

New lizards and rhynchocephalians from the Lower Cretaceous of southern Italy

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The Lower Cretaceous (Albian age) locality of Pietraroia, near Benevento in southern Italy, has yielded a diverse assemblage of fossil vertebrates, including at least one genus of rhynchocephalian (*Derasmosaurus*) and two named lizards (*Costasaurus* and *Chometokadmon*), as well as the exquisitely preserved small dinosaur, *Scipionyx*. Here we describe material pertaining to a new species of the fossil lizard genus *Eichstaettisaurus* (*E. gouldi* sp. nov.). *Eichstaettisaurus* was first recorded from the Upper Jurassic (Tithonian age) Solnhofen Limestones of Germany, and more recently from the basal Cretaceous (Berriasian) of Montsec, Spain. The new Italian specimen provides a significant extension to the temporal range of *Eichstaettisaurus* while supporting the hypothesis that the Pietraroia assemblage may represent a relictual island fauna. The postcranial morphology of the new eichstaettisaur suggests it was predominantly ground-living. Further skull material of *E. gouldi* sp. nov. was identified within the abdominal cavity of a second new lepidosaurian skeleton from the same locality. This second partial skeleton is almost certainly rhynchocephalian, based primarily on foot and pelvic structure, but it is not *Derasmosaurus* and cannot be accommodated within any known genus due to the unusual morphology of the tail vertebrae.

Key words: Lepidosauria, Squamata, Rhynchocephalia, palaeobiogeography, predation, Cretaceous, Italy.

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Introduction

The genus *Eichstaettisaurus* was first described from the Tithonian age Solnhofen Limestones of Wintershof bei Eichstätt, Germany (Broili 1938), although under the name *Ardeosaurus schroederi*. Hoffstetter (1953) recognised that the specimen was distinct from *Ardeosaurus* (another lizard from the same region), and erected a new generic name, *Broilisaurus*. Because this was preoccupied, Kuhn (1958) replaced it with *Eichstaettisaurus*. The single Solnhofen specimen of *Eichstaettisaurus* is well-preserved, but its phylogenetic position has remained controversial. Traditionally, it was placed in the family Ardeosauridae, but the two genera share only a relatively conservative skeletal morphology and there are no synapomorphies to support a close relationship (Evans 1993).

For many years, *Eichstaettisaurus* was represented solely by the Solnhofen holotype, but a second eichstaettisaur was recently described from the basal Cretaceous locality of Montsec, Catalonia, Spain (Evans, Lacasa Ruis, and Erill Rey 1999). This specimen is small and poorly preserved, but its morphology is close to that of *Eichstaettisaurus*, extending the geographical range to another part of the European Mesozoic archipelago. Now a third specimen has been recovered from a substantially younger deposit in Italy.

The Lower Cretaceous (Albian age, Bravi and Garassino 1998) locality of Pietraroia is in southern Italy, roughly 75 km northeast of Naples (Fig. 1). Excavations in the fine-grained marine/lagoonal limestones have been ongoing, albeit intermittently, for more than 150 years (Costa 1851, 1864, 1866; d'Erasmus 1914–15). During this time, the site yielded a rich assemblage of plants, invertebrates (echinoderms, crustaceans, molluscs) and vertebrates, including fishes, amphibians, and reptiles (Leonardi and Teruzzi 1993; Dal Sasso and Signore 1998; Barbera and La Magna 1999; Bravi 1999).

To date, three lepidosaurian taxa have been described from Pietraroia: *Costasaurus rusconi*, a poorly preserved lizard (Estes 1983; Barbera and Macuglia 1988, 1991), *Chometokadmon* (Costa 1864), a second lizard (Barbera and Macuglia 1988, 1991) currently under restudy by us, and *Derasmosaurus* (Barbera and Macuglia 1988), a rhynchocephalian incorrectly attributed to *Chometokadmon* by d'Erasmus (1914–15). In recent years, three further specimens have been recovered. Two of these are described here. The first has a relatively well-preserved skull and a more fragmentary postcranial skeleton. The second is incomplete, comprising the posterior trunk, hind limbs and tail. Although the specimens clearly represent different taxa, they are linked by a coincidence. In the abdominal cavity of the second lepidosaur, there is a partially disarticulated skull matching that of the first.

Geology and materials

The deposits of Pietraroia (Mount Matese, Southern Italy) form part of a Mesozoic carbonate platform sequence. At the locality of “Civita di Pietraroia”, there are two distinct plattenkalk horizons, assigned to the early Albian on the basis of foraminiferal biozonology (Bravi and Garassino 1998). The lower horizon is relatively unfossiliferous. Above it is a thick sequence of lagoonal limestones, overlain by a second plattenkalk horizon with a depth of 8–9 m. The thickness of the second plattenkalk increases to the southwest reaching a maximum (ca. 15 m) at the original “la Cavere” outcrop, and is the source of the major fossil finds from Pietraroia. According to Bausch and Bravi (1999), this fossiliferous plattenkalk was laid down close to a small island, in a shallow lagoonal environment frequently isolated from the open sea but subject to tidal influence and occasional storms. Carannante, Vigorito, and d’Argenio (2001) recently proposed a new model incorporating a submarine channel instead of a lagoon, but further work is needed to clarify this. Freshwater would have flowed into the system from the adjoining landmass, bringing the carcasses of terrestrial animals. The climate was tropical or subtropical (Bravi and Garassino 1998).

In combination, the depositional conditions at Pietraroia have resulted in a fine-grained limestone that preserved soft tissues, such as cartilage and viscera (for example, in the small dinosaur *Scipionyx*, Dal Sasso and Signore 1998), as well as bone.

Institutional abbreviations.—A, excavation number prefix for specimens collected at Pietraroia and held by the Museo di Paleontologia, Università di Napoli, Italy; BSPHM, Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany; IEL, collections of the Institut d’Estudis Ilerdencs, Lleida, Spain; MPN, Museo di Paleontologia, Università di Napoli, Italy.

Systematic palaeontology

Lepidosauria Haeckel, 1866

Squamata Opeel, 1811

Eichstaettisaurus Kuhn, 1958

Type species: *Eichstaettisaurus schroederi* (Broili, 1938).

Other species: *Eichstaettisaurus gouldi* sp. nov.

Distribution.—Late Jurassic (Tithonian), Germany, and Early Cretaceous (Berriasian, Albian), Spain and Italy.

Revised diagnosis.—Squamate genus characterised by the combination of a dorsoventrally compressed head; single frontal with distinct orbital narrowing, strong cristae cranii, and a wide posterior border; simple abutting frontoparietal suture with no overlap surfaces or interdigitation; short maxilla that does not extend beyond midpoint of orbital rim; small unicuspid teeth with labiolingually flattened tips; limbs

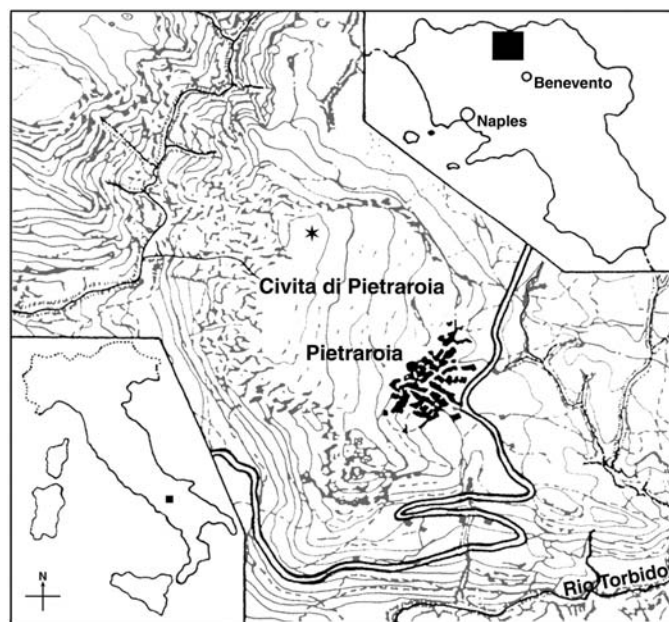


Fig. 1. The locality of Civita di Pietraroia showing the topology of the outcrop (la Cavere, marked by asterisk) and its relationship to the small town of the same name, with insets demonstrating (bottom left) the position of Pietraroia within Italy and (top right) its position in relation to the city of Naples. Modified from Bravi (1996: 148).

short in relation to length of presacral column; epipodials shorter than propodials, but particularly so on the hind limb; manus and pes similar in length to their respective propodials, and without marked disparity in length between the inner and outer digits.

