A NEW BASAL PTEROSAUR GENUS FROM THE UPPER TRIASSIC OF THE NORTHERN CALCAREOUS ALPS OF SWITZERLAND

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Abstract: A lower jaw with multicusped teeth and a number of unique characteristics was discovered in an extensive exposure of the Upper Triassic Kössen Formation in the Northern Calcareous Alps. The ramus of the jaw is high and dominated by a row of large, oval foramina that lies parallel to the tooth row. In addition, the anterior portion of the dentary exhibits a large number of nutritive foramina and small pits, which might indicate an association with a soft tissue structure and/or the presence of a keratinous cover of that area during life. All elements of the jaw are thin-walled and hollow, possibly pneumatic. Two teeth are preserved within the dentary. One is tricuspid and the other bears four cusps. The teeth are noticeably small in comparison with the overall size of the ramus, being only one-third of the height of the ramus. The teeth show a strong similarity to those of the well-known basal pterosaur genus *Eudimorphodon*, whose jaw morphology, however, clearly differs from the specimen described in this study. The dentition and the pneumatic bone structure make an assignment to the Pterosauria plausible. Based on the great number of distinct morphological characters the specimen is described as *Caviramus schesaplanensis* gen. et sp. nov.

Key words: *Caviramus schesaplanensis*, *Eudimorphodon*, Northern Calcareous Alps, pterosaur, Rhaetian, Norian, Late Triassic, Switzerland.

FOSSIL vertebrates with multicusped teeth are relatively abundant in Triassic deposits. Unfortunately, most of the reported finds consist of isolated teeth and only few specimens preserve the appending jaws or more of the cranial or postcranial skeleton. Thus, their taxonomic attribution is primarily based on characters observable in the teeth, such as the number of cusps, their spatial arrangement, the presence of cingula, as well as the overall tooth morphology. On that basis, they have been assigned to several groups of fossil amniotes, including pterosaurs, cynodonts and 'prolacertiformes' with reported geographical occurrences in Europe, North America and India (Clemens 1980; Chatterjee 1986; Murry 1986; Cuny *et al*. 1995; Godefroit 1997; Godefroit and Cuny 1997; Dorka 2002; Datta *et al*. 2004). In the specimen described here, one tricuspid and one four-cuspid tooth are still in place, thus showing that the partially preserved lower jaw bore at least two different tooth types.

The specimen was found in the western part of the Northern Calcareous Alps, the Rätikon. The exact locality is on the western slope of the highest mountain of this region, the Schesaplana (2964 m above sea level), whose ridge also represents the border between Austria and Switzerland (Text-fig. 1). The locality on the western slope of the Schesaplana is situated in Switzerland. The mountain peak represents an extensive outcrop of the Kössen Formation, which is Late Triassic (Late Norian–Early Rhaetian) in age.

In this paper a detailed osteological description and comparison with Triassic tetrapod taxa that possess a multicusped dentition will elucidate the peculiar morphology of specimen PIMUZ A/III 1225, discuss its affiliation with the Pterosauria, and form the basis for the definition of a new genus and species of basal pterosaur.

GEOLOGY AND DEPOSITIONAL ENVIRONMENT

The Kössen Formation that yielded the type specimen of *Caviramus schesaplanensis* gen. et sp. nov. was deposited at the northern margin of the western corner of the Tethys ocean. It belongs to the Austroalpine unit of the Alps that was overthrusted as nappes and folded in several deformation phases during the Alpine orogeny. It is today positioned in the central part of the Alps and represents
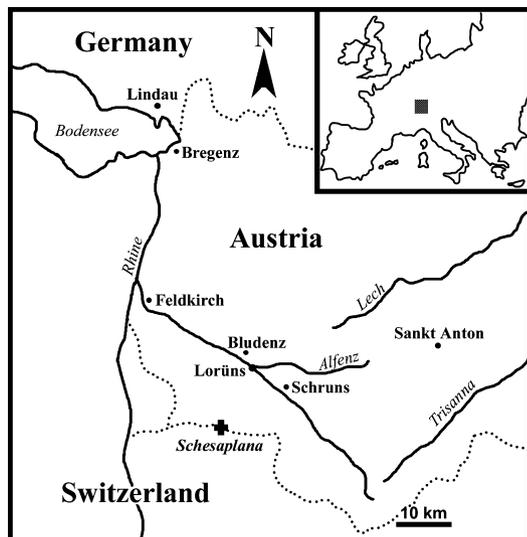
TEXT-FIG. 1. Map of Vorarlberg (western Austria) and northern Graubünden (Switzerland) indicating the locality of Schesaplana mountain, where *Caviramus schesaplanensis* was found (modified from McRoberts *et al.* 1997).

the westernmost extension of the Northern Calcareous Alps at the tectonic border between the Western and Eastern Alps.

