal, orbitosphenoid, parasphenoid, squamosal, quadrate,

prearticular + angular, dentary), vertebrae, pectoral and pelvic girdles and limb bones, which represents an attritional assemblage that is most likely derived from a marshy-lacustrine palaeoenvironment. All fossil skeletal remains described here are housed in the Municipal Museum Pásztó, Hungary. Comparative material used in this study (disarticulated dried skeletons and alcian blue and alizarin red coloured salamandrid specimens) came from the Museo Nacional Ciencias Naturales, Madrid and the Tări Crișurilor Museum, Oradea. Common English terms and the standard anatomical orientation system are used throughout this paper; measurements of salamander vertebrae follow Haller-Probst & Schleich (1994); the classification and nomenclature of salamandrids follows Montori & Herrero (2004), Litvinchuk *et al.* (2005) and Weisrock *et al.* (2006).

Institutional abbreviations used are as follows:

**BMNH**, The Natural History Museum, London;  
**MMGD**, Museum für Mineralogie und Geologie, Dresden;  
**MMP**, Municipal Museum Pásztó, Pásztó, Hungary;  
**MNCN**, Museo Nacional Ciencias Naturales, Madrid;  
**MTC**, Tări Crișurilor Museum, Oradea, Romania;  
**PIUB**, Paläontologisches Institut, Universität Bonn.

## SYSTEMATIC DESCRIPTIONS

### **LISSAMPHIBIA** Haeckel, 1866

### **CAUDATA** Scopoli, 1777

### **URODELA** Duméril, 1806

### **SALAMANDRIDAE** Goldfuss, 1820

### **CARPATHOTRITON** gen. nov.

TYPE SPECIES. *Carpathotriton matraensis* gen. et sp. nov.

ETYMOLOGY. *Carpathan*, geographical name of mountain chain from Central Europe, + *triton*, Greek, a salamander.

DIAGNOSIS. As for the type and only known species.

***Carpathotriton matraensis*** gen. et sp. nov. (Figs 1, 3, 5–7)

2000 *Archaeotriton* sp.; Gál *et al.*, 45, fig. 3.

ETYMOLOGY. *Mátra*, Hungarian, geographical name of mountain range in the vicinity of the locality.

HOLOTYPE. MMP. 2005.361, a partial right frontal missing its postero-medial border and distal section of posterolateral process.

OCCURRANCE AND AGE. Mátraszólós locality 2, a section of road below the Rákóczi Chapel, situated at the northern margin of the small village of Mátraszólós, North Hungary (Gál *et al.* 2000; Hír 2004a; Hír & Kókay 2004). The Miocene lacustrine series with freshwater clays and lignite beds belong to the Sajó Valley Formation (Hír & Kókay 2004). The fossiliferous horizons rich in microvertebrates start with about 20 cm of green clays with freshwater molluscs and gypsum concretions and are followed by about 10 cm of grey clays, with abundant freshwater molluscs. Lignite beds

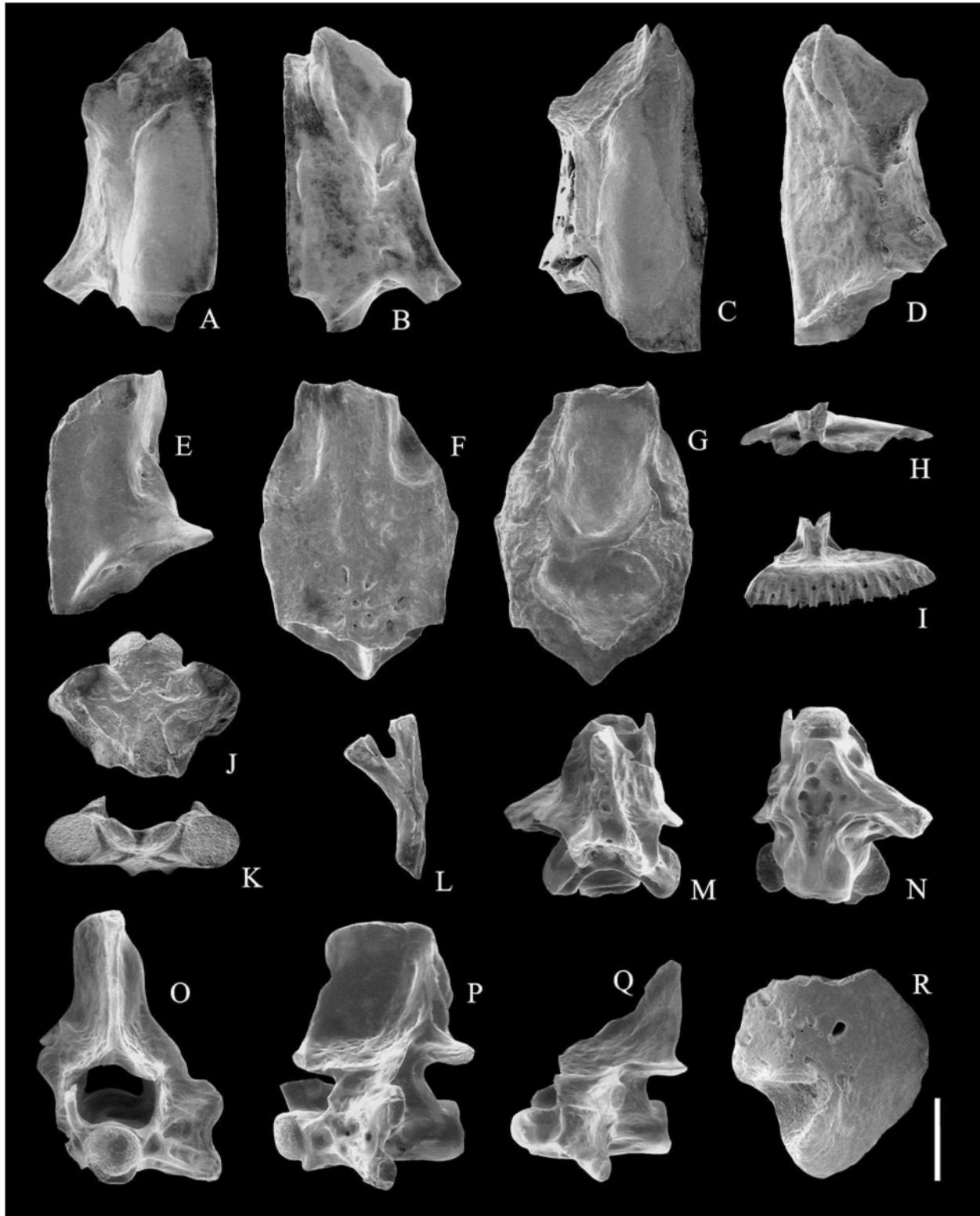
alternating with sands and clays cover the fossiliferous layers. The whole non-marine limnic series is situated between the Rákós Leithakalk (Early Badenian) and Kozárd formations (Early Sarmatian); the microvertebrate bearing sediments are dated to the Astaracian European Mammal age (MN 7) (Hír & Kókay 2004).

REFERRED SPECIMENS. Mátraszólós 1: frontals ( $n=2$ ): MMP. 2005.366, MMP. 2005.369; parietal ( $n=1$ ): MMP. 2005.370; squamosals ( $n=3$ ): MMP. 2005.371/1–3; parasphenoids ( $n=2$ ): MMP. 2005.362, MMP. 2005.372; dentaries ( $n=4$ ): MMP. 2005.373/1–4; vertebrae ( $n=5$ ): MMP. 2005.363/1–4, MMP. 2005.374; humeri ( $n=19$ ): (MMP. 2005.364/1–3, MMP. 2005.367, MMP. 2005.376/1–15; ilia ( $n=3$ ): MMP. 2005.375/1–3; femurs ( $n=47$ ): MMP. 2005.365/1–14, MMP. 2005.368/1–3, MMP. 2005.377/1–30.

Mátraszólós 2: frontals ( $n=26$ ): MMP. 2005.378/1–10, MMP. 2005.388/1–16; premaxillae ( $n=6$ ): MMP. 2005.392/1–6; parietal ( $n=1$ ): MMP. 2005.387; orbitosphenoids ( $n=2$ ): MMP. 2005.389/1–2; parasphenoids ( $n=4$ ): MMP. 2005.380, MMP. 2005.390/1–3; squamosals ( $n=10$ ): MMP. 2005.436/1–3, MMP. 2005.391/1–7; quadrates ( $n=10$ ): MMP. 2005.408/1–10; prearticular+angular ( $n=26$ ): MMP. 2005.379/1–15, MMP. 2005.394/1–11; dentaries ( $n=28$ ): MMP. 2005.437/1–3, MMP. 2005.393/1–25; ceratobranchial ( $n=1$ ): MMP. 2005.403; atlases ( $n=38$ ): MMP. 2005.381/1–8, MMP. 2005.395/1–30; trunk vertebrae ( $n=128$ ): MMP. 2005.382/1–5, MMP. 2005.383/1–63, MMP. 2005.396/1–60; ribs ( $n=4$ ): MMP. 2005.404/1–4; scapulocoracoids ( $n=10$ ): MMP. 2005.386/1–5, MMP. 2005.397/1–5; humeri ( $n=120$ ): MMP. 2005.384/1–30, MMP. 2005.398/1–90; radiuses ( $n=4$ ): MMP. 2005.399/1–4; cubituses ( $n=2$ ): MMP. 2005.400/1–2; ilia ( $n=48$ ): MMP. 2005.438/1–5, MMP. 2005.401/1–43; ischia ( $n=2$ ): MMP. 2005.402/1–2; femurs ( $n=300$ ): MMP. 2005.385/1–105, MMP. 2005.405/1–195; tibiae ( $n=38$ ): MMP. 2005.406/1–38; fibulae ( $n=10$ ): MMP. 2005.407/1–10; malformed specimens: 1 atlas (MMP. 2005.409), 1 ilium (MMP. 2005.410), 3 femurs (MMP. 2005.411/1–3).

DIAGNOSIS. *Carpathotriton matraensis* differs from *Mesotriton*, *Neurergus*, *Oligosomia*, *Lissotriton montandoni*, *L. vulgaris* and *Triturus* in having a large posterolateral process to its frontal. It differs from *Calotriton* and *Euproctus* in having a comparatively shorter frontal and a more prominent supraorbital crest. *Cynops*, *Echinotriton*, *Notophthalmus*, *Pachytriton*, *Paramesotriton*, *Pleurodeles* and *Taricha* have a complete fronto-squamosal arch, but differ in having a more prominent supraorbital crest to the frontal. *Carpathotriton matraensis* further differs from *Cynops*, *Echinotriton* and *Paramesotriton* by its lack of pit and ridge sculpture on the frontal surface. It differs from *Lissotriton boscai*, *L. helveticus* and *Ommatotriton* in having a stouter and posteriorly widening posterolateral process.