Differs from *Ardeosaurus* (Upper Jurassic, Germany: Mateer 1982) in having narrow conjoined frontals (rather than wide and paired), a more open upper temporal fenestra (constricted in *Ardeosaurus*), and a simple rather than interdigitated frontoparietal suture; differs from *Ardeosaurus* and *Meyasaurus* (Lower Cretaceous, Spain: Evans and Barbadillo 1997) in lacking cranial sculpture; resembles *Ardeosaurus*, *Bavarisaurus* (Upper Jurassic, Germany: Hoffstetter, 1964), *Scandensia* (Lower Cretaceous, Spain: Evans and Barbadillo 1998), *Huehuecuetzpalli* (Lower Cretaceous, Mexico: Reynoso 1998), and *Hoyalacerta* (Lower Cretaceous, Spain: Evans and Barbadillo 1999), and differs from *Meyasaurus*, *Chometokadmon* (Lower Cretaceous, Italy: work in progress), and paramacelodids (Upper Jurassic–Lower Cretaceous, Laurasia and Africa: Evans and Chure 1998) in having paired, rather than fused, premaxillae; differs from *Bavarisaurus*, *Meyasaurus*, *Chometokadmon*, and *Huehuecuetzpalli* in having a relatively short symmetrical pes (rather than elongate and strongly asymmetrical), and from *Bavarisaurus*, *Hoyalacerta*, and *Huehuecuetzpalli* in having a broad squamosal; differs from paramacelodids in lacking bony osteoscutes; resembles *Huehuecuetzpalli*, *Bavarisaurus*, and *Scandensia* and differs from *Hoyalacerta*, *Ardeosaurus*, and paramacelodids in having amphicoelous rather than procoelous vertebrae; differs from *Chometokad-*

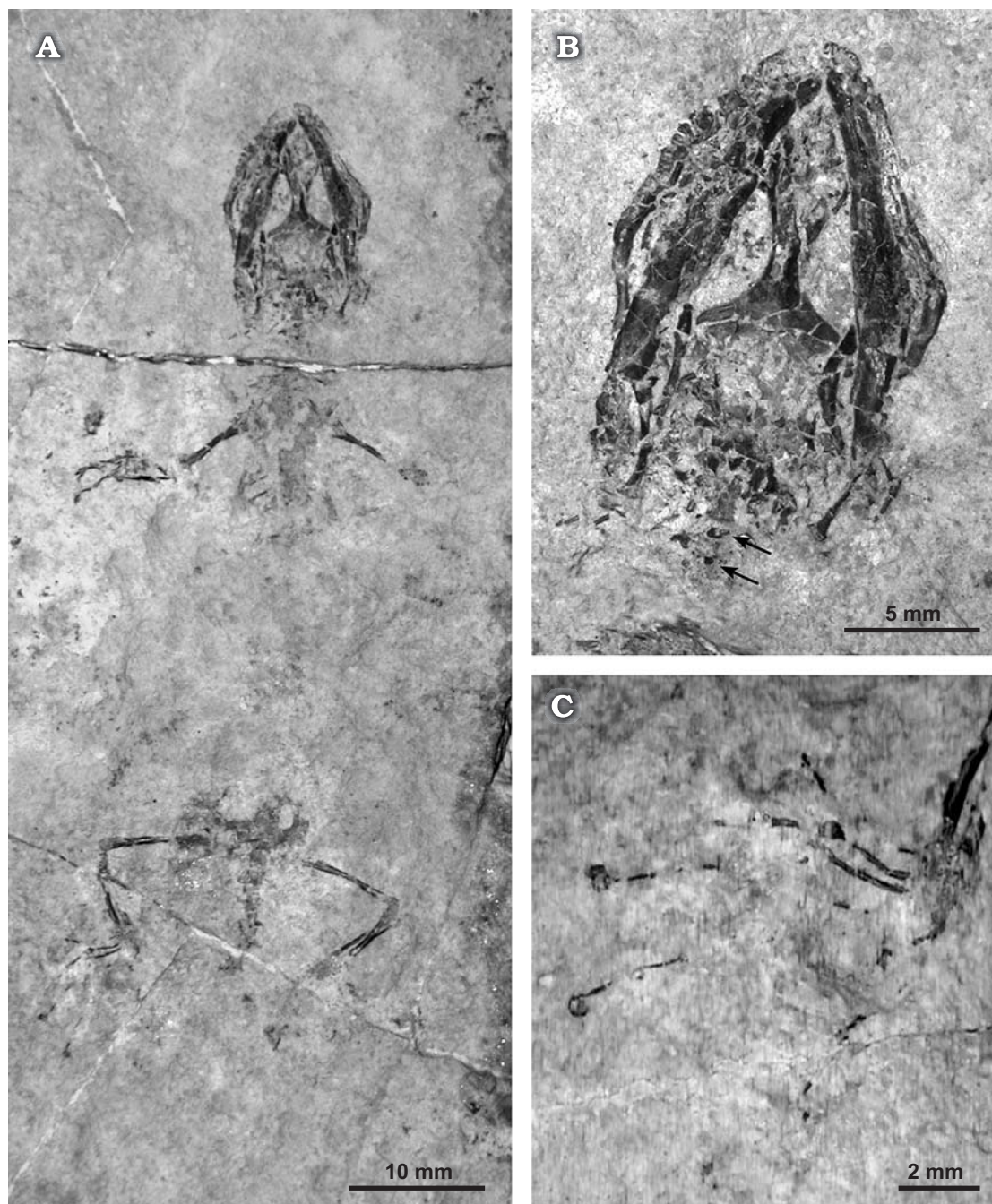


Fig. 2. *Eichstaettisaurus gouldi* sp. nov. Holotype MNP 19457, preserved in ventral view. A. Complete specimen. B. Detail of skull (small arrows mark intercentra). C. Right pes.

mon in the much shorter parietal; differs from *Huehuecuetzpalli* in having short, rather than elongated, premaxillae and larger postfrontals (vestigial in the Mexican form); differs from *Meyasaurus* in frontal morphology (that of *Meyasaurus* is exceptionally narrow); differs from *Scandensia* in lacking the slender, greatly elongated penultimate phalanges; differs from *Sakurasaurus* (Lower Cretaceous, Japan: Evans and Manabe 1999), *Meyasaurus* and *Tarratosaurus* (Lower Cretaceous, Morocco: Broschinski and Sigogneau-Russell 1996) in having a simple homodont dentition (wide

durophagous teeth in *Sakurasaurus*, bicuspid teeth in *Meyasaurus*, few robust teeth in *Tarratosaurus*); differs from the enigmatic *Hodzhakulia* (Lower Cretaceous, Central Asia: Nessov 1985, 1997) in having a longer jaw and smaller teeth; and differs from *Hoyalacerta* in having a broader skull (narrow in *Hoyalacerta*). *Yabeinosaurus* (Lower Cretaceous, China: Endo and Shikama 1942) has never been redescribed in detail, while two new Chinese lizards from the same deposits (*Dalinghosaurus*, Ji, 1998; *Jeholacerta*, Ji, and Ren 1999) have yet to be adequately characterised.

Eichstaettisaurus schroederi (Broili, 1938) Kuhn 1958*Ardeosaurus schroederi* Broili, 1938*Broilisaurus schroederi* Hoffstetter, 1953*Holotype*: BSPHM 1937 I 1, a complete skeleton in dorsal view.*Holotype locality, horizon, and age*: Wintershof bei Eichstaett, Germany. Solnhofen Limestone, Upper Jurassic (Tithonian).

Revised diagnosis.—Species of *Eichstaettisaurus* in which traces of the mid-parietal and mid-frontal suture may remain after the rest of the suture has closed; interorbital frontal width roughly 32 per cent of the width at the frontoparietal suture; frontal and parietal equal in width at suture, in contact laterally, and with postfrontal applied to their lateral margins; frontoparietal suture smooth, with parietal margin broadly convex and frontal margin slightly concave.

Eichstaettisaurus gouldi sp. nov.

Figs. 2–5.

Etymology: For Stephen J. Gould who died in 2002, in recognition of his contributions to evolutionary biology.*Holotype*: MPN 19457, a partial skeleton preserved in ventral view.

Type locality, horizon, and age: La Cavere outcrop, Pietraroraia, Mount Matese, southern Italy. Upper Plattenkalk horizon. I.G.M. [Italian Military Geographic Institute] map sheet 162, III SW-Cusano Mutri (Fig. 1) N4577431, E2482228. Lower Cretaceous, Albian age.

Diagnosis.—Species of *Eichstaettisaurus* differing from the type species as follows: lacking any trace of a median suture on either frontal or parietal; interorbital width of the frontal only 20 per cent of frontoparietal suture width; frontoparietal suture with the parietal slightly embayed by median convexity of frontal; frontal slightly wider than parietal at the frontoparietal suture, with posterolateral tip of frontal apparently emarginated from behind by postfrontal.

Remarks.—Although the narrower frontal could be an artefact of immaturity, the complete fusion of both the frontal and parietal, with no trace of the midline sutures, suggests a pattern of skull development differing from that of *E. schroederi*.

Description of holotype specimen MPN 19457.—The holotype specimen of *E. gouldi* comprises a small (snout-vent length ca. 56 mm) associated skeleton, preserved in ventral aspect, and including the skull, some parts of the axial skeleton, and parts of the fore and hind limbs and their girdles (Fig. 2A). The skeleton is gracile with thin skull roofing bones. This is suggestive of immaturity, as are the poorly ossified carpus and tarsus. The parietal is shattered in MPN 19457, but its anterior and anterolateral borders, and those of the frontal, are complete and they suggest that the skull sutures were already closed (Figs. 2B, 3A). The specimen was therefore well past hatching but probably not yet adult. The body proportions overall are closely similar to those of *E. schroederi*.

