

evolution. Moreover, similarities between the dentition of the basal therizinosaur *Falcarius* and the basal oviraptorosaur *Incisivosaurus*, in combination with their proposed sister relationship (Fig. 3), raises the possibility that the common ancestor of these clades had already undertaken the initial steps in this transition.

The Early Jurassic Chinese jaw from the Lufeng Series in southern China described tentatively as the basal therizinosaurid *Eshanosaurus*²⁷ is more derived in having a lateral shelf and down-turned symphysis, which are absent in *Falcarius*. Its therizinosaurid identification have been considered problematic by some authors^{13,25}. *Falcarius* casts further doubt on the affinities of *Eshanosaurus* by increasing its stratigraphic and phylogenetic inconsistency. Given the discovery of North American members of the therizinosaurid clade, together with the poor record of Middle Cretaceous dinosaurs, it seems that the generally accepted hypothesis of an Asian origin and radiation for Therizinosauridae^{1,2} requires additional testing. □

Methods

Collections from the Crystal Geyser Quarry made so far preserve a minimum of ten individuals based on prepared femora, but the quarry size indicates that perhaps hundreds of disarticulated individuals remain interred, representing multiple growth stages as well as robust and gracile morphotypes. The locality spans about 8,000 m² and the bone-bearing stratum is, on average, 1 m thick, with bone densities in some areas exceeding 100 elements per cubic metre. There is no evidence of another small theropod taxon, so all of the therizinosaurid materials are here referred to *Falcarius*. In addition to the therizinosaurid elements, the quarry contains rare remains of an unidentified ankylosaur. About 99% of all identified bones from the type locality (about 2,000 identifiable bones) represent *Falcarius*.

Several features of these fossils, including neurocentral fusion and fusion of cervical ribs to the vertebrae, indicate that the largest elements represent adult or near-adult individuals. Dorsal ribs and gastralia are the most poorly represented with only two dorsal ribs and one gastralia identified, although many bone fragments in the quarry are thought to be unidentifiable pieces of rib. There are multiple examples of nearly all bones, although much excavation and preparation remains before a detailed taphonomic analysis can be attempted. Overlapping examples of the largest elements are close to the same size, indicating that mature animals had restricted growth. Additionally, associated elements (particularly appendicular elements) indicate the relative proportions of skeletal elements in some individuals. The skeletal reconstruction of *Falcarius* in Fig. 1 was based on the largest preserved elements in the quarry, with vertebral numbers estimated on changing proportions of the vertebrae and comparisons with other maniraptoran theropods.

Phylogenetic relationships were analysed with the use of data from published sources supplemented with novel information (see Supplementary Information). Parsimony analysis of 57 taxa and 231 characters was performed with PAUP 4.0b10 (ref. 28), with all characters weighted equally and a single character ordered, using *Allosaurus* and *Sinraptor* as outgroups (Fig. 3).

Five unambiguous synapomorphies support Therizinosauridae: teeth serrated (reversal); ventral surface of dentary descends strongly posteriorly; ventral edge of anterior ala of ilium hooked anteriorly; distal humerus with large medial condyle, centred on distal end; and preacetabular portion of ilium laterally flaring. The basal position of *Falcarius* is supported by the absence of the following characters: labial face of dentary with lateral ridge and inset tooth row; interdental plates on dentary; obturator process of ischium does not contact pubis; metatarsal I without proximal articulating surface. Therizinosauridae + Oviraptorosauria characterized by basiptyergoid processes abbreviated or absent; suborbital fenestra reduced in size or absent; basiptyergoid processes hollow; symphyseal region of dentary strongly recurved; maxillary and dentary teeth lanceolate and subsymmetrical.

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Discovery of the first Asian plethodontid salamander

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Nearly 70% of the 535 species of salamanders in the world are members of a single family, the Plethodontidae, or lungless salamanders¹. The centre of diversity for this clade is North and Middle America, where the vast majority (99%) of species are found. We report the discovery of the first Asian plethodontid

letters to nature

salamander, from montane woodlands in southwestern Korea. The new species superficially resembles members of North American genera, in particular the morphologically conservative genus *Plethodon*. However, phylogenetic analysis of the nuclear encoded gene *Rag-1* shows the new taxon to be widely divergent from *Plethodon*. The new salamander differs osteologically from putative relatives, especially with respect to the tongue (attached protrusible) and the derived tarsus^{2–6}. We place the species in a new genus on the basis of the morphological and molecular data. The distribution of the new salamander adds to the enigma of Old World plethodontids, which are otherwise restricted to the western Mediterranean region^{7,8}, suggesting a more extensive past distribution of the family.