The name 'Kössener Schichten' (Kössener layers) was first introduced by Suess (1852) for a characteristic dark grey interbedding of carbonates and marls that are rich in brachiopods at an outcrop near Kössen in Tirol, Austria. Furrer (1993) undertook a comprehensive study of the Kössen Formation in various nappes present in the Northern Calcareous Alps, which led to a new lithostratigraphic classification in which he subdivided the 200–350-m-thick formation into five subunits. Specimen PIMUZ A/III 1225 derives from the Alplihorn Member, which is the basalmost unit of the Kössen Formation. It is overlain by the Schesaplana Member, beds of which are almost vertical as a result of gross morphological deformation during the Alpine orogeny.

The Alplihorn Member can reach a thickness of 120 m. It mainly consists of dark grey shaly clays, marls and carbonates, which are characteristically yellowish, brownish or reddish in colour on their weathered surfaces. Occasionally layers of siltstone and dolostone are interbedded. The Alplihorn Member is rich in bivalves such as *Rhaetavicula contorta*, *Gervillia inflata*, *Laternula praecursor* and *Palaeocardita austriaca*. They are typically preserved as isolated shells in densely packed shell banks, probably indicating redeposition (Furrer 1993). Besides the dominating bivalves, foraminifers, ostracods, gastropods, and corals complement the invertebrate fauna. Fossil remains of vertebrates can also be found in abundance, among them sharks, oste-

ichthyans, placodonts and ichthyosaurs, but generally in disarticulated condition in the form of isolated teeth, scales and bones (Furrer 1993; pers. obs.).

The depositional environment of the Kössen Formation has previously been interpreted as shallow lagoon (Furrer 1993) or intrashelf basin (Stanton and Flügel 1995). Both hypotheses describe a depositional change from a semi-restricted basin to a more open marine setting through the Kössen Formation (Golebiowski 1990, 1991). This led to increased water circulation and, therefore, to improved living conditions that allowed the coral and brachiopod reefs to flourish (Furrer 1993).

Despite the great abundance and diversity of fossil remains in the Kössen Formation, its exact age is still controversial in that the lower parts are either interpreted as Late Norian or Early Rhaetian in age (Furrer 1993; Jadoul *et al.* 1994; McRoberts *et al.* 1997). The resolution of its age is problematic owing to the absence of index fossils such as conodonts and identifiable ammonoids. Palynological correlations were attempted in deposits of the Kössen Formation in the Southern Alps of Lombardy and the Apennines by Jadoul *et al.* (1994), who argued for a Late Norian age. This interpretation was adopted by Dalla Vecchia (2003), but 'in the absence of ammonites and conodonts the evidence is not convincing and all these rocks could just as well be Lower Rhaetian' (Hallam 2002, p. 148).

Institutional abbreviations. BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; MCSNB, Museo Civico di Scienze Naturali 'E. Caffi', Bergamo, Italy; MFSN, Museo Friulano di Storia Naturale, Udine, Italy; MGUH, Geological Museum, University of Copenhagen, Denmark; MPUM, Dipartimento di Scienze della Terra dell'Università di Milano, Italy; PIB, Paläontologisches Institut, Rheinische Friedrich-Wilhelms-Universität Bonn, Germany; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich, Switzerland.

SYSTEMATIC PALAEONTOLOGY

REPTILIA Laurenti, 1768
ARCHOSAURIA Cope, 1869
PTEROSAURIA Kaup, 1834

CAVIRAMUS gen. nov.

Derivation of name. Latin, *cavum*, cave, cavity, and *ramus*, branch of the lower jaw, with reference to the pneumaticity of the jaw bones.

Type species. Caviramus schesaplanensis sp. nov.

Diagnosis. As for type and only known species.

Caviramus schesaplanensis sp. nov.
Text-figures 2–4, 6C

Derivation of name. 'Schesaplana', the name of the mountain in the Northern Calcareous Alps where the specimen was found.

Holotype. A right lower jaw ramus, medial and posterior portion partially preserved as imprint and mould (PIMUZ A/III 1225).

Type locality and horizon. Western slope of the mountain Schesaplana in the Northern Calcareous Alps ('Rätikon'), Switzerland; Alplihorn Member of the Kössen Formation, Late Triassic (Late Norian–Early Rhaetian).

Diagnosis. Small lower jaw ramus about 50 mm in length and nearly constant in height throughout its entire length with a blunt, round symphyseal region. Peculiar ventral notch with a finished edge posterior to jaw symphysis. Large number of small foramina, pits and roughness on lateral surface of symphyseal region. A row of large, oval foramina embedded in a shelf parallel to tooth row that adopt a cup-shape in anterior region of dentary. Retroarticular process angled at *c.* 35 degrees posteroventrally. A well-developed pneumaticity in angular, surangular, splenial, articular and dentary bones. Teeth multicusped with main cusp and accessory cusps arranged in one plane. Teeth about one-third of height of ramus. Tooth crown smooth and bulbous, narrowing and flattening in region of tooth neck. Tooth implantation thecodont.

