The Lower Cretaceous lizard genus *Chometokadmon* from Italy

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Abstract

The Lower Cretaceous (Albian) locality of Pietraroia, Italy, has yielded a rich and diverse assemblage of fossil vertebrates, including at least one genus of rhynchocephalian (*Derasmosaurus*) and three named lizards (*Chometokadmon*, *Costasaurus* and *Eichstaettisaurus*). The type and only specimen of *Chometokadmon* is well-preserved but has never been comprehensively described or assessed. It was mistakenly classified as a sphenodontian for many years, but detailed reanalysis has shown that *Chometokadmon* is a squamate. The genus has a relatively unspecialised postcranial skeleton, but the skull is distinctive in having an elongated parietal, expanded squamosal, recurved teeth, and cranial osteoderms. A combination of cranial and postcranial characters (including separable cranial osteoderms, an elongate supratemporal, tooth and pubic morphology) supports a relationship with Anguimorpha, a hypothesis corroborated by cladistic analysis.
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1. Introduction

The Lower Cretaceous (early Albian; Bravi and Garassino, 1998) locality of Pietroroia is in the Apennine Mountains of southern Italy, roughly 75 km northeast of Naples. Excavations have been ongoing, albeit intermittently, for more than 150 years (Costa, 1864, 1866; D'Erasmo, 1915). During this time, the site has yielded a rich assemblage of plants, invertebrates (echinoderms, crustaceans, molluscs) and vertebrates, including fish, amphibians, small reptiles and dinosaurs, most notably the juvenile theropod dinosaur *Scipionyx samniticus* (Leonardi and Teruzzi, 1993; Dal Sasso and Signore, 1998; Bausch and Bravi, 1999; Bravi, 1999). The lepidosaur fauna includes at least one rhynchocephalian, *Derasmosaurus* (Barbera and Macuglia, 1988) and three named lizards, *Chometokadmon* (Costa, 1864), *Costasaurus* (Estes, 1983) and *Eichstaettisaurus* (Evans et al., 2004). Another partial skeleton may represent a second, unnamed, rhynchocephalian (Evans et al., 2004), and a fourth lizard taxon awaits description.

Chometokadmon fitzingeri was described by Costa (1864) on the basis of a single specimen (MPN 539) that he identified as a lizard. In an appendix to the same paper, Costa figured and briefly described another small skeleton (MPN 541) from the same locality. He interpreted this as a second lizard, distinct from *Chometokadmon*, and subsequently named it *Lacerta brevicauda* (Costa, 1866). D'Erasmo (1915) synonymized the two specimens under *Chometokadmon* and referred a third specimen (now lost) to the same genus. Based on the acrodont dentition of Costa's second specimen (MPN 541), D'Erasmo attributed *Chometokadmon* to Rhynchocephalia, despite noting dental inconsistencies in the holotype. Most subsequent reviewers (e.g., von Huene, 1956; Cocude-Michel, 1963; Kuhn, 1969) followed D'Erasmo, although Romer (1956) listed *Chometokadmon* as an indeterminate lizard. The question was resolved by Barbera and Macuglia (1988); Costa was essentially correct. The holotype specimen of *Chometokadmon* is a squamate, but MPN 541 is a rhynchocephalian, and is now the holotype of the genus *Derasmosaurus* (Barbera and Macuglia, 1988).

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Barbera and Macuglia (1988) gave a preliminary description of *Chometokadmon* and tentatively referred it to Scincidae. In the intervening period, however, there has been considerable progress in our knowledge of Jurassic and Early Cretaceous squamates and squamate phylogeny (for a review, see Evans, 2003), prompting a detailed reanalysis of the specimen. Relatively little articulated lizard material exists for the Jurassic and Early Cretaceous, particularly in Euramerica. Furthermore, Pietraroia provides the only European squamate assemblage contemporaneous with mid-Cretaceous (Albian–Cenomanian) lizard assemblages from North America (Nydam, 2000; Nydam and Cifelli, 2002) and Asia (Nessov, 1985, 1988, 1997; Alifanov, 1993).

Institutional abbreviations. BMNH, The Natural History Museum, London, UK; MPN, Museo di Paleontologia, Napoli, Italy.

2. Geology and material

At the locality of "Civita di Pietraroja" (Mt. Matese, southern Italy), two distinct plattenkalk horizons are exposed. The lower horizon is relatively unfossiliferous (Bausch and Bravi, 1999). Above it is a thick sequence of lagoonal limestones, overlain by a second plattenkalk horizon that is the source of the major finds from Pietraroia (early Albian; Bravi and Garassino, 1998). The thickness of this second plattenkalk increases to the southwest reaching a maximum (ca. 15 m) at the original "la Cavere" outcrop. Bausch and Bravi (1999) have reconstructed a shallow lagoonal environment, close to land and frequently isolated from the open sea, but subject to tidal influence and occasional storms. The water would therefore have varied in the level of salinity, and this is reflected in the rock layers that show varying marine or terrestrial influence. The low lying landmass with which the deposit was associated was one of a chain of islands running for perhaps 100–200 km, rather like the Antilles or Bermuda island chain today.

3. Systematic palaeontology

Lepidosauria: Haeckel, 1866
Squamata: Oppel, 1811
Anguimorpha: Fürbringer, 1900
Genus *Chometokadmon* Costa, 1864

Type and only species. Chometokadmon fitzingeri Costa, 1864.

Holotype. MPN 539, articulated skeleton and partial counterpart.

Locality and horizon. La Cavere outcrop, Pietraroia, Mount Matese, Italy. Upper Plattenkalk horizon. IGM (Italian Military Geographic Institute) map sheet 162, III SW-Cusano Mutri, N4577431, E2482228. Lower Cretaceous, Albian.