DESCRIPTION. *Frontal*. The holotype frontal belonged to an adult and is incomplete, with the posteromedial margin and the distal section of the posterolateral process broken off (Fig. 1A, B). In dorsal view, the outer surface of the frontal is slightly convex dorsally and lacks any secondary dermal sculpture. Alongside the medial margin of the frontal there is a less elevated bony surface suggesting that, in life, it was overlapped by its counterpart. The anterolateral section of the frontal is penetrated by several foramina situated in a deep



**Figure 1** *Carpathotriton matraensis* gen. et sp. nov. from Mátraszólós 2. **A, B**, MMP.2005.361 (holotype) frontal; **C, D**, MMP.2005.378/1 frontal; **E**, MMP.2005.387 parietal; **F, G**, MMP.2005.390/1 parasphenoid; **H, I**, MMP.2005.392/1 prefrontal; **J, K**, MMP.2005.395/1 atlas; **L**, MMP.2005.404/1 rib; **M–P**, MMP.2005.382/1 trunk vertebra; **Q**, MMP.2005.382/2 trunk vertebra; **R**, MMP.2005.386/1 scapula. **A, C, F, J, N, R**, ventral views; **B, D, E, G, H, M**, dorsal views; **I**, posterior view; **K, O**, anterior views; **L, P, Q**, lateral views. Scale bar = 1 mm.

groove, which is closed posteriorly. On the anterior section of the table there is a prominent area produced as two divergent ridges, defining a hemi-cylindrical shaped groove for

the premaxillary-frontal contact. This morphology suggests that in the living animal the distal section of the premaxillary dorsal process was almost completely embedded in the

anteromedial section of the frontal. On the anterolateral section of the frontal there is a small laterally inclined surface, which was presumably overlapped by the prefrontal in life. The posterolateral process is relatively wide and presumably was rather long. Its dorsal surface is nearly horizontal, pierced by several pits; and the supraorbital crest is low. A low crest runs from the medial margin of the posterolateral process toward the frontal's posteromedial margin, delimiting a less elevated posterolateral area. In ventral view, the medial surface is concave ventrally and bordered laterally by a prominent ventrolateral ridge. The fronto-orbitosphenoidal contact is marked by an imprint on the medial side of the ventrolateral ridge. The area between the lateral side of the ventrolateral ridge and the supraorbital margin is concave laterally and pierced by several foramina of varying sizes. A bony crest ventrally connects the posterior section of the ventrolateral ridge and the base of the posterolateral process.

The morphology of the remaining frontals closely resembles that of the holotype, exhibiting a relatively narrow range of intraspecific variation. In MMP.2005.378/1, which belonged to a larger individual (Fig. 1C, D), the anterolateral projection marking the contact terminus for the prefrontal is distinctly larger than that in the holotype; the bony crest running from the medial base of the posterolateral process and the posteromedial margin is extremely prominent and inclined posterolaterally. A comparable condition may also be seen in some Recent salamandrids (e.g. *Lissotriton*, *Paramesotriton*; Fig. 2B, C, I). In MMP.2005.378/2 the medial and anterior section of the frontal table is broken off, but there is a well-preserved posterolateral process whose distal section is distinctly widened (Fig. 3A, B). In MMP.2005.378/3 the groove for the fronto-premaxillary contact is distinctly wider and longer than in other specimens. Several fragmentary specimens belonging to large individuals bear a fine dorsal sculpture, produced by extremely shallow pits and ridges.

**Premaxilla.** The premaxillae are completely fused; the *pars dentalis* is relatively long and somewhat arcuate posterolaterally. The best preserved specimen is MMP.2005.392/1 (Fig. 1H, I) with 18 tooth positions preserved, of which 11 teeth are on the right side of the premaxilla, demonstrating that there were at least 22 teeth. The labial surface of the premaxilla is slightly convex and without sculpture. In MMP.2005.392/1 only the broken base of the dorsal process (= alary process) is preserved. The dorsal process, based on specimen MMP.2005.392/2, bears a distinct proximal keel on its labial and lingual surfaces. The rami of the dorsal process are united at their base and diverge slightly dorsally; the free portion is subcylindrical in shape. On the lateral side of the dorsal process there is a distinct recess with a foramen piercing the *lamina horizontalis*. The distal section of the dorsal process in all specimens is broken off. However, based on the morphology of available frontals, I deduce that the premaxillary dorsal processes were rather long and contacted the anteromedial part of the frontal. The *pars palatina* is relatively small when compared to other salamandrids (Fig. 4). It has a slight posterodorsal orientation and is connected medially to the base of the dorsal process.

**Parietal.** The dorsal surface of the parietal is smooth without any secondary sculpture. In MMP.2005.387 (Fig. 1E) the medial margin of the bone is slightly curved dorsally to contact its counterpart. Obviously in the living individual a parietal ridge was present with contributions from both parietals. In MMP.2005.370, which belonged to a somewhat

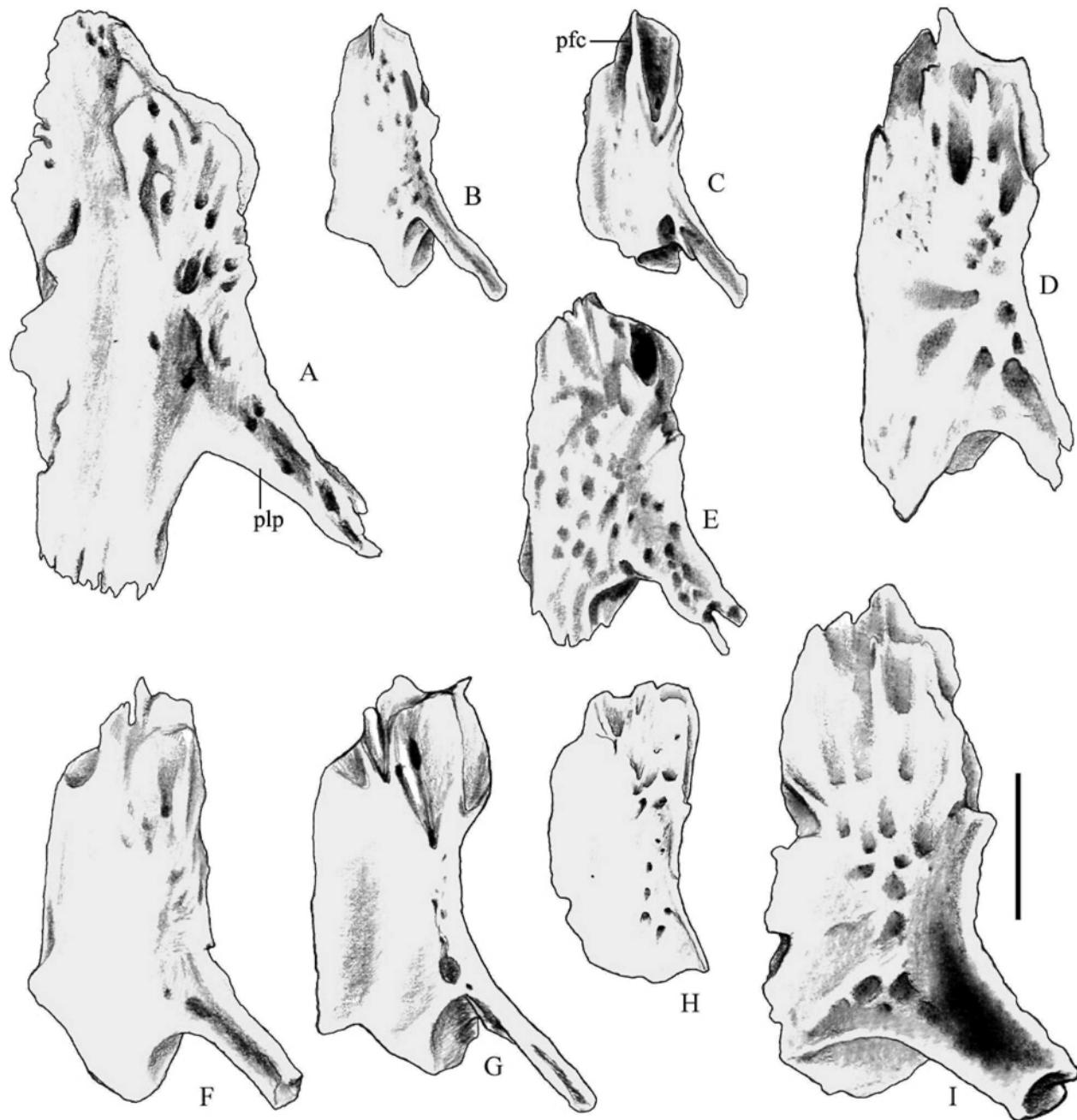
smaller individual, the middle section of the parietal crest is extremely thin and prominent. In MMP.2005.387 the anterior margin of the parietal is slightly damaged but imprints on its dorsal surface suggest that it was overlapped by the frontal. The anterolateral margin is depressed and pierced by several small foramina. The lateral process of the parietal is tapering with a laterodorsal orientation indicating possible contact with the squamosal over the otoccipital. An arch-like ridge extends between the parietal's lateral process and its posterior margin, delimiting a less elevated posterolateral area pierced by several small foramina. The latter structure is also seen in MMP.2005.370.

**Orbitosphenoid.** Specimen MPP. 2005.389/1 (Fig. 3F and see Fig. 7A) in lateral or medial view is oblong-shaped and has a rather simple morphology. The posterior third of the bone is concave laterally and pierced by two foramina: an anterior larger one for the aditus of the optic nerve and a posterior smaller one for the exit of the oculomotor nerve. The anterior section is concave medially and lacks foramina. About two-thirds of the orbitosphenoid's anterior section, facing dorsolaterally, in life was overlapped from above by the frontal; the posterior section, facing dorsomedially, was overlapped by the parietal. The ventral margin of the orbitosphenoid contacted the parasphenoid from above, while its anteriormost section overlapped, dorsally, the vomer. Both the dorsal and ventral margins are slightly widened anteriorly.

**Parasphenoid.** In all specimens the cultriform process is broken off. In MMP.2005.390/1 (Fig. 1F, G) the basal plate is broadly rectangular with some posterior waist; its posterior section is slightly concave. The ventral surface is finely ornamented by small pits and ridges, excepting the post-central area, which is penetrated by several foramina of variable size. On both sides near the base of the cultriform process there is a shallow concavity. A steep bony lamina connects the posterior crest and the posterior margin. The latter tapers posteriorly. In dorsal view the endocranial imprint is exposed in the form of an elongated fossa delimited laterally by sharp bony lamellae. The latter is flanked at the level of the widest extent of the basal plate by a sinuous groove for the carotid duct. In the posterior area there is a smaller concavity delimited by a transverse bony ridge. The ventral surfaces in MMP.2005.372, 380 and 390/2 are flat with some small irregular embayments and a convexity at the base of the cultriform process; the posterior crest projects slightly. MMP.2005.362 resembles other specimens, but its posterior crest is more prominent and there is a low crest detached from the ventral lateral margin running obliquely onto the ventral surface of the cultriform process.

**Quadrata.** The available specimens (MMP.2005.408/1–10) belonged to various-sized individuals. This bone is moderately long and robust and provided with a relatively wide otic process that faces dorsally. The quadrate crest is sinuous, ending in a spur-like process projected dorsally. On the posterolateral area there is an imprint formed by the ventral ramus of the squamosal, which in life would have partially overlapped the quadrate. A prominent process is observed on the anterolateral side of the quadrate, which presumably served for muscular attachment (Fig. 3H, I).