Skull (Figs. 2, 3).—The skull is exposed in ventral view with the lower jaws in articulation (Figs. 2B, 3A, B). Judging by its condition, the skull was probably preserved in this position, with the dorsal surface embedded and little distorted, but with subsequent compression tending to separate the lat-

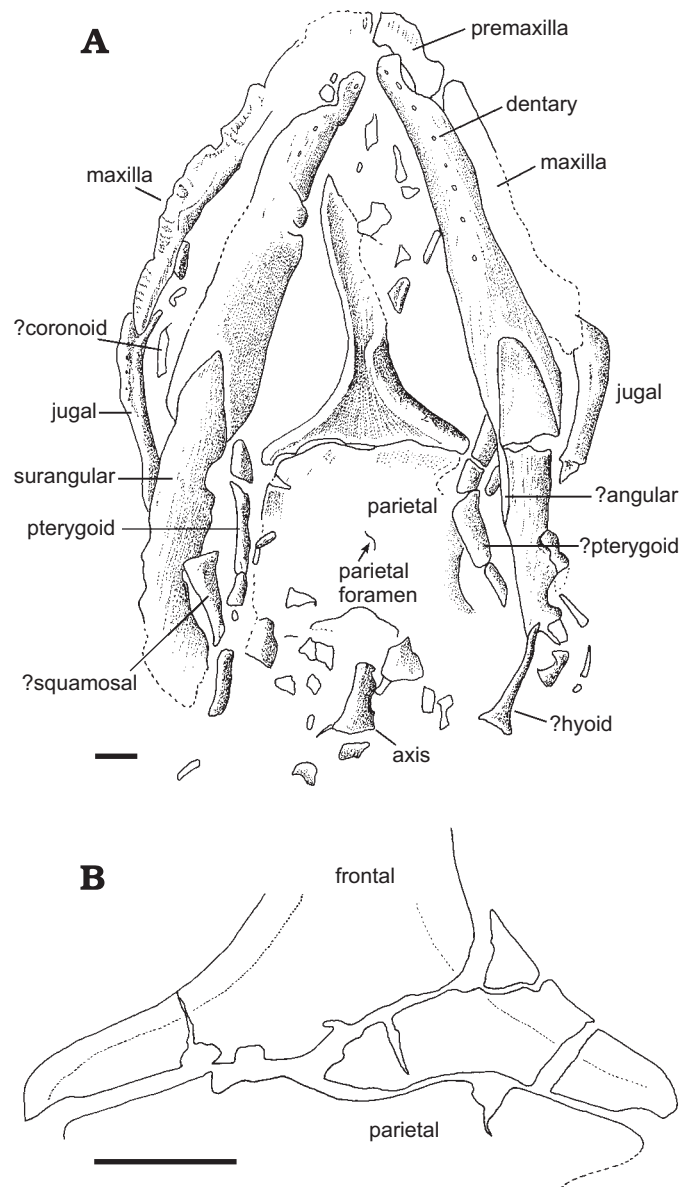


Fig. 3. *Eichstaettisaurus gouldi* sp. nov., holotype MNP 19457. A. Skull. B. Enlargement of frontoparietal region. Scale bars 1 mm.

eral and ventrolateral parts of the skull about the interpterygoid vacuity. The mandibles moved with the maxillae, separating posteriorly but remaining in slight contact at their tips. The orbits are large, rounded and, allowing for compression, somewhat dorsally placed.

The most clearly preserved bone is the long frontal. It is narrow anteriorly, constricts sharply between the orbits, and then widens markedly at the frontoparietal suture (interorbital width roughly 20 per cent of the frontoparietal suture width) (Fig. 3A). The bone is unpaired and has strong cristae cranii (= subolfactory crests or descending flanges) anteriorly and between the orbits, although these do not meet ventromedially. Anterior to the frontal is a damaged mass that probably represents the nasals, suggesting these were quite broad. The frontoparietal suture is well-preserved (Fig.

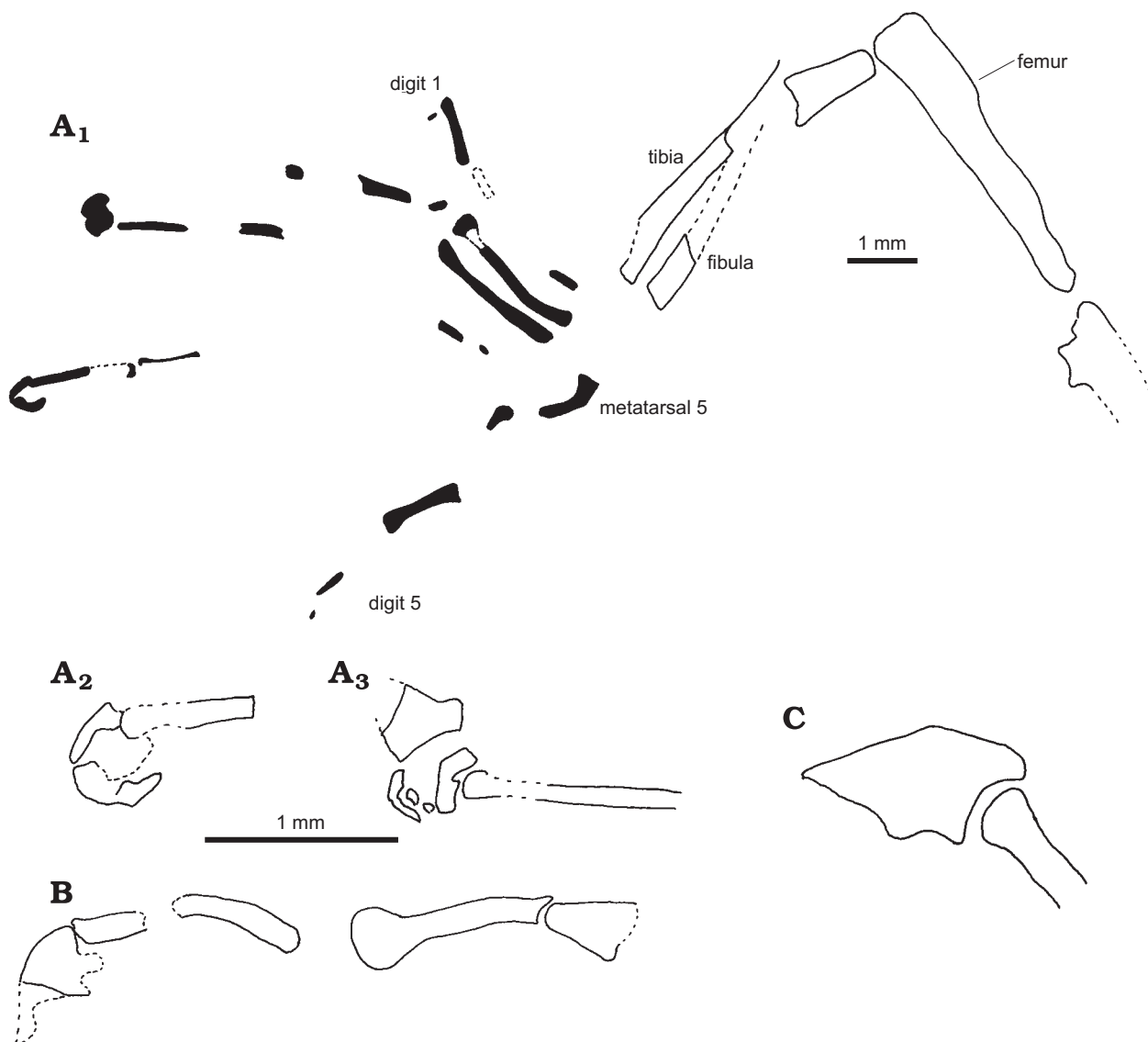


Fig. 4. *Eichstaettisaurus*. **A, B.** *Eichstaettisaurus gouldi* sp. nov., holotype MNP 19457. **A.** Right pes, complete (A₁), enlargements of fourth (A₂) and third (A₃) digits to show how breakage creates the impression of a spatulate tip. **B.** Digit from right manus. **C.** *E. schroederi*, BSPHM 1937 I 1, manus ungual for comparison; not to scale.

3A, B) and has a distinctive shape. It is relatively simple, lacking either interdigitations or overlap surfaces. The central part of the frontal embays the parietal slightly, but then straightens bilaterally, before extending into the lateral processes. This gives the suture a very shallow W-shape. The posterolateral tips of the frontals protrude just beyond the parietal, and their posterior margins are slightly embayed. This suggests the postfrontal may have abutted the back of the frontal, rather than clasping its lateral edge. The parietal plate is damaged but the anterior and anterolateral margins are clearly defined. The anterior margin is intact across the midline and there is no evidence of a midline suture. The posterior part of the bone is too badly damaged to determine the shape of the postparietal processes, but they cannot have been long. The central section of the parietal plate is a mass of thin broken fragments. There is no trace of any localised

thickening that might indicate the presence of ventrolateral crests, but the central section of the bone seems to enclose curved margins pertaining to a parietal foramen (Fig. 3A).

The overlying lower jaws obscure much of the lateral wall of the skull. The maxillae were short, overlapping the jugals but not extending beyond the midpoint of the orbit. They are separated anteriorly by paired premaxillae, each containing six or seven tooth positions. The maxilla had more than 30 tooth positions, but a precise count is not possible. Most of the teeth are either lost or broken, but the few preserved are small and slender, with a relatively shallow pleurodont implantation (as shown by the weak grooves on the maxilla in Fig. 3A).