Diagnosis (emended from Kuhn, 1969). Lizard showing the following combination of derived characters: premaxilla with long nasal process; large maxilla with sharp, recurved teeth; maxilla meets frontal posterodorsally to separate prefrontal and nasal; maxilla with tapering in-turned premaxillary process and posterior process not extending beyond midpoint of orbit; large, ovoid, posteriorly extended external nares; narrow, paired nasals; jugal reaching anterior margin of orbit but separated from prefrontal by lacrimal; maxilla excluded from orbital rim; frontals paired with subparallel orbital margins; nasals and frontals sculptured with low tubercles; small cranial osteoderms associated with orbital and postorbital regions, not attached to skull bones; parietal elongate with long narrow body and long divergent posterior processes; parietal foramen small, anterior to midpoint of bone; supratemporal elongate reaching anterior to level of postparietal notch; squamosal broad with small dorsal process and curved posterior head; anterior margin of supraoccipital overlaps posterior edge of parietal; paroccipital processes long, crested and tapering; vertebrae procoelous, with broad, low neural spines, wide horizontal zygapophyses, but no zygosphene–zygantrum system; anterior caudals with long transverse processes, caudal autotomy septum present (bisecting transverse process); ilium with short narrow blade and small anterior process; pubis directed anteriorly with short symphysis; femur straight, foot longer than femur; fused astragalocalcaneum, wide but proximodistally short, with small groove between tibial and fibular facets; only distal tarsals 3 and 4 retained; fifth metatarsal short and hamate with lateral flange; other metatarsals elongate; phalanges becoming increasingly gracile distally.

4. Description

The type and only specimen (MPN 539) is preserved in dorsal view and is fully articulated (Fig. 1), but both sides of the skull are damaged behind the orbit, and parts of the forelimbs are either obscured by the body (right) or still in the matrix (left). The tail had been autotomised during life and had regenerated to almost its full length. The feet are damaged but are shown in impression on a partial counterpart (mounted in plaster adjacent to the main block).

4.1. Skull

The premaxilla appears to be single, but it is not well preserved and the width of the alveolar region can only be estimated. The dorsal process is narrow and elongate, meeting the tips of the nasals and separating them only for a short distance. A small bifurcate process lies in contact with the tip of the right maxilla, and probably represents the right edge of the premaxillary alveolar margin. (Figs. 1, 2A, B)

The maxilla is well preserved on the right side of the skull, but less so on the left. It is a large bone with a long, deep facial process that had a nearly straight dorsal suture with the nasal and an acute posterior margin that met the prefrontal, lacrimal, and jugal, but was excluded from the anterior and ventral orbital margins. The posterodorsal angle of the bone met the
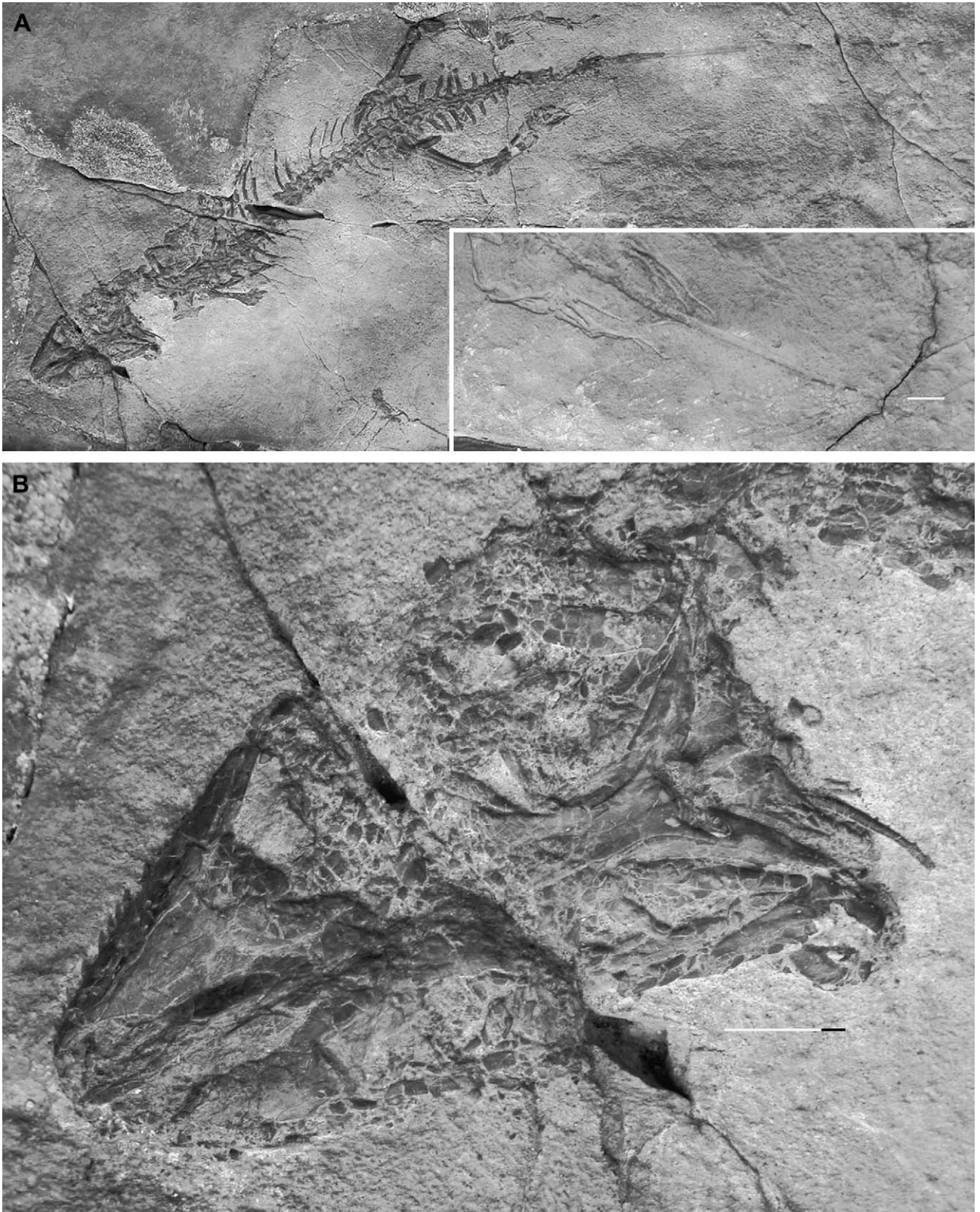
Fig. 1. *Chometokadmon fitzingeri* (MPN 539). A, entire skeleton in dorsal view, with partial counterpart of feet and tail as inset; scale bar represents 10 mm. B, enlargement of skull in dorsal view; scale bar represents 5 mm.