Description

Lower jaw. The specimen consists of a partial right ramus of a lower jaw, which is preserved on the surface of a block of limestone (Text-fig. 2). The jaw is exposed in lateral view anteriorly and in two regions posteriorly. The central and parts of the posterior portion of the ramus are not preserved, but the medial surface of the missing parts can be seen as imprints on the limestone. As a result, the jaw is preserved as three parts of bony elements: anterior, central and posterior parts separated by two sections only showing imprints on the sediment. The anterior end of the ramus is complete except for the anterodorsalmost edge of the dentary. Therefore, although parts of the specimen are missing, the complete length and dimensions of the jaw are preserved. The ramus measures 52 mm from the anteriormost tip of the dentary to the posteriormost extension of the articular, measured to the horizontal of the ramus. At the level of the symphysial region, the dentary forms a rounded edge beyond the level of maximum height. The jaw has a relatively constant height of *c.* 6 mm along most of its length, but it swells out slightly to *c.* 7 mm at the anterior edge of the dentary as well as at the level of the coronoid eminence. The region of the coronoid eminence is bordered by the edge of the slab on which the specimen is preserved. However, the specimen was preserved on
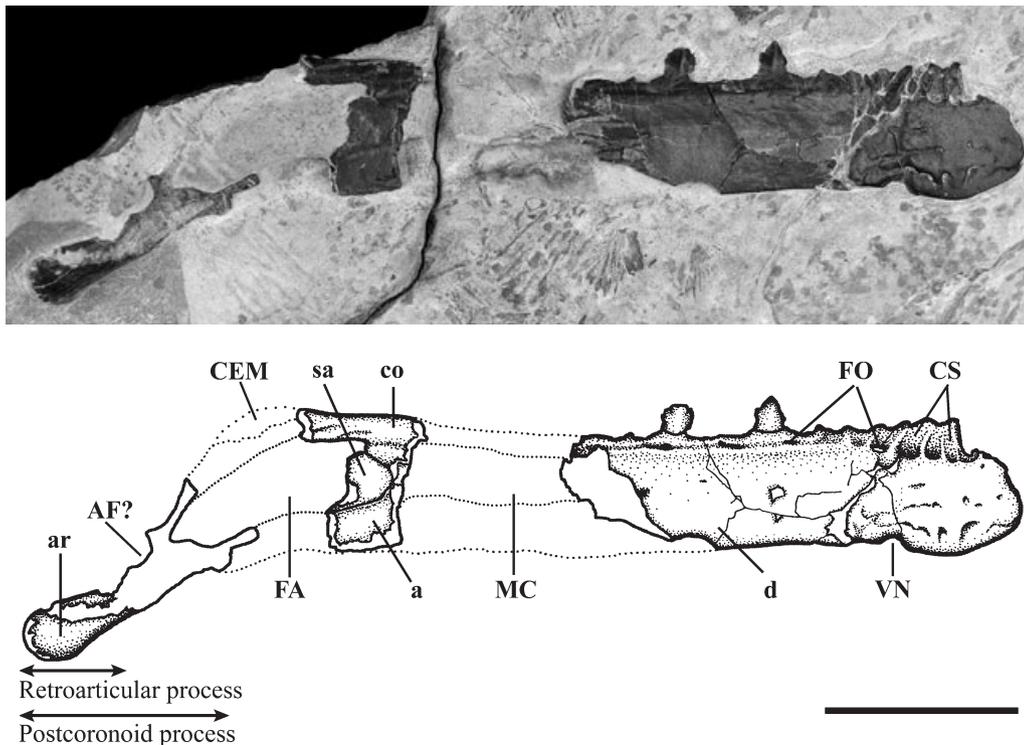
TEXT-FIG. 2. Photograph (A) and drawing (B) of *Caviramus schesaplanensis*. Abbreviations: a, angular; AF?, presumed articulation facet for the quadrate; ar, articular; CEM, presumed outline of the coronoid eminence; co, coronoid; CS, cup-shaped structures; d, dentary; FA, fossa adducctoria; FO, foramen; MC, Meckelian canal; sa, surangular; VN, ventral notch. Scale bar represents 10 mm.

the surface of a large block when we collected it. Complete recovery was not possible, and a further dorsal extension of the preserved bone or the impression of the outline was not observed in the field. In accordance with the impression of the posterior end of the ramus, which runs in a smooth angle towards the preserved part of the coronoid, it is likely that only a shallow coronoid eminence was present rather than a distinct and high coronoid process. The entire postcoronoid region, including the robust retroarticular process, is directed postero-ventrally (Text-fig. 2). Thus, the overall appearance of the jaw is that of a fairly straight, elongate element that is constantly rather high and with a stout, strongly angled postcoronoid process. Although the ramus retains an almost constant height through-out its length and therefore appears quite robust in lateral view, the jaw is a thin, lightly built element that becomes apparent when the cross-section of the broken ramus is examined.