**Squamosal.** MMP.2005.371/1 (Fig. 3C) is tri-radiate-shaped and strongly flattened medio-laterally. The ventral ramus is relatively long (its posterior margin is broken), overlapping the quadrate posterolaterally. The posterior ramus of

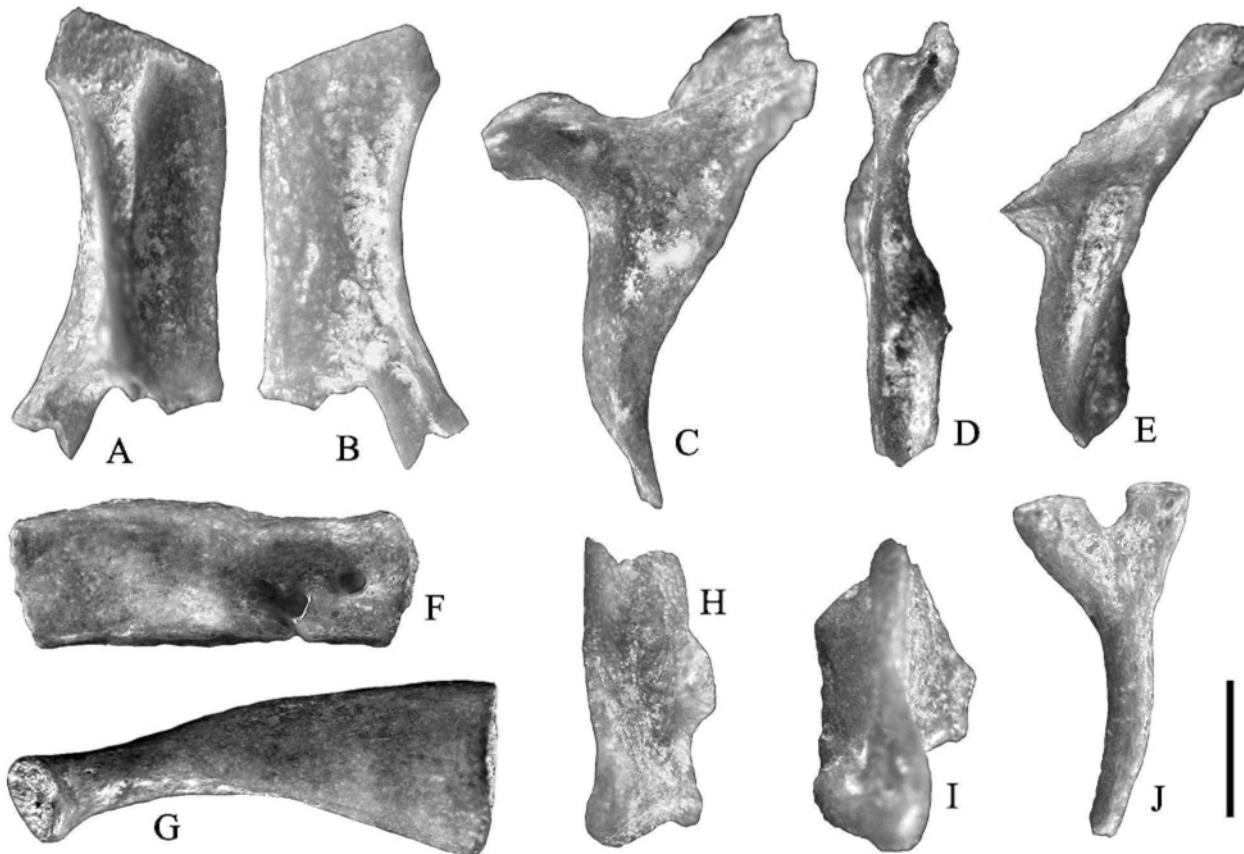


**Figure 2** Right frontals of Recent salamandrids (dorsal views). **A**, *Pleurodeles waltl* (MNCN 19648). **B**, *Lissotriton boscai* (MNCN 18187). **C**, *Lissotriton helveticus* (MNCN 19265). **D**, *Triturus marmoratus* (MNCN 19275). **E**, *Cynops pyrrhogaster* (MNCN 23822). **F**, *Taricha granulosa* (MNCN 11830). **G**, *Ommatotriton vittatus* (MNCN 40462). **H**, *Mesotriton alpestris* (MTC 23450). **I**, *Paromesotriton hongkongensis* (MNCN 23557). Abbreviations: pfc, groove for premaxillary-frontal contact; plp, posterolateral process. Scale bar = 2 mm.

the squamosal is relatively long and directed posterodorsally; its medial side contacts the *crista parotica* of the prootic. The anterior ramus is of the same length or somewhat shorter than the posterior ramus and articulates with the posterolateral process of the frontal, forming a complete fronto-squamosal arch. On the dorsomedial side of the anterior ramus, there is a small but distinct process, which, at least in larger specimens (e.g. MMP.2005.371/1, 436/1) could be in contact with the lateral process of the parietal. In MMP.2005.436/1 the ventral ramus is broken off distally, but both posterior and anterior rami are well developed and the distal anterior

section bears a rostrum directed anteroventrally. On the lateral surface of the squamosal there are two main crista: one is inclined posterolaterally and runs along the lateral side from the posterior process to the distal end of the ventral process; the other starts from the dorsolateral margin of the anterior ramus and meets the lateral crest at the posterolateral corner of the squamosal. At that point a prominent knob-like structure is produced (Fig. 3D, E).

**Dentary.** Although all specimens are fragmentary, available material includes specimens with either the anterior or the posterior section of bone allowing a complete



**Figure 3** *Carpathotriton matraensis* gen. et sp. nov. from Mátraszólós 2. **A, B**, MMP.2005.378/2 frontal; **C**, MMP.2005.371/1 squamosal; **D, E**, MMP.2005.371/2 squamosal; **F**, MMP.2005.389/1 orbitosphenoid; **G**, MMP.2005.403 right first ceratobranchial; **H, I**, MMP.2005.408/1 quadrate; **J**, MMP.2005.404/1 rib; **A**, ventral view; **B, G**, dorsal views; **C, E, F, I, J**, lateral views; **D**, posterior view; **H**, anterior view. Scale bar = 1 mm.

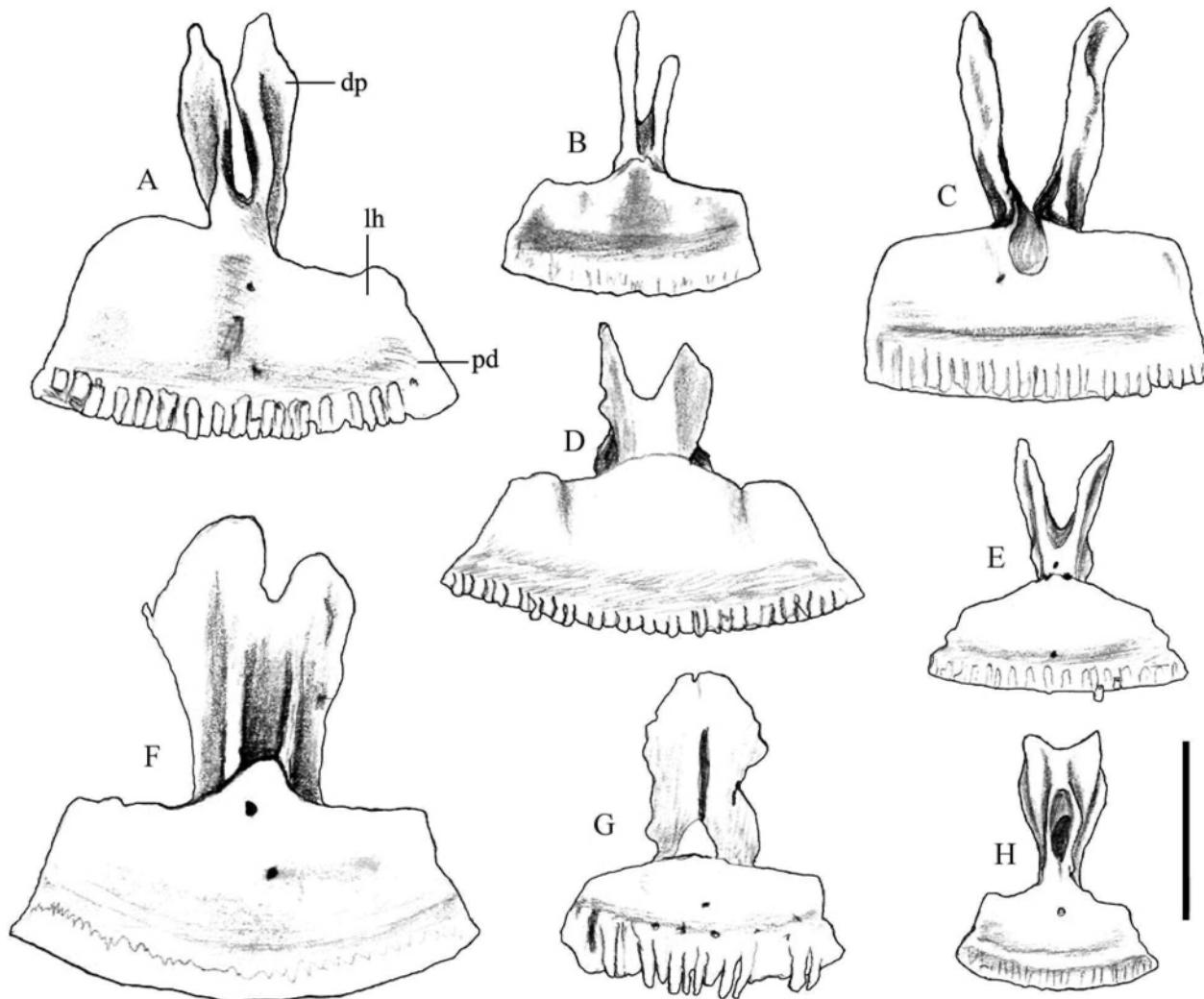
reconstruction. The labial surface is broadly convex and smooth, with a shallow groove along the labial side of the base of the dental parapet. In MMP.2005.437/1, representing a distinctly larger specimen (Fig. 5F), the labial surface is sculptured with longitudinal striations, grooves and foramina and there is a well-defined keel along the lower dental margin. The anterior (i.e. toothed) section of the dentary is relatively short and strongly curved medially, the dental parapet projects strongly above the level of the posterior ramus and is provided with pleurodont teeth or loci and the subdental shelf is moderately widened. Tooth counts of different fragmentary specimens suggest that the complete dentary had a total of 23–25 loci. The posterior ramus behind the tooth row is extremely long and has an unusual morphology: the dorsal edge bears a continuous lingual crest, which presumably articulates with the prearticular. The labial crest is also continuous (e.g. MMP.2005.437/3) and is pierced behind the tooth row by a foramen, or more typically intersected by a groove extending onto the labial surface (e.g. MMP.2005.393/1-2; Fig. 5A, B, D). Behind this groove the labial crest is developed into a well defined dorsal flange with its dorsal margin twisted lingually and overlapping the coronoid process of the prearticular, as observed in specimen MMP.2005.437/1, in which the anterior ramus of the prearticular is also preserved (Fig. 5E). The Meckelian groove is deep and widened posteriorly but narrows in its anterior section below the tooth

row and closes completely at the level of the seventh or eighth tooth position. The symphysis is rather small.

**Prearticular+angular.** The prearticular is elongate and slightly compressed medio-laterally and is provided with a relatively high coronoid process and a low lateral flange bordering the Meckel's groove lingually. The dorsal margin of the coronoid process bears an imprint indicating that it was overlapped by the dorsal process of the dentary posterior ramus (see above). The surface of the Meckelian cartilage is orientated posterodorsally.

**Hyobranchial skeleton.** The only referable bony element is MMP.2005.403, a right first ceratobranchial (Fig. 3G). This is curved mediolaterally, the head is slightly dilated and has an oval shape and the stem is thickened distally and slightly flattened dorsoventrally. The distal plate presumably contacts the epibranchial.