Amphibia L., 1758

Urodela Duméril, 1806

Plethodontidae Gray, 1850

Karsenia koreana gen. et sp. nov.

Etymology. The genus name honours the discoverer, Stephen J. Karsen. The species name refers to the Korean peninsula. The suggested vernacular name is Korean crevice salamander (Korean: Ikkee dorongyong).

Holotype. EWNHM (Ewha Women's University Natural History Museum) 80314, an adult male from the vicinity of Jangtae-san, Daejeon-si, Chungcheongnam-do, Korea (36° 13' N, 127° 20' W), elevation 210 m, in a rocky, forested habitat, collected 12 April 2003 by Karsen.

Paratypes. MVZ (Museum of Vertebrate Zoology) 246033, 247157, Daedun-san, Keoncheon-ri, Nami-myeon, Kumsan-gun, Chungcheongnam-do, Korea (36° 7.4' N, 127° 19.3' E); MVZ 247156 (Fig. 1), Daea-ri, Dongsang-myeon, Wanju-gun, Cheollabuk-do, Korea (35° 59' N, 127° 16.4' E); MCZ (Museum of Comparative Zoology)-A-136691, MVZ 247154–247155, MMS (Laboratory of Mi-Sook Min) 27–29, 32–44 Yeomchi, Yeomchi-ri, Munui-myeon, Cheongwon-gun, Chungcheongbuk-do, Korea (35° 32' N, 127° 32' E); SIUC (Southern Illinois University Collections) H7890–7897, MMS 1–3, 9–20, same locality data as holotype.

Diagnosis of genus and species. A plethodontid salamander on the basis of its lunglessness, absence of a pterygoid bone in adults, large patches of paravomerine teeth, and nasolabial groove. Differs from phenotypically similar *Plethodon* in ankle morphology: distal tarsal 5 (d5) is relatively large and articulates with the centrale, while d4 is relatively small and is separated from the fibulare by d5 (Fig. 2). This arrangement is known only in the plethodontids *Aneides* and

Chiropterotriton^{2,3,6}. *Karsenia* differs from both in having paired premaxillaries rather than a single bone, from *Aneides* in having small hands and feet with short, pointed digits rather than long, terminally expanded digits, and from *Chiropterotriton* in having a tongue that is attached to the front of the mouth and epibranchials that are shorter than the ceratobranchials (rather than being much longer).

This is a relatively small, moderately robust species. Adult males are 38.5–47.7 mm snout-to-vent length (svl) (mean \pm s.d. 41.8 mm \pm 3.6 mm, $n = 8$) and adult females, 38.5–47.7 mm svl (mean \pm s.d. 41.8 \pm 3.7 mm, $n = 12$). A well-defined, relatively broad head (0.13–0.17 \times svl (mean 0.15) in males, 0.13–0.16 \times svl (mean 0.14) in females), is delimited from the body by a marked gular fold. The nasolabial groove is shallow, terminating in a small swelling on the lip. Snouts are more rounded in females than in males, and nostrils are separated by approximately 2.5 mm in both. There are 14–15 costal grooves (mean 14.3 in males, 14.7 in females). Limbs and digits are relatively short, and digits are slightly webbed (Fig. 2). The combined limb length is 0.51–0.55 (mean 0.54) \times axilla–groin length in males, 0.52–0.58 (mean 0.54) in females, and appressed limbs leave three to four intercostal folds uncovered. The tail is round basally but laterally compressed more distally in some individuals, tapering to a sharp tip; the tail is partly regenerated in many specimens, but complete tails are about equal in length to the svl (longest tail 1.1 \times svl). Small eyes (horizontal opening 2.6–2.7 mm) are moderately protuberant and separated by 3.3–4 mm. The rounded tongue, attached anteriorly by genio-



Figure 1 Paratype of *Karsenia koreana* (MVZ 247156) in life.