The anteriorly preserved part of the ramus is also the largest, with a length of *c.* 24 mm, and is composed of only the dentary. This bone is the dominant element in the jaw with its dorsal and ventral margins running approximately parallel to one another. The posterior extension of the dentary is uncertain as information on sutural contacts is not available from the imprints. Nonetheless, on the medial side of the jaw, the dentary extends far backwards to at least the posterior end of the central, preserved part, which can be observed in cross-section (see below). A peculiar feature of the specimen is a distinct notch at the ventral margin of the bone just posterior to the level of maximum height, at the anterior edge of the dentary. It is *c.* 1 mm in length, has a semicircular shape and a finished edge. The notch might be associated with a soft tissue structure or a keratinized covering of the bone in this area. This function could be supported by the presence of numerous large foramina, channel-like grooves as well as smaller pits at the whole anterior part of the dentary back to the level of the posterior end of the notch, indicating strong vascularization of this area (Text-fig. 2). Posterior to the ventral notch the lateral surface of the ramus is flat and smooth.

Along the dorsal margin of the jaw there are 12 distinct alveoli, two of which still bear teeth. The dorsal rim of each alveole is concave in shape and separated from neighbouring alveoli by a small dorsal projection of bone (Text-figs 2–3). On the dorsolateral side of the jaw there is a distinct shelf running parallel to the tooth row along most of the length of the dentary. On top of this shelf, there are a number of large, oval foramina that seem to be positioned approximately at the level of every second tooth. The depressions of these foramina show a distinct V-shaped form before they enter the bone as a rounded canal, which is a feature commonly observed in archosaurs (H. C. E. Larsson, pers. comm. 2004).

A further unique feature of specimen PIMUZ A/III 1225 is a number of large, cup-shaped indentations at the anterodorsal edge of the dentary with elongated dorsoventral extension. They end in foramina at their ventralmost point (Text-fig. 2) and form the anterior continuation of the row of foramina embedded in the lateral shelf described above. These structures cannot represent further alveoli as the row of the latter continues further dorsal to the cup-shaped structures on the same level and in the same manner as the more posteriorly positioned alveoli. The cup-shaped depressions are unusual structures that have to our knowledge not been reported for any other taxon. Despite this, there is no reason to assume a pathological cause for their presence, as they are symmetrically spaced and there is no sign of a fracture or unnatural hypertrophic bone growth or exostosis that could indicate an infection or trauma. It is, therefore, likely that they indeed represent natural anatomical structures. Large nutritive vessels probably left the cup-shaped depressions in the bone. Because the position of these shallow depressions approximately coincides with the level of the ventral notch and the area of distinct pits, roughness and foramina along the anterior region of the dentary, they might also have been associated with a soft tissue structure and/or keratinous covering in that area.

Alternatively, these depression found at the anteroventral edge of the ramus could be interpreted as overbite structures from anterior teeth or fangs of the upper jaw, indicating a heterodont dentition. It is notable, however, that these structures distinctly widen ventrally, resulting in a peculiar cup shape of individual indentations. For the depressions being caused by an overbite of fangs of the upper jaw, one would expect a shape that tapers to

TEXT-FIG. 3. Photograph showing the two multicusped teeth that are preserved in the ramus of *Caviramus schesaplanensis.* Anterior is to the right. Scale bar represents 2 mm.

a point ventrally rather than widening and being cup-shaped. Furthermore, the posterior depressions point posteroventrally while the anterior ones project anteroventrally and all are separated from each other by distinct, elevated bony ridges that would have hindered the teeth of the upper jaw from smoothly gliding into these depressions on closure of the jaws. For these structural and biomechanical reasons, the depressions in the anterior portion of the dentary are here interpreted as depressions of nutritive vessels that might have supplied as well as assisted in anchoring soft tissue in that area of the ramus.

The central part of the specimen has a maximum anteroposterior extension of *c.* 6 mm. It is built by a complex pattern of interdigitating bones, of which not all elements are observable in lateral view. A more complete picture of the arrangement of the individual elements can be gained by considering a cross-section of the jaw at the anterior end of this central portion (Text-fig. 4). The ventral edge is formed by the splenial bone, which is solely observable in cross-section, because the ramus is broken along the ventral edge of the lateral side. The splenial extends over the full width of the jaw. Further dorsally, the angular bone ventrally forms a large portion of the lateral as well as medial sides of the jaw. Laterally, the angular slightly overlaps the surangular bone that is also best seen in cross-section. In lateral view, the suture between angular and surangular runs approximately parallel to the ventral margin of the bone, but strongly curves dorsally at the anterior boundary of the preserved central bony part of specimen PIMUZ A/III 1225 (Text-fig. 2).