The shape of the postfrontal, or postorbitofrontal, can be inferred only from the embayment on the frontal. The only representative of the postorbital series clearly preserved is the

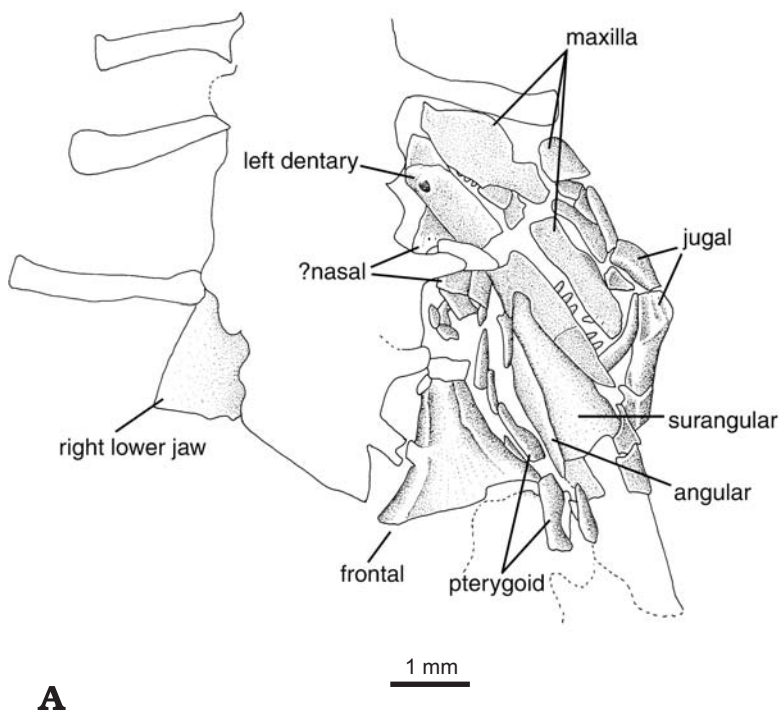


Fig. 5. *Eichstaettisaurus gouldi* sp. nov. Disarticulated skull within the body cavity of Pietraroia specimen MPN A01/82. **A.** Drawing of skull components. **B.** As preserved in the specimen.

jugal, exposed on both sides as a strong, curved arch of bone between the posterior end of the maxilla and the posterior orbital margin. It had no posterior spur or process. At the right maxillary-jugal junction, the thin, tapering posterior process of the maxilla underlies the jugal, and a thin splint of bone running along the medial aspect of the maxilla suggests the jugal extended forward to the antorbital margin. The posterodorsal ramus of the jugal obviously contributed to a complete postorbital bar but the lower jaw obscures its dorsal extremity, and therefore its relation to the postorbital and squamosal. On the right side of the skull, between the back of the jaw and the quadrate ramus of the pterygoid, there is a curved bar of bone (in two parts, Fig. 3A) that may be a squamosal, or possibly hyoid. The quadrates are not exposed.

The mandibles also obscure the palatal elements, leaving only the pterygoids partly exposed. These are represented by a pair of well-ossified bars running roughly parallel to the margins of the parietal and then, on the left side, curving anterolaterally. The interpterygoid vacuity appears very broad, but allowance must be made for both immaturity and postmortem compression. Adjacent to the posterior tip of the left mandible, there is a rod-like structure, expanded posteriorly, that may be either the epipterygoid or, from its position, the first hyoid ceratobranchial (Fig. 3A).

Both lower jaws are in association, the left ramus being almost complete. The dentary is comparatively slender throughout, but becomes particularly so towards the weak symphysis. No teeth are visible. The lateral surface is marked with a series

of eight small neurovascular foramina. The rear of the dentary is deeply bifurcate, with long dorsal and ventral rami of roughly equal length. The anterior tip of the large surangular is correspondingly tapered. A small mass of bone along the dorsal edge of the right mandible at this point may be the coronoid (Fig. 3A), while a thin ventral splint visible on the opposite mandible probably represents the angular (Fig. 3A).

Axial skeleton (Figs. 2A, B, 3A).—Elements of the cervical, dorsal, sacral and anterior caudal vertebral column are visible (Fig. 2A), but the preservation is poor. The cervical count is estimated at six or seven, but dorsal number is unknown. The first recognisable vertebra lies immediately behind the head and is probably the axis (Fig. 3A). Its centrum is simple, cylindrical, and lacks any trace of a posterior condyle. Between it and the next vertebra is a robust intercentrum (see arrows, Fig. 2B). The next centrum is shorter and apparently keeled. Again it seems to be separated from the next vertebra by an intercentrum. The sacrum is obscured by overlying elements of the pelvis. Behind it, there is a short series of at least six anterior caudal vertebrae bearing strong transverse processes. In most cases, the distal ends of the processes are damaged, but the second caudal has a process with a distinct posterior angulation. The caudal centra are broad, cylindrical, and again apparently amphicoelous. None preserves a trace of a fracture plane (autotomy septum), but this is not surprising. The fracture plane typically develops in a more distal position along the tail, and may explain the short caudal series in this specimen.

Pectoral girdle and forelimb (Figs. 2A, 4B).—The forelimbs are partially preserved on each side and are short in relation to the axial skeleton. They are represented by slender right and left humeri, parts of the right radius and ulna, and parts of each manus. The proximal ends of the humeri lie against irregular bone and cartilage masses pertaining to the pectoral girdle, but these provide no anatomical detail. The right manus preserves parts of at least three long slender digits (probably the central three). Traces of the carpus are visible between the remnants of the epipodials, suggesting that it may have been only partially ossified. An accurate phalangeal count is not possible, but the longest digit (four) seems to have had five components (presumably a metacarpal and four phalanges). The individual phalanges are relatively long, with slender shafts and more expanded rounded extremities. Only two of the unguis phalanges are reasonably complete (Fig. 4B). The unguis is short and rather deep with a strongly concave proximal surface (meeting the small rounded head of the penultimate phalanx), a well-developed flexor tubercle, and a sharply tapering tip.

Pelvic girdle and hind limb (Figs. 2A, C, 4A₁–A₃).—The pelvic girdle is poorly preserved, but the ventral elements enclose a large thyroid fenestra. The pubes taper anteriorly and have strongly concave medial margins. The ischia are represented only by bone masses, and the ilia are obscured. Again, the hind limbs are short in relation to the snout-vent length (SVL, estimated in a fossil as the distance between the tip of the premaxillae and the posterior edge of the second caudal, the approximate position of the cloaca in living taxa). The femora are slender with little expansion of the articular ends and only a slight sigmoid curvature; the tibia and fibula are considerably shorter (roughly 50 per cent of femoral length). The tibia is widest proximally, narrowing markedly at midshaft. The right foot is only partially preserved, but there is enough to demonstrate its dimensions (Figs. 2C, 4A). As a whole, the foot is of similar length to the femur (Fig. 2A), and therefore much longer than the crus. The second and third metatarsals are incomplete and rather thin; the fifth is short and was apparently hooked, a conclusion supported by the divergent position of the fifth digit. This digit is also comparatively long. The foot thus lacks the strong asymmetry seen in many fast running modern lizards where the fourth digit is markedly longer than the third or fifth. On first inspection, the unguis of digits three and four look highly unusual (Figs. 2C, 4A₁). The distal end of each penultimate phalanx is small and rounded, but it seems to meet a flared, ring-like, expansion, as though the lizard had rounded tips to the digits (Fig. 4A₁). However, this is an artefact of preservation. Superimposing a scaled image of the hand claws onto the pedal digital tips shows that the ring-like effect results from a combination of breakage and distortion (Fig. 4A₂, A₃). In fact, the pedal unguis resemble those of the manus, with a strongly concave proximal margin for the penultimate phalanx, a short deep proximal blade, a pointed distal tip, and a strong ventral tubercle for the attachment of digital flexors. There is also a suggestion of a small proximodorsal tubercle for

extensor muscle attachment. Overall, the appearance is that of a claw capable of being strongly flexed.

Description of the Eichstaettisaurus skull within MPN A01/82 (Fig. 5).—A second skull of *Eichstaettisaurus* has been identified within the body cavity of another Pietrarovia reptile specimen, MPN A01/82 (see below). The associated, but disarticulated, skull remains (Fig. 5) are attributable to *E. gouldi* on the basis of several distinctive features: the form of the single frontal (marked interorbital constriction, but note that the posterior sutural edge is broken); the general morphology of the dentary (tapering symphyseal region, generally shallow profile, deeply bifurcate posterior margin); a surangular of similar depth; and a slender ventral angular. The proportions of the dentary and postdentary bones also correspond.

The frontal is preserved in ventral view and lies just behind the anterior edge of the block (inverted in Fig. 5 to aid interpretation). It is flanked by the left mandible, and then by the left maxilla. Both are exposed in lateral view. The maxilla has a deep facial process with a rounded profile, and a shallower orbital process. Curving behind the maxilla (anatomically) is an arc of bone bearing a smooth orbital margin. This is presumably the jugal, displaced and rotated from its articulation with the orbital process of the maxilla. Immediately in front of the frontal are several flat bone fragments that may pertain to the anterior part of the frontal and the nasals. The right mandible lies along the right edge of the vertebral mass of the predator but is largely obscured (Fig. 5).

Both the left dentary and maxilla bear teeth. In most positions, the roots of the teeth can be seen through the thin bone of the alveolar margins, showing that they were pleurodont, but with relatively shallow attachment surfaces. Towards the rear of the jaws, several tooth crowns are exposed. They are small, pointed and slightly spatulate, suggesting a degree of labiolingual compression at the tips.

Lepidosauria Haeckel, 1866
Rhynchocephalia Günther, 1867
Genus indet.

Figs. 6–10.

Description.—MPN A01/82 preserves the posterior half of a small reptile in dorsal view, from the mid-trunk through to the tip of the long tail, and including parts of the pelvis and hind limbs (Fig. 6). Given the preserved remains, the original snout-vent length of this animal may be estimated as ca. 70 mm, depending on the relative length of the trunk. The specimen is of particular interest in containing part of the original gut contents, in the form of recognisable bones (see above), bone fragments, and organic matrix.

Vertebral structure (Figs. 6A, B, 7, 8).—The specimen preserves a series of large, but crushed, posterior trunk vertebrae. Each bears either a short straight rib or a long lumbar transverse process (the junction between rib and vertebral body is not always clear). These posterior vertebrae are followed by two sacrals. The first is partially obscured by the posterior gut mass, but reveals strong, distally expanded ribs.