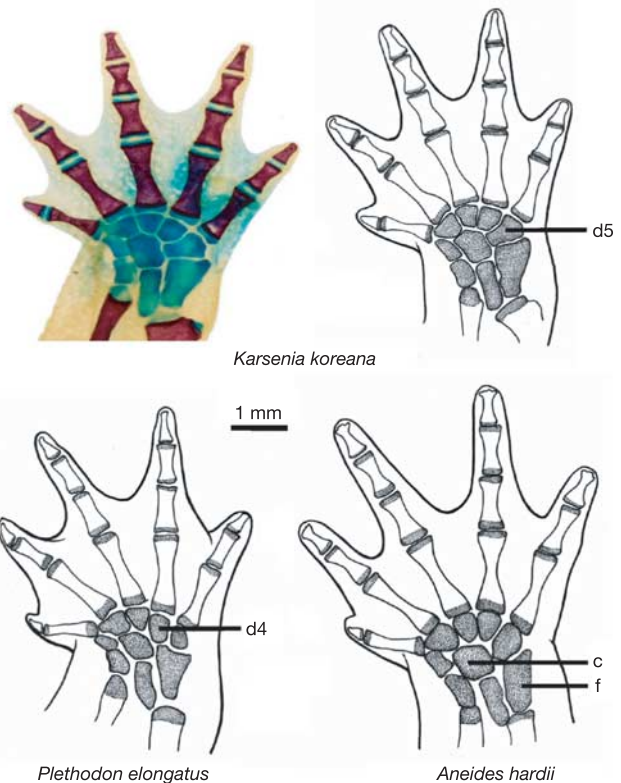


Figure 2 Right foot of three species of plethodontid salamanders. Top, paratype of *Karsenia koreana* (SIUC H7894), stained (alcian blue for cartilage; alizarin red for bone) and cleared in trypsin and glycerine (left) and drawn (right). Bottom, *Plethodon elongatus* and *Aneides hardii*. The arrangement of distal tarsals 4 (d4) and 5 (d5), and the fibulare (f) is diagnostic. c, centrale. Cartilage is stippled; bone and contour of limb are outlined. The pattern observed in *Karsenia* was absent in large samples of *Plethodon* (40 *P. elongatus*, 96 *P. glutinosus*, 98 *P. hoffmani*) and most *Desmognathus* (one asymmetrical variant in *D. monticola*, but absent in 77 others, in 42 *D. quadramaculatus* and 136 *D. ochrophaeus*).

glossal muscles, lacks posterior flaps. When manipulated in an anaesthetized individual, the tongue formed a well-defined, highly protrusible pad. All teeth are small, undifferentiated and weakly bicuspid. Premaxillary teeth number 4–7 (mean 6.4) in males, 6–10 (mean 7.9) in females; maxillary teeth 43–50 (mean 45.6) in males, 40–56 (mean 49.3) in females; vomerine teeth 13–21 (mean 15.5) in males, 12–20 (mean 17.8) in females.

The species is darkly pigmented with a broad dorsal stripe that varies from being prominent and bright, to being heavily invaded by melanic pigment that obscures the stripe on the head and trunk. The stripe arises as a triangular patch on the snout and extends along the dorsum nearly to the tip of the tail. In life, the stripe is reddish to yellowish brown, tan, or dark brown with some reddish highlights. The stripe is always clearest and brightest in the tail base and anterior tail regions. A canthus rostralis is accentuated by the contrasting colours of the snout. Lateral surfaces are uniformly dark with an obscure overlay of small, whitish speckles. Abundant silvery dots and flecks (about 1 mm in diameter maximum) are concentrated on the dark ventrolateral surfaces and are largest and most numerous where the flanks meet the ventrum. Ventral surfaces are pale, especially in the gular area, and are marked with moderately large, whitish flecks except along the midline.

A single cleared and stained specimen (SIUC H7894) and radiographs of it and seven more (SIUC H7890–7897) reveal that the skull is fully articulated with a small, anteriorly placed intermaxillary foramen and no dorsal fontanelle. Premaxillaries are

paired and relatively stout, with short, expanded frontal processes that do not articulate with each other behind the short foramen. The septomaxillaries are unusually large, articulating on one side with the relatively large prefrontal that lies between but mainly posterior to the nasals and maxillaries. The otic capsule bears small, projection-like lateral crests but no dorsal crests. The operculum has a well-developed, rod-like stylus. The vomers are well formed and bear small, truncated, preorbital processes. Teeth are in short series between the internal nares, usually not on the process. Large, paired patches of paravomerine teeth, well separated from the vomerine teeth, are borne on the ventral surface of the parasphenoid.

Vertebrae include one cervical, 16 ($n = 7$) or 17 ($n = 1$) trunk, one sacral, three caudosacral and a variable number of caudals (maximum 42). Biconcave centra of the trunk vertebrae are relatively stout and posteriorly directed parapophyses are relatively long and slender. The centrum length is shorter than the distance from the tip of one parapophysis to the other. Long bicapitate ribs are about the same length as the centrum and are present on all or all but the last trunk vertebrae.