The dorsalmost third of the cross-section is formed by the coronoid bone. It slightly overlaps the surangular laterally and wraps around the entire dorsal part of the dentary, thereby forming the dorsal margin of the jaw in its central region (Text-fig. 4). In lateral view, the extension of the sutural contact of the coronoid on the surangular bone is indicated by a smooth facet and bordered by a sigmoidal-shaped edge. The latter is only visible because the ventralmost edge of the coronoid bone is slightly damaged. At the dorsal margin of the ramus, the coronoid bone is furrowed by oblique grooves.

The dentary forms an inverted U-shaped structure, which is covered dorsally by the coronoid and continues in a very long, slender blade that contributes to an essential part of the medial side of the jaw (Text-fig. 4). A crack separates the two parts of the dentary, but the perfect fit of the unfinished bony surfaces leaves no doubt that both portions are part of the same element. Ventrally, the dentary blade approaches the angular bone at the medial side of the jaw, revealing a distinct terrace between these two bones, which represents a remnant of the medial groove for the Meckelian cartilage. The Meckelian canal is preserved as a mould on the imprints between the preserved bony parts of the jaw. It is particularly well developed along the posterior imprint where the canal widens to form the fossa adductoria (Text-fig. 2).

The posteriormost of the three preserved portions of the jaw represents the retroarticular process and additionally some parts of the postcoronoid region. It points posteroventrally at an angle of *c.* 30 degrees to the longitudinal axis of the ramus, and terminates in a stout, rounded end. A semicircular indentation at the posterodorsal margin of this process might represent the facet for articulation with the quadrate (Text-fig. 2). Most of the
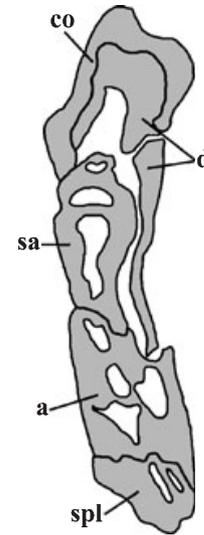
TEXT-FIG. 4. Drawing of the cross-sectional view of the centrally preserved bony part of *Caviramus schesaplanensis*. Bone is grey and matrix is white. Note the well-developed pneumaticity of the dentary (d), surangular (sa), angular (a) and splenial (spl); co, coronoid.

bony surface is damaged and no more information can be extracted from this part of the jaw. However, in concert with the imprint of the medial side of the lower jaw, the general shape of the posterior part of the specimen becomes evident.

All elements of the lower jaw exhibit a distinct pneumatic structure, which is clearly visible when observing the cross-sectional view of the central, preserved portion of the specimen. In particular, the angular and surangular show large cavernous structures, but cavities are also visible in the medial portion of the splenial, as well as the articular and dentary bones.

Dentition. Two teeth, the seventh and the tenth, are preserved and still in place. Anterior to the seventh tooth six alveoli are clearly visible and a seventh was possibly present where the anterodorsal edge of the dentary is broken off. Posterior to the tenth tooth, two further alveoli are identifiable, therefore indicating the presence of a minimum of 12 teeth. Estimated from the approximate length of the dentary, no more then 17 teeth (or 18, if an additional alveole is assumed to have been present at the anterior broken edge of the dentary) could have been present in the jaw, assuming that they retained the same size throughout the entire length of the dentary.

The seventh tooth is tricuspid with a large, slightly bulbous and well-defined main cusp and two small accessory cups mesial and distal of it, which are arranged in a single plane. The accessory cusps are nestled close to the base of the main cusp rather than being set off from it. Slightly basal of each of the two accessory cusps, a small bump is visible that can be interpreted as two additional miniature cuspules.

The tenth tooth is clearly four-cuspid. The tip of the dominant, bulbous main cusp is broken off. Distally two well-defined accessory cups are visible, of which the apical one is nestled close to the main cusp. The basal accessory cusp is somewhat

more separated from the apical accessory cusp than is the latter from the main cusp, with its tip pointing apicodistally. A third accessory cusp is positioned mesially. Its tip is more pointed than that of the two distal accessory cusps, and it is well separated from the main cusp by a smooth, V-shaped indentation. The surface of the crown is smooth.

In general, the tooth crowns narrow and flatten ventrally into a tooth neck that sits in the alveole and the teeth appear small in comparison with the ramus of the jaw, having only about one-third of the height of the ramus.

