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A LONG-BODIED LIZARD FROM THE LOWER CRETACEOUS OF JAPAN

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Abstract: Platynotan lizards underwent a dramatic Late Cretaceous radiation into marine habitats. Beginning with small-bodied forms, the lineage culminated with the mosasaurs, large predatory lizards with a world-wide distribution in the Santonian–Campanian. Moreover, the marine squamate radiations of the Cenomanian–Turonian are remarkable in having produced a range of long-bodied, reduced-limbed swimmers (dolichosaurs, adriosaurs, coniasaurs and limbed snakes) that seem to have thrived in the shallow coastal environments of the Western Tethys region. Until now, none of these long-bodied aquatic squamates has been recorded prior to the Cenomanian, none has been recovered from a non-marine locality and none is known from Asia. Here we describe a small, gracile, long-bodied mosasauroid lizard from a swampy continental deposit in the Lower Cretaceous of Japan.

Key words: Cretaceous, Tetori Group, Japan, Squamata, Mosasauroidea, lizard.

PLATYNOTAN squamates (*sensu* Pregill *et al.* 1986) form a conspicuous and important group with a wide past and present distribution (including the living *Varanus*). The earliest putative stem-platynotan is *Parviraptor* (Evans 1994, 1998), from the Middle Jurassic of Britain, the Upper Jurassic of Portugal (Broschinski 2000) and the USA (Evans 1996), and the Lower Cretaceous of England (Evans 1994). The first recorded crown-group platynotan is the helodermatid *Primaderma* (Nydam 2000) from the Albian–Cenomanian of North America. In the Cretaceous, one or more platynotan lineages underwent a dramatic marine radiation. As currently recorded, this radiation began in the Cenomanian with a series of relatively small-bodied lizards, loosely referred to as dolichosaurs, from the North American Seaway (*Coniasaurus*; Caldwell and Cooper 1999), southern Britain (*Coniasaurus*, *Dolichosaurus*; Caldwell 1999*a*, 2000*a*), Croatia and Slovenia (*Adriosaurus*, *Aigialosaurus*, *Mesoleptos*, *Pontosaurus*, e.g. Cornalia and Chiozza 1852; von Meyer 1860; Kramberger 1892; Kornhuber 1893, 1901; Nopsca 1908, 1923; Calligaris 1988, 1993; Caldwell *et al.* 1995; Lee and Caldwell 2000; Pierce and Caldwell 2004); Lebanon (*Aphanizocnemus*; Del Sasso and Pinna 1997; Dal Sasso and Renesto 1999; *Pontosaurus*; Caldwell and Dal Sasso 2004) and Palestine (*Haasiasaurus*; Polcyn, Tchernov and Jacobs 1999). They shared these shallow coastal waters with a diversity of limbed marine snakes (e.g. Haas 1979, 1980*a*, *b*; Rage 1984, 1988; Cuny *et al.* 1990; Rage and Escuillié 2000, 2002), although whether these represent part of the same radiation or a completely separate one remains highly contentious (e.g. Caldwell and Lee 1997; Lee 1997, 1998; Lee and Caldwell 1998, 2000; Zaher 1998; Caldwell 1999*b*, 2000*a*, *b*, 2002; Caldwell and Cooper 1999; Lee *et al.* 1999a, *b*, Zaher and Rieppel 1999, 2000, 2002; Coates and Ruta 2000; Greene and Cundall 2000; Rieppel and Zaher 2000*a*, *b*; Tchernov *et al.* 2000; Caldwell and Albino 2001; Rieppel and Kearney 2001; Lee and Scanlon 2002). One platynotan lineage, the mosasauroids (*sensu* Bell 1997), subsequently gave rise to the large predatory mosasaurs, which made their first appearance in the Coniacian but had spread world-wide by the Santonian–Campanian. To date, the pre-Cenomanian history of mosasauroids has remained unrecorded.

The Lower Cretaceous (Berriasian–Hauterivian) rocks of the Tetori Group in north-central Honshu, Japan (Text-fig. 1), have yielded rich and varied assemblages of aquatic and terrestrial taxa including fish (Yabumoto 2000), amphibians (Evans and Manabe 1998; Matsuoka 2000*a*), synapsids (mammals and tritylodonts) (Rougier *et al.* 1999; Setoguchi *et al.* 1999*a*, *b*; Manabe *et al.* 2000;

Matsuoka 2000*b*; Takada *et al.* 2001), dinosaurs (Azuma and Tomida 1995; Hasegawa *et al.* 1995; Manabe 1999; Manabe and Barrett 2000; Manabe *et al.* 2000; Azuma and Kobayashi 2003), pterosaurs (Unwin *et al.* 1996, 1997; Unwin and Matsuoka 2000), turtles (Hirayama 1996, 1999, 2000), choristoderes (Evans and Manabe 1999*a*; Matsumoto *et al.* 2002) and a diversity of Early Cretaceous squamates (Evans *et al.* 1998; Evans and Manabe 1999*b*, 2000, work in progress). The squamate assemblage includes representatives of a new genus that shows similarities to the long-bodied, limb-reduced dolichosaurs of the early Late Cretaceous.

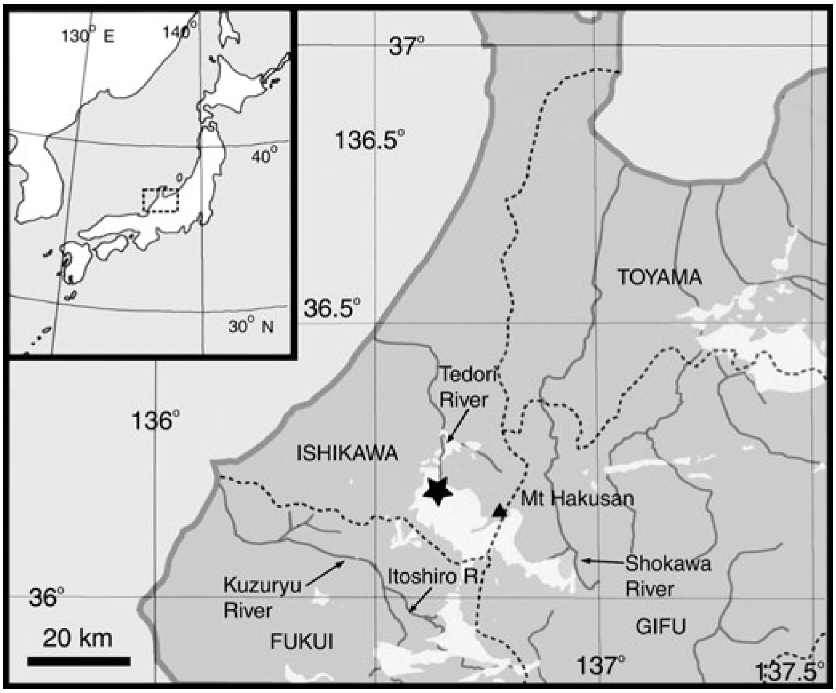
GEOLOGY AND MATERIAL

Rocks of the Tetori Group of central Honshu, Japan, span an interval from the Middle Jurassic to the Early Cretaceous (Maeda 1961; Matsukawa and Obata 1994; Kusuhashi *et al.* 2002; Fujita 2003; Isaji *et al.* 2005). They are represented by the Kuzuryu, Itoshiro and Akaiwa subgroups in ascending stratigraphic order (Maeda 1961). All the fossil material described in this paper came from the upper part of the Kuwajima Formation, Itoshiro Subgroup, at a single locality, the Kaseki-kabe or 'fossil-bluff', in the village of Shiramine (now Kuwajima District, Hakusan City), Ishikawa Prefecture, western Honshu, Japan (Text-fig. 1). These deposits have been variously dated as early 'Neocomian' (Kusuhashi *et al.* 2002), Kimmeridgian–Hauterivian (Matsukawa and Obata 1994), Valanginian (Isaji *et al.* 2005) and Late Hauterivian (Fujita 2003). The last age estimate (*c.* 132 Ma, Gradstein and Ogg 2004) is based on the finding of a Hauterivian ammonite in a marine horizon (Kamihambara Formation) in the central part of the Itoshiro Subgroup at another locality. This is in agreement with a zircon fission-track date of 135 ± 7 Ma for the laterally equivalent (Maeda 1961) Okuradani Formation at Shokawa, Gifu Prefecture (Gifu-ken Dinosaur Research Committee 1992). A Berriasian–Hauterivian age for the Kuwajima Formation is also supported by a Middle–Late Jurassic (Callovian–Oxfordian) age for the underlying Kuzuryu Subgroup (based on ammonites) and a Barremian (or Late Hauterivian) to Aptian age for the overlying Akaiwa Subgroup (based on non-marine molluscs, pollen and spore assemblages, and zircon fission-track dates; Matsukawa and Obata 1994; Fujita 2003; Isaji *et al.* 2005).

In the Kaseki-Kabe, the Kuwajima Formation is represented by alternating beds of fine-grained sandstones, mudstones and thick, coarse-grained sandstones. The coarse-grained sandstones contain pebbles, muddy gravels and driftwood and are interpreted as channel deposits (Isaji *et al.* 2005). Plant and animal remains are found in the fine sandstones and mudstones (interpreted as inter-channel deposits), and include *in situ* tree trunks (0·5–3 m in height, 0·1–1 m in diameter; Isaji *et al.* 2005), rootlets and occasional coals indicative of a well-vegetated inland floodplain. Three dominant facies can be recognized among the bone-bearing rocks (Isaji *et al.* 2005). The deposits of facies 1 consist of massive coarse-grained carbonaceous sandstones. The fossil assemblage is dominated by compressed and fragmented plant remains and poorly preserved molluscs, and is thought to represent a peat marsh environment containing sediments reworked from other levels. Facies 2 is represented by fine-grained, dark grey silty sandstones containing unionid bivalves (often in life position; Isaji *et al.* 2005), freshwater gastropods, ostracods and charophytes, and is interpreted as a shallow lake deposit. Together facies 1 and 2 yield a predominantly freshwater aquatic vertebrate fauna including fish, turtles and choristoderes. These taxa are also found in facies 3 (dark greenish grey mudstones), but are rarer and terrestrial components (tritylodonts, mammals, lizards, dinosaurs) predominate. Facies 3 also contains concentrations of eggshell and occasional compressed eggs (Isaji *et al.* 2005). Although many of the vertebrate remains are disarticulated, this facies has produced a number of articulated specimens, suggesting quiet conditions. Molluscs and plant remains are rare, but there are numerous *in situ* rootlets (200 mm or more in length; Isaji *et al.* 2005). Facies 3 is interpreted as representing a vegetated subaerial swamp environment, subject to short periods of flooding (Isaji *et al.* 2005).

Specimens of the long-bodied lizard described here come from both facies 2 and facies 3. The articulated holotype specimen was recovered from deposits of facies 3, and has rootlets passing through it at right angles to the plane of the skeleton. This feature, together with the relatively undisturbed state of the skeleton, suggests the lizard was not transported far prior to burial. However, most of the attributed specimens were also derived from facies 3. This material is largely disarticulated, but several associations are known.

The fossiliferous deposits were extracted mechanically in bulk (*c.* 16,700 m^3) during the construction of a road tunnel through the fossil cliff in 1997. With the co-operation of the mayor's office and the Board of Education of Shiramine Village, the excavated material was collected and stored. Although much of the material was processed for plant remains, a sample of 210 m^3 of facies 1, 2 and 3 was set aside for detailed examination. To date, a little over one-third of this has been prospected and the work is ongoing. Since the matrix is acid-resistant, each block is broken into manageable pieces, the exposed surfaces are examined, and then any traces of bone are prepared. This time-consuming work (mostly under the direction of Ichio Yamaguchi and Mikiko Yamaguchi) has yielded more than 1000 catalogued vertebrate



TEXT-FIG. 1. Map showing the distribution of Tetori Group deposits (white) in the region of Mount Hakusan, north-central Honshu, Japan, and the location (black star) of the Kaseki-Kabe, type locality of *Kaganaias hakusanensis* gen. et sp. nov., Kuwajima Formation, Lower Cretaceous (Berriasian–Hauterivian). The inset shows the position of the main map in relation to the rest of Japan (redrawn from Maeda 1961).

specimens, including many associations. Unavoidably, some parts of associated specimens have been lost, as with the skull and anterior vertebral series of the long-bodied lizard described here.

To provide supplementary information on vertebral morphology and pelvic structure, the part and counterpart of the type specimen (SBEI 1568) and both the type (BMNH R49002) and a second specimen (BMNH R32268) of *Dolichosaurus* were imaged by the High Resolution X-ray Computed Tomography (HRCT) Facility at the University of Texas (Austin), Geological Sciences, and then digitally reconstructed.

Institutional abbreviations. BMNH, Natural History Museum, London; GBA, Austrian Geological Survey, Vienna, Austria; SBEI, Shiramine Board of Education, Shiramine village, Ishikawa Prefecture, Japan (the collection retains this name although it is now under the auspices of the Hakusan City Council).

Abbreviations used in the figures. a.rb, ribs from vertebrae anterior to the preserved section; CaV1–4, caudal vertebrae; CeV, cervical vertebrae; co, condyle; cot, cotyle; d.hd, dorsal head of quadrate; d.pr, dorsal process on rib; D.V, dorsal vertebra; fe, femur; f.pr, facial process of maxilla; ha1–3, haemal arches 1–3; H, humerus; HL, hindlimb; hy, hypapophysis; il, ilium; is, ischium; l.fe, left femur; l.il, left ilium; l.pk, lateral pocket in vertebra; md.lm, medial lamina of quadrate; n.sp, neural spine; ph, phalanges; pu, pubis; pyg, pygal vertebra (first caudal without haemapophysis); q.co, quadrate conch; rb, rib; rb.ft, rib facet; r.il, right ilium; Sa1, first sacral vertebra; Sa2, second sacral vertebra; sk, skull; ssp, suprastapedial process; syn, synapophysis; un, ungual phalanx; V.ft, facet for attachment to vertebra; v.pr, ventral process on rib; zy, zygosphene-zygantral system.

SYSTEMATIC PALAEONTOLOGY

SQUAMATA Oppel, 1811
ANGUIMORPHA Fürbringer, 1900
PLATYNOTA Duméril and Bibron, 1836

KAGANAIAS gen. nov.

Derivation of name. From Kaga, an old name for Ishikawa Prefecture, Japan, and *naias* (Latin), a water nymph.

Type specimen. SBEI 1568 (Shiramine Board of Education), part and counterpart of an articulated partial skeleton comprising parts of the dorsal vertebral series, and parts of the tail, pelvis and hind limbs. Housed in the collections of the Shiramine Board of Education, Kuwajima District, Hakusan City, Japan (formerly Shiramine Village).

Material. SBEI 195, partial left and right dentaries; SBEI 196–197, 199, 258, 260–261, 567, 834, 836–838, 845, 1266, 1532, 1793–1796, 1800, 2007, 2012, blocks bearing cervical, dorsal or caudal vertebrae and ribs; SBEI 1799, association of vertebrae, ribs, a partial right maxilla and a left quadrate.

Diagnosis. As for type and only known species.

Occurrence. From the ‘Kaseki-Kabe’, or fossil cliff, at Kuwajima, Hakusan City, Ishikawa Prefecture, Honshu, Japan, 36° 12′ N, 136° 38′ E (Text-fig. 1). The material comes from the Neocomian Kuwajima Formation, Itoshiro Subgroup, Tetori Group.