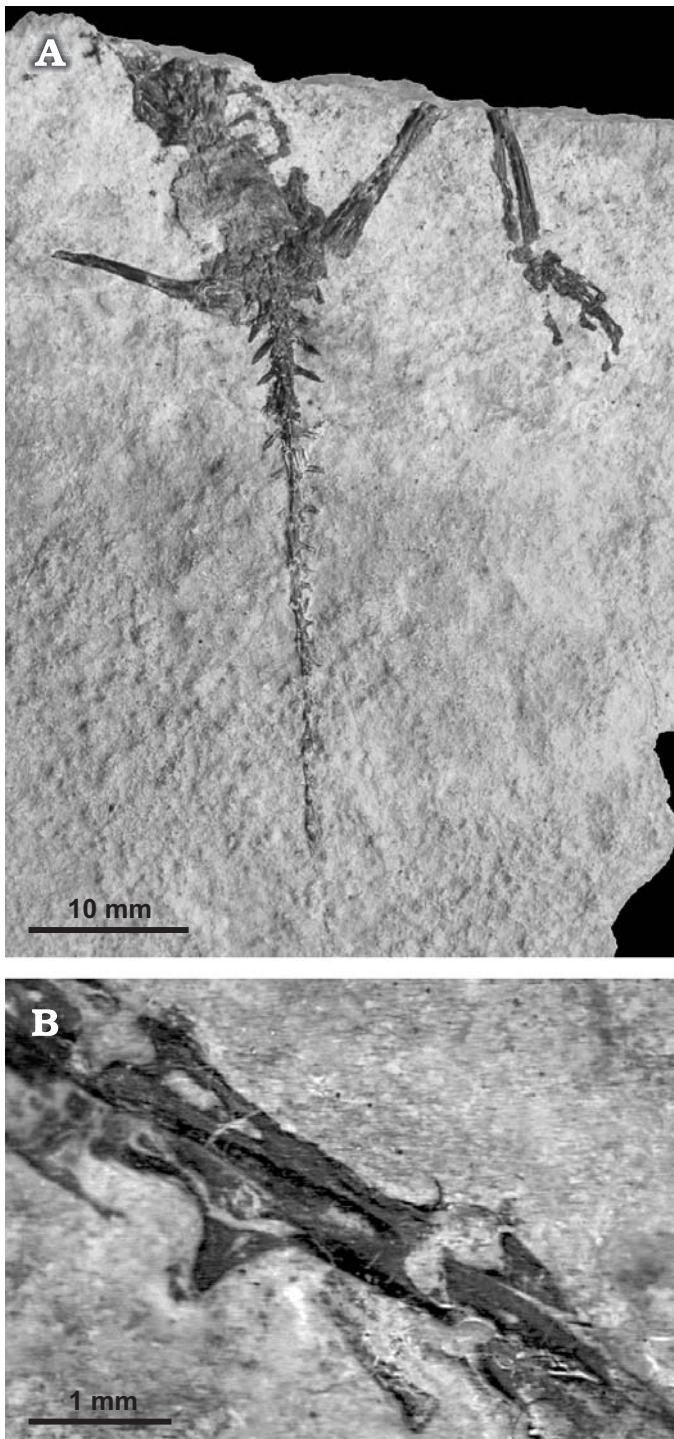


Fig. 6. *Petraroia* specimen MPN A01/82. **A.** Complete specimen (but without distal one third of tail). **B.** Midcaudal vertebra.

The second sacral shows one of two slightly smaller sacral ribs. The tip is again expanded but shows no bifurcation. The tail is long and slender, with at least 25 distinctive caudal vertebrae (note that the distal third of the tail is omitted from Fig. 6A). The eight proximal caudals are relatively elongate, with long horizontal zygapophyseal surfaces and small, horizontally-directed spines. Their transverse processes are long, ta-

pering, and angled sharply backward (Fig. 8). The processes disappear around the level of caudal vertebra nine and the vertebrae become increasingly attenuated. The zygapophyses come closer to the midline, eventually forming a single midline process, and there is no neural spine. Rather, the dorsal surface of the arch bears a sulcus or depression, flanked on each side by a shallow ridge running from anterior to posterior zygapophysis (Figs. 6B, 7). The ridge and depression are also present on more anterior caudals, but are difficult to see because the region is crushed. Ventrolateral to the zygapophysial ridge, there is a second sulcus running along the side of the neural arch, above the level of the transverse process. The first ten caudals show no trace of a fracture plane. Further distally, several of the vertebrae are grooved, but there is no consistency of position and the vertebrae do not appear to be autotomous. The haemal arches are nearly horizontal and do not increase the depth of the tail to any significant degree.

Pelvis and hind limb (Figs. 8, 9).—The pelvic girdle has been compressed and is partially obscured anteriorly by the gut contents and sacrum (Fig. 8). The right ilium has fallen medially, exposing the lateral surface and the acetabulum; it had clearly not fused to the other pelvic bones. There is a small anterior iliac prominence, but the upper part of the blade has been crushed into the sacrum and its margins are not visible. The pubis lies anteroventral to the ilium. It forms a broad plate delimiting a posteromedial thyroid fenestra (the edge of which is just visible in front of the ilium). The most distinctive feature is a large, flange-like pectineal process that extends anterolaterally. From this point, the anterodorsal edge of the bone curves towards the midline rather than running forward. This suggests a short, broad pubic ramus, with a wide pubic symphysis. The ischium lies under the ilium and femur and is more clearly visible on the right side. It has a strong posterior process.

The right hind limb and most of the left femur are exposed (Figs. 6, 9). The remainder of the left limb is within the matrix, but it was not possible to prepare this region further because the matrix is hard and the bone rather fragile. There is an apparent disparity in the widths of the right and left femora, but this is an artefact of crushing and a slight smearing on the right side. On the left, the borders are intact and the bone is quite

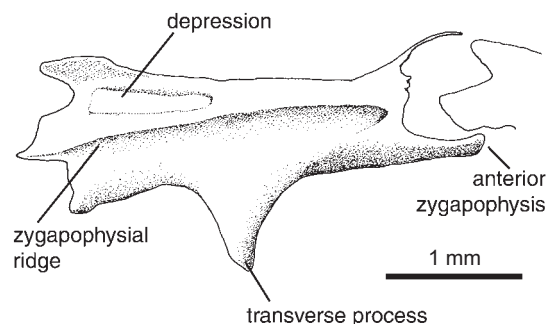


Fig. 7. *Petraroia* specimen MPN A01/82. Posterior caudal vertebra showing lateral zygapophysial ridge and dorsal depression.

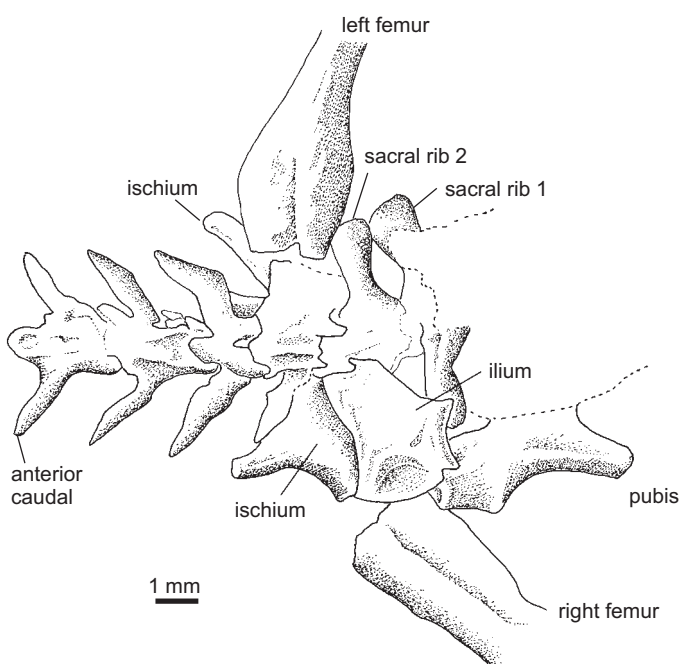


Fig. 8. *Pietrarroia* specimen MPN A01/82, pelvic, sacral and caudal morphology.

gracile. Allowing for the absence of the distal femoral head and the proximal tibia, the right femur is not substantially longer than the bones of the crus, a marked difference between this specimen and MPN 19457. The tibia and fibula run in parallel, with both bones of almost constant width, although the tibia, as usual, is thicker. The right hind foot is preserved in its entirety, but, like the femur, the individual bones are crushed and somewhat smeared, so that boundaries between elements are difficult to see. Thus although the proportions of the digits shown in Fig. 9 can be taken as accurate, the lengths of individual elements, and the positions of the joints between them, are shown with less confidence. There is a single ovoid proximal tarsal close to the end of the fibula and the lateral edge of the tibia. This is probably the calcaneus, but there is no trace of the astragalus, unless it is crushed into the proximal ends of the inner metatarsals. There is at least one distal tarsal, probably the fourth, between the calcaneus and the heads of metatarsals four and five.

The foot as a whole is shorter than the crus, another significant difference with MPN 19457. Metatarsals 1–4 appear to be short and thick; metatarsal 5 is expanded proximally but the degree of hooking is unclear. The individual phalanges are also relatively shorter than those of MPN 19457. The penultimate phalanges are longest and have a distinctive shape—wide proximally, narrowing in the distal part of the shaft, and then expanding slightly at the distal articular head (mostly still cartilage). The unguals are narrow and tapering. As reconstructed, the phalangeal formula is 2: 3: 4: 4/5?: 3?.

Soft tissues (Fig. 10B, C).—To the left and right of the trunk vertebrae and ventral to the short ribs, there is an irregular

mass made up of three distinct components (Fig. 10B, C). An anterior mass consists of identifiable small bones comprising the disarticulated lizard skull discussed above. Under the Scanning Electron Microscope these elements show slight acid etching. The more posterior mass comprises finely comminuted bone fragments embedded in an organic ground substance. Linking the two regions is a narrow wavy strip of stained rock containing indeterminate particulate material.

The lizard skull lies with its anterior tip directed backwards and with the ventral side uppermost. This suggests the prey may have been swallowed head first with the rest of the skeleton following (and on the missing part of the block), although it is equally possible that the lizard was decapitated or scavenged.