COMPARISON

A variety of taxa from Upper Triassic sediments are known to possess a dentition with multicusped teeth. These are 'Prolacertiformes' (*Tanystropheus*, *Langobardisaurus*), cynodonts, as well as the pterosaur *Eudimorphodon*.

'Prolacertiformes'. Representatives of the genus *Tanystropheus* are known in two size clusters. Only the small animals that were formerly interpreted as juveniles (Wild 1973) but are now believed to be distinct taxa (Fraser *et al.* 2004) possess a multicusped dentition. The multicusped teeth of *Tanystropheus* are somewhat more dorsoventrally elongated than the teeth found in PIMUZ A/III 1225 and evidently tricuspid only, throughout the whole tooth row (Wild 1973, 1980; pers. obs.). Moreover, in *Tanystropheus* the main cusp is set well off the well-developed mesial and distal accessory cusps.

Another late Triassic 'prolacertiform' possessing multicusped teeth is *Langobardisaurus* from the Norian of northern Italy (Renesto and Dalla Vecchia 2000). It has a series of tricuspid teeth in the cheek region, consisting of a large central and lower lateral cusps, one on each side of the main cusp. Just as in *Tanystropheus*, the teeth are clearly tricuspid only. *Langobardisaurus* moreover possesses a molar-like crushing tooth posterior to the last tricuspid tooth and monocuspid teeth in the anterior region of the jaw. As no teeth are preserved in the posterior and anterior region of PIMUZ A/III 1125 it cannot be ruled out that a similar dentition was present in *Caviramus schesaplanensis*. However, the multicuspid dentition of the latter differs from *Langobardicus* in that the posterior preserved tooth is four-cuspid. Moreover, the jaw morphology of *Langobardisaurus* is very different from that of *Caviramus*. It tapers to a sharp point anteriorly, whereas the anterior end is slightly bent ventrally. It possesses a prominent, stout coronoid process and the postcoronoid process points straight posteriorly rather than in a distinct ventral direction as seen in PIMUZ A/III 1125.

Cynodontia. There are a number of cynodont taxa that possess a multicusped dentition, but only the possibly paraphyletic 'dromatheriid' non-mammalian cynodonts lack features of more derived cynodonts, such as a cingulum or spatial arrangement of their cusps, which clearly sets their dentition apart so that they are easily recognizable even in isolated tooth samples. In fact, isolated teeth of 'dromatheriid' cynodonts could easily be mistaken for teeth of the early pterosaur *Eudimorphodon* and vice versa, although Hahn *et al.* (1984) proposed a number of criteria that can help to distinguish teeth of both taxa.

These authors specifically used *Pseudotriconodon wildi* as a basis for establishing distinguishing characteristics, which, however, are variable among 'dromatheriids'. These characters include the structure of the enamel, which is smooth in 'domatheriids' but shows enamel ribs in *Eudimorphodon*. This feature on its own, however, is not sufficient to distinguish the taxa, because juvenile specimens of *Eudimorphodon* have weakly developed or lack the enamel ribs as well. *Caviramus* also lacks enamel ribs. Another character is the shape of the crown in apical view, which is elliptical in *Eudimorphodon*, a character shared by *Caviramus*, but labiolingually parallel in *Pseudotriconodon*. Sues (2001) also reported an elliptical outline of the teeth in *Microconodon* in occlusal view. Furthermore, cutting edges on all cusps are often sharp in members of the 'Dromatheriidae', but are rounded and only weakly developed in *Eudimorphodon* and *Caviramus*. The root is set off from the crown by a more or less well-developed incision in *Eudimorphodon* and *Caviramus*, but is continuous in *Pseudotriconodon* and other 'dromatheriids'. Additionally, a further character that is often used to identify derived cynodonts on the basis of isolated teeth is the development of a double-rootedness (Shapiro and Jenkins 2001; Sues 2001; Datta *et al.* 2004). In contrast, as far as is known, all pterosaurs possess a single, undivided root. Because no isolated teeth are available for study in *Caviramus*, the condition remains unknown in this taxon.

Almost complete jaws are only known from the two earliest described 'dromatheriid' taxa *Dromatherium sylvestre* (Emmons, 1857) and *Microconodon tenuirostris* (Osborn, 1886; see also Sues 2001). Furthermore, 'dromatheriid' teeth associated with jaw fragments are reported for *Lepagia gaumensis* (Hahn *et al.* 1987) and *Pseudotriconodon chatterjeei* (Lucas and Oakes 1988).