**Atlas.** The available material consists of atlantal centra from individuals of various sizes (Fig. 1J, K). Centrum length approximately equals centrum width. The subcentral area is arrow-shaped and concave ventrally, displaying several pits bordered by bony ridges. The articular surface of the paired atlanteal condyles is faintly convex and elliptical in shape. The odontoid process is relatively wide and displays two well separated and shallowly convex ventrolateral articular surfaces of oval shape. The atlanteal cotyle is circular. The foramina for the exit of the first spinal nerves are situated

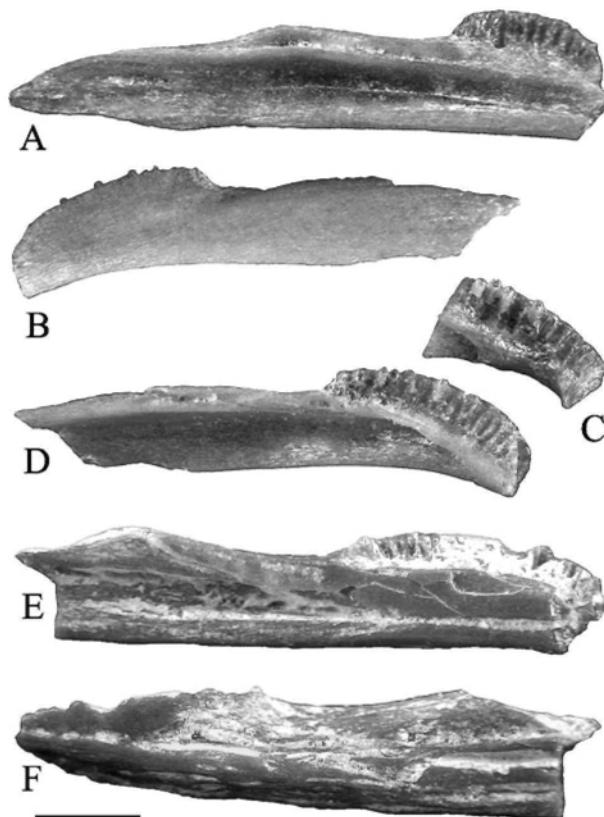


**Figure 4** Premaxillae of Recent salamandrids in posterior views. **A**, *Triturus marmoratus* (MNCN 19275); **B**, *Cynops pyrrhogaster* (MNCN 23822); **C**, *Taricha granulosa* (MNCN 11830); **D**, *Ommatotriton vittatus* (MNCN 40462); **E**, *Lissotriton helveticus* (MNCN 19265); **F**, *Paramesotriton hongkongensis* (MNCN 23557); **G**, *Calotriton asper* (MNCN 16132); **H**, *Lissotriton boscai* (MNCN 18187). Abbreviations: dp, dorsal process; lh, lamina horizontalis; pd, pars dentalis. Scale bar = 2 mm.

posterior to the ventrolateral margins of the atlanteal condyles. In one atlas (MMP.2005.409) the odontoid process is rather small and asymmetric lacking its left lobe and the left articular surface on its ventrolateral side, respectively.

**Trunk vertebrae.** MMP 2005.382/1 (Fig. 1M–P) represents an anterior trunk vertebra in which both prezygapophyseal areas and the right transverse processes (=rib bearers) are broken off. In lateral view, the centrum is opisthocoelous and moderately elongated. The condyle is relatively small, rounded and separated from the vertebral centrum by a distinct constriction. The transverse processes are widely spaced and, except for their distal end, are connected with a bony lamina. The rib-articulating surface of the diapophysis is oval, while that of the parapophysis is nearly circular. There is a distinct spinal nerve foramen at the posterior base of the diapophysis. The subcentral lamina is prominent ventrally and connected to the parapophysis. The neural spine is about 2.5 times the height of the centrum, without any anterior or posterior overhang. There is a lateral enlargement of the dorsal surface. The postzygapophyseal

area is completely delimited by a sharp dorsolateral crest, which runs from the posterolateral border of the neural lamina to the diapophysis. The postzygapophyseal crest extends anterodorsally, merging into the dorsolateral crest. On the right lateral side, the dorsolateral crest is comparatively lower in height. In anterior view, the condyle is circular and without a notochordal fossa. The neural canal is pear-shaped, while the neural spine is extremely high with a thin leading edge and a somewhat thickened dorsal surface. In ventral view, the centrum is somewhat constricted medially between the condyle and the cotyle. Prominent bony ridges extend between the ventrolateral sides of the condyle and cotyle and the ventral surface of the parapophyses, respectively. The resulting diamond-shaped subcentral area is deeply concave and penetrated by several foramina of different size. In dorsal view, the neural arch is relatively short. The dorsal surface of the neural spine is relatively thin with a gradual posterior enlargement bearing pit and ridge sculpture. In posterior view, the cotyle is deeply concave and circular. MMP. 2005.382/2 closely resembles MMP. 2005.382/1 (Fig. 1Q) but has more



**Figure 5** Dentaries of *Carpathotriton matraensis* gen. et sp. nov. from Mátraszólós 2. **A**, MMP.2005.393/1 dentary; **B**, **D**, MMP.2005.393/2 dentary; **C**, MMP.2005.393/3 dentary; **E**, **F**, MMP.2005.437/1 dentary. **A**, **C**, **D**, **E**, lingual views; **B**, **F**, labial views. Scale bar = 1 mm.

widely spaced transverse processes. The remaining material is rather fragmentary, but closely resembles the described specimens. Intraspecific variations mainly concern the morphology of the subcentral area, which sometimes displays a midline bony pillar across the subcentral pit. The transverse processes are variable in shape, length and spacing, mostly dependent on their position within the vertebral column.

**Ribs.** The ribs are bicapitate (Figs 1L, 3J) and display ovoid articular surfaces. At least some were provided with dorsal spines.

**Scapulocoracoid.** In most specimens the scapular shaft is missing (Fig. 1R), the glenoid is relatively narrow and the supracoracoid foramen is always present. Two specimens preserve the scapular shaft, which is relatively long and moderately widened with a thin anterior rim.

**Humerus.** The humeral shaft is straight and the proximal articular surface rounded and connected to the moderately prominent ventral humeral crest (Fig. 6A). The surface of the humeral crest, especially in larger individuals, is covered with lateral striae and pierced by several small foramina. The dorsal humeral crest is a thin and rather short bony lamella of roughly triangular shape, its height usually diminishing well above the level of the ventral humeral crest. The distal section of the humeral shaft is slightly widened and provided with a rather shallow ventral cubital fossa (Fig. 6D). The entepicondyle is slightly larger than the ectepicondyle.

**Ilium.** The iliac shaft is extremely long, bears a fine longitudinal striation on its lateral surface and is roughly the same thickness along its length with some waisting in the preacetabular area (Fig. 6B, E). In dorsal or ventral view the iliac shaft is curved medially, the acetabulum is oval and placed near the anterior margin of the acetabular region and there is a distinct posteroventral expansion (= *pars descendens*). MMP.2005.410 represents a pathological ilium with the acetabular area and proximal section of iliac shaft preserved. The bony surface is swollen in the acetabular and preacetabular area suggesting that the ilium was not securely articulated to the femur.

**Ischium.** Available specimens (MMP.2005.402/1, 402/2) come from relatively small individuals and display a very simple morphology. The ischiadic plate is slightly elongated with a convex medial margin; the ischiadic process is orientated posterolaterally and there are two small foramina piercing the ischiadic plate near its base.

**Femur.** In anterolateral or posteromedial view, this bone has a faintly sigmoidal shape. In larger (i.e. older) individuals the epiphyses are completely ossified (Fig. 6C). The



**Figure 6** *Carpathotriton matraensis* gen. et sp. nov. from Mátraszólós 2. **A**, **D**, MMP.2005.398/1, 398/2 humeri; **B**, **E**, MMP.2005.401/1 left ilium; **C**, **F**, MMP.2005.405/1 femur. **A-C**, lateral views, **D-F**, ventral views. Scale bar = 1 mm.

head of the bone is rounded and slightly thickened while the ventral margin is concave and delimits a relatively shallow ventral depression. The trochanter possesses a spur-like process connected to a well-defined *crista trochanterica* running along the anteroventral margin of the femur (Fig. 6C, F). The distal part of the shaft is moderately widened and dorsoventrally flattened with a shallow distal embayment. MMP.2005.411/1–3 represent well-preserved femurs, each with a tuberosity just below the trochanter. Because there is no fracture line present, the femoral shaft was presumably deformed due to pathological proliferation of bony tissue.

**REMARKS.** The frontal in *Carpathotriton* is like those seen in some members of *Lissotriton* (e.g. *L. boscai* and *L. helveticus*) and *Ommatotriton* (*O. ophryticus* and *O. vittatus*) with a complete fronto-squamosal arch, but its posterolateral process is stouter and tends to widen distally (Fig. 3A, B). In other salamandrids the frontal bears a secondary pustular sculpture, as in *Tylototriton* and related genera (e.g. *Chelotriton*, *Echinotriton*: Nobel 1928; Westphal 1978, 1980; Estes 1981; Bailon 1989, 1991; Haller-Probst 1998), or a pit and ridge sculpture as in *Cynops*, *Pachytriton*, *Paramesotriton* and *Salamandrina* (Chan *et al.* 2001; pers. obs.) (Fig. 2E, I). The sculpture is somewhat attenuated in *Pleurodeles*, *Taricha* (Fig. 2A, F) and in members of the *Triturus* group (except *T. marmoratus* which has an extensive dorsal sculpture: Fig. 2D) and, usually, is reduced to the orbital margin in *Calotriton*, *Euproctus*, *Lissotriton*, *Mesotriton*, *Ommatotriton* (Fig. 2B, C, G) and *Carpathotriton* (Fig. 1B, D). The frontal is devoid of sculpture in members of the *Salamandra* group. The dorsal surface of the frontal is flat or slightly concave in the *Tylototriton* group and in *Cynops*, *Pachytriton*, *Paramesotriton* and *Pleurodeles*. In the remaining genera and *Carpathotriton* the dorsal surface of the frontal is more or less convex. In the members of one *Tylototriton* group the sculpture covers the fronto-squamosal arch (e.g. see Roček 2005: text-fig. 2B, C) and the supraorbital crest is extremely prominent. Comparison with *Brachycormus* is equivocal because of conflicting published interpretations. The monotypic *B. noachicus* was seen by Estes (1981) as a member of ‘Group II’ salamanders and included with *Pleurodeles*, *Tylototriton* and related extinct genera (e.g. *Chelotriton* and *Palaeopleurodeles*). In the absence of a holotype Estes (1981) designated specimen SUB 1307 as the neotype of *Brachycormus noachicus* and gave the following diagnosis: ‘skull longer than broad; fronto-squamosal arches well developed; skull roof broad, sculptured with irregular dermal bone that on the squamosals becomes pustular; vertebrae with relatively high neural spines capped with pustular dermal bone...’. Roček (1996a), reviewing the type material from Orsberg, Germany, observed that the neotype designated by Estes (SUB 1307= PIUB Ro 4429), is in fact the holotype figured by Goldfuss (1831: pl. 13, figs 6, 7). The diagnosis given by Roček (1996a: 481) stated: ‘*Brachycormus* is closely related to *Triturus* but differs from it in that (1) it is neotenous, with ossified hyobranchial skeleton, specifically the copula anterior, ceratobranchial 1, ceratohyal and epibranchials, and with external gills apparently present, and (2) the skeleton shows incomplete ontogenetic development, with frontotemporal arch absent...’. Moreover, both authors also referred to BMNH 30268, which represents a complete salamander skeleton in dorsal view (Estes 1981: 79; Roček 1996a: 483). According to the figure of Estes (1981: fig. 20A)