Limbs are relatively short; a proximal spur is present but partly attached to the shaft of the tibia. Digits in order of decreasing length are 3–2–4–1 and 3–4–2–5–1. Phalangeal formulas are 1–2–3–2 and 1–2–3–3–2. The tarsus and carpus are unmineralized cartilage and cannot be visualized in radiographs. The arrangement of the tarsus in the cleared specimen was confirmed in a dissected specimen (Fig. 2). Tips of terminal phalanges are bluntly rounded, but those of the longest digits can be slightly knobbed.

The tongue skeleton is largely cartilaginous and closely resembles that in *Plethodon*, *Aneides* and *Desmognathus*^{4,5}. The first ceratobranchial is the longest element (1.2 × basibranchial length), whereas the epibranchial is slightly shorter than the basibranchial. The basibranchial, which is mostly ossified, has a pronounced anterior projection in front of the very elongate and slender cornua (which are about 0.6 × basibranchial length). A small, bowed urohyal is ossified (about 0.35 × basibranchial length).

Teeth are moderate in number. In the cleared and stained individual there are four teeth on each premaxilla, 20 and 21 on the two maxillae, 27 on each mandible, five on each vomer, and 70 and 77 in the two well-separated paravomerine patches.

In external morphology *Karsenia* most closely resembles species of *Plethodon* from western North America, but is smaller (closest in size to *P. larselli*, which reaches 57 mm svl⁹). It is shorter-bodied, less robust and has less prominent jaw muscles than members of the *P. elongatus* group from northwestern California and southwestern Oregon, but its hands and feet are nearly identical in shape, length of digits and degree of webbing (Fig. 2). *Karsenia* resembles western *Plethodon* in most features of osteology, including paired premaxillae and general pattern of the skull roof, tongue skeleton and vertebral dimensions. However, its tarsus and vomer resemble those of *Aneides*, from which it differs in critical features of osteology and in having much shorter toes with little or no terminal expansion. Its jaw muscles are much less swollen than in *Aneides*.

Analysis of the nuclear encoded gene *Rag-1* from an array of taxa representing all salamander families shows that *Karsenia* is a plethodontid (Fig. 3). Within a monophyletic Plethodontidae *Karsenia* is nested in a well-supported clade that includes the desmognathine salamanders and *Aneides*. *Hydromantes* and *Ensatina* also have strong affinities to this clade. The sister taxon of all of the above is *Plethodon*, which is monophyletic in agreement with recent molecular studies^{10,11}. There is no support for *Karsenia* as a member of *Plethodon*. *Rag-1* is an evolutionarily conserved gene, and the minimal divergence (4.6% to *Phaeognathus*) is relatively high, greater than that between several other plethodontid genera¹⁰.

The new species occurs in damp, mossy talus slopes and rock-slides of limestone in forests of hardwoods and mixed hardwood/pine (*Pinus densiflora* and *Quercus mongolica* dominate). Forests range from 15 to 50 years in age. Most individuals were found under