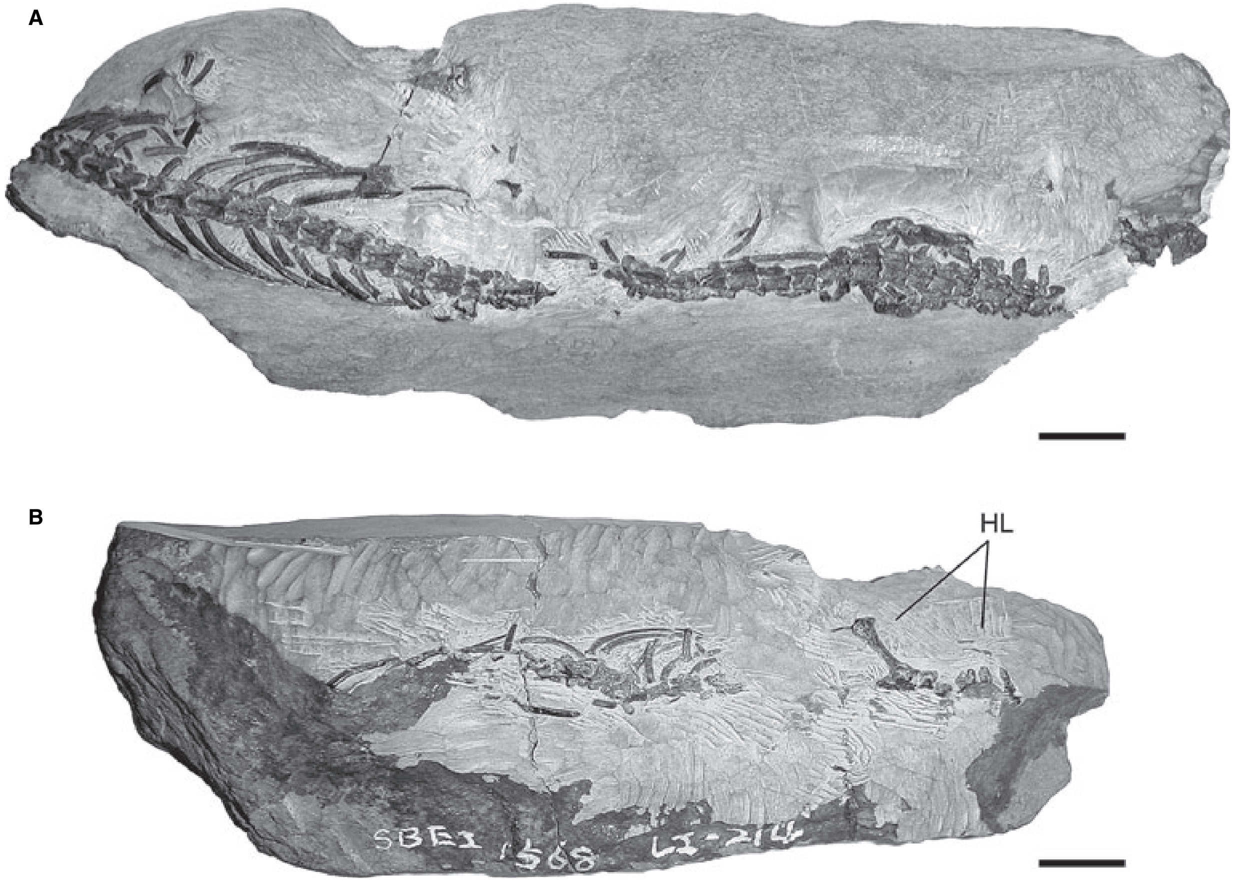
Kaganaias hakusanensis sp. nov.

Plates 1–2; Text-figures 2–8, 12

Derivation of name. From Hakusan, the mountain that gives its name to the region and to Hakusan City.

Diagnosis. A small (*c.* 300 mm snout–pelvis length) gracile lizard with a bilaterally compressed body; an elongated trunk with at least 36–46 dorsal vertebrae bearing deep lateral recesses, low roughened neural spines and well-developed zygosphene-zygantral articulations in which the zygosphene faces ventrolaterally; thickened ribs with dorsal and ventral tubercles; a sacrum in which the second sacral rib is broader than the first; a single pygal vertebra, haemal arches that are fused to pedicles on the caudal vertebrae; a long slender ilium; and hindlimbs that were small in relation to trunk length, with a straight robust femur.

Remarks. Resembles mosasauroids in having well-developed zygosphene-zygantral articulations (with the zygosphene facing ventrolaterally rather than dorsolaterally) on trunk vertebrae (weakest in *Adriosaurus*, *Aphanizocnemus*) and in the general reduction of the limbs; differs from mosasaurs and aigialosaurs, but resembles *Adriosaurus*, *Aphanizocnemus*, *Coniasaurus*, *Dolichosaurus* and *Pontosaurus* in having an elongated dorsal series; resembles *Aphanizocnemus* and *Dolichosaurus*, and differs from *Pontosaurus* in having a deep, laterally compressed body in which the ribs are weakly curved; resembles *Dolichosaurus* but differs from *Adriosaurus* in having a sacral series in which the first sacral rib is narrow and the second conspicuously broader (first sacral wider in *Adriosaurus*), anterior caudal ribs that are dorsoventrally flattened and blade-like (narrower based but more rounded in *Adriosaurus*), prominent synapophyses on the vertebrae and a single pygal vertebra (uncertain in *Adriosaurus*); differs from *Adriosaurus*, *Coniasaurus* and *Dolichosaurus*, and resembles *Aphanizocnemus* in having almost no elevation of the neural spines in the trunk, but differs from *Aphanizocnemus* in also lacking spines in the tail; resembles *Dolichosaurus*, but differs from *Adriosaurus*, *Aphanizocnemus* and *Pontosaurus* in having an excess of 36 dorsal vertebrae (36–46 vs. 27 for *Aphanizocnemus*, 29 for *Adriosaurus*, 29–30 in *Pontosaurus* and an estimated 38 for *Dolichosaurus*); resembles *Adriosaurus* and *Aphanizocn-*



TEXT-FIG. 2. *Kaganaias hakusanensis* gen. et sp. nov. Type specimen, SBEI 1568. A, part. B, counterpart showing the small hind limb (HL). Scale bars represent 10 mm.

emus, and differs from *Dolichosaurus* in having less angled ribs, narrower, less waisted vertebral neural arches, a single short-ribbed 'lumbar' vertebra and proportionally much shorter sacral ribs; differs from *Adriosaurus*, *Coniasaurus* and *Dolichosaurus* in the fusion of the first (and presumably subsequent) haemal arch to the ventral pedicels (no fusion of haemal arches in the tail of *Aphanizocnemus*). The first haemal arch (caudal 2) of *Kaganaias* is also low, more like a cervical hypapophysis, and the second and third are deep. The unique combination of characters supports generic distinction for the Japanese lizard.

MORPHOLOGY

The description is based primarily on the holotype, SBEI 1568, supplemented by other specimens as relevant. The type specimen is in two parts: a main block and a counterpart block containing part of the axial skeleton and one limb (Text-figs 2–3; Pl. 1). On the main block (Text-fig. 2A), the specimen has an overall length of 194 mm, but this probably represents only the central third of the body (see below). The skeleton is fully articulated and is preserved in three dimensions. The main block was prepared from the dorsal aspect, so that the exposed parts include the dorsal vertebrae and ribs, parts of the left and right pelvis, a right femur, a single phalanx and the base of the tail. There is no trace of a pectoral girdle or forelimb and, if present, this must have been placed anterior to the front end of the block. The counterpart (Text-fig. 2B) bears a few ribs, the three and a half vertebrae missing from the dorsal region of the main block (two preserved in ventral view, three and one-half neural arches) and a near complete left femur. The crus, tarsus and metatarsus are missing, but the block bears traces of the pedal phalanges and one claw. HRCT scans provide further details of the pelvis (pubis and ischium) and of the ventral and lateral aspects of the ribs and vertebrae.

Vertebral column

A total of 30 dorsal vertebrae are preserved, but the anterior end of the block bears the remains of six additional ribs that clearly belonged to more anterior dorsal vertebrae (Text-fig. 4A–B), giving a minimum dorsal count of 36. Even if the animal had a reduced pectoral girdle and forelimb (and it may equally have been of normal size), then 5–10 additional dorsals would need to be added as there is no trace of the forelimb on the block. This fits with observations made on *Adriosaurus* (BMNH R2867), *Dolichosaurus* (BMNH R49002, R32268) and *Pontosaurus* (cast of Vienna specimen, GBA 1873/4/2 in Museo di Storia Naturale, Milan; Pierce and Caldwell 2004). The overall length and proportions of the ribs in the anterior part of the preserved skeleton of *Kaganaias* match those of dorsals 9–10 in *Dolichosaurus*. This is the region just behind the level of the pectoral girdle and forelimb. In *Adriosaurus*, a lizard of similar size to *Kaganaias*, the skeleton consists of three principal parts: the head, neck and pectoral region (which are curved); the main dorsal region, which is held rigid by the long, thick, overlapping ribs; and the tail, again curved. By our interpretation, the preserved section of *Kaganaias*, which is also held straight, would correspond to the central part of *Adriosaurus*. Putting these observations together, *Kaganaias* had at least 36 dorsal vertebrae (36–46). With the squamate average of seven or eight cervical vertebrae, the total presacral count would probably have approached 50; if the neck were elongated, the count would be higher. This falls within the range of modern limb-reduced lizards that move with a serpentine mode of locomotion (e.g. *Anguis*, *Ophisaurus*, many scincids; Gans 1962, 1975; Hoffstetter and Gasc 1969; Wiens and Slinghuff 2001; Caldwell 2002). However, the deep body profile suggests that the animal was at least partially aquatic and moved primarily by lateral body undulation, with the limbs used mainly for steering and stabilization.

The neurocentral sutures are closed and the vertebral arches are well developed with low rugose neural crests. This suggests that the animal was skeletally fairly mature despite its small size (less than half that of the largest known *Dolichosaurus* specimen). However, the collection also contains vertebrae matching those of SBEI 1568, but about twice the size (e.g. SBEI 1799), suggesting either further growth during life or sexual dimorphism in body size.

Cervical vertebrae. No cervicals are preserved in SBEI 1568, but SBE1 1799 contains at least one partial cervical vertebra with a midventral ridge (Text-fig. 5A).

Dorsal vertebrae and ribs. On SBEI 1568, the dorsal vertebrae are generally similar to one another, but become slightly shorter towards the sacrum. The vertebral arch is characterized by a low neural spine that tapers to a point anteriorly where it meets, or nearly meets, the back of the preceding vertebra (Text-figs 3–5, 6A; Pls 1–2). The spines have little elevation and they become wider and more rugose towards the rear of the column. In the HRCT scans, the more anterior dorsal spines appear notched anteriorly (Text-fig. 4C), but this is because the anterior part of the spine is thin; more posteriorly, they develop narrow rugose spine tables that probably contacted the overlying skin (Pl. 1, fig. 1). The anterior zygapophyses are quite large and horizontal; behind them, the arch swells into a prominent synapophysis, posterior to which there is a slight waisting (least in the posterior dorsal and sacral vertebrae). Overall, however, the arch is rather narrow and of nearly constant width. The anteromedial part of the arch is raised and contributed to the formation of a well-developed zygosphene-zygantral system of accessory articulations between the neural arches. This system varies in its morphology amongst lepidosaurs (Hoffstetter and Gasc 1969), with the zygapophyseal-zygosphenic angle ranging from obtuse (with the anterior zygosphene facing dorsolaterally) to acute (with the zygosphene facing ventrolaterally, as in *Kaganaias*), and with full separation of the zygapophyseal and zygosphenic surfaces in snakes and some large lizards (Hoffstetter and Gasc 1969). Seen in lateral view (Text-figs 4C, 5B, 6A), the pedicel is marked by a strong anteroposterior crest between the zygapophyses, a large anterior synapophysis and a conspicuous posterolateral pocket. This lateral pocket is bounded dorsally by a prominent interzygapophysial ridge (margo lateralis; Hoffstetter and Gasc 1969) and ventrally by the edge of the depressed centrum (margo ventralis; Hoffstetter and Gasc 1969). In the HRCT scans, it looks as though the arch pedicel is sometimes perforated in the deepest, anterior part of the recess, but this is probably an artefact (thin bone may not be resolved). Comparison with extant lizards (e.g. the serpentiform scincid *Feylinia*; Gasc 1981) suggests these crests and deep lateral recesses may have accommodated expanded intercostal musculature.

The centra on the main block are mostly obscured, but where they have been prepared from the underside, they are seen to be dorsoventrally depressed with a deep procoelous intervertebral articulation. The posterior dorsal centra are also visible on the second, smaller, block. The articular surface of the condyle is mostly dorsal and that of the cotyle is mostly ventral; thus the articulation is strongly oblique. Centrum morphology is seen most clearly in the HRCT images (Text-fig. 4A; Pls 1–2). They show that the condyles are not waisted at their boundary with the centrum and that the ventral margins of the centrum are subparallel, tapering slightly towards the rear, with the condyle forming the apex. The centra broaden slightly towards the sacral region. Subcentral foramina are not obvious in the exposed vertebrae close to the sacrum, but are visible in more anterior dorsals (HRCT images), lying in grooves that begin on either side of the cotyle and converge towards the centre.

SBEI 1799 includes an association of disarticulated vertebrae that match those of the holotype block in having well-developed zygosphene-zygantral articulations, a deep lateral recess behind the rib facet and a dorsoventrally compressed centrum with an oblique condylar surface. However, the neural spines are taller, suggesting a more anterior position in the column (perhaps associated with the pectoral girdle) and the elements are about twice the size of the vertebrae on the holotype, indicating that *Kaganaias* could grow to a larger size. The zygosphene system is preserved very clearly in these elements (Text-fig. 5D).

The ribs are robust and thick-walled with a reduced central cavity suggesting at least incipient pachyostosis. Isolated ribs on the SBEI 1799 block may come from the anterior part of the dorsal series. The proximal ends are unicapitate but they bear a distinct ventral flange that creates a triangular process below the rib head, and a smaller dorsal tubercle (Text-fig. 5E–H). These rib features are more pronounced in the anterior part of the holotype skeleton. The longest rib preserved (in the anterior part of the specimen) is between five and six vertebral lengths. These ribs extend ventrally with only a weak medial curvature (Text-fig. 3; Pl. 1), giving the animal a narrow, deep cross-sectional profile. More posterior ribs associated with the holotype replace the ventral flange with a smaller tubercle (Text-fig. 6B). The last eight ribs anterior to the sacrum are more slender than those preceding them, with the last two presacrals bearing short ‘lumbar’ ribs, although they are not fused to the centrum.

Sacral vertebrae. There are two sacral vertebrae (Pl. 2). The first has a narrow, backwardly directed rib with a circular cross-section; the second is about twice that width. The second sacral rib is broken on the left but complete on the right. It is expanded distally and applied against the medial side of the iliac blade. Both sacrals have short, wide, neural arches and low rugose spines that notch into one another. The spine tables on these vertebrae are wider than those on the dorsal vertebrae, forming distinct, anteriorly tapering triangles (Pl. 2, fig. 1). The centrum of the first sacral is hidden by the pelvis, but that of the second is visible (HRCT, Pl. 2, fig. 2) as a broad, flattened body with a small posterior condyle.