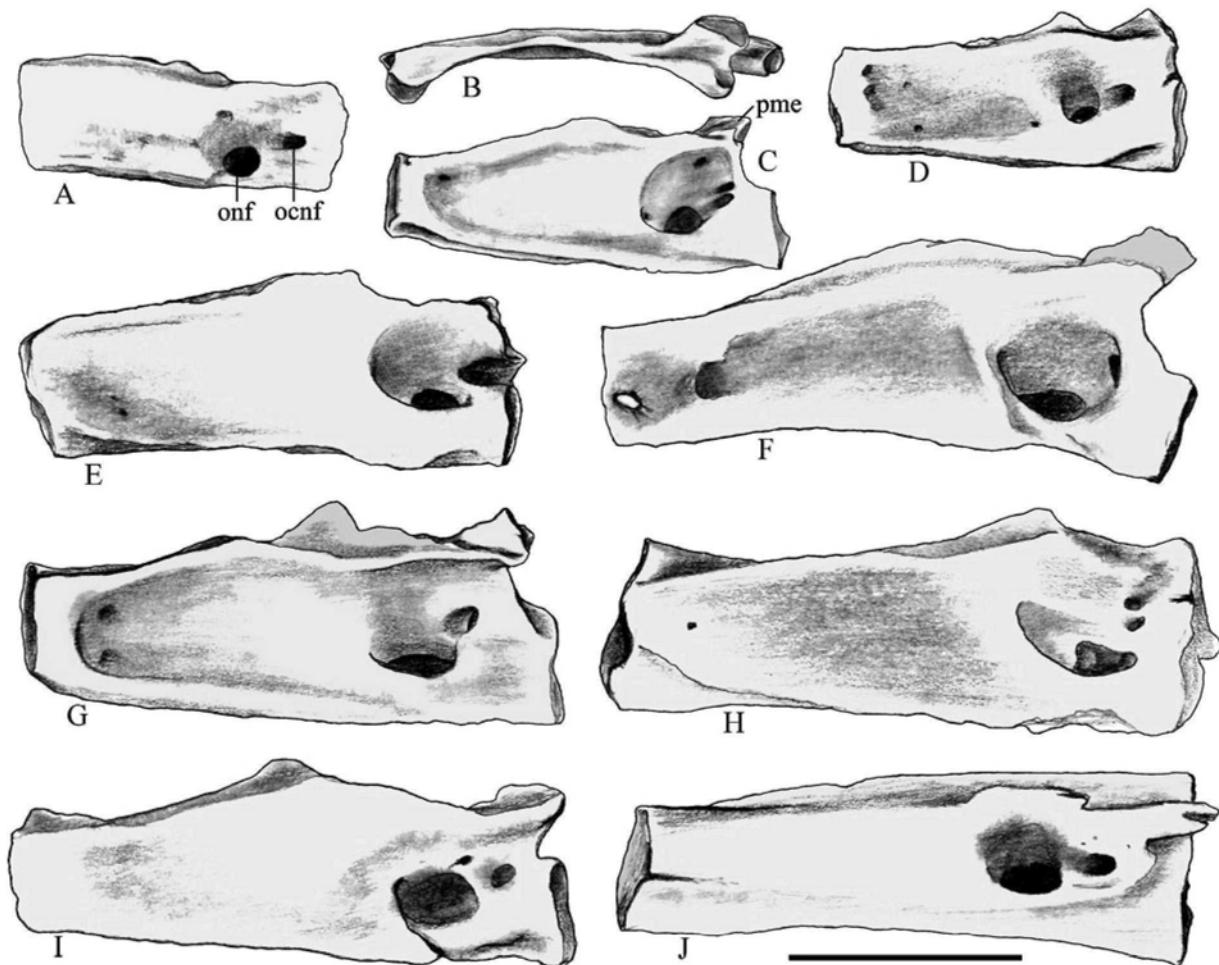
this has a complete fronto-squamosal arch with secondary sculpture on the frontals, parietals and squamosals. From the figure of Roček (1996a: text-fig. 5) the only discernable elements of the head region are the epibranchials. Finally, comparing the orientation of the appendicular skeleton and tail in the above figures, it is clear that Estes and Roček figured part and counterpart of the same specimen and came to different conclusions. In a different article, Roček (1996b: 196) stated that *Brachycormus* is closely related to *Chelotriton* and that both have a fronto-squamosal arch. Thus, it is not clear yet if the material referred to *Brachycormus* by Estes and Roček represent two different genera (one close to the *Tylototriton* group and the other close to *Triturus*) or different ontogenetic stages (including pre- and postmetamorphic individuals) of the same genus.

The fused premaxillae assigned to *Carpathotriton* are unique in having an undeveloped palatine process. The premaxillae are paired in *Archaeotriton*, *Chelotriton*, *Chiloglossa*, *Echinotriton*, *Mertensiella*, *Salamandra*, *Salamandrina*, *Pleurodeles* and *Tylototriton*, but they are fused in the remaining salamandrid genera. In most taxa with fused premaxillae the distal section of the dorsal processes end free with their stem laterally compressed. In contrast, when the dorsal processes are fused distally, as exemplified by *Calotriton*, *Paramesotriton*, some *Lissotriton* and *Triturus*, they are dorsoventrally flattened (Fig. 4F–H). In *Carpathotriton* the dorsal process is reminiscent of newts having distally free and divergent premaxillary dorsal processes, as observed in *Taricha*, *Triturus* and in some species of *Cynops* and *Lissotriton*. However, in *Carpathotriton* the imprint left on the anteromedial side of the frontal by the premaxillary dorsal process suggests that the distal section of the latter was dorsoventrally flattened.

The parietal in *Carpathotriton* has a tapering lateral process, which probably contacted the squamosal over the otoccipital, as in several other salamandrid genera (e.g. *Salamandra*, *Cynops*, *Calotriton*, *Neurergus*, *Paramesotriton*, *Pleurodeles* and members of the *Tylototriton* group: Duellman & Trueb 1986; Haller-Probst & Schleich 1994; Chan *et al.* 2001). In the *Tylototriton* group, the parietal dorsal surface bears a secondary pustular sculpture, while in some oriental genera (e.g. *Paramesotriton*) a pit and ridge sculpture is present.

The orbitosphenoid in *Carpathotriton*, compared to other newts, has a rather simple morphology, with a relatively small optic nerve foramen, a posteriorly situated oculomotor nerve foramen and no posteromedial extension. In all newts, including *Carpathotriton*, the optic nerve foramina are situated within the orbitosphenoid border (Fig. 7). In the members of *Lissotriton*, *Mesotriton*, *Ommatotriton*, *Triturus* and, to a lesser degree, in *Cynops*, *Paramesotriton* and *Taricha*, the posterior section of the orbitosphenoid is produced into a distinct posteromedial extension facing posterodorsally. In the *Salamandra* group the oculomotor nerve foramen is situated close to the posterior border or is sometimes marginal (pers. obs.).

The squamosal in the *Salamandra* group is rather simple with a relatively long ventral ramus, but without well developed anterior and posterior rami. The rami in *Mesotriton* and *Triturus* are only slightly expanded, while in *Lissotriton* the posterior ramus is always longer than the anterior ramus. In *Pleurodeles* there is a long anterior ramus and a relatively reduced posterior one. In *Cynops*, *Paramesotriton*, *Taricha*



**Figure 7** Orbitosphenoids of fossil and Recent salamandrids. **A**, *Carpathotriton matraensis* gen. et sp. nov. (MMP.2005.389/1); **B, C**, *Lissotriton helveticus* (MNCN 19265); **D**, *Cynops pyrrhogaster* (MNCN 23822); **E**, *Taricha granulosa* (MNCN 11830); **F**, *Triturus marmoratus* (MNCN 19275); **G**, *Lissotriton boscai* (MNCN 18187); **H**, *Parameotriton hongkongensis* (MNCN 23557); **I**, *Ommatotriton vittatus* (MNCN 40462); **J**, *Pleurodeles walti* (MNCN 19648). Abbreviations: onf, optic nerve foramen; ocnf, oculomotor nerve foramen; pme, posteromedial extension. **A, C–J**, lateral views; **B**, dorsal view. Scale bar = 2 mm.

and related genera the squamosal is roughly T-shaped (Fig. 8E, G), while in *Calotriton* the ventral ramus is comparatively shorter. The morphology of the squamosal in *Carpathotriton* approaches the condition seen in some members of *Lissotriton* (e.g. *L. helveticus*, *L. boscai*) in which the fronto-squamosal arch is well-developed (Fig. 8D, F).

The quadrate is relatively short in *Calotriton* and *Salamandrina* and moderately long in the remaining genera. Except for *Salamandrina*, the dorsal process on the quadrate is well defined in all genera. The lateral surface of the quadrate in *Carpathotriton* has a well-developed process orientated antero-laterally. A similar structure is present in *Echinotriton* (Nussbaum & Brodie 1982; Rage & Hossini 2000), which may be homologous. In several salamandrid genera there is a spur-like process facing laterally near the proximal end of the quadrate (Haller-Probst 1998; Rage & Hossini 2000; pers. obs.).

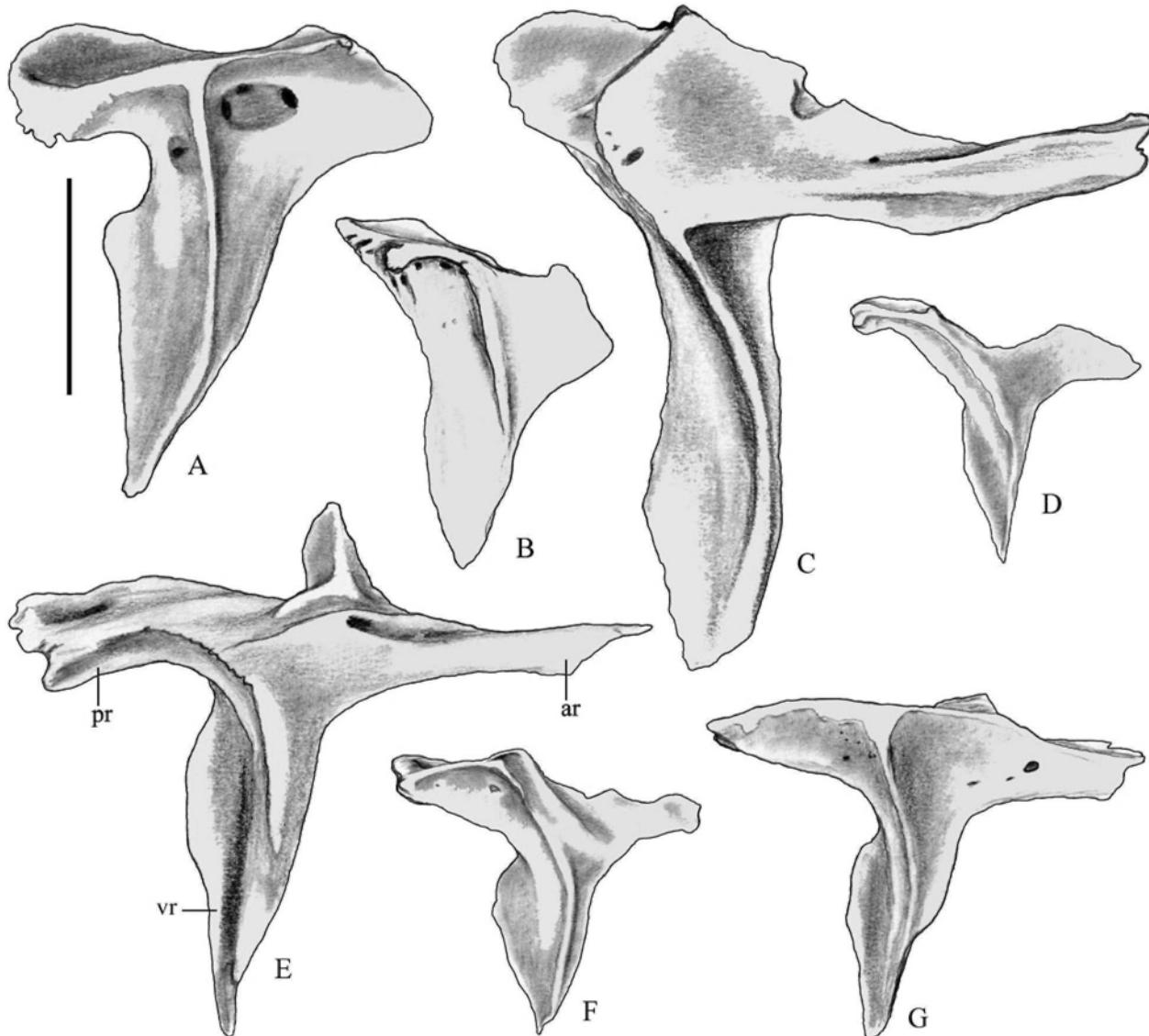
The prearticular+angular is elongated in *Calotriton*, *Pleurodeles* and *Salamandra*, and Meckel's groove is closed in the anterior half of the dentary. In all newts the prearticular+angular is entirely fused with Meckel's cartilage. Conversely, in several macerated skeletons of *Salaman-*

*dra salamandra* the prearticular+angular was not fused with Meckel's cartilage (pers. obs.).