In addition to the differences in the dentition, all 'dromatheriid' and more derived cynodonts, of which the jaws are known, are characterized by a jaw morphology that shows a prominent coronoid process with major contribution of the dentary (Sues 2001; Sidor 2003). In contrast, the coronoid region in PIMUZ A/III 1225 only shows a rather shallow coronoid eminence and the dentary is not exposed laterally at this level (Text-fig. 6). Although the 'Dromatheriidae' do not show the mammalian jaw articulation of dentary and squamosal (Sues

2001), the postdentary jaw elements are strongly reduced in size, whereas in PIMUZ A/III 1225 the posterior third of the jaw ramus is built by the angular, surangular and articular, with the articular forming the articulation with the skull. Distinctly cavernous bone structures as revealed by *Caviramus schesaplanensis* have to our knowledge not been reported for cynodonts.

Pterosauria. A comparison with the pterosaur genus *Eudimorphodon* reveals great similarities with PIMUZ A/III 1225 in the structure of individual teeth (Text-fig. 5). Aside from *Eudimorphodon*, a multicusped dentition has been described for another Upper Triassic (Norian) pterosaur genus, *Austriadactylus* from Tyrol, Austria (Dalla Vecchia *et al.* 2002). Although the teeth figured are different from those found in *Caviramus* in that they possess a large number of small cuspules along the cutting edge (Dalla Vecchia *et al.* 2002, fig. 3), *Austriadactylus* has pentadactyl teeth similar to those of *Eudimorphodon* in the mid-posterior region of the mandible that were not figured (F. Dalla Vecchia, pers. comm. 2005). However, since no figures are available, no further comparison of the dentition can be made at present.

Three species of *Eudimorphodon* are known from Norian and Rhaetian deposits: *E. ranzii* (Zambelli, 1973), *E. rosenfeldi* (Dalla Vecchia, 1995) and *E. cromptonellus* (Jenkins *et al.*, 2001). *E. cromptonellus* is solely represented by the holotype MGUH VP 3393, which possesses only fragmentarily preserved mandibles and, therefore, is not suitable for direct comparison of the jaw morphology. However, the multicusped teeth are similar in structure and form of the main and accessory cusps to those of *Caviramus schesaplanensis*.

All described *Eudimorphodon* species possess variable numbers and sizes of accessory cusps that are arranged in a single plane (Dalla Vecchia 2003, 2004). Compared with the multicusped teeth found in *Tanystropheus*, the main cusp is usually less clearly set off from the accessory cusps. The arrangement and size of the cups and cuspules, as well as the slightly bulbous form of the tooth crown and the narrowed and flattened tooth neck of PIMUZ A/III1225 greatly resemble the dentition of the three known *Eudimorphodon* species (Zambelli 1973; Wild 1978, 1994; Dalla Vecchia 1995, 2004; Jenkins *et al.* 2001). Two large fangs are present in the ramus of the lower jaw of *E. ranzii*, but are not reported in the other two *Eudimorphodon* species, owing to insufficient preservation of the *E. rosenfeldi* and *E. cromptonellus* specimens (Wild 1978; Jenkins *et al.* 2001; Dalla Vecchia 2004). They are, however, also present in disarticulated eudimorphodontid mandibular rami of an undescribed specimen (Dalla Vecchia 2004; Text-fig. 5). The presence of fangs in PIMUZ A/III 1225 cannot be ruled out, as the teeth of the anterior region of the dentary are not preserved. In *E. ranzii* the fangs exhibit a significantly larger cross-section than the posterior multicusped teeth, therefore requiring larger alveoli. Moreover, the alveoli of the fangs are slightly displaced ventrally with respect to the tooth row of the multicusped dentition. In *Caviramus schesaplanensis* the anteriormost alveoli are approximately the same dimensions as the posterior ones and the tooth row forms a straight line throughout the length of the dentary. It therefore seems unlikely that large fangs were present in *Caviramus schesaplanensis*, indicating that it might have had an isodont dentition in the lower jaw, rather than a heterodont dentition as found in *Eudimorphodon*. The lower jaw of the well-preserved holotype of *Eudimorphodon ranzii* (MCSNB 2888) still contains 25 multicusped teeth, and one tooth in the middle of the tooth row that has evidently fallen out, therefore giving a count of 26 multicusped teeth in that specimen. Two further completely preserved *Eudimorphodon* mandibles possess 13 multicusped teeth in specimen MPUM 6009 (34 mm long), one of which again has fallen out, therefore leading to a count of 14 teeth, and 19 multicusped teeth in specimen MFSN 21545 (53 mm long)


TEXT-FIG. 5. Lower jaw ramus of *Eudimorphodon* cf. *ranzii*, BSP 1994I 51.

(Dalla Vecchia 2004). *Caviramus schesaplanensis* (52 mm long) had at least 12, and a maximum of 18 teeth in its dentary, therefore having a comparatively smaller number of teeth. As PIMUZ A/III 1225 represents the only specimen known from *Caviramus schesaplanensis*, no assessment about the ontogenetic age of this individual can be made, which however, could have a strong influence on the number of teeth present in the jaw in case the number of teeth increases with ontogentic age in this taxon.