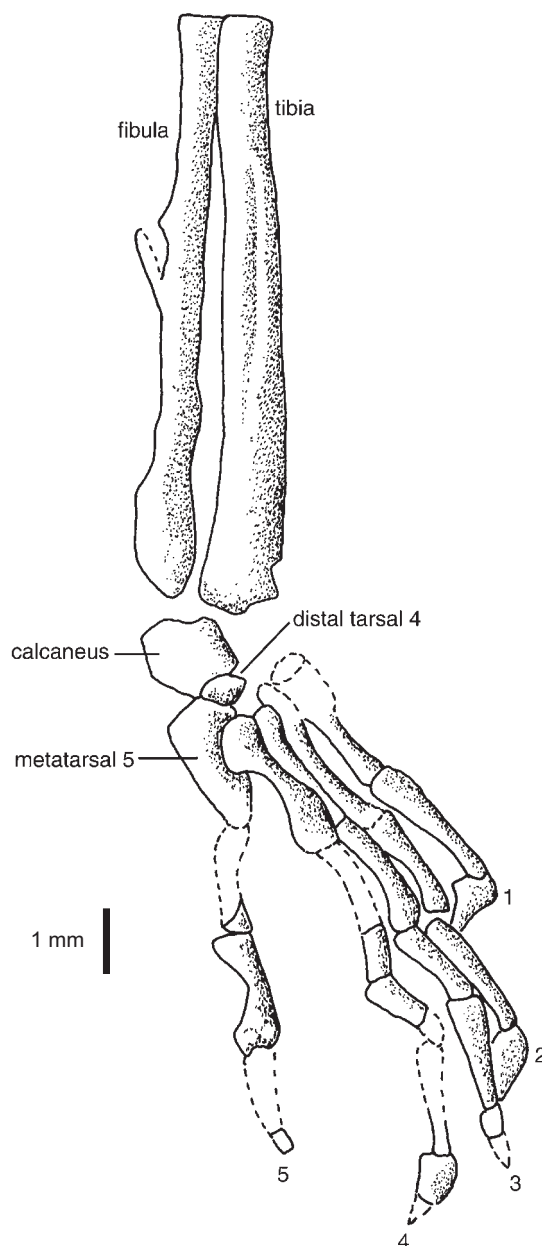


Fig. 9. *Pietrarroia* specimen MPN A01/82. Right crus and pes of MPN A01/82, digits numbered 1–5.

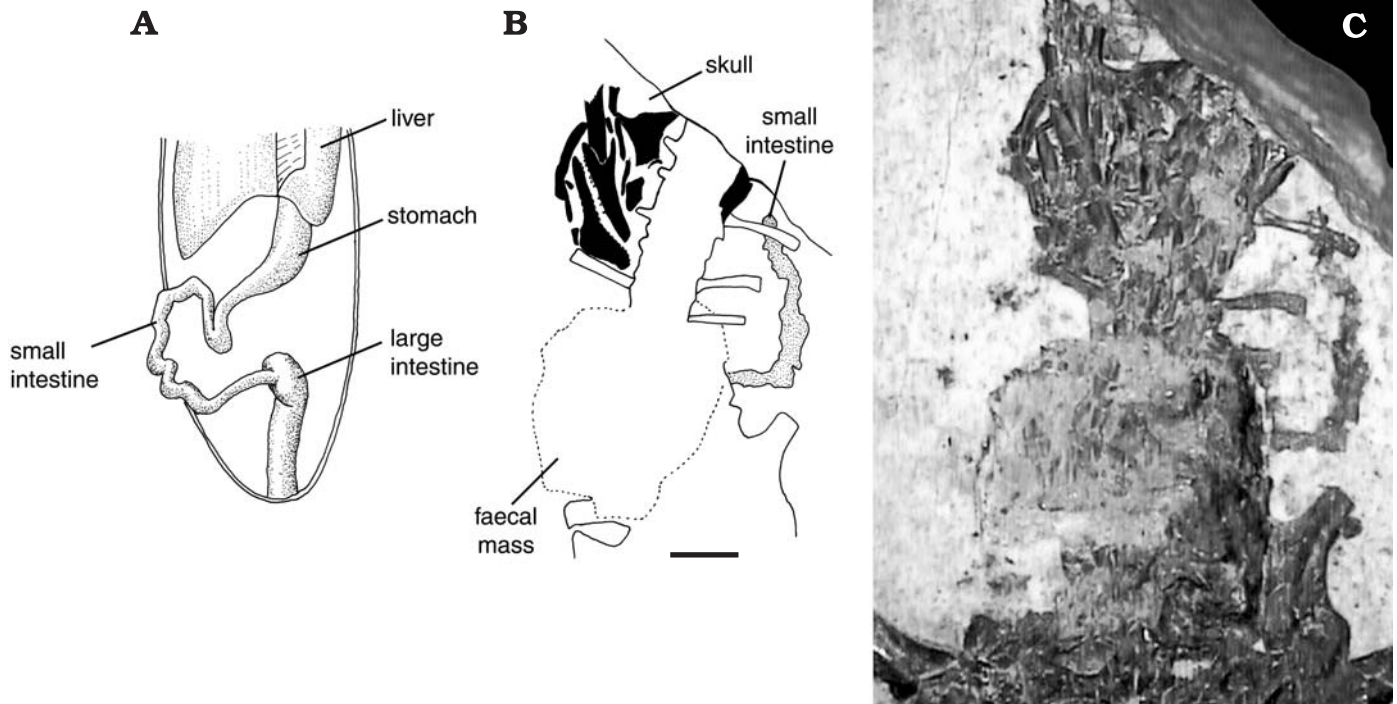


Fig. 10. Visceral structures. **A.** The gut of *Sphenodon punctatus* (redrawn from Guibé 1970: fig. 403); not to scale. **B, C.** Pietraroia specimen MPN A01/82, abdominal region; scale bars 2 mm. **B.** Simplified figure showing arrangement of gut parts. **C.** The central part of the specimen.

Discussion

The phylogenetic position of MPN 19457.—The slender gracile body form, divergent fifth digit, and wide open thyroid fenestra support the attribution of MPN 19457 to the Lepidosauria, while the combination of fully pleurodont teeth, a short dentary, an incomplete lower temporal arcade, a relatively simple (non-overlapping, non-interdigitating) frontoparietal suture, and a slender, anteriorly extended pubis, provide strong evidence that it is a squamate. As such, the first issue is a comparison with the other lizards of Pietraroia.

Examination of the holotype of *Chometokadmon* (MPN 539) demonstrates marked differences between it and MPN 19457, even allowing for the difference in size. The parietal of *Chometokadmon* is narrow and elongated, with long postparietal processes; in MPN 19457, it is nearly square with straight lateral margins and, probably, short postparietal processes. In *Chometokadmon* the frontals are paired and relatively broad, in MPN 19457 they are fused and very narrow between the orbits. The antorbital region of *Chometokadmon* is elongated and rather pointed, while that of MPN 19457 is short and rounded. Although both lizards have a relatively elongated presacral vertebral column and short limbs, *Chometokadmon* has a long, asymmetric pes with relatively robust phalanges, while MPN 19341 has a more symmetrical pes with more gracile phalanges. The differences go well beyond normal levels of variation between species.

Comparison with *Costasaurus* is more problematic because the type and only specimen is very fragmentary, with a badly damaged skull, parts of the axial skeleton, but only traces of the limbs (personal observations). *Costasaurus* is more generally similar to MPN 19457 than either is to *Chometokadmon*, particularly in having a short, rather rounded skull, slender pterygoids, a wide interpterygoid vacuity, a gracile jaw with a flared retroarticular region, and amphicoelous notochordal vertebrae with simple intercentra (but smaller in *Costasaurus*). Unfortunately, the potential for further comparison is limited. MPN 19457 has a poorly preserved vertebral column but distinctive limbs; *Costasaurus* has relatively well preserved vertebrae, but only fragments of the limbs. Similarly, *Costasaurus* preserves a distinctive quadrate, but this element is unknown in MPN 19457.

Of known fossil squamates, MPN 19457 (and the skull within the gut of MPN A01/82) most closely resembles the Solnhofen genus *Eichstaettisaurus* (Fig. 11A). *Eichstaettisaurus schroederi* and MPN 19457 are closely similar in their skull and body proportions. Both have relatively large heads with rounded snouts and large circular orbits; a long presacral vertebral column; and relatively short limbs. In both, the propodials are longer than the epipodials; the pes lacks the strong asymmetry seen in the feet of many modern lizards; the fifth toe is strongly divergent; the penultimate phalanges are narrow and elongate (particularly so in MPN 19457); and the unguals have a closely similar shape with a deep proximal section and a rather short but acutely pointed