In most salamandrid genera the dentary displays a relatively large subdental shelf, a relatively long tooth row and a relatively short posterior ramus. The tooth row in *Carpathotriton* is strongly curved medially and is approximately two times shorter than the toothless posterior ramus (Fig. 5). Another taxon with similar morphology is *Archaeotriton*. In *Archaeotriton*, based on specimen MMGD-Hw97 (see Böhme 1998: figs 3, 4), the length of the tooth row and the toothless posterior ramus are approximately the same length. Among recent salamandrids the only genus with a relatively long posterior ramus is *Calotriton* (Fig. 9E).

The trunk vertebrae bear a rather low neural spine in *Chioglossa*, *Mertensiella*, *Salamandra*, *Pleurodeles* and *Triturus*. The neural spine is moderately high in the members of *Lissotriton*, *Mesotriton*, *Ommatotriton*, *Calotriton* and *Salamandrina*, but is very high in *Cynops*, *Pachytriton*, *Paramesotriton* and *Archaeotriton* (Fig. 10).

In *Carpathotriton* and *Archaeotriton* the humeral length/distal width and the femoral length/distal width ratios are distinctly higher than in other salamandrids, while



**Figure 8** Squamosals of Recent salamandrids in right lateral view. **A**, *Triturus marmoratus* (MNCN 19275); **B**, *Mesotriton alpestris* (MTC 23450); **C**, *Pleurodeles waltli* (MNCN 19648); **D**, *Lissotriton helveticus* (MNCN 19265); **E**, *Taricha granulosa* (MNCN 11830); **F**, *Lissotriton boscai* (MNCN 18187); **G**, *Cynops pyrrhogaster* (MNCN 23823). Abbreviations: ar, anterior ramus; pr, posterior ramus; vr, ventral ramus. Scale bar = 2 mm.

the relative length of the ilium is similarly higher. In both *Carpathotriton* and *Archaeotriton* these three attributes may relate to their adaptation to an aquatic mode of life.

## PHYLOGENETIC RELATIONSHIPS OF CARPATHOTRITON

*Carpathotriton* falls within newts based on two apomorphies (fused premaxillae provided with long alary processes, well-developed fronto-squamosal arch). To assess the monophyly and relationships of newts, a set of 23 morphological characters was used. These were derived from the published data sets of Wake & Özeti (1969), Titus & Larson (1995) and Wang & Evans (2006). A further 12 morphological characters, depicting attributes of the premaxilla, frontal, parietal, squamosal, quadrate, dentary and angular + articular, were scored for 14 Eurasian salaman-

drid taxa (see Appendix and Table 1). Character scores were based mainly on first hand examination of dissociated salamandrid skeletons or on alcian blue and alizarin red coloured specimens, but some data were obtained from the literature (Duellman & Trueb 1986; Zhao & Hu 1988; Haller-Probst & Schleich 1994; Roček 1996a; Böhme 1998; Haller Probst 1998; Rage & Hossini 2000; Chan *et al.* 2001).

A hypothetical ‘all zero’ ancestor and *Salamandra salamandra*, a member of the ‘true’ salamander’s group, were designated as outgroups, and the most parsimonious trees were found using the branch-and-bound algorithm in PAUP\* (Swofford 2001). Polarity decision for character states is based on outgroup comparison (Bryant 2001). All characters were unordered and equally weighted and both the accelerated transformation (ACCTRAN – favouring reversals over convergences if both interpretations are equally probable) and delayed transformation (DELTRAN – favouring convergences over reversals if both interpretations are

**Table 1** Data matrix of 35 characters for two outgroup taxa (*Salamandra salamandra* and an 'all zero' hypothetical ancestor) and 13 ingroup taxa.

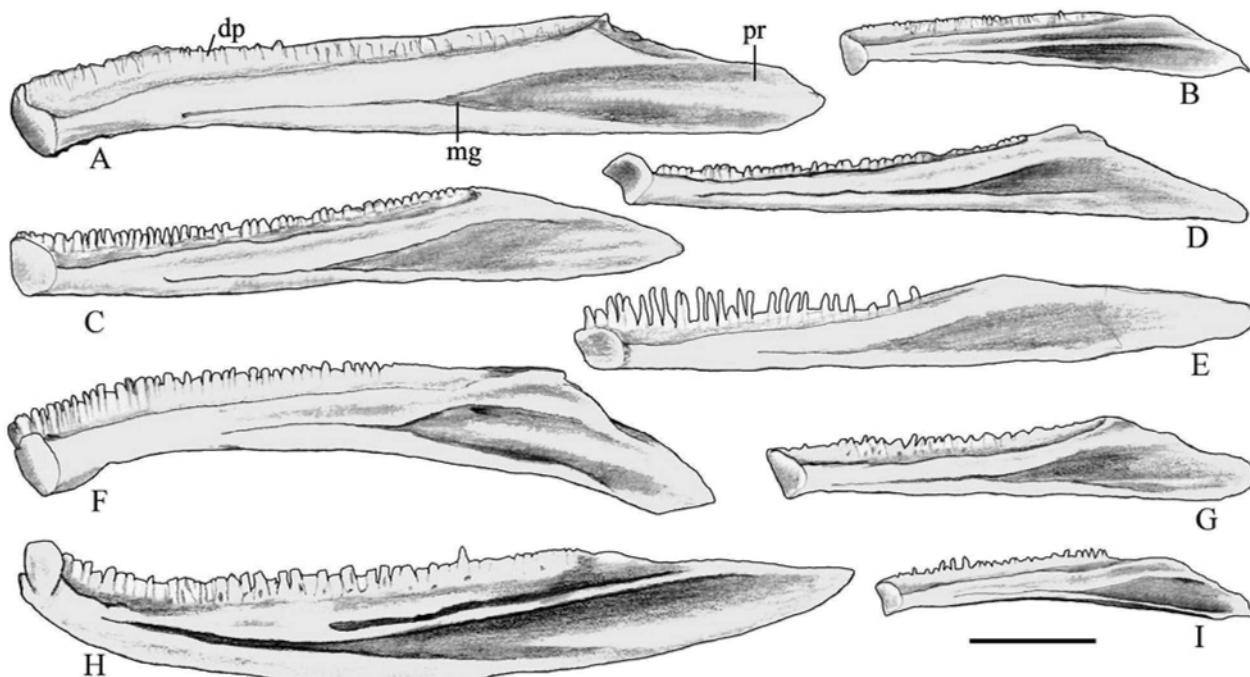
Terminal taxa	Characters								% missing
	0 0 0 0 0	0 0 0 0 1	1 1 1 1 1	1 1 1 1 2	2 2 2 2 2	2 2 2 2 3	3 3 3 3 3		
	1 2 3 4 5	6 7 8 9 0	1 2 3 4 5	6 7 8 9 0	1 2 3 4 5	6 7 8 9 0	1 2 3 4 5		
Hypothetical ancestor	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0
<i>Salamandra salamandra</i>	0 0 1 1 0	0 0 0 0 0	0 0 0 0 0	0 0 0 1 0	0 1 0 0 1	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0
<i>Pleurodeles waltl</i>	0 0 0 0 1	1 0 0 0 0	0 0 1 0 0	1 0 1 0 0	1 0 0 2 0	0 0 1 0 1	1 0 1 0 1	0	
<i>Tylototriton</i>	0 0 0 0 2	1 1 1 0 0	1 0 1 1 0	0 0 1 0 0	1 0 0 1 0	0 0 1 1 1	1 0 1 1 1	0	
<i>Echinotriton</i>	0 0 0 0 2	1 1 1 0 0	1 0 1 1 1	0 0 1 0 0	1 0 0 1 0	0 0 1 1 1	1 0 1 1 1	0	
<i>Salamandrina</i>	0 0 0 0 1	1 0 0 1 1	0 0 1 1 0	0 0 1 1 1	1 0 0 2 1	1 0 0 0 0	0 0 0 0 0	0	
<i>Calotriton asper</i>	1 1 1 1 1	1 0 1 0 1	0 2 1 1 0	1 0 1 1 1	1 1 1 1 0	1 1 1 1 1	1 1 1 2 1	0	
<i>Ommatotriton</i>	1 1 0 1 1	1 0 1 1 1	0 2 1 1 0	1 0 1 1 0	1 0 1 2 0	1 1 1 1 1	1 1 1 2 1	0	
<i>Lissotriton helveticus</i>	1 1 1 1 1	1 0 1 1 1	0 2 0 1 0	1 0 1 1 0	1 0 1 2 0	1 1 1 1 1	1 1 1 2 1	0	
<i>Mesotriton</i>	1 1 1 1 1	0 0 0 1 1	0 2 0 0 0	1 0 1 1 0	1 0 1 2 0	1 1 1 1 1	1 1 1 2 1	0	
<i>Triturus</i>	1 1 1 1 1	0 0 0 1 1	0 2 0 0 0	1 0 1 1 0	1 0 1 2 0	1 1 1 1 1	1 1 1 2 1	0	
<i>Carpathotriton</i> gen. nov.	1 0 1 1 1	1 0 1 0 ?	0 0 1 1 1	1 1 1 ??	?? ? ? ?	?? ? 1 ?	?? ? ? ?	?? ? ? 1	46
<i>Archaeotriton</i>	0 0 0 0 1	1 0 0 1 1	0 ? 1 0 0	? 1 1 ??	?? ? ? ? 1	?? ? ? ?	?? ? ? ?	?? ? ? ?	51
<i>Cynops pyrrhogaster</i>	1 0 0 0 1	1 0 1 0 0	0 1 1 1 0	1 0 1 0 0	1 0 1 2 0	1 1 1 1 1	1 1 1 2 1	0	
<i>Paramesotriton</i>	1 1 1 1 2	1 1 1 0 0	0 1 1 1 0	1 0 1 1 0	1 0 1 2 0	1 1 1 1 1	1 ? 1 2 1	3	

0, 1, 2, represent character states; ?, unknown. The final column lists the percentage of missing records.