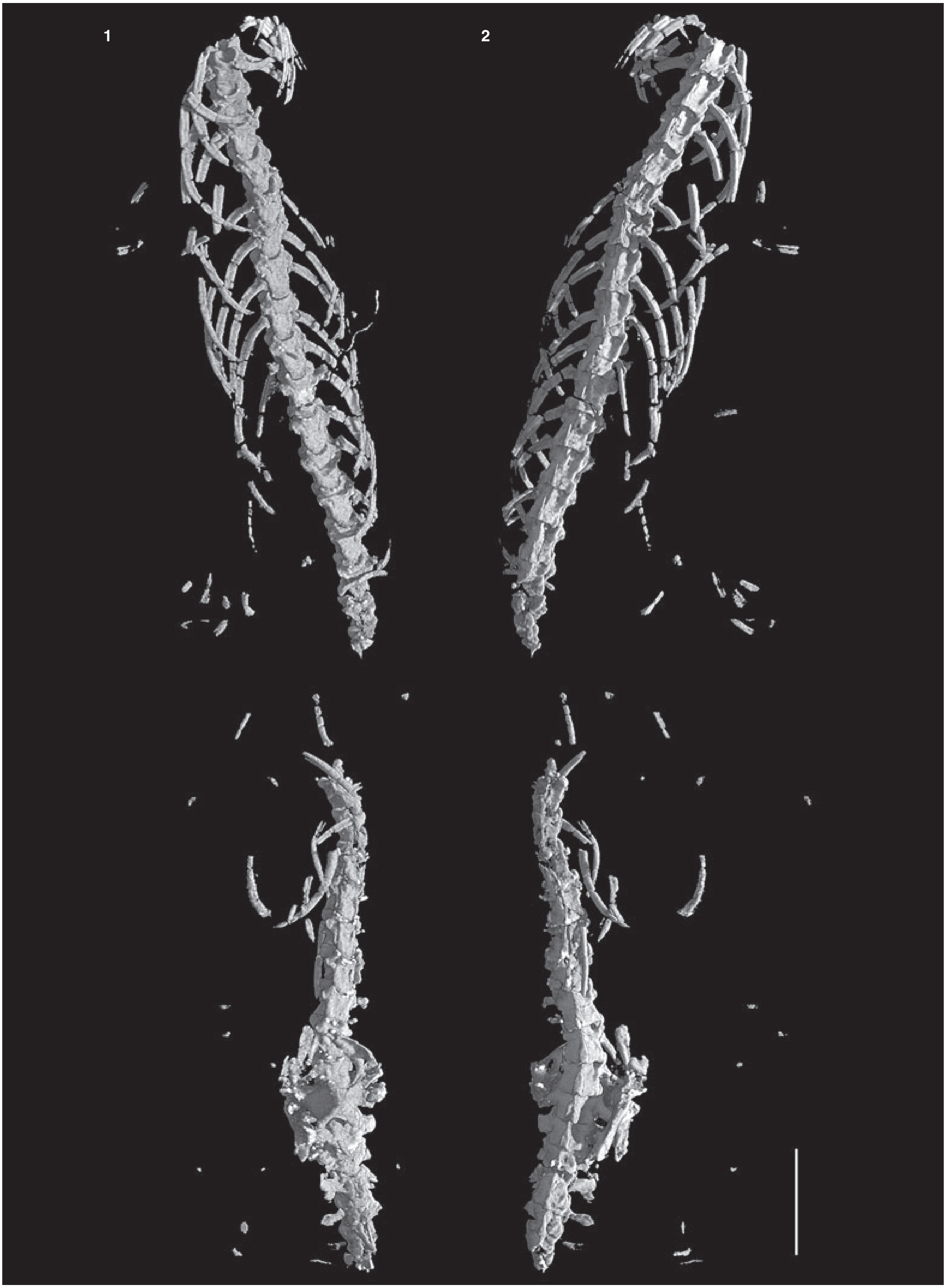
Caudal vertebrae. Four caudal vertebrae are preserved in articulation after the sacrum, and two more are displaced further back. The vertebrae are shorter than those of the dorsal series, but retain the low, anteriorly tapering neural spines. The zygasphene-zygantral articulation is still present, but is less developed than in the trunk. These vertebrae are characterized by dorsoventrally flattened caudal transverse processes that taper distally. The first transverse process is directed laterally and is broad-based, but broken. The second is angled anteriorly; it widens slightly before tapering at the tip, but also twists about the long axis so that part of the blade angles posteroventrally. The third transverse process is narrower but also has the anterior curvature. The more posterior transverse processes are directed laterally.

The first caudal lacks any trace of a ventral haemal arch and therefore meets the definition of a pygal vertebra (marking the position of the cloacal outlet). It is, however, grooved on the underside (HRCT, Pl. 2, fig. 2; Text-fig. 6C) with a least one subcentral foramen. Behind it, the second caudal vertebra bears shallow ventral pedicels fused on either side of the midline, but it is not clear whether these are rudiments or whether a larger haemal arch has broken away. It resembles the condition in *Lanthanotus* (Rieppel 1980) where the second caudal has a pedicel onto which a haemal arch attached. The third caudal has a strong, deep, fully fused haemapophysis, angled posteriorly. These processes would have deepened the ventral part of the tail but there is no corresponding elevation of the neural spine. However, the zygapophyses are particularly well developed in this region, with a larger overlap than in the presacral region. The last two vertebrae on the holotype are too poorly preserved for description (and are omitted from the HRCT images because they provided no information).

Isolated caudal vertebrae resembling those on SBEI 1568 are found on several blocks. SBEI 197 (not illustrated) is an anterior caudal retaining transverse processes, but with fused haemapophysial flanges (open distally) and a more rounded posterior condyle than that of presacrals. There is a low neural spine that projects posteriorly. None of the attributed caudals shows any trace of an autotomy septum.

EXPLANATION OF PLATE 1

Figs 1–2. *Kaganaias hakusanensis* gen. et sp. nov., Kuwajima Formation, Lower Cretaceous, Japan. Type specimen (SBEI 1568), high-resolution X-ray computed tomography reconstructions of the skeleton. 1, ventral view, hidden surface. 2, dorsal view, as partially exposed. Scale bar represents 10 mm.



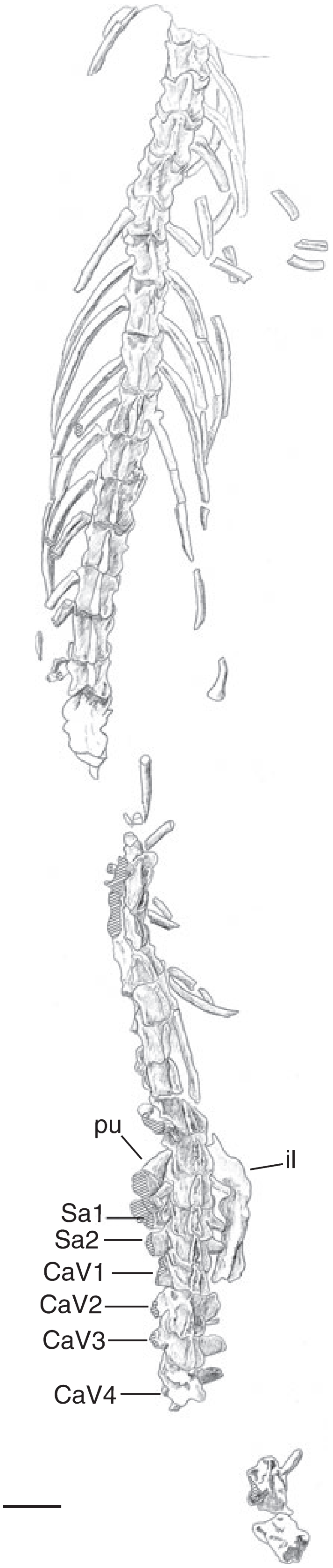
EVANS *et al.*, *Kaganaias*

Pelvis and hind limb

SBEI 1568 exposes the right ilium, parts of the right and left pubes, and a fragment of the left ilium (Text-fig. 7; Pl. 2). In addition, part of the right femur is preserved as a short, straight bone fragment that runs ventral and subparallel to the iliac blade. On the second block, an almost complete left femur is preserved, as well as a small group of pedal phalanges (Text-fig. 7A). The HRCT scans permit a view of the underside of the specimen, showing the pubes and ischia in greater detail (Pl. 2, fig. 2). Unfortunately, no additional parts of the hind limbs were revealed.

The right ilium is relatively long (three vertebral lengths) and slender (Pl. 2). Overall, the complete bone is L-shaped, with a smooth, curving anterior margin that lacks any trace of an anterior iliac tubercle. The iliac blade is horizontal, deepest anteriorly but tapering to the rear (incomplete). On the medial surface there is a strong anteroposterior ridge that marks the position of the sacro-iliac joint (second sacral rib in articulation). The left ilium adds little to this description (Text-fig. 7B–C). It is broken both anteriorly and posteriorly, so that only the central portion of the blade, with the medial ridge, is preserved. The right pubis is badly damaged and provides no useful information. The left pubis (HRCT, Pl. 2) is damaged proximally and distally, but shows several important features. It is directed anteriorly and tapers into the symphysial region. The lateral edge is in-turned and bears a small inflected pectineal process that is closer to the proximal head. The ischia are both preserved (HRCT, Pl. 2, fig. 2), but the left bone is the more complete. The element is strongly built, with a relatively narrow neck and a well-developed ischial tuberosity. The bone is widest in its midsection, but then tapers obliquely towards the anterior symphysis. Overall, the pubo-ischiadic plate in *Kaganaias* covers three vertebral lengths (four in the living *Varanus*, two in some aigialosaurs; Carroll and deBraga 1992).

Fragments of a right femur are associated with the right pelvis on the main block, but nothing else of this limb remains except for the distal part of a penultimate phalanx bearing prominent condyles for articulation with the ungual. On the left side, a pronounced rounded condyle in the region of the acetabulum may be the femoral head (Text-fig. 6C). The remainder of the bone is on the counterpart block. It is a robust bone with expanded proximal and distal ends (paired condyles) but no sigmoid curvature. The shaft is comparatively thick (*c.* 50 per cent of proximal width as compared with 27 per cent in *Varanus*). The femur as preserved (Text-fig. 7) is 14 mm in length (*c.* 4 dorsal vertebral lengths vs. 6 in *Varanus salvator*, *c.* 3 in aigialosaurs; Carroll and deBraga 1992), while there is a gap of 11·5 mm between its distal end and the small group of pedal phalanges (Text-fig. 7A). No trace of the crus, tarsus or metatarsus remains, but given the general preservation of the skeleton, these elements were presumably accommodated roughly within this short gap. Remains of two very short pedal phalanges are preserved in what appears to be a life position, curving towards the axial skeleton and with one bearing a short ungual phalanx



TEXT-FIG. 3. *Kaganaias hakusanensis* gen. et sp. nov. Type specimen, SBEI 1568, drawing of skeleton on main block. Scale bar represents 5 mm.

(note that because of their size and thin walls, these elements are not visible in the HRCT scans). A gap of 16·5 mm exists between the tip of the ungual and the distal end of the femur. If this was roughly the length of the crus and foot combined, then the total hind limb length was about 31 mm, less than one-quarter of the length of the trunk (*c.* 8 dorsal vertebral lengths vs. 15 in *Sphenodon*).

Skull remains

SBEI 1799 consists of an association of disarticulated vertebrae matching those of the holotype (see above). Preserved with them are a quadrate and a partial maxilla (Text-fig. 8A–C). The maxilla is represented by the anterior part of a right bone, preserving two long, slender, strongly recurved teeth (allowing for breakage) (Text-fig. 8A). The maxilla resembles that of living varanoids in having a long anterior subnarial margin. Tooth implantation is a modified pleurodonty with the teeth set in deep recesses separated by interdental laminae formed from bone of attachment (Text-fig. 8A). The large, clearly squamate, left quadrate lacks a medial pterygoid wing and has a small (but damaged) lateral conch and a large, posteriorly extended, head with a small suprastapedial process (Text-fig. 8B–C). The ventral condyle for the articular is a single saddle-shaped surface rather than the double condylar structure found in many lizards.

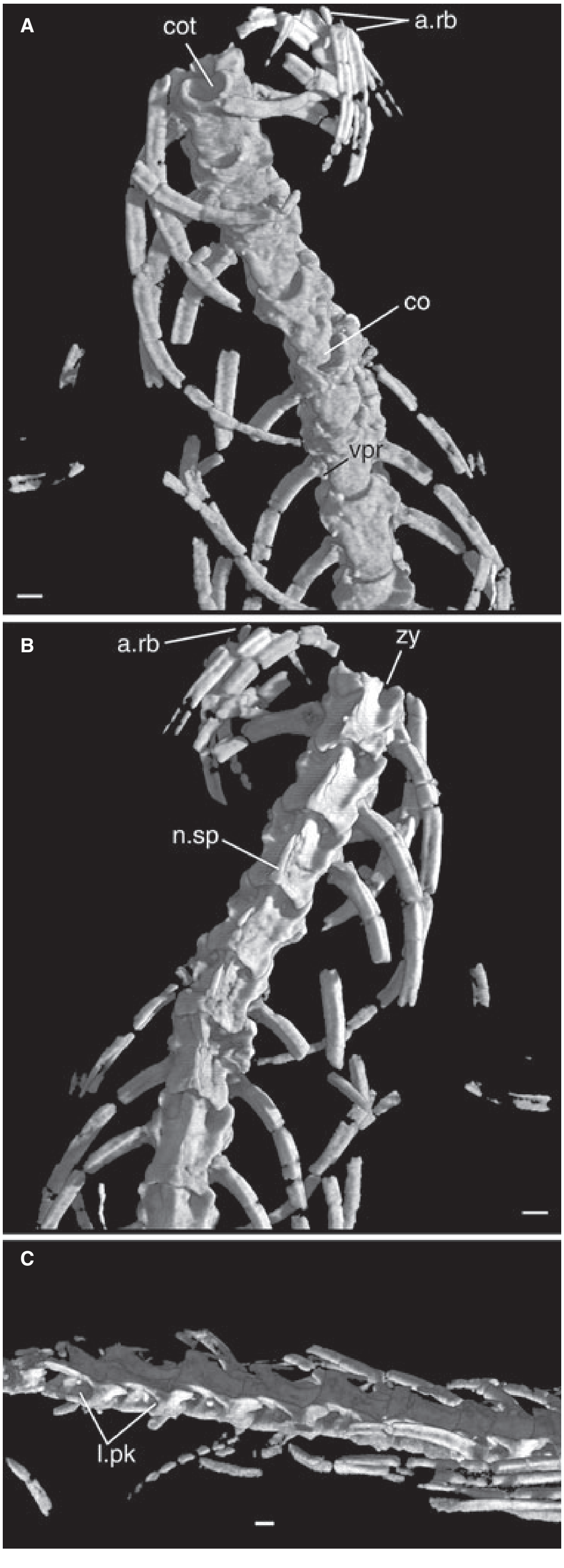
SBEI 195 is an association of left and right dentaries (Text-fig. 8D–E) referred to *Kaganaias* on the basis of the similarities in tooth implantation with SBEI 1799. The jaws are not complete but the left bone preserves seven small tooth recesses separated by interdental ridges (all teeth are missing), and a ventrally sloping subdental shelf. The Meckelian canal is displaced to a ventral position. On the right side, only a small section of the jaw is present but it contains a single tooth base without basal plicidentine.