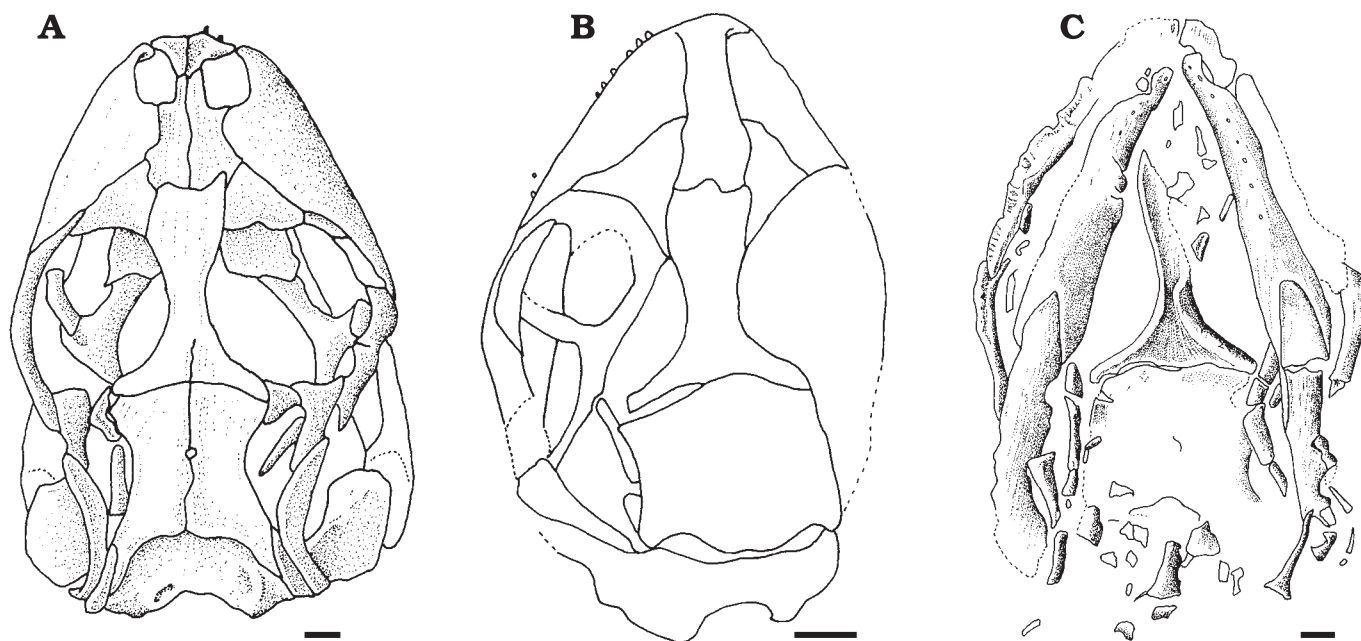


Fig. 11. Comparison of skulls in *Eichstaettisaurus*. **A.** *Eichstaettisaurus schroederi*, BSPHM 1937 I 1, Solnhofen, Germany. **B.** *Eichstaettisaurus* sp., IEI LP-3400, Montsec, Catalonia, Spain. **C.** *Eichstaettisaurus gouldi* sp. nov., MPN 19457, Pietraroia, Italy. A, B, dorsal views, C, ventral view. Scale bars 1 mm.

distal end (Fig. 4A–C). Estes (1983) describes the vertebrae of *Eichstaettisaurus* as procoelous but the vertebrae of the holotype specimen are articulated and preserved in dorsal view. It is simply not possible to determine the structure of the centra with any confidence (Evans, personal observations). In the skull, both taxa have a single fused (or nearly fused) frontal. The bone is narrow anteriorly, constricted between the orbits, and expands into a broad simple suture with the parietal. Both have a nearly square parietal (allowing for the crushing in MPN 19457) with a small central parietal foramen and short postparietal processes. Both taxa have a small bifurcate postfrontal, although MPN 19457 appears to differ in the relation of the frontal to the postfrontal (see description above). Both taxa have paired premaxillae, a relatively short maxilla with a deep, rounded facial process and a rather short orbital process that does not extend beyond the midpoint of the orbital margin. In both taxa, the teeth are small and rather weakly pleurodont, with some labiolingual compression at their tips (Evans, personal observations of *E. schroederi*). Both have slender pterygoids and a wide interpterygoid vacuity.

We ran *Eichstaettisaurus gouldi* through a phylogenetic analysis (PAUP 3.1.1, Swofford 1993) using a corrected matrix (based on Evans and Chure 1998) with 24 terminal taxa (Rhynchocephalia, modern squamate clades including snakes, dibamids and amphisbaenians, and the Solnhofen taxa *Bavarisaurus*, *Ardeosaurus*, and *Eichstaettisaurus schroederi*). The analysis yielded 14 optimal trees (length 877; CI 0.761; RI 0.57); in every tree *Eichstaettisaurus gouldi* emerged as the sister taxon of *E. schroederi*.

MPN 19457 is separated from *Eichstaettisaurus schroederi* by a temporal gap of more than 40 million years (Gradstein et al. 1995), but their morphological differences are minor and do not justify distinction at the generic level. The temporal and geographical gap between Solnhofen and Pietraroia is partly bridged by the specimen recently described from the Berriasian age locality of Montsec, Catalonia, northern Spain (Evans, Lacasa-Ruiz, and Erill Rey 1999) (Fig. 11B), although this specimen cannot be attributed reliably to one or other species.

Most recent analyses of Squamata recognise two major clades, Iguania (iguanids, agamids, and chamaeleons) and Scleroglossa (gekkotans, scincomorphs, anguimorphs, amphisbaenians and snakes) (e.g., Estes et al. 1988; Reynoso 1996, 1998; Evans and Barbadillo 1998, 1999). Cocude-Michel (1963), Hoffstetter (1964, 1966), and Estes (1983) all referred *Eichstaettisaurus* to the Gekkota. A single frontal with deepened crista cranii is among characters listed by Estes et al. (1988) as diagnosing gekkotans (although the frontals are typically fused beneath the olfactory tracts), but a similar morphology is found in members of several other groups (e.g., many gymnophthalmids, varanoids, and some scincids, Evans, personal observations). Both *Eichstaettisaurus schroederi* and *E. gouldi* also share the wide interpterygoid vacuity, narrow pterygoids, and lightly built skeleton found in gekkotans, as well as the broad, short snouted, rather flattened skull morphology. However, these may be phenetic similarities, since the skeletons lack any unique gekkotan traits. Most notably, the large, curved jugal indicates a complete postorbital bar, a feature found in no living

gekkotan, where the jugal is, at best, a tiny ventral remnant and both postorbital and upper temporal bars are lost completely. The only described exception to that pattern is the Late Cretaceous *Myrmecodaptrya microphagosa* from Mongolia (Gao and Norrell 2000). This genus, based on a single, isolated (but well-preserved) skull, has been attributed to the Gekkotata, but differs from all known gekkotans in the presence of complete postorbital and upper temporal bars. This renders its attribution problematic.

Like *Ardeosaurus* and *Eichstaettisaurus*, the Solnhofen genus *Bavarisaurus* was also first classified as a gekkotan, in this case on the basis of its amphicoelous vertebrae (Hoffstetter 1964; Estes 1983), but subsequent analyses have interpreted it as stem squamate (e.g., Reynoso 1996, 1998; Evans and Barbadillo 1997, 1998, 1999). A similar position has been suggested for the amphicoelous *Huehuecuetzpalli* (Aptian/Albian, Mexico: Reynoso 1998), for the genera *Scandensia* and *Hoyalacerta* (Barremian, Spain: Evans and Barbadillo 1998, 1999), and also for both *Eichstaettisaurus* and *Ardeosaurus* (Reynoso 1996, 1998; Evans and Barbadillo 1998, 1999). Whether all these taxa are genuinely stem squamates or stem scleroglossans remains uncertain, however, and a detailed reanalysis of basal squamate relationships is overdue. In our preliminary analysis, *Bavarisaurus*, *Ardeosaurus* and *Eichstaettisaurus* (including *E. gouldi*) all fell outside the Iguania-Scleroglossa clade.

Functional morphology.—The skeleton is gracile in both known species of *Eichstaettisaurus*, with limbs (and especially epipodials) that are relatively short in relation to the presacral axial skeleton. The manus and pes are rather symmetrical, not elongated, and have slender digits but strong claws. *Eichstaettisaurus* was certainly not built for speed. There is an established relationship between the length of the hind limbs and high sprint speeds (e.g., Losos 1990; Melville and Swain 2000). In a study of species variation in the scincid lizard *Niveoscincus*, Melville and Swain (2000) identified three basic morphotypes that they correlated with life-style and habitat usage: relatively large animals, with a short interlimb index and long hind limbs (rock climbers); smaller lizards with similar proportions (tree climbers); and small to medium-sized animals with a long interlimb index and short hind limbs (ground-dwellers in thick undergrowth). The latter group were the slowest runners, using cover rather than speed to evade predators. They also had difficulty climbing on restricted surfaces because the undulatory movements of the body compromised balance. However, other authors have correlated short limbs with climbing, at least on inclined or vertical planar surfaces (e.g., Vanhooydonck, Van Damme, and Aerts 2000), using the argument that short limbs, and particularly short epipodials, bring the animal's centre of gravity closer to the substrate and thus give it greater stability. There is also general agreement that long, strong forelimbs are an advantage to a climber in pulling the animal forward against gravity. That said, it is worth remembering that many small modern lizards are very versatile,

changing between horizontal and vertical surfaces with relative ease.

It is difficult to get accurate measurements of the body proportions in *E. gouldi*, but the fore limbs seem particularly short in relation to body length (FL/SVL ca. 20 per cent in *E. gouldi* v. 24 per cent in *E. schroederi*; HL/SVL c. 38 per cent in *E. gouldi* v. 32 per cent in *E. schroederi*). The body proportions of *Eichstaettisaurus gouldi* (long interlimb length, short limbs) are most like Melville and Swain's (2000) secretive ground dwellers, although given the short epipodials and dorsoventral flattening this body shape would also be appropriate for climbing on inclined surfaces. In reality, Zaaf et al. (2001), showed that the basic body proportions of climbing and non-climbing gekkotans were closely similar. The short forelimbs and rather delicate manus and pes in *Eichstaettisaurus* argue against propulsive strength, although the strong flexor muscle attachment points and strongly concave articulation facets on the claws suggest a strong grip. According to a recent analysis (Zani 2000), short, deep, recurved claws are the optimal design for clinging to rough surfaces. *E. gouldi* was thus plausibly a relatively slow-moving, secretive ground lizard with some capacity for climbing on broad inclined rock surfaces, and perhaps for crevice dwelling. MPN A01/82 demonstrates that *E. gouldi* had reason to be secretive.