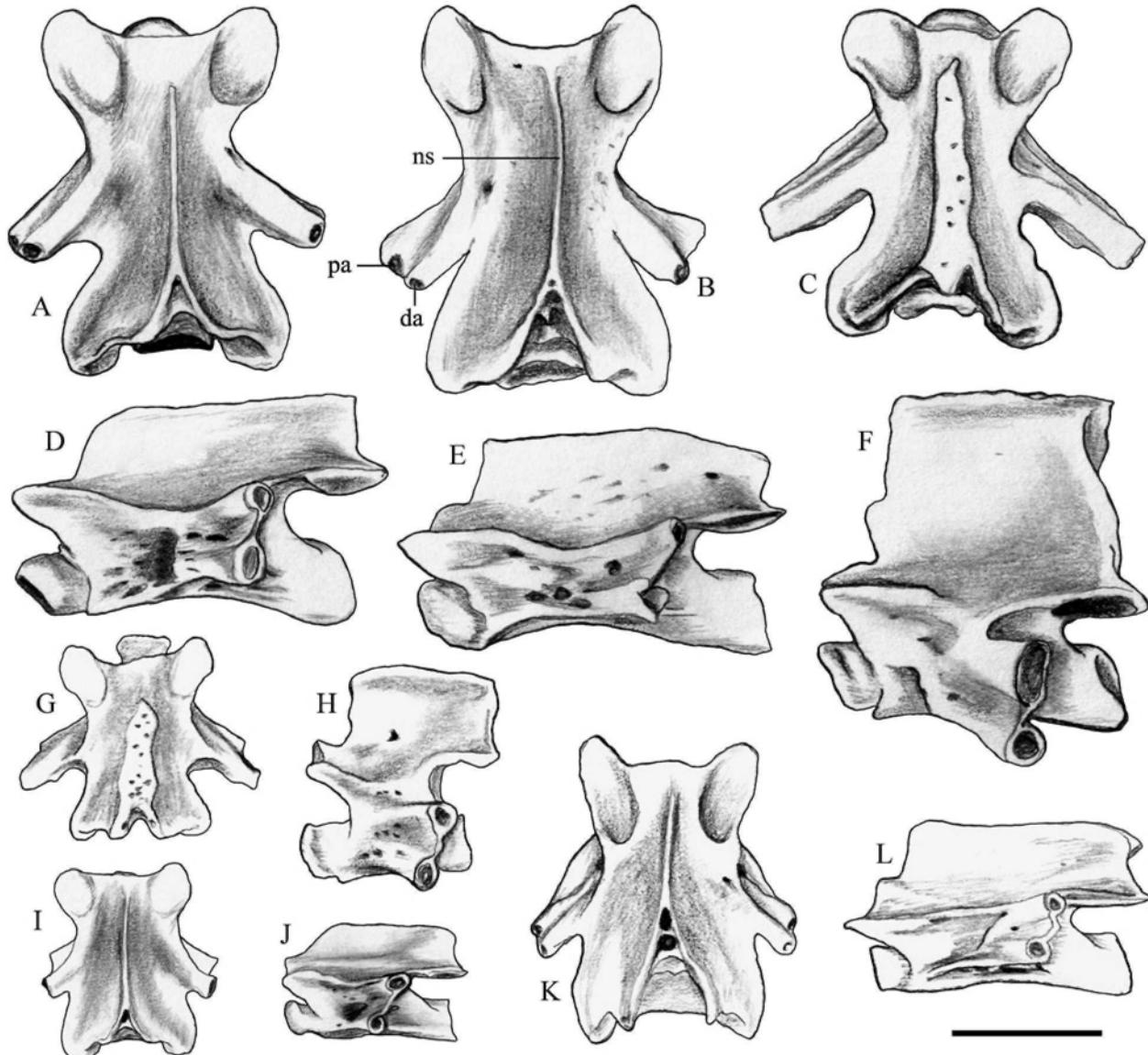
equally probable) optimisations were applied in mapping the distribution of character states on trees. The branch-and-bound search was used also for the bootstrap and decay analyses. Bootstrap values resulted from 2000 replicates, while the decay indices (steps) of Bremer (1994) were obtained by a search for trees successively longer than the shortest tree until all branches collapsed and the consensus of all cladograms appeared as unresolved.

The branch-and-bound search yielded a single shortest tree (tree length = 62 steps, consistency index = 0.63, re-

tention index = 0.81: Fig. 11). The monophyly of newts is well supported (bootstrap = 93%, decay index = 4 steps) by six derived character states [5(1), 6(1), 13(1), 18(1), 21(1), 24(1)] independent of optimisation (Fig. 12). *Carpathotriton* forms an unnamed clade along with *Cynops*, *Paramesotriton*, *Calotriton*, *Ommatotriton*, *Lissotriton*, *Mesotriton* and *Triturus*. This clade is supported by six apomorphies using both the ACCTRAN and the DELTRAN optimisations [1(1), 23(1), 26(1), 27(1), 32(1), 34(2)] and two more characters by either ACCTRAN [12(1)] or DELTRAN optimisation [16(1)]



**Figure 9** Right dentaries of Recent salamandrids in lingual view. **A**, *Parimesotriton hongkongensis* (MNCN 23557); **B**, *Lissotriton helveticus* (MNCN 19265); **C**, *Ommatotriton vittatus* (MNCN 40462); **D**, *Taricha granulosa* (MNCN 11830); **E**, *Calotriton asper* (MNCN 16132); **F**, *Triturus marmoratus* (MNCN 19275); **G**, *Cynops pyrrhogaster* (MNCN 23822); **H**, *Pleurodeles waltl* (MNCN 19648); **I**, *Lissotriton boscai* (MNCN 18187). Abbreviations: dp, dental parapet; mg, Meckelian groove; pr, posterior ramus. Scale bar = 2 mm.

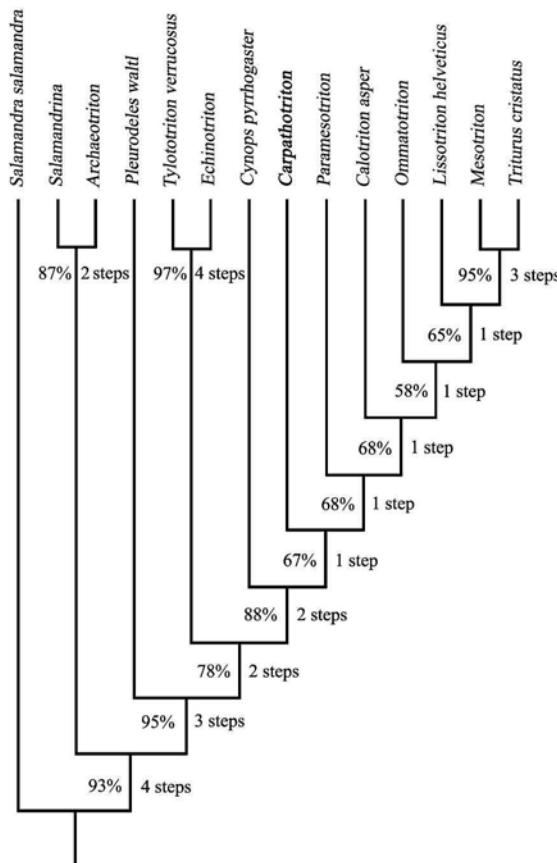


**Figure 10** Trunk vertebrae of Recent salamandrids. **A, D**, *Taricha granulosa* (MNCN 11830); **B, E**, *Triturus marmoratus* (MNCN 19275); **C, F**, *Parimesotriton hongkongensis* (MNCN 23557); **G, H**, *Cynops pyrrhogaster* (MNCN 23822); **I, J**, *Lissotriton helveticus* (MNCN 19265); **K, L**, *Ommatotriton vittatus* (MNCN 40462). Abbreviations: da, diapophysis; pa, parapophysis; ns, neural spine. **A–C, G, I, K**, dorsal views; **D–F, H, J, L**, lateral views. Scale bar = 2 mm.

(Fig. 12). The robustness of this clade is indicated by its relatively high bootstrap value (88%) and decay index (2 steps). The best supported clade within this unnamed clade is that of *Mesotriton* and *Triturus* (bootstrap = 95%, decay index = 3), with *Lissotriton* as a sister taxon. The branches situated stemward to the *Mesotriton*–*Triturus* clade received weak support from bootstrap analysis (58–68%) and collapse if one more step is added to the shortest tree. The strict consensus of trees one step longer redistribute the remaining genera (*Cynops*, *Carpathotriton*, *Parimesotriton*, *Calotriton*, *Ommatotriton*, *Lissotriton*) in an unresolved polytomy. The sister-group of the clade containing the above eight genera is the clade with *Tylototriton* and *Echinotriton*, and then *Pleurodeles*. The clade containing *Archaeotriton* and *Salamandrina* is shifted to the basalmost position. This clade is relatively well supported (bootstrap = 87%, decay index = 2). Since less than

50% of the included characters in *Archaeotriton* could be scored, its position may be problematic.

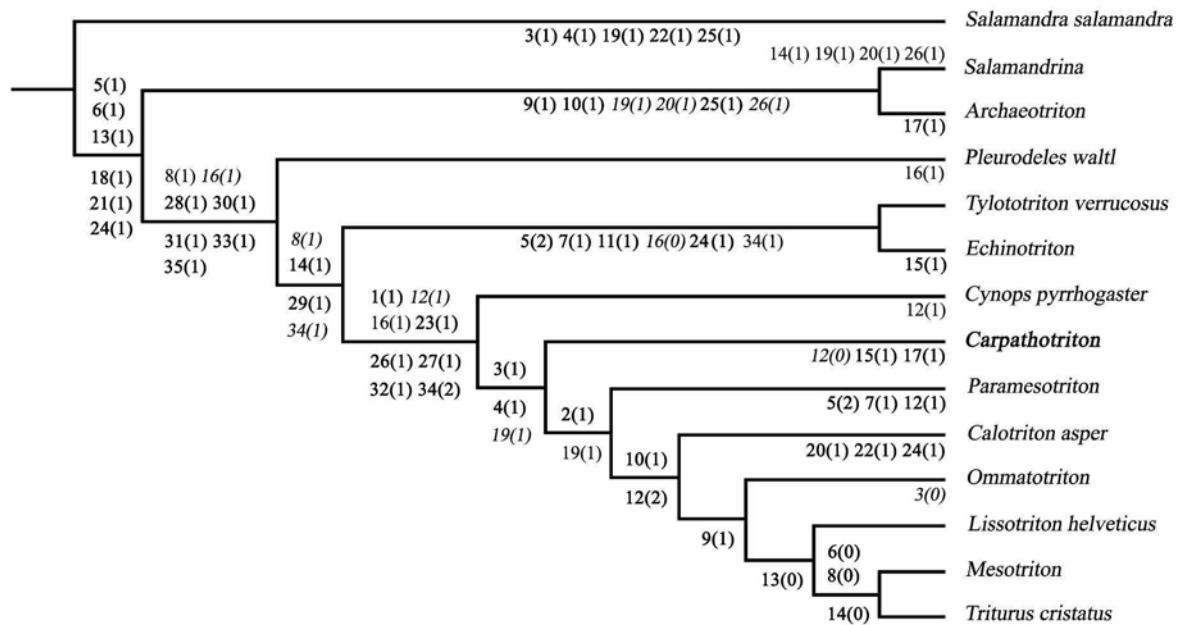
The genera *Ommatotriton*, *Lissotriton*, *Mesotriton* and *Triturus*, partitioned recently from the genus *Triturus* (Montori & Herrero 2004; Litvinchuk *et al.* 2005), are shifted crownward and appear as a monophyletic assemblage. This arrangement differs significantly from those obtained from molecular and morphological data, or from a combination of these (e.g. Titus & Larson 1995; Larson *et al.* 2003; Montori & Herrero 2004; Weisrock *et al.* 2006), in which two or more genera (or species) of the former genus *Triturus* appear as a paraphyletic assemblage or remain unresolved. A more extensive morphological data set (including cranial, axial and appendicular characters) is, therefore, needed to obtain a robust solution.