DISCUSSION

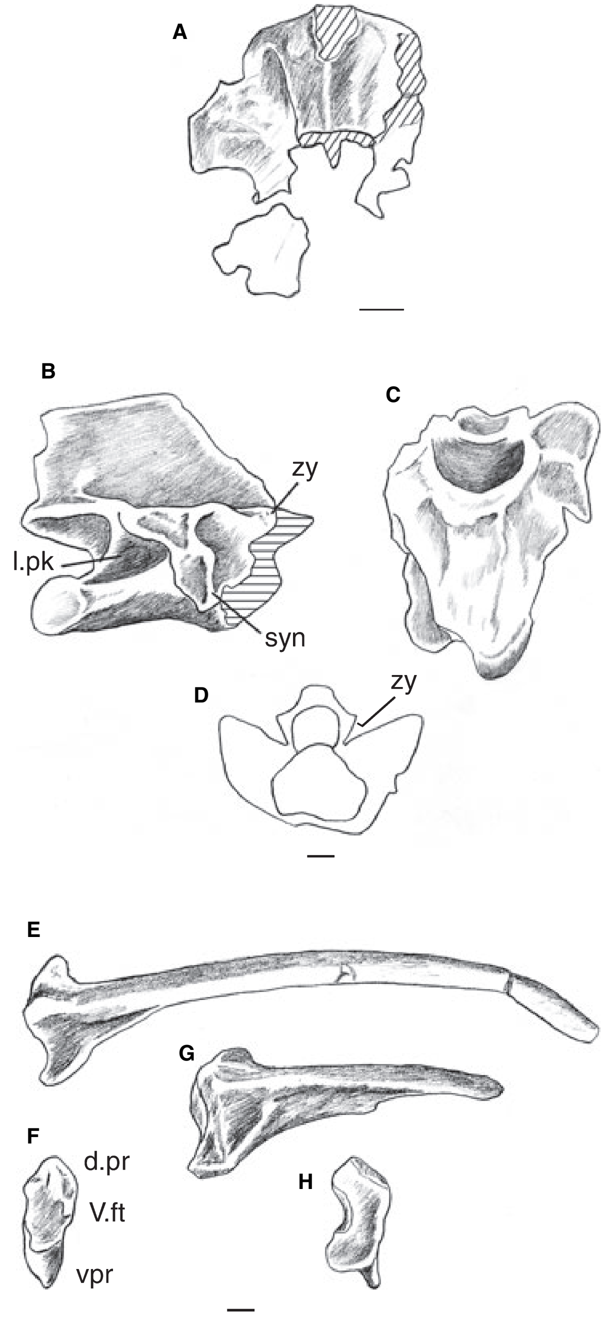
Phylogenetic position within Squamata

The combination of procoelous vertebrae, strong zygosphenoidal joints, and a pelvis with a large thyroid fenestra and anteriorly tapering pubis identifies *Kaganaias* as a squamate, a conclusion supported by the attributed quadrate and maxilla.

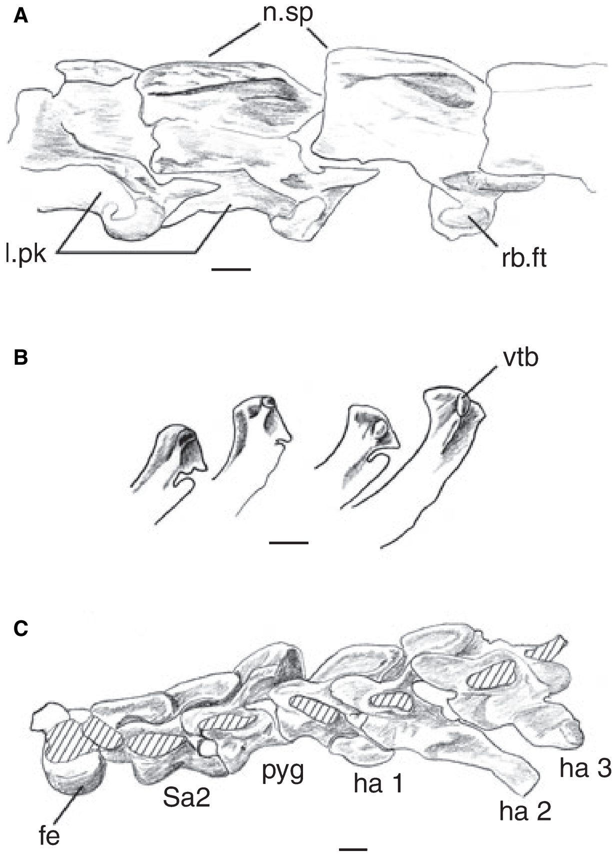
All recent cladistic analyses of squamates using morphological characters have recognized two major clades, Iguania and Scleroglossa (e.g. Estes *et al.* 1988; Evans and



TEXT-FIG. 4. *Kaganaias hakusanensis* gen. et sp. nov. Type specimen, SBEI 1568, High-resolution X-ray computed tomography reconstructions giving details of the vertebral column. A, ventral aspect of anterior dorsal vertebrae showing ribs and articular condyles. B, as A, in dorsal view showing reduced neural spines and accessory articulations. C, right lateral view of more posterior dorsal vertebrae showing the pockets in the sides of the vertebral arches. Scale bars represent 1 mm.



TEXT-FIG. 5. *Kaganaias hakusanensis* gen. et sp. nov. Specimen SBEI 1799, association of bones. A, partial cervical vertebra in ventral view. B–D, anterior dorsal vertebra in B, lateral, C, ventral, and D, anterior views. E–H, anterior dorsal ribs in E and G, lateral, and F and H, proximal views (respectively) to show dorsal tubercle and ventral crest. Scale bars represent 1 mm.



TEXT-FIG. 6. *Kaganaias hakusanensis* gen. et sp. nov. Type specimen, SBEI 1568. A, lateral view of posterior dorsal vertebrae, main block. B, mid-dorsal ribs in ventral view on the counterpart block. C, sacral and anterior caudal vertebrae, left lateral view to show development of haemal arches. Scale bars represent 1 mm.

Barbadillo 1997, 1998, 1999; Evans and Chure 1998; Lee 1998; Reynoso 1998; but see Townsend *et al.* 2004). Scleroglossa incorporates all gekkotan, scincomorph and anguimorph clades, as well as the derived amphisbaenians and snakes. The absence of a skull makes a comprehensive cladistic analysis of *Kaganaias* difficult, as skull characters play a major role in classification. However, no known iguanian or basal squamate shows a long-bodied limb-reduced morphology: this is confined to Scleroglossa (the gekkotan pygopodids, dibamids, amphisbaenians, snakes, and various scincomorphs and anguimorphs). The oblique intercentral articulations of *Kaganaias* resemble those of anguimorphs more than scincomorphs. Similarly,

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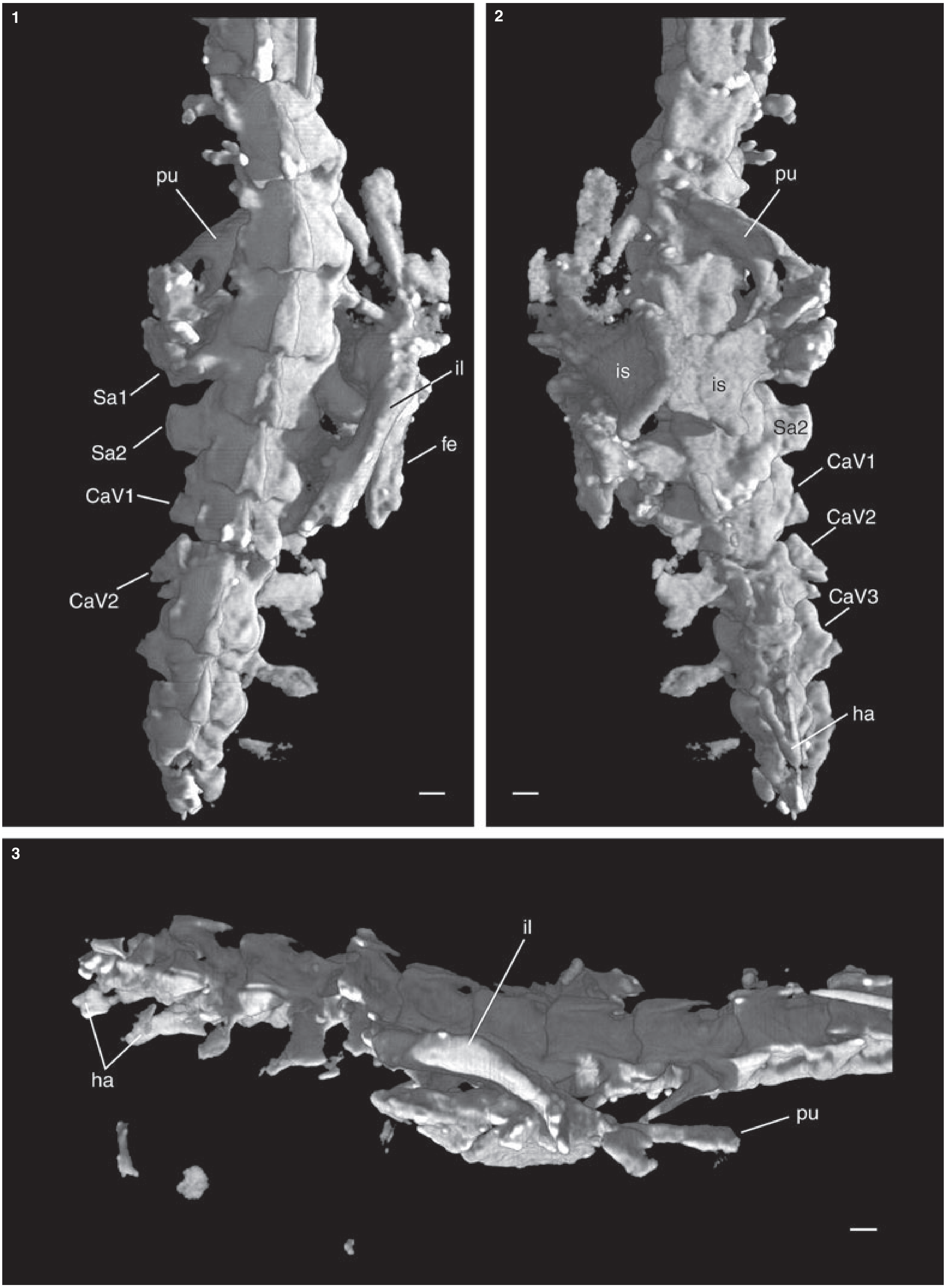
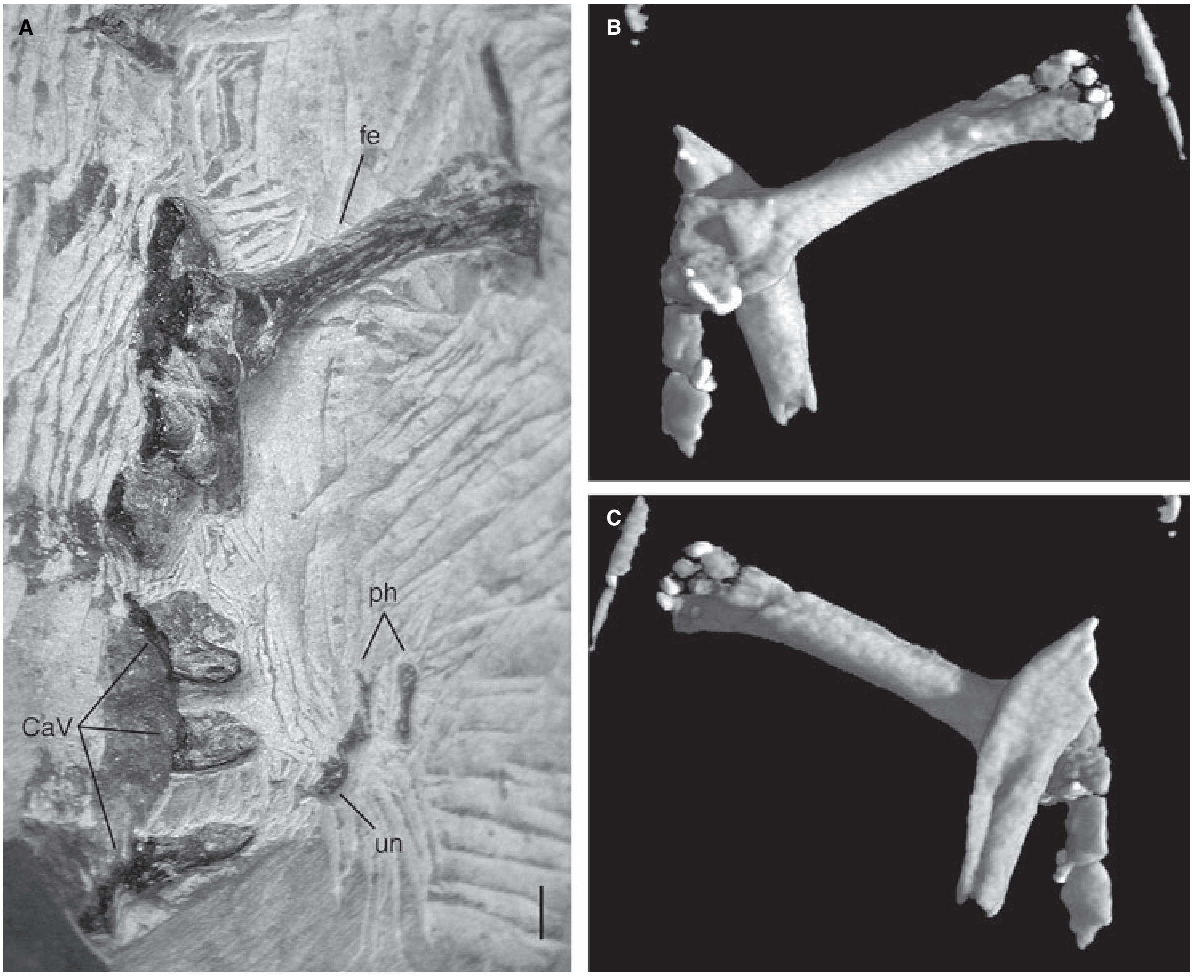
EXPLANATION OF PLATE 2

Figs 1–3. *Kaganaias hakusanensis* gen. et sp. nov., Kuwajima Formation, Lower Cretaceous, Japan. Type specimen (SBEI 1568), high-resolution X-ray computed tomography reconstructions of the pelvic region. 1, dorsal view. 2 ventral view. 3, right lateral view. Scale bars represent 1 mm.