anterolateral process of the frontal. The facial process was probably medially inclined rather than vertical in life, so that the snout was somewhat depressed. The anterior premaxillary process is tapering and curved, whereas the posterior process is relatively short, not extending beyond the midpoint of the orbital margin. On the right side, the alveolar margin is seen to bear 12 teeth with gaps between them. These teeth are sharp, narrow and posteriorly recurved.

The nasals are narrow bones with roughly parallel medial and lateral margins and an extended anteromedial premaxillary process. The anterior margins are deeply excavated by the external nares while laterally each bone has a long straight suture with the maxilla. The nasal does not meet the prefrontal. The right bone has been rotated slightly about its long axis so that its medial margin faces slightly dorsally. It is a simple surface and the two nasals met in a butt joint. Posteriorly, the nasal tapers into an apex that fits into a notch in the anterior margin of the frontal.

The frontals are also paired with a simple median suture. The left bone is almost intact but the posterior half of the right bone is shattered. The dorsal surface is weakly sculptured in a tuberculate pattern. The frontals are longer than wide, slightly wider posteriorly than anteriorly, and only slightly narrowed between the orbits. The anterior margin is deeply notched for the nasal, with a short median process and a longer lateral process that met the posterior tip of the maxilla. Anterolaterally, the bone has a shallow notch for the orbital process of the prefrontal but nothing of the ventral surface is visible. The posterior margin appears straight but part of the bone is missing so that the contact surface for the parietal is not preserved (reconstructed in Fig. 2B).

The unpaired parietal is probably the most distinctive bone of the entire skull. The parietal plate is slightly shorter than the overall length of the frontals, but with the long divergent postparietal processes, the parietal is much longer. The dorsal surface is flat, with no trace of a dorsal crest and no sculpture. The lateral margins are sloping and relatively deep, providing the surface of attachment for the adductor muscles. The bone is narrowest between the large ovoid supratemporal fenestrae, widening anteriorly and posteriorly, but not strongly so. A small parietal foramen persists roughly one third of the way from the anterior margin of the bone. The postparietal processes are strongly divergent, enclosing a posterior angle of around 110°. The medial and lateral surfaces of the processes are both strongly oblique, creating a narrow dorsal crest between them. Posteriorly, these sloping surfaces accommodated epaxial neck muscles. Centrally, the posterior margin is slightly recessed and is overlapped by the supraoccipital, suggesting that metakinesis was at best limited.

Along the antorbital margin of the maxilla, there are three bones. The most dorsal of these is the prefrontal. It has a narrow orbital portion that runs parallel to the frontal, notching the lateral margin of that bone, and a more expanded ventral part that contributes to the antorbital skull wall. Below the prefrontal is a narrow lacrimal and this, in turn, meets the jugal ventrally. The jugal is preserved on the right side as a long narrow bar running along the dorsal surface of the maxilla,

notching it slightly, before contacting the lacrimal. Nothing of the posterior part of the jugal is visible.

A crack divides the anterior and posterior parts of the skull, disrupting the postorbital region. A short region of the skull roof is missing. The problem is exacerbated by a scatter of osteoderms that obscure some of the underlying morphology (see below). The posterolateral corner of the left frontal is flanked by a small oblique bar of bone and a similar structure contacts the anterolateral edge of the parietal on the right side. These bony fragments are here tentatively interpreted (Fig. 2) as anterior and posterior parts of a bone straddling the lateral edge of the frontoparietal suture, but with the central part lost in the cracked region. The only bone with these relations in a squamate is the postfrontal or postorbitofrontal, if the postfrontal is fused to the more ventrolaterally placed postorbital.

Distinctive squamosals are preserved on both sides of the skull. They have blade-like anterior processes and long curved terminal portions offset from the anterior blade. At the junction between the two parts there is a slight dorsal expansion. Neither squamosal shows an obvious postorbital or postorbitofrontal facet, and both are rotated so that the anterior blade is directed anteroventrally. This suggests, at least, that the articulation between the squamosal and postorbital bar was not strong. The anterior process of the squamosal would not have reached beyond the midpoint of the upper temporal fenestra. On the left side, the squamosal contacts an anteroposterior series of bone fragments. Some of these must pertain to the lower jaw but more dorsal fragments may belong to an upper temporal bar, placed well lateral to the parietal.

On both sides, long slender supratemporals lie medial to the squamosals and overlap the lateral margins of the parietals. Both streptostylic quadrates are in situ but are rather obscured by overlying bones.

The braincase is well preserved but only partially visible. The supraoccipital is fully exposed behind the parietal, despite the length of the parietal plate. It has a strong dorsal crest and, somewhat unusually, its anterior margin is drawn into short processes that overlap the posterior margin of the parietal (a similar condition was recently reported in the Late Cretaceous mosasauroid, *Pontosaurus*; Pierce and Caldwell, 2004). Bilaterally, the supraoccipital is sutured to a large otooccipital. Each otooccipital extends posterolaterally into a long slender paroccipital process that meets the squamosal and supratemporal but apparently not the parietal. The foramen magnum is also visible with the basioccipital forming its ventral margin. The prootics are largely obscured by the parietal, but their lateral margins are exposed below the parietal plate. They extend well forward suggesting the presence of strong alary processes.