The phylogenetic position of MPN A01/82.—MPN A01/82 can be attributed to the Lepidosauria based on a combination of factors including the divergent fifth digit, pelvic structure (iliac shape, thyroid fenestra), and the presence of only two sacral vertebrae (primitive). However, in the structure of the pelvis, MPN A01/82 resembles rhynchocephalians more than squamates in having a rather short, broad, medially inturned pubis, with a laterally extended pectineal process (pubic tubercle), and a strong posterior process on the ischium. By comparison, the lizard pubis is typically narrower and more elongated anteriorly, with a pectineal process in the plane of the blade (Gauthier et al. 1988).

Despite the imperfect preservation, MPN A01/82 shows a series of distinctive features: a "lumbar" region with rather long vertebrae bearing short, straight ribs or long transverse processes; an elongated tail with vertebrae that lack neural spines, bear dorsal and lateral gutters and zygapophyseal crests, and have elongate zygapophyses close to the dorsal midline. The pectineal process on the pubis is unusually large, the posterior ischial process is strong, the ilium has a small, but distinct, anterior tubercle, and the second sacral rib does not appear to be bifurcated. This combination of features is not found in the Pietrarovia rhynchocephalian *Derasmosaurus* (Barbera and Macuglia 1988, 1991) (nor in any of the Pietrarovia lizards). Although the *Derasmosaurus* holotype is clearly juvenile, the tail vertebrae already have distinct neural spines.

In the rather long "lumbar" region, MPN A01/82 resembles specimens of the Late Jurassic/Early Cretaceous European genera *Kallimodon* (e.g., Cocude-Michel 1963; Renesto and Viohl 1997) and *Sapheosaurus* (Cocude-Michel

1963), and the mid-Cretaceous *Ankylosphenodon* from Mexico (Reynoso 2000). However, none of these taxa has the strong pectineal flange on the pubis. The Late Jurassic *Homoeosaurus* (Solnhofen, Germany; Cerin, France) has longer limbs (and particularly longer feet) in relation to vertebral length than MPN A01/82 (Evans, personal observation). The only other Jurassic or Cretaceous rhynchocephalian taxa for which corresponding postcranial remains are known are the European *Pleurosaurus* (Late Jurassic/Early Cretaceous) and *Palaeopleurosaurus* (Late Jurassic). Both have tall caudal neural spines (unlike MPN A01/82); neither shows long the long lumbar transverse processes/ribs; and both have a pelvis that is small relative to both the hind limbs and the vertebral column (Fabre 1981; Carroll 1985). Going further back, the mainly Triassic *Clevosaurus* shows similarities in pelvic structure (anterior angle on ilium, some development of the pectineal process), but the caudals have neural spines rather than gutters and depressions (Fraser 1988), while *Polysphenodon* and *Brachyrhinodon* are too poorly preserved in this region for detailed comparison.

If we are correct in our identification of MPN A01/82 as a rhynchocephalian, it appears to represent either a new taxon or one for which the postcranial skeleton is not yet fully known (e.g., the mid-Cretaceous Mexican *Pamizinsaurus*, Reynoso 1997). We are, however, reluctant to name the animal because the available material is so limited.

Feeding biology.—The abdominal cavity of MPN A01/82 clearly preserves traces of the gut contents. Comparison with living lepidosaurs suggests that the anterior mass corresponds to the position of the stomach while the more posterior mass, just in front of the pelvis, lay in the hindgut (Fig. 10B, C). The narrower wavy strip between them matches the position of the small intestine of living taxa (Guibé 1970, Fig. 10A). The specimen therefore preserves the remains of two distinct meals, one relatively recent, and one ready to be voided.

Digestion rates and gut passage times depend on the size and content of the meal, the metabolic physiology of the animal and, for reptiles, the ambient temperature (e.g., Skoczylas 1978). The living *Sphenodon* has a low metabolic rate and lives in cool temperate conditions. Recent studies suggest it feeds sporadically, especially in winter (e.g., Fraser 1993; Cree et al. 1999). Juvenile and female tuatara feed mainly on invertebrates (Cree et al. 1999). Males take vertebrate prey more often (mainly petrel chicks [4 per cent of total], but occasionally lizards and juvenile tuatara [3 per cent of total food], Walls 1981). There are no data on digestion times for vertebrate meals (Alison Cree, personal communication 2002), although vertebrate bones are sometimes found in the faecal pellets (Walls 1978). One study (Fraser 1993) suggests that an average meal spends 48 hours in the stomach in winter and 24 hours in summer, with at least some invertebrate meals taking six or seven days to pass through the gut. However, although extinct rhynchocephalians might have had a lower metabolic rate than their squamate contemporaries (and this is not cer-

tain), digestion and passage times for a rhynchocephalian living in a warm tropical or subtropical environment, such as that of Cretaceous *Pietraroia*, may have been considerably faster than in the living *Sphenodon*. The condition of the lizard skull in MPN A01/82 (disarticulated but not dissociated; slight acid etching; teeth not yet dissolved) suggests the meal was relatively recent, probably in the 24–48 hours before death (Skoczylas [1978] gave data for a 250–300 g rat eaten by a 7 kg snake; decalcification was taking effect by 22 hours). The second mass in the hindgut is the remnant of the previous meal, presumably taken at least one day earlier.

Biogeography.—Squamates probably diverged from the lepidosaurian stem in the Middle to Late Triassic, but are first recorded from Early–Middle Jurassic localities in Britain, India and Central Asia (Fedorov and Nessov 1992; Evans 1998a; Evans, Prasad, and Manhas 2002). Jurassic and basal Cretaceous assemblages tend to be dominated by archaic lineages that became extinct before the end of the Mesozoic, while Late Cretaceous assemblages have a much more modern aspect and contain representatives of extant lineages. The Early to Mid-Cretaceous may therefore have been a period of transition (Evans 1998b), with the gradual disappearance of older lineages (for example, paramacellodids, Laurasian rhynchocephalians) and the first records of newer ones such as helodermatids (Nydham 2000), polyglyphanodont teioids (Nydham 1999), snakes (Gardner and Cifelli 1999), and xenosaurs (Nessov 1997; Gao and Nessov 1998). To date, the Early Cretaceous also provides the first records of true gekkotans (*Hoburogecko* from the Aptian–Albian of Khobur, Mongolia, Alifanov 1989), although the phylogeny predicts that this group must have originated much earlier.

Despite this general trend, however, mid-Cretaceous localities show sharp regional differences in the composition of their assemblages. The Albian–Cenomanian assemblages of western North America (e.g., Cifelli et al. 1997, 1999; Nydam et al. 1997; Nydam and Cifelli 2002a, b) and of Central Asia (e.g., Nessov 1985, 1988, 1997; Alifanov 1993; Gao and Nessov 1998) lack rhynchocephalians and show a relatively derived squamate assemblage. However, other, roughly contemporaneous localities (e.g., Tepexi de Rodriguez, Mexico, Reynoso 1996, 1998, Reynoso and Callison 2000), have an apparently archaic assemblage (rhynchocephalians, basal squamates). The region around Tepexi de Rodriguez was an island at the time of deposition, and may therefore have served as a refugium for relict taxa (much as the islands of New Zealand do today for *Sphenodon*). Similarly, for most of the Mesozoic, Western Europe was an archipelago of fairly small landmasses. This may explain the relatively archaic character of European Early Cretaceous lepidosaurian assemblages. Apart from the Iberian teioid genus *Meyasaurus* (Montsec, Las Hoyas, Uña, Galve; Hoffstetter, Crusafont and Aguirre 1965; Richter 1994; Evans and Barbadillo 1997), most known lizards from Jurassic and Early Cretaceous European assemblages belong either to the basal scincoid paramacellodids, or to groups currently placed on the squamate stem. *Pietraroia* fits this pattern.

In the mid-Cretaceous, the area that is now Pietraroia formed a small emergent carbonate platform that was part of a longer island arc close to the shores of Gondwana, although the recovered tetrapod fauna is primarily Laurasian in character. The only known amphibian, the albanerpetontid *Celtekens*, has its closest relatives in Britain (Berriasian, Purbeck Limestone) and Spain (Barremian, Las Hoyas) (McGowan and Evans 1995). With *Pamizinsaurus* and a sapeosaurid from Tepexi de Rodriguez, Mexico (Albian), *Derasmosaurus* (and probably MPN A01/82) shares the distinction of being one of the last recorded rhynchocephalians from Laurasia. The identification of *Eichstaettisaurus* from Pietraroia provides another archaic Laurasian link with both Germany (Tithonian, Solnhofen) and Spain (Berriasian, Montsec). Determining the affinities of the other members of this relatively well-preserved faunal assemblage will further our understanding of the history of European Mesozoic small vertebrate assemblages.

Conclusions

New lizard material from the Lower Cretaceous (Aptian) locality of Pietraroia in Italy can be referred to a new species of the genus *Eichstaettisaurus*, first described from the Upper Jurassic (Tithonian) of Germany, and more recently from the Lower Cretaceous (Berriasian) of Spain. Based on body and limb proportions, *Eichstaettisaurus* appears to have been predominantly ground-dwelling.

The identification of *Eichstaettisaurus* at Pietraroia (in association with late surviving Laurasian rhynchocephalians) contributes to the idea that this was an archaic island assemblage, a refugium for relicts.

A second new Pietraroia reptile is tentatively referred to the Rhynchocephalia and appears to represent a new generic record for Pietraroia, although it cannot be named from available material. It is clearly distinct from the other Pietraroia rhynchocephalian, *Derasmosaurus*. The presence of a skull of *Eichstaettisaurus* within the gut cavity of this reptile provides a rare glimpse of trophic biology in the Lower Cretaceous.

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