PLATE 2



EVANS *et al.*, *Kaganaias*

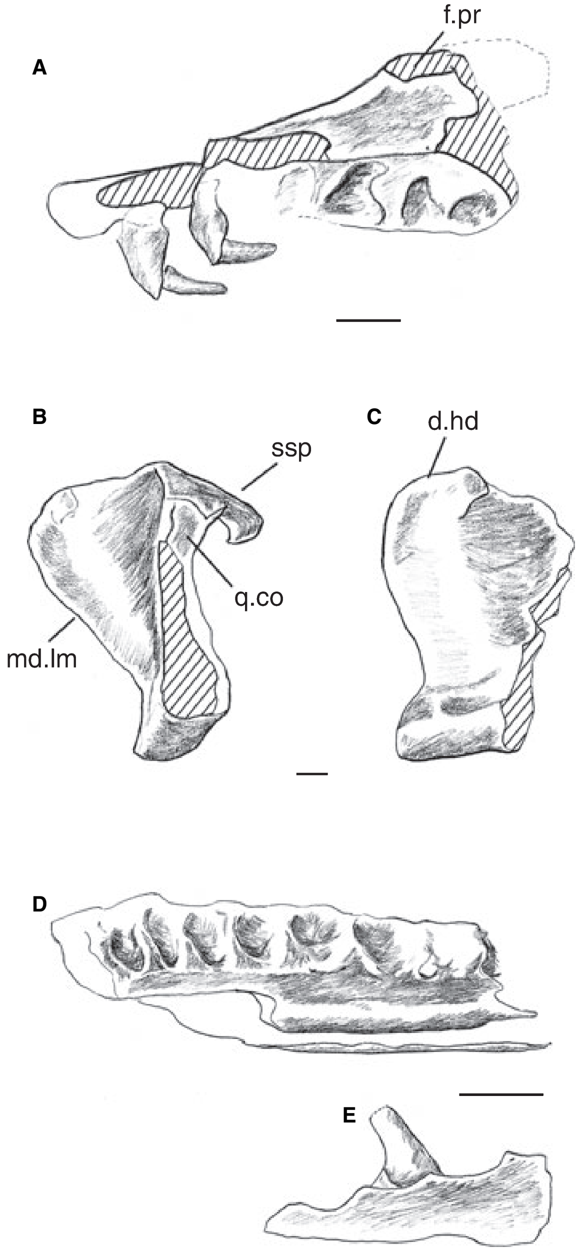


TEXT-FIG. 7. *Kaganaias hakusanensis* gen. et sp. nov. Type specimen, SBEI 1568, counterpart block, left hindlimb and tail. A, photograph of the specimen. B–C, High-resolution X-ray computed tomography reconstructions of the femur and ilium, in B, ventral and C, dorsal views. Scale bar represents 1 mm.

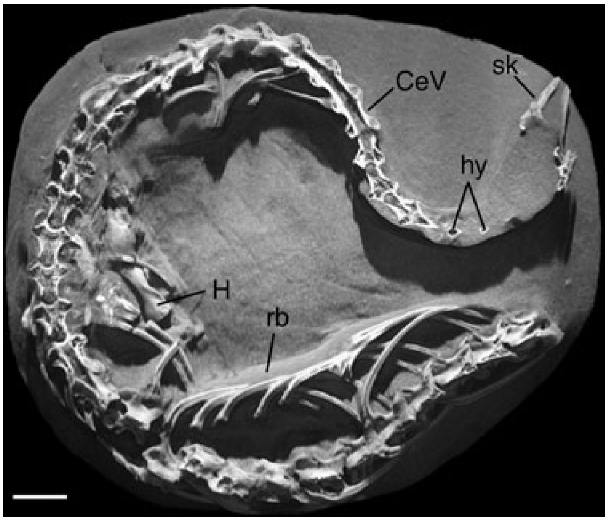
if the jaw elements are correctly attributed, the tooth implantation resembles that of anguimorphs (little or no subdental ridge, posterior replacement) more than that of scincomorphs (strong subdental shelf, medial replacement).

Anguimorphs are widely recognized as a monophyletic group (e.g. Estes 1983; Borsuk-Białynicka 1984; Estes *et al.* 1988; Evans and Barbadillo 1998; Evans and Chure 1998; Gao and Norell 1998; Lee 1998; Caldwell 1999*a*, *b*; Macey *et al.* 1999), comprising the anguids and the platynotans (helodermatids, *Lanthanotus*, varanids and related fossil groups); the status of 'xenosaurs' (*Xenosaurus* and *Shinisaurus*) is more problematic (see review by Bever *et al.* 2005) with some authors recognizing them as sister taxa (e.g. Estes *et al.* 1988; Gao and Norell 1998) and others arguing against a close relationship (e.g. Conrad 2004; Townsend *et al.* 2004). There is also general agreement among morphologists that snakes were derived from within Platynota (but see the recent molecular trees of Townsend *et al.* 2004; Vidal and Hedges 2004). The position and affinities of amphisbaenians remain controversial, the main recent hypotheses being gekkotan (e.g. Lee 1998), teioid (e.g. Wu *et al.* 1993, 1996; Townsend *et al.* 2004) and snake (Zaher and Rieppel 1999, 2000) relationships.

Platynotans are a distinctive group characterized by a range of features including: retracted nares; sharp recurved teeth (except *Coniasaurus* and perhaps *Dolichosaurus*; Caldwell 2000*a*); interdental ridges formed by bone of attachment; tooth replacement from behind; reduction of the nasals; reduction or loss of the subdental shelf on the lower jaw. Within Platynota, *Kaganaias* is strikingly different from members of the Varanidae that have plicidentine on the teeth, lack zygosphenes and have waisted vertebral condyles, strong hind limbs, a shorter dorsal vertebral series, and strong triangular ilia with anterior tuberosities. Among living taxa, the pelvis of *Kaganaias* is closer to that of *Lanthanotus* and *Heloderma*



TEXT-FIG. 8. *Kaganaias hakusanensis* gen. et sp. nov. A–C, SBEI 1799, association of vertebrae, ribs, maxilla and quadrate. A, medial view of right anterior maxilla. B–C, left quadrate, in B, lateral and C, anterior views. D–E, SBEI 195, associated dentaries. D, medial view of anterior region of left bone. E, lateral view of fragment of right bone and partial tooth. Scale bars represent 1 mm.

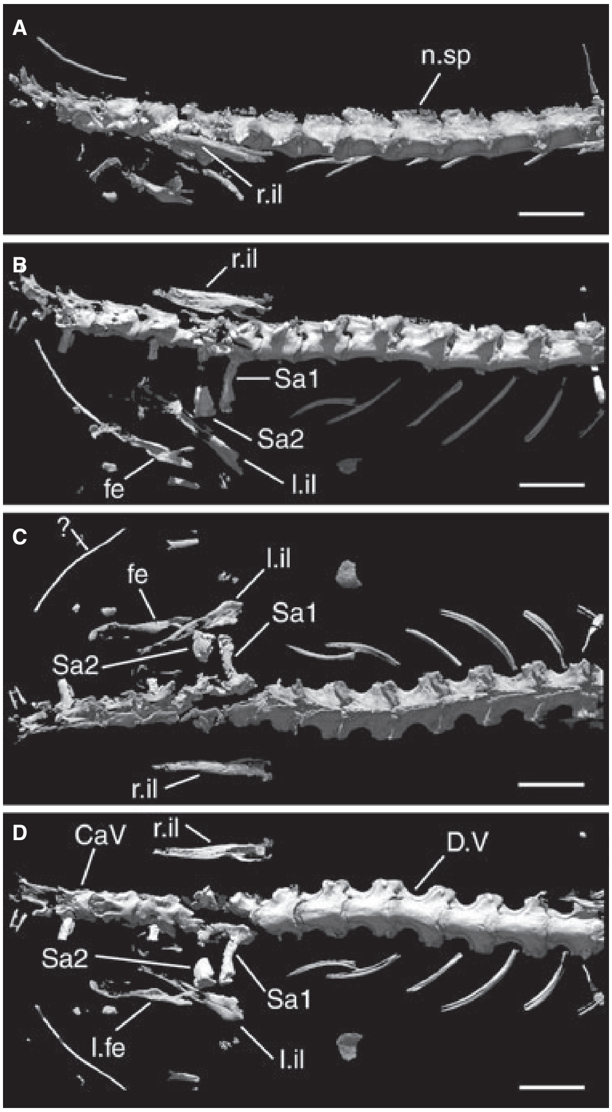


TEXT-FIG. 9. *Dolichosaurus longicollis*, type specimen, BMNH R49002. High-resolution X-ray computed tomography reconstruction with vertebral column partially cut-away to show vertebral articulations (centrum) and cervical hypapophyses. Scale bar represents 10 mm.

in having a long, slender ilium. In terms of vertebral structure (low spines, waisted vertebrae, ventrolaterally facing zygosphenes, elongate dorsal series), *Kaganaias* most closely resembles the long-bodied marine taxa of the Cenomanian–Turonian – *Adriosaurus*, *Aphanizocnemus*, *Coniasaurus*, *Dolichosaurus* (Text-figs 9–10) and *Pontosaurus* – loosely called dolichosaurs, although they may not be a monophyletic group (Caldwell 2000*a*).

Most recent authors have recognized dolichosaurs as relatives of mosasaurs and aigialosaurs within a larger platynotan clade, Mosasauroidea (e.g. Bell 1997; Lee 1998; Caldwell 1999*a*, *b*, 2000*a*, *b*; Rieppel and Zaher 2000*a*, *b*). At the present time, opinions as to the relationships between this clade, varanoids, snakes and amphisbaenians are divided between authors who regard snakes as being mosasauroid derivatives (e.g. Caldwell and Lee 1997; Lee 1997, 1998; Lee and Caldwell 1998, 2000; Caldwell 1999*a*, *b*, 2000*a*, *b*; Rage and Escuillié 2000, 2002; Caldwell and Albino 2001; Lee and Scanlon 2002) and those who place snakes closer to amphisbaenians (Zaher 1998; Zaher and Rieppel 1999, 2000, 2002; Rieppel and Zaher 2000*a*, *b*; Tchernov *et al.* 2000; Rieppel and Kearney 2001; Rieppel *et al.* 2003). The two different relationship hypotheses are linked to ecological hypotheses, and thus the environment in which snakes developed their unique body form, as marine swimmers (mosasauroid ancestry) or burrowers (amphisbaenian relationships).

Kaganaias is clearly not a snake (vertebral morphology, limb morphology) but as a long-bodied, dolichosaur-like lizard, it impacts on some aspects of the current debate. In order to maintain a relatively neutral position, we coded *Kaganaias* into three data matrices: those of Lee (1998), Lee and Caldwell (2000) and Rieppel and Zaher (2000*b*). We ran branch and bound analyses using PAUP version 3.1.1 (Swofford 1993). Some taxa not immediately relevant to the discussion were deleted from each matrix



TEXT-FIG. 10. *Dolichosaurus longicollis*, BMNH R32268. High-resolution X-ray computed tomography reconstructions of the posterior dorsal vertebrae and pelvic region. A, right lateral view. B, right ventrolateral view. C, dorsal view. D, ventral view. Scale bars represent 10 mm.

to shorten the running time (up to 4 weeks), but only after repeated heuristic searches to ensure as far as possible that their removal did not affect tree topology. The results are shown in Text-figure 11.

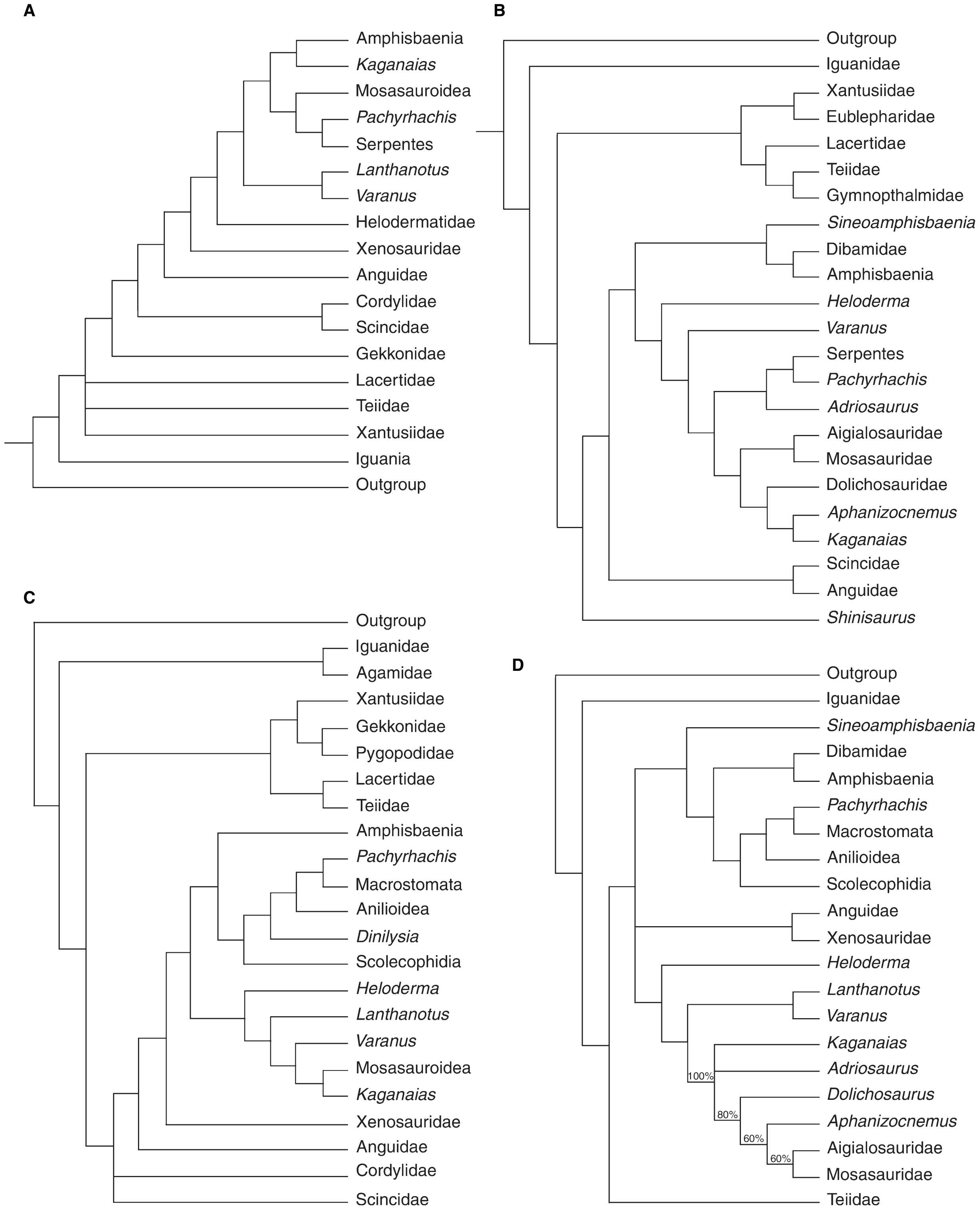
The first analysis used the matrix of Lee (1998), but with characters unordered. Text-figure 11A shows a strict consensus of 16 MPTs (maximum parsimony trees) (L = 809, CI = 0·74, RC = 0·5). *Kaganaias* emerged as the sister group of Amphisbaenia, with this clade as the sister taxon of mosasauroids and snakes. This is the only analysis that placed *Kaganaias* with Amphisbaenia. When the character states actually coded are examined, the only derived states shared by *Kaganaias* and Amphisbaenia are the dorsal and ventral tubercles on the rib heads (also found in snakes).

The second analysis used the matrix of Lee and Caldwell (2000), with some modifications to the coding for the Lebanese *Aphanizocnemus* (Dal Sasso and Pinna, 1997) based on a re-examination of the specimen (see Appendix). The Lee and Caldwell (2000) matrix is closely similar to that of Lee (1998) but includes a greater range of fossil taxa. The difference in the position of *Kaganaias* in the resulting trees highlights the effects of the differential incorporation of taxa in analyses. Text-figure 11B shows a strict consensus of 66 MPTs (L = 471, CI = 0·57, RC = 0·38) resulting from the second analysis. *Kaganaias* is nested within Mosasauroidea as the sister taxon of *Aphanizocnemus*. However, of the derived characters that can be coded for both *Kaganaias* and *Aphanizocnemus*, only one (185, ridge-like dorsal neural spines) actually links these two genera. We left the original coding of the fossil *Sineoamphisbaena* unchanged in the Lee and Caldwell (2000) matrix, but it should be noted that subsequent work by Kearney (2003*b*) has failed to support a relationship between *Sineoamphisbaena* and amphisbaenians.