The palate is not exposed and since the specimen is embedded in a block of plaster, it is not possible to prepare the ventral surface. However, a slender element running back lateral to the left prootic is presumably the posterior ramus of the pterygoid. A small columnar epipterygoid runs perpendicular to it to reach the anterior part of the prootic.
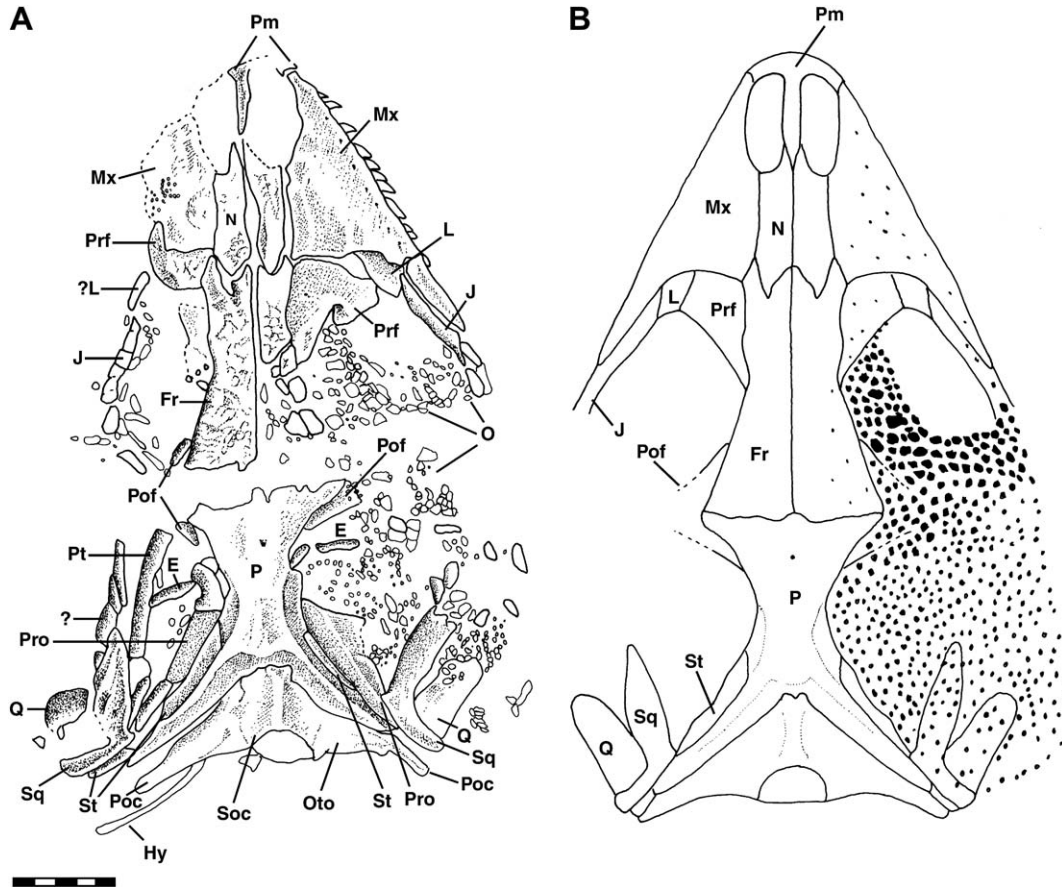
Fig. 2. The skull of *Chometokadmon fitzingeri* (MPN 539). A, dorsal view as preserved. B, reconstruction of skull and osteoderms. Scale bar represents 5 mm. Abbreviations: E, epipterygoid; Fr, frontal; Hy, hyoid; J, jugal; L, lacrimal; Mx, maxilla; N, nasal; O, osteoderms; Oto, oto-occipital; P, parietal; Pm, premaxilla; Poc, paroccipital process; Pof, postfrontal or postorbitofrontal; Prf, prefrontal; Pro, prootic; Pt, pterygoid; Q, quadrate; Soc, supraoccipital; Sq, squamosal; St, supratemporal; ?, fragments of lower jaw and/or upper temporal bar.

The exposed right side of the skull is damaged posterolaterally due to the break in the block, and several of the skull bones have fragmented. However, the right orbital and temporal regions show a tessellate pattern of bone fragments that are too many to have come from broken skull bones, and, in the orbit at least, are too orderly in their arrangement. The skull therefore seems to have been covered, at least partially, by a mosaic of small osteoderms that were not fused to the underlying skull bones. Small patches of these are preserved in situ on the left maxilla, on the front of the parietal, and over the right squamosal and quadrate (Fig. 2A, B). Although a few of these osteoderms have been displaced inwards, they seem to map the boundaries of the eye opening (Fig. 3A). There is no trace of the scleral ossicles, but these presumably collapsed inward with the eyeball. The osteoderms do not extend postcranially.

4.2. Postcranial skeleton

4.2.1. Vertebral column

The cervical column is disrupted behind the skull and again at the level of the twelfth presacral vertebra. The atlanto-axial region has been dislocated from the braincase and moved towards the right side, where it lies adjacent to the right quadrate. Small rectangular elements in this region may be parts of the atlantal arch. Immediately adjacent to these is an irregular bony element here interpreted as the axis in left lateral view. It has a low, anteriorly overhanging neural spine with a prominent anterior zygapophysis. The neural arch pedicels are notably shorter but the centrum is exposed and is seen to have a posterior condyle, establishing that the vertebrae were procoelous. At least one additional vertebra lies between the axis and the main vertebral series as the column returns into dorsal view. The pectoral girdle is mostly obscured and this makes it difficult to judge the level of the first rib long enough to reach the sternum. Presacral vertebrae (PS) 5−7 bear short sturdy ribs that may have supported the girdle. PS 8 has a longer rib, and that on PS 9 was probably, but not certainly, the first dorsal. This would give a conservative cervical count. In all, there seem to have been ca. 25 presacrals (thus cervical:dorsal as 7:18, 8:17 or 9:16). The presacral vertebrae are fully exposed and are of generalised form (Fig. 3B). The neural arches are relatively short, with large, widely spaced zygapophyses but no accessory zygosphenes. There is little development of a neural spine.