**Figure 11** Shortest tree based on 35 informative characters scored for 14 salamandrid terminal taxa and a hypothetical 'all zero' ancestor. Indices of support for clades are given to the left of each node (bootstrap value (%)) for 2000 replicates, while the decay index (steps) is given to the right of each node.

## PALAEOENVIRONMENTAL AND PALAEOGEOGRAPHICAL IMPLICATIONS

The fossil assemblages from Mátraszólós 1 and 2 suggest a marshy-lacustrine palaeoenvironment. Of the 38 gastropod taxa identified, 20 are terrestrial while 18 are freshwater; a single species (*Theodoxus pictus*) consisting of small individuals might indicate oligo-miohaline conditions (Hír & Kókay 2004). A freshwater environment is also supported by the abundance of limnic ostracods (e.g. *Heterocypris salina*, *Candona luminosa*, *Ilyocypris* sp.: Szurominé-Korecz & Nagy-Bodor 2002). The anurans from Mátraszólós 1 and 2 include *Latonia gigantea*, *Discoglossus* sp., *Palaeobatrachus hiri*, *Pelobates sanchizi*, *Hyla cf. arborea* and *Rana esculenta* (Venczel 2004). Anuran taxa closely associated with marshy-lacustrine environments (*Palaeobatrachus hiri*, *Rana esculenta*) are significantly more common than those connected with terrestrial habitats. In samples processed from Mátraszólós 1 the frequency of *Palaeobatrachus* varied between 28.4–37.7%, while that of *Rana esculenta* is between 65.1–74.3%. In Mátraszólós 2, the frequency of *Palaeobatrachus* ranges between 8.8–16.3%, while that of *Rana esculenta* ranges between 52.7–55.7%. The frequency of other anurans was much lower: *Latonia* (2.5–9.3%), *Discoglossus* (0–1.8%), *Pelobates* (2.3–6.8%) and *Hyla* (0.8–7%) (pers. obs.). *Lissotriton* (= *Triturus*) sp. has been listed from Mátraszólós 1, while *L. roehrsi* is known from Mátraszólós 2 only (Gál et al. 1999b, 2000). Most of the birds described from both Máraszólós localities (*Bucephala* sp., aff. *Anhinga* sp., *Mergus* sp., *Clangula* sp., *Porzana* aff. *estramosi*, *Rallus* sp., *Proardeola walkeri*, *Mionetta consobrina*) probably preferred marshy-lacustrine habitats (Gál et al. 1999b, 2000). The presence of brackish water conditions is indicated by the fossil flamingo (*Megapaloelodus goliath*), described from Máraszólós 2 (Gál et al. 2000). The insectivore



**Figure 12** Shortest tree with distribution of derived character states mapped using ACCTRAN and DELTRAN optimisations. Characters in italics are supported by ACCTRAN optimisation only; characters in Roman type are supported by DELTRAN optimisation only; characters in bold are supported by both optimisations.

*Desmanella* sp. probably also lived in the surrounding area of freshwater lakes (Gál *et al.* 1999b). Based on the faunal list published by Hír & Kókay (2004) the rodent fauna was rather diverse (*Eurolagus fontannesi*, *Spermophilinus bredis*, *Muscardinus* aff. *sansaniensis*, *Eliomys truci*, *Bransatoglysp.*, *Eomyops oppligeri*, *Keramidomys mohleri*, *Megacricetodon minor*, *Democricetodon mutilus*, *D. cf. freisingensis*, *Cricetodon* sp., *Eumyriarion mediis*, *Anomalomys gaudryi*) but, with the exception of *Megacricetodon minor* they are very infrequent.

The surrounding vegetation of the Mátraszólós localities was reported in a preliminary study by Szurominé-Korecz & Nagy-Bodor (2002). They found a dominance of *Pinus sylvestris* and *Picea* sp. with the presence of subtropical elements (e.g. *Tsuga*, *Zelkova*, *Pterocarya*, *Platycarya*) and few tropical species (Sapotaceae, *Symplocos*) indicating mild temperate conditions, rather than a tropical climate. A marshy-lacustrine habitat is suggested by the abundance of planktonic algae (*Spirogyra scorbiculata*, *Botryococcus braunii*) and the cormophyte *Myrica* (Szurominé-Korecz & Nagy-Bodor 2002).

Sedimentation at Mátraszólós 1 started with an accumulation of fine-grained green clays followed by yellow diatomaceous mud (Gál *et al.* 1999b). At Mátraszólós 2 the green and grayish clays are overlain by a series of lignitic beds (Gál *et al.* 2000). Sediment transportation was presumably of low energy and short distance, enabling the preservation of many small and fragile amphibian bones with no signs of abrasion. Thus the allochthonous assemblage consisted mainly of the remains of local fauna (freshwater molluscs, fishes, newts, palaeobatrachids, green frogs and emydid turtles), and only occasionally contained remains of vertebrates from the surrounding terrestrial environments (Gál *et al.* 1999b, 2000; Venczel 2004). In both Mátraszólós 1 and 2 the abundant remains of *Carpathotriton matraensis*, including individuals representing various ontogenetic stages, indicate that these newts might have had a long aquatic phase similar to palaeobatrachid and green frogs. The relatively long and distally very slightly widened limb bones, in combination with the extremely high neural spine of trunk vertebrae, may also strengthen this view.

Except for the Oligocene *Archaeotriton*, forms resembling *Carpathotriton* have never been reported from the western part of the European continent, suggesting that this genus never extended into the western Parathethys. Phylogenetic analysis shows that *Carpathotriton* is closely related to some Asiatic forms (*Cynops*, *Pachytriton*, *Paramesotriton*). Based on mitochondrial-DNA sequence analysis, the earliest divergence among these Asiatic genera is estimated as early Miocene (about 16 Myr) by Larson *et al.* (2003). A possible palaeobiogeographical scenario may therefore be: (1) the common ancestor of the above genera and *Carpathotriton* might have arisen during the wet tropical conditions of the so-called Miocene Climatic Optimum (Böhme 2003); (2) the geographical range of this ancestral taxon was then fragmented during the early Middle Miocene climatic turnover and gave rise to several distinct lineages, of which *Cynops*, *Pachytriton* and *Paramesotriton* survived to the Recent; (3) the extinct *Carpathotriton* survived in the Central Parathethys area until late Astaracian times (MN 7+8).

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#### Cranial characters

1. Premaxillae: paired (0), fused (1) (Wake & Özeti 1969 [1]; Titus & Larson 1995 [1]; Wang & Evans 2006 [1]).
2. Premaxillary alary processes: free (0), at least 50% of their length fused (1).
3. Premaxillary–frontal contact: absent (0), present (1) (Wang & Evans 2006 [2, modified]).
4. Nasal contact: present (0), absent (1) (Wake & Özeti 1969 [4]; Titus & Larson 1995 [5]; Wang & Evans 2006 [5, modified]).
5. Frontal sculpture: absent (0), weak sculpture present (1), strong sculpture present (2).
6. Fronto-squamosal arch: absent (0), at least partially developed (1) (Wake & Özeti 1969 [2]; Titus & Larson 1995 [2, modified]).
7. Parietal sculpture: absent (0), present (1).
8. Parietal: longer than frontal or equals it in length (0), shorter (1).
9. Parietal squamosal contact: absent (0), present (1) (Wang & Evans 2006 [37]).
10. Maxillary length: reaches or nearly reaches the quadrate (0), extends beyond the eye, or falls short of the posterior margin of the eye (1) (Wake & Özeti 1969 [3]; Titus & Larson 1995 [3, modified]; Wang & Evans 2006 [3, modified]).
11. Maxillary–pterygoid joint: absent (0), present (1) (Wake & Özeti 1969 [40]; Titus & Larson 1995 [4]).
12. Orbitosphenoid postero-dorsal extension: absent (0), postero-dorsal extension small (1), postero-dorsal extension large (2).
13. Squamosal frontal process: absent or reduced to a small process (0), long (1).
14. Squamosal posterior process: absent or reduced to a small process (0), long (1).
15. Quadrate anterolateral process: absent (0), present (1).
16. Parasphenoid posterior ventral crest: absent (0), present (1).
17. Dentary tooth row: long (0), tooth row about half the length of whole dentary or shorter (1).
18. Prearticular + angular: not fused with articular (0), fused (1).
19. Operculum: ossified or mineralised (0), composed of unmineralised cartilage (1) (Wake & Özeti 1969 [5]; Titus & Larson 1995 [6]).

#### General anatomical characters

20. Lung reduction: well developed lungs (0), lungs weakly developed or absent (1) (Wake & Özeti 1969 [8]; Titus & Larson 1995 [8]).
21. Skin texture: smooth (0), rough or keratinised (1) (Wake & Özeti 1969 [9]; Titus & Larson 1995 [9]).
22. Epidermis: presence of an epidermal lining in the anterior half of the female cloacal chamber (0), absence (1) (Titus & Larson 1995 [18]).
23. Pseudopenis: absent (0), present (1) (Titus & Larson 1995 [19]).

#### Hyoid apparatus

24. Second basibranchial: present (0), rudimentary (1), absent (2) (Wake & Özeti 1969 [13]; Titus & Larson 1995 [23]).
25. Epibranchial: present (0), absent (1) (Wake & Özeti 1969 [14]; Titus & Larson 1995 [24]).

## APPENDIX: LIST OF CHARACTERS

The figures in square brackets refer to original numbering in the cited reference.

26. Radii: two pairs of radii present (0), single pair of radii present (1) (Wake & Özeti 1969 [15], Titus & Larson 1995 [26]).
27. Interradial cartilage: absent (0), present (1) (Wake & Özeti 1969 [16]; Titus & Larson 1995 [27, modified]).
28. First ceratobranchial: cartilaginous (0), bony (1) (Wake & Özeti 1969 [18]; Titus & Larson 1995 [29]).

#### *Hyobranchial musculature*

29. Rectus cervicis profundus: inserted via a single head (0), with several insertions (1) (Wake & Özeti 1969 [23]; Titus & Larson 1995 [34]).
30. Hebosteoypsiloideus muscle: more differentiated (0), less differentiated (1) (Wake & Özeti 1969 [25]; Titus & Larson 1995 [36]).
31. Inter-oss-quadrata muscle fibres: fall entirely short of the raphe (0), few fibres extend to the medial raphe or, the muscle is well developed (1) (Wake & Özeti 1969 [26]; Titus & Larson 1995 [37, modified]).

32. The rectus abdominis profundus and the rectus abdominis superficialis: the muscles are differentiated and separate (0), the muscles are not distinct from each other (1) (Wake & Özeti 1969 [30]; Titus & Larson 1995 [40]).
33. The geniohyoideus and genioglossus muscles: they are unconnected (0), or attached by dense connective tissue at the anterior ends of the ceratohyals (1) (Wake & Özeti 1969 [32]; Titus & Larson 1995 [42, modified]).
34. Rectus cervicis profundus: insertion of slips of the rectus cervicis profundus may be absent from the first basibranchial and radii (0), present on the posterior part of the first basibranchial (1), or present on both the first basibranchial and radii (2) (Wake & Özeti 1969 [34]; Titus & Larson 1995 [44]).

#### *Axial skeleton*

35. Atlantal centrum roughly of same length as postatlantal centra (0), much shorter than postatlantal centra (1) (Wang & Evans 2006 [62, modified]).