The third analysis used the matrix of Rieppel and Zaher (2000*b*), again slightly reduced. Text-figure 11C shows a strict consensus tree obtained from two MPTs (L = 475, CI = 0·566, RC = 0·399), in which *Kaganaias* is placed as the sister taxon of mosasauroids. We then added *Adriosaurus* (Lee and Caldwell 2000; SEE, pers. obs.), *Aphanizocnemus* (SEE, pers. obs. 2004), *Dolichosaurus* (Caldwell 2000*a*; SEE, pers. obs. 2004), aigialosaurs (Carroll and deBraga 1992) and mosasaurs (based on *Platycarpus*; Russell 1967), and re-ran the analysis. The strict consensus of 60 MPTs (L = 447, CI = 0·58, RC = 0·4) left the mosasauroid taxa, including *Kaganaias*, in an unresolved polytomy. Text-figure 11D shows the 50 per cent Majority Rule Consensus tree from the same analysis. The inclusion of *Kaganaias* within Mosasauroidea is well supported, but its position in relation to other members of the group is poorly resolved. Given the absence of skull or neck characters for the Japanese lizard, and the equally limited information on dolichosaur skull anatomy generally, this is hardly surprising.

Morphological comparison

Although the precise position of *Kaganaias* within mosasauroids cannot be determined at this stage, a suite of characters supports its attribution to Platynota. From the data set of Rieppel and Zaher (2000*b*) these are: 146 (shallow thecodont tooth implantation, with interdental bone and wide tooth spacing); 165 (the oblique articulation of the vertebral condyles); 172 (the increased number



TEXT-FIG. 11. The phylogenetic position of *Kaganaias hakusanensis* based on four phylogenetic analyses. A, strict consensus of 16 MPTs using the matrix of Lee (1998). B, strict consensus of 66 MPTs using the matrix of Lee and Caldwell (2000). C, strict consensus of two MPTs based on the matrix of Rieppel and Zaher (2000*b*). D, 50 per cent Majority Rule Consensus Tree from 60 MPTs based on the extended Rieppel and Zaher (2000*b*) matrix.
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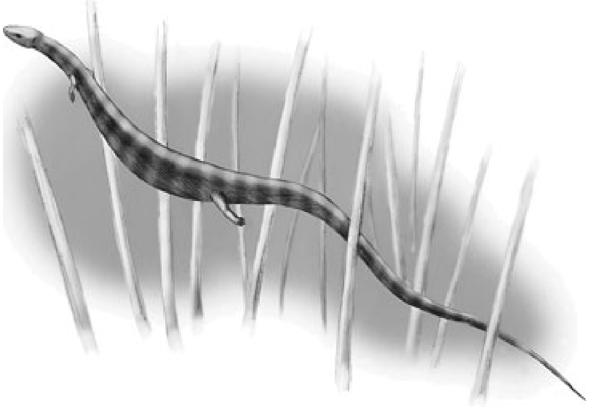

TEXT-FIG. 12. Tentative life reconstruction of *Kaganaias hakusanensis*, allowing for the absence of information on the anterior region of the body.

of presacral vertebrae); 183 (the presence of pedestals on caudal vertebrae for the attachment of haemapophyses); 185 (the posterior position of the haemapophysial attachment); and 207 (the lack of fusion of pelvic elements). Another smaller suite supports the attribution to mosasauroids: 168 (the low ridges on dorsal vertebrae); 169 (the well-developed zygosphene-zygantral system); 212 (the short robust femur); and 213 (the straight femur). The quadrate referred to *Kaganaias* differs from that of aigialosaurs and mosasaurs in having only a small suprastapedial process. In the more derived taxa, a large recurved suprastapedial process contributes to the conch of the middle ear (deBraga and Carroll 1993). The quadrate of the dolichosaur *Pontosaurus* (Pierce and Caldwell 2004) also approaches this shape, but the bone remains unknown in the other basal mosasauroids (*Dolichosaurus*, coniasaurs, *Adriosaurus*, *Aphanizocnemus*) making it difficult to plot the evolutionary history of mosasauroid quadrate structure.

Character 172 separates snakes and amphisbaenians clearly from fully limbed squamates, but the range of vertebral numbers (27–50) given for character state 1 does not separate the long-bodied dolichosaurs from aigialosaurs and mosasaurs. Aigialosaurs have 7–8 cervicals and 20 dorsals (Carroll and deBraga 1992; deBraga and Carroll 1993), while mosasaurs have 7–8 cervicals and 22–35 dorsals (Russell 1967). *Dolichosaurus* has around 18 cervicals and 32–38 dorsals (Caldwell 2000*a*; SEE, pers. obs. 2004), *Aphanizocnemus* has 10–11 cervicals and 25 dorsals (Dal Sasso and Pinna 1997; SEE, pers. obs. 2004), while *Adriosaurus* has *c.* 11 cervicals and 29 dorsals (Lee and Caldwell 2000; SEE, pers. obs. 2004), and *Pontosaurus* has 11 cervicals and a maximum of 30 dorsals (SEE, pers. obs. 2004). The cervical count in *Kaganaias* is unknown, but with a dorsal count in excess of 36, the only taxon that it approaches in overall presacral length is *Dolichosaurus* (Text-figs 9–10).

Kaganaias also resembles *Dolichosaurus* in the shape and thickness of the ribs (elongate, not strongly curved, reduced cavity, 5–6 vertebral lengths). These ribs differ from those of *Adriosaurus* and *Pontosaurus* where the stronger curvature gives the body a more circular profile. *Aphanizocnemus* resembles *Kaganaias* and *Dolichosaurus* in rib shape (even less curvature than *Kaganaias*), but differs in that the ribs are very gracile. However, this feature, with the thin skull bones and weakly developed pelvis, suggests that the *Aphanizocnemus* holotype may be juvenile. The size, shape and orientation of the zygosphene-zygantrum, the rib facets and the mid-vertebral waisting are broadly similar in *Kaganaias* and *Dolichosaurus*, but *Dolichosaurus* has wider neural arches, with more anterior and posterior flaring and a greater difference in size between anterior and posterior trunk vertebrae (Text-fig. 10C–D). However, none of the other dolichosaur taxa has the deep lateral vertebral recesses found in *Kaganaias.* The posterior neural spines of *Kaganaias* are shorter than those of *Adriosaurus* or *Dolichosaurus* (Text-fig. 10A), but resemble those of *Aphanizocnemus* in being little more than ridges. In *Dolichosaurus*, the sacral ribs are longer and narrower than those of *Kaganaias* (Text-fig. 10C–D), but both taxa (and *Aphanizocnemus*) have wide and dorsoventrally compressed transverse processes on the anterior caudals. *Kaganaias* resembles *Aphanizocnemus*, *Dolichosaurus* and *Lanthanotus* in having a single pygal vertebra, but differs from *Aphanizocnemus* in that the first haemal arch in that genus is long. In *Adriosaurus* the first visible haemal arch is between caudals 3 and 4, so the state of any more anterior element is not known. Unlike *Kaganaias*, however, the haemal arches of *Aphanizocnemus* do not seem to be fused to the centra (although again this could be age related).

In *Kaganaias*, the femur is 14 mm long but the space left for the rest of the limb between the end of the femur and the terminal phalanges is about 11·5 mm. This suggests that the femur was at least 50 per cent of total limb length. This is different from the situation in mosasaurs and aigialosaurs (femur *c.* 33 per cent of entire limb) and *Varanus* (femur *c.* 27 per cent), but it does resemble *Aphanizocnemus*, as reconstructed by Dal Sasso and Pinna (1997), in which the tibia and fibula are strongly reduced, the foot is short and simple, and the femur is rather slender but short and flattened. The phalanges of *Aphanizocnemus* are short and broad, but differ from those of *Kaganaias* in that there is no differentiation between head and shaft (although again this might be a juvenile feature); the claws are thick, short and triangular. The femur of *Dolichosaurus* is poorly preserved, but appears robust without obvious waisting or sigmoid curvature; nothing is known of the more distal parts of the limb. The femur of *Kaganaias* is roughly four dorsal vertebral lengths (VL). This is short relative to the femur of *Varanus* (6 VL), but relatively long compared with the femora of *Adriosaurus* (3 VL), *Aigialosaurus* (2·7 VL), *Aphanizocnemus* (2·4 VL) or mosasaurs (2–2·5 VL).

Ecological niche

Remains of *Kaganaias* are found in both the aquatic and the swampy terrestrial facies of the Kuwajima Formation at Shiramine, although they are more abundant in the latter. However, the depositional environment need not be the life environment, and morphology has to be the arbiter. The deep, narrow body profile of *Kaganaias*, combined with thickened ribs and relatively small hind limbs, suggests a predominantly, though not exclusively, aquatic lifestyle (Text-fig. 12). The low, ridge-like neural spines may seem inconsistant with this, but a similar morphology is found in other dolichosaurs. Long-bodied terrestrial taxa, both burrowers and surface taxa, are typically rounded in cross-section (e.g. amphisbaenians, dibamids, feylinids, limbless anguids, *Anniella*; SEE pers. obs.). Based on sedimentary evidence, *Kaganaias* is interpreted as having lived in a well-vegetated, freshwater swampy environment on a continental floodplain (Isaji *et al.* 2005). It presumably used lateral body movements (strong ribs, strong intercostal musculature as suggested by accessory rib processes and deep lateral cavities on the vertebrae) to swim, with the limbs used to steer. However, the limbs, although relatively small, are strongly built, as is the pelvis to which they are attached. The ends of the small pedal phalanges have strong joint surfaces and the claw has attachment points for flexor muscles. This suggests that the limbs could also have been used actively on land, perhaps to grip a muddy substrate and provide additional leverage. The presence of a large ischium with a well-developed posterior tuberosity suggests that this element was still important for muscle attachment. In living lizards, the ischial tuberosity provides a surface of origin for the flexor tibialis (flexor of knee) and the ischiotrochantericus (which raises the femur upwards; Romer 1956), while the inner and outer surfaces of the plate itself give origin to the puboischiofemoralis internus and externus, abducting and adducting the femur. Thus *Kaganaias* was probably an amphibious wetland lizard, but without information on skull and forelimb morphology, total body length or neck length, we cannot speculate further on lifestyle.

Implications

To date, all known long-bodied platynotans and aquatic limbed snakes have been recovered from Late Cretaceous (Cenomanian–Turonian) nearshore or shallow-marine deposits in the North American Seaway and the western Tethys Basin (Britain, North Africa, Portugal, France, Croatia, Slovenia, Lebanon, Palestine). *Kaganaias* is the first representative from the Early Cretaceous (Valanginian/Hauterivian), showing that this morphotype had arisen some 20–40 myr earlier than previously recorded. It is also the first from an eastern Asian locality, and the first from a non-marine facies. At the time of deposition of the Kuwajima Formation, Japan lay on the eastern edge of the Asian continent, but Ishikawa Prefecture was some distance (at least 100 km) from the sea.

In reality, the recovery of an early long-bodied platynotan in swampy floodplain deposits is not surprising. Extant varanid lizards frequently swim in both freshwater and saltwater environments. The ancestral mosasauroid presumably had a niche similar to that of modern taxa, becoming increasingly amphibious (freshwater/brackish) before entering the sea, initially in warm shallow coastal waters and then, with the mosasaurs, in deeper oceans (deBraga and Carroll 1993). *Kaganaias* may represent an early stage in that transition (or a relict of that stage), or an independent radiation with a similar body plan. More data are needed on platynotans from Upper Jurassic and Lower Cretaceous deposits, but perhaps the appearance and apparently sudden diversification of marine platynotans in the western Tethys region in the Late Cretaceous followed the Early Cretaceous re-association of Asia and Euramerica, with continental aquatic or semi-aquatic squamates emerging into new shallow-marine habitats. The presence of a basal platynotan lizard (*Parviraptor*) in the Middle Jurassic of Britain (Evans 1994) suggests that the group had evolved prior to the separation of Asia from Euramerica and, perhaps, of Laurasia from Gondwana. If early platynotans were globally distributed (or even if they were limited to Laurasia), then there was scope for more than one radiation. Again, more information is needed on skull and limb morphology (in *Kaganaias* but also other long-bodied taxa), in order to gauge the degree or likelihood of convergent evolution. At the very least, *Kaganaias* demonstrates that there is still much to learn about the early history and radiation of these specialized long-bodied squamates; that they were more widely dispersed than recent evidence suggested; and that not all Cretaceous long-bodied platynotans were marine.

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REFERENCES

AZUMA, Y. and KOBAYASHI, Y. 2003. A new iguanodontian (Dinosauria: Ornithopoda) from the Lower Cretaceous Kitadani Formation of Fukui Prefecture, Japan. *Journal of Vertebrate Paleontology*, **23**, 194–202.

—— and TOMIDA, Y. 1995. Early Cretaceous dinosaur fauna of the Tetori Group in Japan. 125–131. *In* SUN, A. L. and WANG, Y. Q. (eds). *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota: short papers*. China Ocean Press, Beijing, 250 pp.

BELL, G. L. 1997. A phylogenetic revision of North American and Adriatic Mosasauroidea. 281–292. *In* CALLAWAY, J. M. and NICHOLLS, E. L. (eds). *Ancient marine reptiles*. Academic Press, London and New York, 448 pp.

BEVER, G. S., BELL, C. J. and MAISANO, J. A. 2005. The ossified braincase and cephalic osteoderms of *Shinisaurus crocodilurus* (Squamata, Shinisauridae). *Palaeontologia Electronica*, **8**, 1–36.

BORSUK-BIAŁYNICKA, M. 1984. Anguimorphans and related lizards from the Late Cretaceous of the Gobi Desert, Mongolia. *Palaeontologia Polonica*, **46**, 5–105.

BROSCHINSKI, A. 2000. The lizards from the Guimarota mine. 59–68. *In* MARTIN, T. and KREBS, B. (eds). *Guimarota, a Jurassic ecosystem*. Verlag Dr Friedrich Pfeil, Munich, 155 pp.

CALDWELL, M. W. 1999*a*. Description and phylogenetic relationships of a new species of *Coniasaurus* Owen, 1850. *Journal of Vertebrate Paleontology*, **19**, 438–455.

—— 1999*b*. Squamate phylogeny and the relationships of snakes and mosasauroids. *Zoological Journal of the Linnean Society*, **125**, 115–147.

—— 2000*a*. On the aquatic squamate *Dolichosaurus longicollis* Owen, 1950 (Cenomanian, Upper Cretaceous) and the evolution of elongate necks in squamates. *Journal of Vertebrate Paleontology*, **20**, 720–735.

—— 2000*b*. On the phylogenetic relationships of *Pachyrhachis* within snakes: a response to Zaher (1998). *Journal of Vertebrate Paleontology*, **20**, 181–184.

—— 2002. From fins to limbs to fins: limb evolution in fossil marine reptiles. *American Journal of Medical Genetics*, **112**, 236–249.

—— and ALBINO, A. M. 2001. On the palaeoenvironment and palaeoecology of three Cretaceous snakes: *Pachyophis*, *Pachyrhachis*, and *Dinilysia*. *Acta Palaeontologica Polonica*, **46**, 203–218.

—— CARROLL, R. L. and KAISER, H. 1995. The pectoral girdle and forelimb of *Carsosaurus marchesetti* (Aigialosauridae) with a preliminary phylogenetic analysis of mosasauroids and varanoids. *Journal of Vertebrate Paleontology*, **15**, 516–531.

—— and COOPER, J. 1999. Redescription, palaeobiogeography, and palaeoecology of *Coniasaurus crassidens* Owen, 1850 (Squamata) from the English Chalk (Cretaceous: Cenomanian). *Zoological Journal of the Linnean Society*, **127**, 423–452.