The sacrum consists of two vertebrae with strong, sacral ribs. Following these are five anterior caudals with long
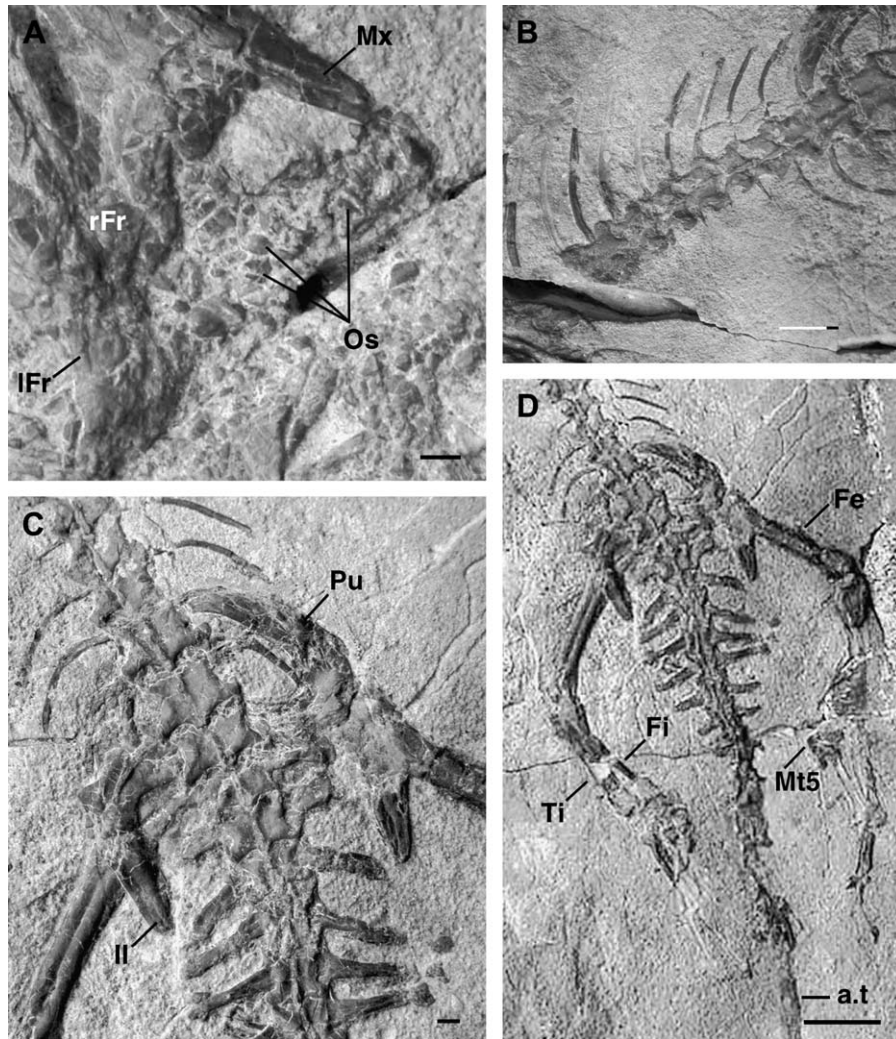
Fig. 3. *Chometokadmon fitzingeri* (MPN 539). A, enlargement of right orbital region to show detail of the osteoderms. B, mid-dorsal vertebrae. C, enlargement of pelvic region and sacrum. D, hindlimbs and tail. Scale bars represents 1 mm in A and C, 5 mm in B, and 10 mm in D. Abbreviations: a.t, autotomised tail replacement; lFr, left frontal; Il, ilium; Mx, maxilla; Os, cranial osteoderms; Pu, pubis; rFr, right frontal.

transverse processes (length greater than the width of the neural arch), and then a further six with processes that decrease in size. On the third of these, an autotomy septum passes through the transverse process. The tail apparently fractured in life through the fourteenth caudal and then regenerated to a length roughly equal to that of the trunk. An impression of the soft tissue replacement is preserved on the block (Fig. 3D, a.t).

4.2.2. Pectoral girdle and forelimb

The pectoral girdle is largely obscured by the vertebrae and ribs, except for some of the cartilaginous epicoracoid parts on the right. Lying below presacral vertebrae 4−5, and overlain by the short ribs of the neck, is a pair of bony rods connected in a roughly V-shape. This is probably part of an emarginated coracoid plate. There is a similar rod contralaterally. The left humerus is almost complete (ca. 18 mm in length), with a narrow proximal head and a broader distal head bearing a strong entepicondyle and a weak ectepicondyle. There is no obvious ectepicondylar foramen. The proximal end of the ulna is in articulation, with a fully ossified olecranon and no trace of the epiphysial suture, suggesting the animal was mature (but see below). The rest of the forearm and hand extends into the block but further preparation has not been possible.

4.2.3. Pelvic girdle and hind limb

The pelvis is better preserved than the pectoral girdle (Fig. 3C, D). Somewhat surprisingly, despite the strong ossification in other parts of the body, the components of the pelvis are not conjoined. This is a feature usually found either in immature squamates or aquatic ones, but this is problematic given the fusion of the epiphyses. Both ilia are exposed in medial view (since they have fallen outwards). Each has a long, rather narrow blade. This is almost horizontal and the sacral rib facets are placed in a relatively proximal position.

Each bone has a small anterior tuberosity of a kind frequently found in living terrestrial lizards that show some tendency to raise the trunk on the hind limbs, either in standing (varanids) or bipedal running (many iguanians, some teiids and varanids: Snyder, 1949, 1952, 1954; Brian Ruth, pers. comm. July 2004). Each pubis is elongate, with curved medial and lateral borders, and a short, anteriorly placed, symphysial region. The pectineal process is not obvious and was either reduced or dorsally placed and obscured. The ischia are obscured by the sacrum.