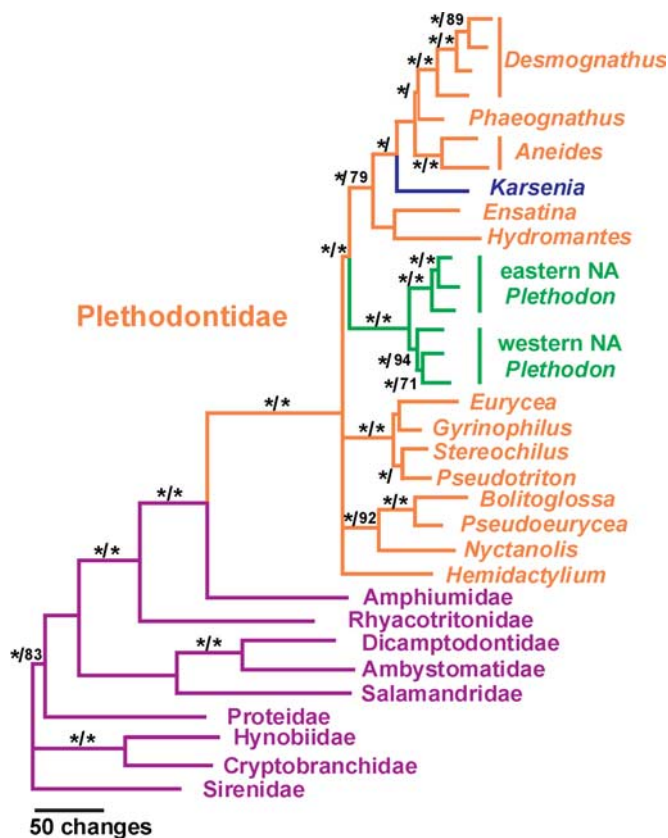


Figure 3 Bayesian phylogram based on 1,503 base pairs of *Rag-1*, showing strong support for the placement of *Karsenia* relative to other salamanders. Bayesian branch lengths demonstrate the relative distinctiveness of *Karsenia* among other plethodontids. Support for nodes is estimated from bayesian posterior probabilities and maximum-likelihood bootstrap values (separated by slash). Values $\geq 95\%$ indicated by star symbol; maximum-likelihood bootstrap values between 70% and 95% are given. The genus *Plethodon* is highlighted in green, *Karsenia* in blue, and remaining plethodontids in orange. For details of molecular and phylogenetic analyses see Supplementary Information.

small rocks or rock flakes scattered among larger boulders on fine-grained soil.

The discovery of *Karsenia* has important biogeographical implications. Plethodontidae is now seen to have a Holarctic distribution, although it is impressively disjunct. The nearest plethodontids are found along the central coast of British Columbia, Canada (*P. vehiculum*, *Ensatina eschscholtzii*). To the west, no plethodontids are known until central Italy. Disjunctions between Asia and North America are recorded for many taxa, and for plants of eastern Asia and eastern North America. About 65 flowering plant genera¹² display such disjunctions, typically with Asian species in a given clade being more numerous¹³, a strong contrast with plethodontids, which are represented by many species in eastern North America. Phylogenetic relationships of the plants and estimated divergence times suggest multiple historical events at different periods in geological time, with disjunctions typically dating from the Miocene or earlier^{12–14}. Disjunct taxa usually are not cladistically close¹⁴. These conclusions apply to *Karsenia* as well. The species has no close relatives in North America, and the amount of genetic divergence suggests a long period of independent evolution, possibly pre-Tertiary^{8,10}. Plethodontids are known to be very old, with fossils of *Plethodon* and *Aneides* known from the Arikarean (Oligocene) of Montana^{15,16}.

Mammalian fossils indicate strong physical and phylogenetic connections between east Asia and North America at least until the Late Miocene¹⁷, and polar sea temperatures are estimated to have averaged about 15 °C 70 million years ago and more than 20 °C at 90 million years ago¹⁸. Such temperatures would have been favourable for plethodontid salamanders. Accordingly, there have been many opportunities for early migrations between the continents. An important implication of current distributions is that Old World plethodontids have had lower rates of speciation than those in the New World, but also may have been disproportionately subject to extinction. The discovery of plethodontids in Asia encourages further efforts to find more of these secretive animals. □

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An extant cichlid fish radiation emerged in an extinct Pleistocene lake

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The haplochromine cichlid fish of the East African Great Lakes represent some of the fastest and most species-rich adaptive radiations known¹, but rivers in most of Africa accommodate only a few morphologically similar species of haplochromine cichlid fish. This has been explained by the wealth of ecological opportunity in large lakes compared with rivers. It is therefore surprising that the rivers of southern Africa harbour many, ecologically diverse haplochromines. Here we present genetic, morphological and biogeographical evidence suggesting that these riverine cichlids are products of a recent adaptive radiation in a large lake that dried up in the Holocene. Haplochromine species richness peaks steeply in an area for which geological data reveal the historical existence of Lake palaeo-Makgadikgadi^{2,3}. The centre of this extinct lake is now a saltpan north of the Kalahari Desert, but it once hosted a rapidly evolving fish species radiation, comparable in morphological diversity to that in the extant African Great Lakes. Importantly, this lake seeded all major river systems of southern Africa with ecologically diverse cichlids. This discovery reveals how local evolutionary processes operating during a short window of ecological opportunity can have a major and lasting effect on biodiversity on a continental scale.

Lake Victoria (LV) and Lake Malawi (LM) are known for their extremely diverse flocks of haplochromine cichlid fish and have received much attention as model systems for explosive speciation and ecomorphological diversification^{1,4}. Together comprising more than 800 species, geological and mitochondrial (mt)DNA evidence suggests that these flocks evolved in a very short time period (Lake Victoria, 15,000–250,000 years^{5,6}; Lake Malawi, up to 5 million years⁷) from one or a few common ancestors^{8,9}. In contrast, the