—— and DAL SASSO, C. 2004. Soft-tissue preservation in a 95 million year old marine lizard; form, function and aquatic adaptation. *Journal of Vertebrate Paleontology*, **24**, 980–985.

—— and LEE, M. S. Y. 1997. A snake with legs from the marine Cretaceous of the Middle East. *Nature*, **386**, 705–709.

CALLIGARIS, R. 1988. I rettili fossili degli 'strati calcarei ittiolitici di Comeno' e dell'isola di Lesina. *Atti del Museo Civico di Storia Naturale di Trieste*, **41**, 85–125.

—— 1993. *Acteosaurus crassicostatus*, nuova specie di Dolichosauridae negli 'strati calcarei ittiolitici' di Comeno. *Atti del Museo Civico di Storia Naturale di Trieste*, **45**, 29–34.

CARROLL, R. L. and DEBRAGA, M. 1992. Aigialosaurs: mid-Cretaceous varanoid lizards. *Journal of Vertebrate Paleontology*, **12**, 66–86.

COATES, M. and RUTA, M. 2000. Nice snake, shame about the legs. *Trends in Ecology and Evolution*, **15**, 503–507.

CONRAD, J. L. 2004. Skull, mandible, and hyoid of *Shinisaurus crocodilurus* Ahl (Squamata, Anguimorpha). *Zoological Journal of the Linnean Society*, **141**, 399–434.

CORNALIA, E. and CHIOZZA, L. 1852. Cenni geologici sull′ Istria. *Giornale dell'Imperiale Reale Instituto Lombardo di Scienze Lettere ed Arte e Biblioteca Italiana*, **3**, 1–35.

CUNY, G., JAEGER, J. J., MAHBOUBI, M. and RAGE, J. C. 1990. Les plus anciens serpents (Reptilia, Squamata) connus. Mise au point sur l'age geologique des serpents de la partie moyenne du Cretace. *Comptes Rendus des Séances de l'Academie des Sciences, Paris II*, **311**, 1267–1272.

DAL SASSO, C. and PINNA, G. 1997. *Aphanizocnemus libanensis* n. gen. n. sp., a new dolichosaur (Reptilia, Varanoidea) from the Upper Cretaceous of Lebanon. *Paleontologia Lombarda della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, Nuova Serie*, **7**, 3–31.

—— and RENESTO, S. 1999. Aquatic varanoid reptiles from the Cenomanian (Upper Cretaceous) lithographic limestones of Lebanon. *Rivista della Museo Civico di Storia Naturale, 'E.Caffi', Bergamo*, **20**, 63–69.

DEBRAGA, M. and CARROLL, R. L. 1993. The origin of mosasaurs as a model of macroevolutionary patterns and processes. *Evolutionary Biology*, **27**, 245–322.

DUMÉRIL, A. M. C. and BIBRON, G. 1836. *Erpétologie générale, ou histoire naturelle complète des Reptiles*. Volume 3. Libraire Encyclopédique de Roret, Paris, 517 pp.

ESTES, R. 1983. *Sauria terrestria, Amphisbaenia*. *In* WELLNHOFER, P. (ed.). *Handbuch der Paläoherpetologie,* **10A**. Gustav Fischer Verlag, Stuttgart, 245 pp.

—— DE QUEIROZ, K. and GAUTHIER, J. 1988. Phylogenetic relationships within Squamata. 119–281. *In* ESTES, R. and PREGILL, G. (eds). *Phylogenetic relationships of the lizard families*. Stanford University Press, Stanford, 631 pp.

EVANS, S. E. 1994. A new anguimorph lizard from the Jurassic and Lower Cretaceous of England. *Palaeontology*, **37**, 33–49.

—— 1996. *Parviraptor* (Squamata: Anguimorpha) and other lizards from the Morrison Formation at Fruita, Colorado. *Bulletin of the Museum of Northern Arizona*, **60**, 243–248.

—— 1998. Crown group lizards from the Middle Jurassic of Britain. *Palaeontographica, Abteilungen A*, **250**, 123–154.

—— and BARBADILLO, L. J. 1997. Early Cretaceous lizards from las Hoyas, Spain. *Zoological Journal of the Linnean Society*, **119**, 23–49.

—— —— 1998. An unusual lizard from the Early Cretaceous of Las Hoyas, Spain. *Zoological Journal of the Linnean Society*, **124**, 235–265.

—— —— 1999. A short-limbed lizard from the Early Cretaceous of Spain. *Special Papers in Palaeontology*, **60**, 73–85.

—— and CHURE, D. 1998. Paramacellodid lizard skulls from the Jurassic Morrison Formation at Dinosaur National Monument, Utah. *Journal of Vertebrate Paleontology*, **18**, 99–114.

—— and MANABE, M. 1998. Early Cretaceous frog remains from the Okurodani Formation, Tetori Group, Japan. *Paleontological Research*, **2**, 275–278.

—— —— 1999*a*. A choristoderan reptile from the Lower Cretaceous of Japan. *Special Papers in Palaeontology*, **60**, 101–119.

—— —— 1999*b*. Early Cretaceous lizards from the Okurodani Formation of Japan. *Geobios*, **32**, 889–899.

—— —— 2000. Fossil lizards. 105–106. *In* MATSUOKA, H. (ed.). *Fossils of the Kuwajima 'Kaseki-kabe' (Fossil-bluff). Scientific report on a Neocomian (Early Cretaceous) fossil assemblage from the Kuwajima Formation, Tetori Group, Shiramine, Ishikawa, Japan.* Shiramine Village Board of Education, Ishikawa Prefecture, Japan, 277 pp. [In Japanese, English abstract].

—— —— COOK, E., HIRAYAMA, R., ISAJI, S., NICHOLAS, C. J., UNWIN, D. and YABUMOTO, Y. 1998. An Early Cretaceous assemblage from Gifu Prefecture, Japan. *Bulletin of the New Mexico Museum of Natural History and Science*, **14**, 183–186.

FUJITA, M. 2003. Geological age and correlation of the vertebrate-bearing horizons in the Tetori Group. *Memoir of the Fukui Prefectural Dinosaur Museum*, **2**, 3–14.

FÜRBRINGER, M. 1900. Beitrag zur Systematik und Genealogie der Reptilien. *Jenaischen Zeitschrift für Naturwissenschaften*, **34**, 596–682.

GANS, C. 1962. Terrestrial locomotion without limbs. *American Zoologist*, **2**, 167–182.

—— 1975. Tetrapod limblessness: evolution and functional corrrelaries. *American Zoologist*, **15**, 455–467.

GAO, K. and NORELL, M. A. 1998. Taxonomic revision of *Carusia* (Reptilia: Squamata) from the Late Cretaceous of the Gobi Desert and phylogenetic relationships of the anguimorphan lizards. *American Museum Novitates*, **3230**, 1–51.

GASC, J. P. 1981. Axial musculature. 355–435. *In* GANS, C. and PARSONS, T. S. (eds). *Biology of the Reptilia*, **11**. Academic Press, New York, 475 pp.

GIFU-KEN DINOSAUR RESEARCH GROUP 1992. The Tetori Group in Ogamigo area, Shokawa-mura, Gifu Prefecture, Japan. *Bulletin of the Gifu Prefectural Museum*, **13**, 9–16. [In Japanese].

GRADSTEIN, F. M. and OGG, J. G. 2004. Geologic time scale 2004, why, how, and where next? *Lethaia*, **37**, 175–181.

GREENE, H. W. and CUNDALL, D. 2000. Limbless tetrapods and snakes with legs. *Science*, **287**, 1939–1941.

HAAS, G. 1979. On a new snake-like reptile from the Lower Cenomanian of Ein Jabrud, near Jerusalem. *Bulletin du Museum National d'Histoire Naturelle de Paris*, **1**, 51–64.

—— 1980*a*. Remarks on a new ophiomorph reptile from the lower Cenomanian of Ein Jabrud, Israel. 177–192. *In* JACOBS, L. L. (ed.). *Aspects of vertebrate history: essays in honor of Edwin Harris Colbert.* Museum of Northern Arizona Press, Flagstaff, 407 pp.

—— 1980*b*. *Pachyrhachis problematicus* Haas, snakelike reptile from the Lower Cenomanian: ventral view of the skull. *Bulletin du Museum National d'Histoire Naturelle de Paris*, **2**, 87–104.

HASEGAWA, Y., MANABE, M., ISAJI, S., OHKURA, M., SHIBATA, I. and YAMAGUCHI, I. 1995. Terminally resorbed iguanodontid teeth from the Neocomian Tetori Group, Ishikawa and Gifu Prefecture, Japan. *Bulletin of the National Science Museum, Tokyo, Series C*, **21**, 35–49.

HIRAYAMA, R. 1996. Fossil land turtles from the Early Cretaceous of Central Japan. *Journal of Vertebrate Paleontology*, **16** (Supplement to No. 3), 41A.

—— 1999. Testudinoid turtles from the Early Cretaceous (Neocomina) of Central Japan. *Journal of Vertebrate Paleontology*, **19** (Supplement to No. 3), 51–52A.

—— 2000. Fossil turtles. 75–92. *In* MATSUOKA, H. (ed.). *Fossils of the Kuwajima 'Kaseki-kabe' (Fossil-bluff). Scientific report on a Neocomian (Early Cretaceous) fossil assemblage from the Kuwajima Formation, Tetori Group, Shiramine, Ishikawa, Japan.* Shiramine Village Board of Education, Ishikawa Prefecture, Japan, 277 pp. [In Japanese, English abstract].

HOFFSTETTER, R. and GASC, J. P. 1969. Vertebrae and ribs of modern reptiles. 201–310. *In* GANS, C., BELLAIRS, A. d'A. and PARSONS, T. S. (eds). *Biology of the Reptilia*, **1**. Academic Press, London, 373 pp.

ISAJI, S., OKAZAKI, H., HIRAYAMA, R., MATSUOKA, H., BARRETT, P., TSUBAMOTO, T., YAMAGUCHI, M., YAMAGUCHI, I. and SAKUMOTO, T. 2005. Depositional environments and taphonomy of the bone-bearing beds of the Lower Cretaceous Kuwajima Formation, Tetori Group, Japan. *Bulletin of the Kitakyushu Museum of Natural History and Human History, Series A, Natural History*, **3**, 123–133.

KEARNEY, M. 2003*a*. Systematics of the Amphisbaenia (Lepidosauria: Squamata) based on morphological evidence from recent and fossil forms. *Herpetological Monographs*, **17**, 1–74.

—— 2003*b*. The phylogenetic position of *Sineoamphisbaena hexatabularis* reexamined. *Journal of Vertebrate Paleontology*, **23**, 394–403.

KORNHUBER, A. 1893. *Carsosaurus marchesettii*, ein neuer fossiler Lacertilier aus den Kreideschichten des Karstes bei Komen. *Abhandlungen der Kaiserlich-Koenigliche Geologischen Reichsanstalt Wien*, **17**, 1–16.

—— 1901. *Opetiosaurus bucchichi*, eine neue Eidechse aus der unteren Kreide von Lesina in Dalmatien. *Abhandlungen der Kaiserlich-Koenigliche Geologischen Reichsanstalt Wien*, **17**, 1–24.

KRAMBERGER, K. G. 1892. *Aigialosaurus*, eine neue Eidechse aus den Kreideschiefern der Insel Lesina mit Rucksicht auf die bereits beschriebenen Lacertiden von Comen und Lesina. *Glasnik Huvatskoga Naravolosovnoga Derstva (Societas Historico-Matulis Croatica) u Zagrebu*, **7**, 74–106.

KUSUHASHI, N., MATSUOKA, H., KAMIYA, H. and SETOGUCHI, T. 2002. Stratigraphy of the late Mesozoic Tetori Group in the Hakusan Region, central Japan: an overview. *Memoirs of the Faculty of Science, Kyoto University, Geology and Mineralogy Series*, **59**, 9–31.

LEE, M. S. Y. 1997. The phylogeny of varanoid lizards and the affinities of snakes. *Philosophical Transactions of the Royal Society of London, Series B*, **352**, 53–91.

—— 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate phylogeny. *Biological Journal of the Linnean Society*, **65**, 369–453.

—— BELL, G. and CALDWELL, M. W. 1999*a*. The origins of snake feeding. *Nature*, **400**, 655–659.

—— and CALDWELL, M. W. 1998. Anatomy and relationships of *Pachyrhachis problematicus*, a primitive snake with hindlimbs. *Philosophical Transactions of the Royal Society of London, Series B*, **353**, 1521–1552.

—— —— 2000. *Adriosaurus* and the affinities of mosasaurs, dolichosaurs, and snakes. *Journal of Paleontology*, **74**, 915–937.

—— —— and SCANLON, J. D. 1999*b*. A second primitive marine snake: *Pachyophis woodwardi* from the Cretaceous of Bosnia-Herzegovina. *Journal of Zoology*, **248**, 509–520.

—— and SCANLON, J. D. 2002. Snake phylogeny based on osteology, soft anatomy and ecology. *Biological Reviews*, **77**, 333–401.

MACEY, J. R., SCHULTE, J. A., LARSON, A., TUNIYEV, B. S., ORLOV, N. and PAPENFUSS, T. J. 1999. Molecular phylogenetics, tRNA evolution, and historical biogeography in anguid lizards and related taxonomic families. *Molecular Phylogenetics and Evolution*, **12**, 250–272.

MAEDA, S. 1961. On the geological history of the Mesozoic Tetori Group in Japan. *Journal of the College of Arts and Science, Chiba University*, **3**, 369–426. [In Japanese, English abstract].

MANABE, M. 1999. The early history of the Tyrannosauridae in Asia. *Journal of Paleontology*, **13**, 477–482.

—— and BARRETT, P. M. 2000. Dinosaurs. 93–98. *In* MATSUOKA, H. (ed.). *Fossils of the Kuwajima 'Kaseki-kabe' (Fossil-bluff). Scientific report on a Neocomian (Early Cretaceous) fossil assemblage from the Kuwajima Formation, Tetori Group, Shiramine, Ishikawa, Japan.* Shiramine Village Board of Education, Ishikawa Prefecture, Japan, 277 pp. [In Japanese, English abstract].

—— —— and ISAJI, S. 2000. A refugium for relicts? *Nature*, **404**, 953.

—— ROUGIER, G. W., ISAJI, S. and MATSUOKA, H. 2000. Fossil mammals. 107–108. *In* MATSUOKA, H. (ed.). *Fossils of the Kuwajima 'Kaseki-kabe' (Fossil-bluff). Scientific report on a Neocomian (Early Cretaceous) fossil assemblage from the Kuwajima Formation, Tetori Group, Shiramine, Ishikawa, Japan.* Shiramine Village Board of Education, Ishikawa Prefecture, Japan, 277 pp. [In Japanese, English abstract].

MATSUKAWA, M. and OBATA, I. 1994. Dinosaurs and sedimentary environments in the Japanese Cretaceous: a contribution to dinosaur facies in Asia based on molluscan palaeontology and stratigraphy. *Cretaceous Research*, **15**, 101–125.

MATSUMOTO, R., EVANS, S. E. and SHIMOJIMA, S. 2002. The dentary of a choristodere (Reptilia: Archosauromorpha) from the Okurodani Formation, Tetori Group (Early Cretaceous), Japan. *Bulletin of the National Science Museum, Tokyo*, **28**, 43–48.