The femur is essentially straight (ca. 20 mm) and featureless. The tibia and fibula are shorter (ca. 16.5 mm), with a robust tibia and a markedly more slender fibula. The ankle is preserved on the left side. It shows a fully co-ossified astragalocalcaneum that is proximodistally short but quite wide. The tibial facet is narrow and covers part of the medial margin; the fibular facet is separated from the tibial facet by a narrow groove, but is raised above the surface of the bone and extends further onto the dorsal surface. The lateral border of the astragalocalcaneum curves distally, expanding into a small lateral wing close to the position of metatarsal 5. The distal border is concave medially where it receives a large distal tarsal (dt) 4, and straighter laterally where it extends towards the lateral wing. There are only two distal tarsals, the large dt4 and a small, trapezoid dt3. The proximal surface of dt4 appears to have two condylar surfaces but these merge distally into a single body. Dt4 meets the fourth and fifth metatarsals. With the exception of the fifth metatarsal (see below), the metatarsals are long and straight with strong proximal heads. They were undoubtedly the strongest part of the foot and make the greatest contribution to its length. The fifth metatarsal is much shorter, proximally displaced, and has both a plantar tubercle and a distolateral flange. The phalanges are relatively short but quite slender and the pedal phalangeal formula is 2:3:4:5:4. The unguals are slender. In total, the foot (ca. 32.5 mm along digit 4) is nearly as long as the femur and tibia combined (ca. 36.5 mm), with a robust proximal part and a rather more delicate distal region.

5. Phylogenetic position of *Chometokadmon*

The genus *Chometokadmon* has remained in obscurity for more than a century, yet the type specimen is one of the relatively few articulated lizard fossils known from the Early Cretaceous of Euramerica (with, for example, Las Hoyas, Spain, Evans and Barbadillo, 1997, 1998, 1999; Tepexi de Rodriguez, Mexico, Reynoso, 1998, Reynoso and Callison, 2000; Pietraroia, Evans et al., 2004).

Chometokadmon is clearly a squamate (Costa, 1864) and not a rhynchocephalian (D'Erasmo, 1915), as demonstrated by the dentition; the structure of the quadrate and its suspension; the procoelous vertebrae; the emarginated coracoid; the elongated anterior ramus of the pubis; and the derived tarsal morphology. Today, most squamate systematists recognise four major clades: Iguania, Gekkota, Scincomorpha, and

Anguimorpha, with Serpentes and Amphisbaenia (+Dibamidae) variously placed (e.g., Estes et al., 1988; Rieppel, 1988; Evans and Barbadillo, 1998; Lee, 1998). Most workers unite all squamates except iguanians into the clade Scleroglossa (for a detailed discussion of different hypotheses of relationship, see Evans, 2003, but see also Townsend et al., 2004, for an alternative view). Osteologically, Scleroglossa are characterised, amongst other features, by a bifurcate medial ramus of the postfrontal/postorbitofrontal (Estes et al., 1988). In addition, with the exception of the marine iguana *Amblyrhynchus* (de Queiroz, 1987), no iguanian is known to have either cranial or postcranial osteoderms, and this feature has not been reported in any of the Jurassic—Cretaceous taxa placed on the squamate stem in recent analyses (e.g., Evans and Barbadillo, 1998, 1999; Evans and Chure, 1998; Reynoso, 1998). The Jurassic *Ardeosaurus* (Mateer, 1982) and the Early Cretaceous *Yabeinosaurus* (Evans et al., 2005), for example, have cranial ornament but there is no evidence that this results from the attachment of osteoderms. Within Scleroglossa, osteoderms are rare in Gekkota (but not unknown, e.g., *Gekkonia*, SEE, pers. obs.), absent in teiids, xantusiids and gymnophthalmids, and variable in *Varanus* (Estes et al., 1988). They are highly developed in anguids, scincids, cordylids, and the extinct Paramacellodidae (scincoid relatives; Evans and Chure, 1998), and are also present in helodermatids, *Lanthanotus* (Maisano et al., 2002), *Xenosaurus* and *Shinisaurus* (Bever et al., 2005). Indeed, the presence of dorsal body osteoderms has been listed as a synapomorphy of Anguimorpha (e.g., Estes et al., 1988; Gao and Norell, 1998). However, although cranial osteoderms occur in all of these groups, body osteoderms may be reduced. Thus *Xenosaurus* and *Shinisaurus* have cranial osteoderms but there are relatively few on the body (Bever et al., 2005); in *Lanthanotus*, osteoderms are thin and scattered within the skin (Maisano et al., 2002), and in *Varanus*, they are reduced or absent.

In their preliminary study, Barbera and Macuglia (1988) suggested that *Chometokadmon* might be a scincoid, but the absence of dorsal and ventral body osteoderms argues against this, as does the attachment of the jaw adductor musculature to the lateral rather than ventral surfaces of the parietal. The combination of slender, recurved, and well-separated teeth; the small, loosely attached cranial osteoderms; reduced or absent body osteoderms; paired frontals with subparallel margins; a slight retraction of the nares; a long, anteriorly extended supratemporal; a relatively elongated pubis; and the non-fusion of the pelvic components are all features variably found in non-anguid anguimorphs (Estes et al., 1988; Lee, 1998). Conflicting characters include the slight dorsal process/thickening of the squamosal (but also in the anguimorph *Xenosaurus*), the relatively short presacral series (fewer than 26; also in *Xenosaurus* and *Shinisaurus*, Estes et al., 1988), and the retention of autotomy septa in the tail. Unfortunately, many key characters of the braincase, the palate, and the jaws (Estes et al., 1988; Gao and Norell, 1998; Lee, 1998) remain unknown for *Chometokadmon*.

Chometokadmon bears a general resemblance to two other Late Jurassic/Early Cretaceous Euramerican genera, *Dorsetisaurus* (Hoffstetter, 1967) and *Parviraptor* (Evans, 1994), both of which have been attributed to Anguimorpha (Hoffstetter, 1967; Evans, 1994; Nydam, 2000). All three genera have long, crested postparietal processes, and all three show a reduction of mobility between the parietal and the braincase, although in different ways. In *Parviraptor* (Fig. 4), a posteromedian parietal process overlapped the supraoccipital, while in *Chometokadmon* (Fig. 2) and *Dorsetisaurus* anterior processes of the supraoccipital overlap the parietal. All three have paired, parallel-sided frontals, but these are sculptured in *Chometokadmon* and *Dorsetisaurus* (Fig. 5) and smooth in *Parviraptor*. *Parviraptor* differs from both *Chometokadmon* and *Dorsetisaurus* in having paired parietals (but this may be a paedomorphic trait, given the very slow completion of the vertebral condyles in this taxon; Evans, 1994), whereas *Chometokadmon* is characterised by the small dorsal flange on the squamosal. Both *Chometokadmon* and *Parviraptor* have an elongated parietal table in which the adductor musculature attached to narrow lateral edges; in *Dorsetisaurus* the parietal table is shorter (Fig. 5). *Chometokadmon* and *Parviraptor* share the possession of recurved maxillary teeth in a tooth row that extended posteriorly below the anterior part of the orbit, but unfortunately the implantation and tooth replacement pattern of *Chometokadmon* cannot be verified. In *Dorsetisaurus*, the mature teeth are distinctive in forming triangular blades (Hoffstetter, 1967). The maxillae also differ in other significant ways. The facial process is long and low in *Parviraptor* but tall and triangular in *Chometokadmon* and *Dorsetisaurus* (Fig. 5). In *Parviraptor*, the smooth dorsomedial margin of the maxilla suggests it was free for much of its length (forming the margin of a retracted naris), whereas the maxilla of the other two genera certainly met the nasal in the posterior part of the naris.
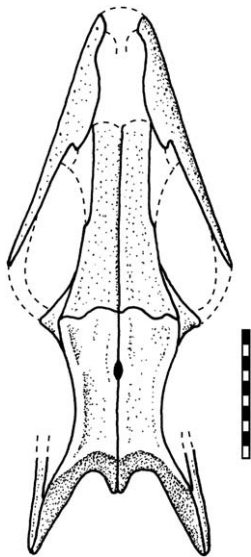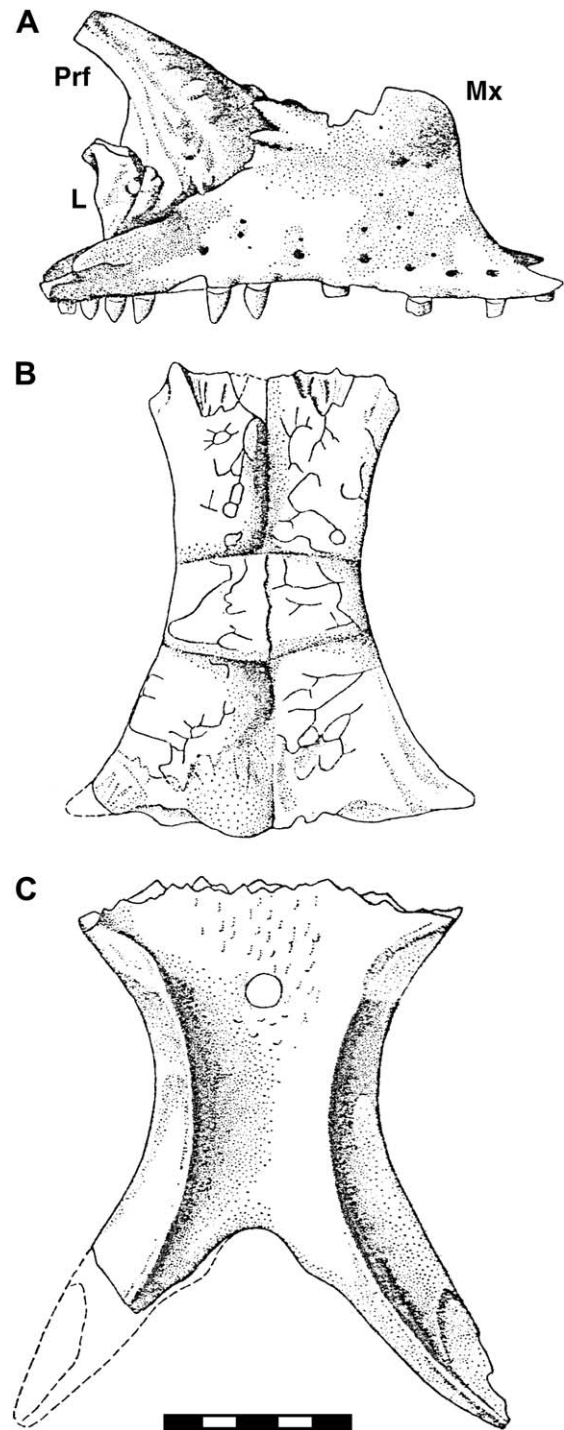

Fig. 5. Skull bones of *Dorsetisaurus purbeckensis* (BMNH R.8129). A, right maxilla, prefrontal, and lacrimal, inlateral view. B, frontals in dorsal view. C, parietal in ventral view. Modified from Hoffstetter (1967, fig. 11); abbreviations as in Fig. 1. Scale bar represents 5 mm.

Fig. 4. Reconstruction of the skull of *Parviraptor estesi*, dorsal view; reproduced from Evans (1994, text-fig. 5). Scale bar represents 10 mm.