MATSUOKA, H. 2000*a*. A frog fossil. 50–52. *In* MATSUOKA, H. (ed.). *Fossils of the Kuwajima 'Kaseki-kabe' (Fossil-bluff). Scientific report on a Neocomian (Early Cretaceous) fossil assemblage from the Kuwajima Formation, Tetori Group, Shiramine, Ishikawa, Japan.* Shiramine Village Board of Education, Ishikawa Prefecture, Japan, 277 pp. [In Japanese, English abstract].

—— 2000*b*. Tritylodonts (Synapsida, Therapsida). 53–74. *In* MATSUOKA, H. (ed.). *Fossils of the Kuwajima 'Kaseki-kabe' (Fossil-bluff). Scientific report on a Neocomian (Early Cretaceous) fossil assemblage from the Kuwajima Formation, Tetori Group, Shiramine, Ishikawa, Japan.* Shiramine Village Board of Education, Ishikawa Prefecture, Japan, 277 pp. [In Japanese, English abstract].

MEYER, H. VON 1860. *Acteosaurus tommasinii* aus dem schwarzen Kreide-Schiefer von Comen am Karste. *Palaeontographica*, **7**, 223.

NOPSCA, F. 1908. Zur kenntnis der fossilen Eidechsen. *Beitrage zur Palaontologie und Geologie Osterreich-Ungarns und des Orients*, **21**, 33–62.

—— 1923. *Eidolosaurus* and *Pachyophis*. Zwei neue Neocom Reptilien. *Palaeontographica*, **65**, 97–154.

NYDAM, R. L. 2000. A new taxon of helodermatid-like lizard from the Albian–Cenomanian of Utah. *Journal of Vertebrate Paleontology*, **20**, 285–294.

OPPEL, M. 1811. *Die Ordnungen, Familien und Gattungen der Reptilien, als Prodrom einer Naturgeschichte derselben*. Joseph Lindauer, Munich, 87 pp.

PIERCE, S. and CALDWELL, M. W. 2004. Redescription and phylogenetic position of the Adriatic (Upper Cretaceous; Cenomanian) dolichosaur, *Pontosaurus lesinensis* (Kornhuber, 1873). *Journal of Vertebrate Paleontology*, **24**, 373–386.

POLCYN, M. J., TCHERNOV, E. and JACOBS, L. L. 1999. The Cretaceous biogeography of the eastern Mediterranean with a description of a new basal mosasauroid from 'Ein Yabrud', Israel. 259–290. *In* TOMIDA, Y., RICH, T. H. and VICKERS-RICH, P. (eds). *Proceedings of the Second Gondwanan Dinosaur Symposium.* National Science Monographs, **15**, Tokyo, 296 pp.

PREGILL, G. K., GAUTHIER, J. A. and GREENE, H. W. 1986. The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. *Transactions of the San Diego Society of Natural History*, **21**, 167–202.

RAGE, J. C. 1984. Serpentes. *In* WELLNHOFER, P. (ed.). *Handbuch der Palaoherpetologie*, **11**. Gustav Fisher Verlag, Stuttgart, New York, 80 pp.

—— 1988. Un serpent primitif (Reptilia, Serpentes) dans le Cenomanian (base du Cretace superieur). *Comptes Rendus des Séances de l'Academie des Sciences, Paris*, **307**, 1027–1032.

—— and ESCUILLIÉ, F. 2000. Un nouveau serpent bipède du Cénomanien (Crétacé). Implications phylétiques. *Comptes Rendus de l'Academie des Sciences, Paris, Sciences de la Terre et des Planètes*, **330**, 513–520.

—— —— 2002. *Eupodophis*, new name for the genus *Podophis* Rage and Escuillie, 2000, an extinct bipedal snake, preoccupied by *Podophis* Wiegmann, 1843 (Lacertilia, Scincidae). *Amphibia-Reptilia (Leyden)*, **23**, 232–233.

REYNOSO, V. H. 1998. *Huehuecuetzpalli mixtecus* gen. et sp. nov: a basal squamate (Reptilia) from the Early Cretaceous of Tepexi de Rodríguez, central México. *Philosophical Transactions of the Royal Society of London, Series B*, **353**, 477–500.

RIEPPEL, O. 1980. The phylogeny of anguimorphan lizards. *Denkschriften der Schweizerischen Naturforschenden Gesellschaft*, **94**, 1–98.

—— and KEARNEY, M. 2001. The origin of snakes: limits of a scientific debate. *Biologist*, **48**, 110–114.

—— and ZAHER, H. 2000*a*. The braincases of mosasaurs and *Varanus*, and the relationships of snakes. *Zoological Journal of the Linnean Society*, **129**, 489–514.

—— —— 2000*b*. The intramandibular joint in squamates, and the phylogenetic relationships of the fossil snake *Pachyrachis problematicus* Haas. *Fieldiana, Geology, New Series*, **43**, 1–69.

—— —— TCHERNOV, E. and POLCYN, M. J. 2003. The anatomy and relationships of *Haasiophis terrasanctus*, a fossil snake with well-developed limbs from the mid-Cretaceous of the Middle East. *Journal of Paleontology*, **77**, 536–558.

ROMER, A. S. 1956. *Osteology of the reptiles*. University of Chicago Press, Chicago, 772 pp.

ROUGIER, G. W., ISAJI, S. and MANABE, M. 1999. An Early Cretaceous Japanese triconodont and a revision of triconodont phylogeny. *Journal of Vertebrate Paleontology*, **19** (Supplement to No. 3), 72A.

RUSSELL, D. A. 1967. Systematics and morphology of American mosasaurs. *Peabody Museum of Natural History, Yale, Bulletin*, **23**, 1–241.

SETOGUCHI, T., MATSUOKA, H. and MATSUDA, M. 1999*a*. New discovery of an early Cretaceous tritylodontid (Reptilia, Therapsida) from Japan and the phylogenetic reconstruction of Tritylodontidae based on dental characters. 117–124. *In* WANG, Y. Q. and DENG, T. (eds). *Proceedings of the Seventh Annual Meeting of the Chinese Society of Vertebrate Paleontology*. China Ocean Press, Beijing, 274 pp.

—— TSUBAMOTO, T., HANAMURA, H. and HACHIYA, K. 1999*b*. An early Late Cretaceous mammal from Japan, with reconsideration of the evolution of tribosphenic molars. *Paleontological Research*, **3**, 18–28.

SWOFFORD, D. L. 1993. PAUP* – (Phylogenetic Analysis Using Parsimony), version 3.1.1. University of Illinois, Urbana-Champaign.

TAKADA, T., MATSUOKA, H. and SETOGUCHI, T. 2001. The first multituberculate from Japan. 55–58. *In* DENG, T. and WANG, Y. (eds). *Proceedings of the Eighth Annual Meeting of the Chinese Society of Vertebrate Paleontology*. China Ocean Press, Beijing, 301 pp.

TCHERNOV, E., RIEPPEL, O., ZAHER, H., POLCYN, M. J. and JACOBS, L. L. 2000. A fossil snake with limbs. *Science*, **287**, 2010–2012.

TOWNSEND, T. M., LARSON, A., LOUIS, E. and MACEY, J. R. 2004. Molecular phylogenetics of Squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. *Systematic Biology*, **53**, 735–757.

UNWIN, D. M., BAKHURINA, N. N., LOCKLEY, M. G. and MANABE, M. J. 1997. Pterosaurs from Asia. *Journal of the Palaeontological Society of Korea*, **2**, 43–65.

—— MANABE, M., SHIMIZU, K. and HASEGAWA, Y. 1996. First record of pterosaurs from the Early Cretaceous Tetori Group: a wing-phalange from the Amagodani Formation in Shokawa, Gifu Prefecture, Japan. *Bulletin of the National Science Museum, Tokyo, Series C, Geology and Paleontology*, **22**, 37–46.

—— and MATSUOKA, H. 2000. Pterosaurs and birds. 51–54. *In* MATSUOKA, H. (ed.). *Fossils of the Kuwajima 'Kaseki-kabe' (Fossil-bluff). Scientific report on a Neocomian (Early Cretaceous) fossil assemblage from the Kuwajima Formation, Tetori Group, Shiramine, Ishikawa, Japan.* Shiramine Village Board of Education, Ishikawa Prefecture, Japan, 277 pp. [In Japanese, English abstract].

VIDAL, N. and HEDGES, S. B. 2004. Molecular evidence for a terrestrial origin of snakes. *Proceedings of the Royal Society of London, Series B*, **271**, 226–229.

WIENS, J. J. and SLINGHUFF, J. L. 2001. How lizards turn into snakes: a phylogenetic analysis of body-form evolution in anguid lizards. *Evolution*, **55**, 2303–2318.

WU, X. C., BRINKMAN, D. B. and RUSSELL, A. P. 1996. *Sineoamphisbaena hextabularis*, an amphisbaenian (Diapsida, Squamata) from the Upper Cretaceous redbeds at Bayan Mandahu (Inner Mongolia, People's Republic of China), and comments on the phylogenetic relationships of the Amphisbaenia. *Canadian Journal of Earth Sciences*, **33**, 541–577.

—— —— —— DONG, Z., CURRIE, P. J. and HOU, L. G. 1993. Oldest known amphisbaenian from the Upper Cretaceous of Chinese Inner Mongolia. *Nature*, **366**, 57–59.

YABUMOTO, Y. 2000. Fossil fishes. 46–49. *In* MATSUOKA, H. (ed.). *Fossils of the Kuwajima 'Kaseki-kabe' (Fossil-bluff). Scientific report on a Neocomian (Early Cretaceous) fossil assemblage from the Kuwajima Formation, Tetori Group, Shiramine, Ishikawa, Japan.* Shiramine Village Board of Education, Ishikawa Prefecture, Japan, 277 pp. [In Japanese, English abstract].

ZAHER, H. 1998. The phylogenetic position of *Pachyrhachis* within snakes (Squamata, Serpentes). *Journal of Vertebrate Paleontology*, **18**, 1–3.

—— and RIEPPEL, O. 1999. The phylogenetic relationships of *Pachyrhachis problematicus*, and the evolution of limblessness in snakes (Lepidosauria, Squamata). *Comptes Rendus des Séances de l'Academie des Sciences, Paris*, **329**, 831–837.

—— —— 2000. A brief history of snakes. *Herpetological Review*, **31**, 73–76.

—— —— 2002. On the phylogenetic relationships of the Cretaceous snakes with legs, with special reference to *Pachyrhachis problematicus* (Squamata, Serpentes). *Journal of Vertebrate Paleontology*, **22**, 104–109.

APPENDIX

Matrices of characters used in phylogenetic analyses

The MPTs shown in Text-figure 11 were derived using the matrices of Lee (1998), Caldwell and Lee (2000) and Rieppel and Zaher (2000*b*). Each of these matrices is large in terms both of characters and of taxa used. Rather than repeat each matrix and its character list, reference is made to the original papers. Below are listed the codings for *Kaganaias* in each of these matrices, with *Aphanizocnemus* added under Caldwell and Lee (2000) since our codings for this genus have been changed slightly after examination of the specimen. We added several mosasauroid taxa to the Rieppel and Zaher (2000*b*) matrix in order to explore the relationships of *Kaganaias* further: *Adriosaurus* (Caldwell and Lee 2000), *Aphanizocnemus* (Dal Sasso and Pinna 1997; SEE, pers. obs. 2004), *Dolichosaurus* (Caldwell 1999*b*; SEE, pers. obs, 2004), aigialosaurs (Carroll and deBraga 1992), and *Platycarpus* (mosasaurs, Russell 1967).

Codes for variable or uncertain states: A = 0/1; B = 1/2; C = 0/2; D = 3/4.

Caldwell and Lee (2000)

Aphanizocnemus

```
1????  ?????  ????0  0????  ?????  ?0010  ?0?1?  ???1?  0001?  ????0  1????
?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????
?????  ?????  ?????  ?????  ?0???  1????  ?????  00???  ???0?  ?????  ?????
?????  ?????  ?????  ???11  0??33  0????  00-01  ???0?  ?????  ?????  ?????
?????  ?????  ?????  ?????  ?????  ?????  ?????  ???
```

Kaganaias

```
?????  0????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????
?????  11?11  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????
?????  ?????  ?1???  00?1?  ?????  ?????  ?????  ?????  ?????  ?????  20010
?????  ?????  ????0  10111  0013?  0????  00-0?  ?1101  ?1100  1????  ?????
?????  ?????  A2111  1111?  ?0?00  ?????  ????1  ??0
```

Lee (1998)

Kaganaias

```
????0  0????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????
?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????
?????  ?????  ?????  ?????  ?????  ?????  ?????  11011  ?????  ?????  ???AB
00000  1D???  20???  ??110  ?110?  ?????  ?????  ?????  0B1??  011??  00???
?????  ?????
```

Rieppel and Zaher (2000*b*)

Adriosaurus

```
???01  01???  ?0?0?  1?11?  ?0211  ????1  ?0001  0?0?0  ?0???  ?????  ?????
?1???  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ???0?
?????  ?????  ?????  ?????  ?????  ????0  0??1?  ?????  ?????  ?????  ?????
??1??  ?32??  ??0?0  1?10?  00001  ?????  ?????  ???1?  0111?  01100  000??
0????  ?0???  ???01  0???0
```

Aigialosauridae

```
???01  0100?  ?01??  B000?  10?11  ???01  ?0001  00000  100??  ???1?  0??0?
1010?  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ???0?
?02??  ??010  ????0  ???0?  ?0???  ????1  1??10  21?00  1010?  ?1???  1??00-

0102?  13000  000??  1?000  ???00  11???  ?????  ???00  11100  011?0  000??
0????  ?0???  ??001  0?0?0
```

Aphanizocnemus

```
?????  ?????  ?????  ??00?  10???  ????1  ?0001  ?????  ?????  ?????  ?????
?????  ??0??  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????
?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????
??11?  ?32??  ??0?0  1?0C0  ?0000  1????  ?????  ???01  12?0?  011??  000??
0????  ?????  ???01  0????
```

Dolichosaurus

```
?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????
?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????  ?????
?????  ????0  ?????  ??!??  ?0???  ?????  ?????  ?????  ?????  ?????  ???02
0112?  1321?  200?0  1????  ???00  000??  ?????  ???0?  111??  011??  000??
?????  ?????  ???01  0????
```

Kaganaias
???0? ????? ????? ????? ????? ????? ????? ????? ????? ??1?? ?1???
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
????? ????? ????? ????? ????? ????? ????? 2001? ????? ????? ???02
0112? 13??? ????? ??111 ?11?? ????? ????? ????? 01121 011?? 00???
????? ????? ???01 0????

Platycarpus (Mosasauridae)
?1001 01000 001?1 1000? 20211 10101 10001 00000 10011 10112 01?01
01100 01011 10000 00011 10000 01001 1??10 ??1?0 ?0?00 00011 11101
00201 12010 21011 0110? 00011 ?1011 11000 21111 10100 0111? 01?00
11020 13000 000?0 1?100 00000 0100? ?0100 ?0?00 12120 01100 000??
0???? ????? 00001 00000

NOTE ADDED IN PROOF

After acceptance of the manuscript our attention was drawn to the following record of a dolichosaur vertebra from the upper Cenomanian–Turonian horizon of Kazakhstan. Although clearly Asian, at the time of deposition this region was on the fringes of the western Tethys, and thus within the same biogeographical region as other contemporaneous early Late Cretaceous dolichosaurs.

AVERIANOV, A. O. 2001. The first find of a dolichosaur (Squamata, Dolichosauridae) in Central Asia. *Paleontological Journal*, **35**, 525–527.