Chometokadmon resembles *Dorsetisaurus* in having a free lacrimal and an anteriorly elongated prootic; both have long narrow paroccipital processes. There is no trace of osteoderms on the associated specimens of *Dorsetisaurus* (Hoffstetter, 1967; SEE, pers. obs.) but the presence or absence of cranial osteoderms cannot be confirmed in

Parviraptor (Evans, 1994). Postcranially, *Dorsetisaurus* is virtually unknown but whereas *Parviraptor* vertebrae have some development of the zygosphene−zygantral system, *Chometokadmon* appears to lack this. The remainder of the skeleton cannot be compared. Thus *Chometokadmon* shows both similarities with and differences from *Dorsetisaurus* and *Parviraptor*, and the three genera are clearly distinct.

In order to test the possible anguimorph affinities of *Chometokadmon*, we added it (+*Dolichosaurus*, Caldwell, 2000 and SEE, pers. obs.; *Dorsetisaurus*; and *Parviraptor*) to a matrix combined from Evans and Barbadillo (1997, 1998, 1999) and Evans and Chure (1998), using the 212 characters of the latter study. The analysis was run using PAUP version 3.1.1 (Swofford, 1993), rooting by outgroup (Rhynchocephalia). Xenosauridae has been left as a single entry because preliminary runs with both *Xenosaurus* and *Shinisaurus* always grouped them as sister taxa. We do, however, recognise arguments for a separate Shinisauridae (e.g., Conrad, 2004; Bever et al., 2005). Similarly, because the preliminary heuristic searches (not shown) found a monophyletic Scincomorpha (Paramacellodidae, Scincidae, Cordylidae, Xantusiidae, Teiidae, Gymnophthalmidae, Lacertidae), they were grouped simply as Scincomorpha in the main analysis. A Branch and Bound search yielded 14 MPTs (Maximum Parsimony Trees: Tree length = 642; Consistency Index = 0.841; Rescaled Consistency Index = 0.414). The strict and semistrict consensus trees (not shown) gave almost no resolution above Rhynchocephalia and *Bavarisaurus*, yielding a polytomy with only two small clades (one of living anguimorphs and the other of snakes and *Dolichosaurus*). However, the 50% Majority Rule Tree (Fig. 6) places *Chometokadmon* within crown-group Squamata and within Scleroglossa, as one of three Jurassic/Cretaceous lizards (*Chometokadmon*, *Dorsetisaurus*, *Parviraptor*) forming

a series of consecutive sister taxa to living anguimorphs. This is a relatively well-supported grouping (jaw and tooth morphology, palate structure, the position and attachment of cervical intercentra), but unfortunately *Chometokadmon* lacks information for almost all of these characters. With living anguimorphs it shares the presence of separate frontals (reversal of character 6), cephalic osteoderms (108), and cranial rugosities (109), but this hypothesis of relationship must remain tentative pending further analyses and more data. Previous analyses (e.g., Evans, 1994; Nydam, 2000) have placed *Parviraptor* in a more crownward position. Similarly, snakes, *Dolichosaurus*, and amphisbaenians lie one step outside the traditional Anguimorpha on this tree, but allowance must be made for the almost total lack of useful cranial data for *Dolichosaurus*, our limited knowledge of early snakes, and the absence of information on basal amphisbaenian morphology.

Acknowledgments

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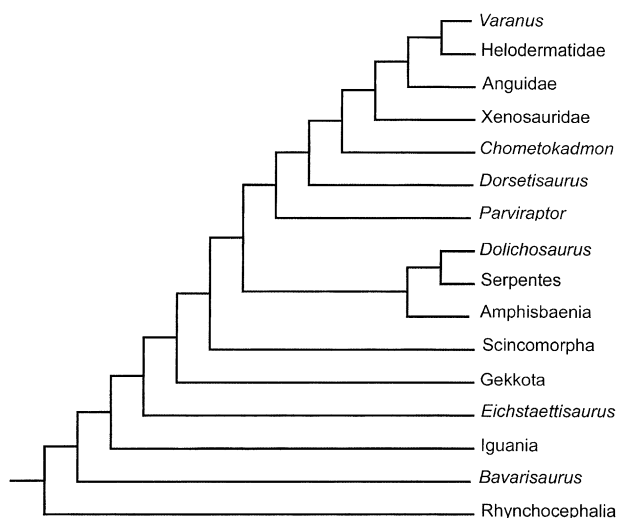

Fig. 6. Strict Consensus of 14 MPTs derived from a Branch and Bound search using a matrix combined from Evans and Barbadillo (1997, 1998, 1999) and Evans and Chure (1998), showing a hypothesis of relationship for *Chometokadmon* within Squamata.

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Appendix

The full character list can be found in Evans and Chure (1998). Below we list the codings for taxa added to the original matrix.

Chometokadmon

?0010	00???	0????	00??2	000?1	?000?	?????	?????	?1???	0????	?????	?????
?????	?????	?????	00???	?200?	?00?0	???1?	?????	???1?	0011?	?????	?????
?????	????1	1111?	?????	1??1?	???1?	111??	???1?	?121?	?????	?????	?????
?????	?????	1?0?1	111??	?????	????2	??					

Dolichosaurus

?????	?????	?????	0????	?????	?????	?????	?????	?????	?????	?????	?2??1
?0???	?????	?????	?????	12024	10230	2?000	?0???	??3??	?0000	?????	?????
?????	?????	??1?0?	?????	????1	21110	1????	?????	??1??	?????	?????	?????
?????	?????	?????	?????	??01?	0????	??					

Dorsetisaurus

100?0	00000	0????	01000	01001	?????	?????	?01??	?100?	00??0	00010	00010
000??	???1?	01121	00???	020??	?????	?????	?????	?????	0000?	?????	?????
?????	?????	1????	111??	2?1?1	2????	1????	?????	?????	?????	?????	?????
?????	?????	?????	?????	0?01?	0????	?2					

Parviraptor

?1??0	00?11	00???	00002	00???	?01??	??1??	00100	1????	00012	?????	?????
?????	?????	02221	00???	0201?	1?0??	?????	?????	?????	??00?	?????	?????
?????	????1	11?1?	?11??	???1?	?11??	?????	?????	?????	?????	?????	?????
?????	?????	1????	?1???	0????	?????	?2					