The morphology of the mandible of the three *Eudimorphodon* species differs in a number of aspects from PIMUZ A/III 1225. In all three *Eudimorphodon* taxa, the ramus is an elongate, slender element that narrows anteriorly and tapers to a point towards the symphyseal region (Text-fig. 5). In contrast, the mandible of *Caviramus schesaplanensis* is a stout element with a constant, rather great height over its entire length and a blunt, round symphyseal region. In *E. ranzii* the coronoid process is very shallow and the retroarticular process is short and almost horizontal (Wild 1978; Dalla Vecchia 2004). The anterior, symphyseal region of the lower jaw ramus is not preserved in *E. rosenfeldi*, but the coronoid process is somewhat higher in that taxon and pointed dorsally. The retroarticular process is directed posteroventrally and approaches the condition found in PIMUZ A/III 1225, although the downward angle of the postcoronoid region of the latter is even stronger. A morphology similar to that of *E. rosenfeldi* can also be found in the mandible of *E.* cf. *ranzii*, specimen BSP 1994I 51 (Wellnhofer 2003). The retroarticular process terminates in a spheroidal, strong end in PIMUZ A/III 1225, but is flattened and more angular or axe-shaped in *E. rosenfeldi* and *E.* cf. *ranzii* (specimen BSP 1994I 51) (Text-fig. 5).

PIMUZ A/III 1225 clearly differs from the Triassic 'prolacertiforms' *Tanystropheus* and *Longobardisaurus* in characteristics of the dentition and the jaw morphology. The latter also clearly sets *Caviramus* apart from cynodonts, which have a distinct shape and characteristic upward curvature of their mandible with a high coronoid processes, which is very different from the jaw morphology of *Caviramus* (Text-fig. 6). Strong similarities, particularly of the multicusped dentition, exist with the basal pterosaur taxon *Eudimorphodon*. The well-developed pneumaticty of the elements of the mandible revealed in cross-sectional view is supportive evidence for the affinity of *Caviramus* to the Pterosauria, which are known to possess pneumatic long bones as a means to lighten the skeleton for flight (de Ricqlès *et al.* 2000). However, cross-sectional views of jaw bones have not been studied in most taxa; hence, no definite statement about presence of pneumaticity can be made for the taxa used for comparison in this study.
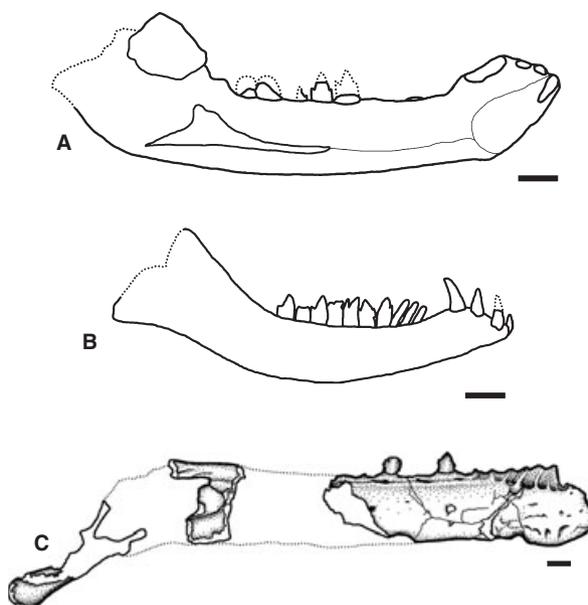
TEXT-FIG. 6. Comparison of the jaw morphology of A, *Microconodon tenuirostris*, modified from Sues (2001), B, *Dromatherium sylvestre*, modified from Simpson (1926), and C, *Caviramus schesaplanensis*. Scale bar represents 2 mm.

CONCLUSIONS

Caviramus schesaplanensis exhibits a number of unique characteristics that clearly differentiate it from other Triassic tetrapod taxa known to have a multicusped dentition and which make a clear diagnosis of this taxon possible. Moreover, although PIMUZ A/III 1225 is solely a lower jaw ramus, an assignment of it to the Pterosauria is possible on the basis of the close resemblance of its dentition to that of the well-known pterosaur genus *Eudimorphodon*. The short and slightly bulbous form of the tooth crown, exhibiting a variable number of accessory cusps aside from a large main cusp, and the narrowed, flattened tooth neck are found in *Eudimorphodon* as well as in *Caviramus schesaplanensis*. The dentition of *Eudimorphodon* and *Caviramus* bears similarities to the teeth of 'dromatheriid' cynodonts, although a number of characteristics are suitable to differentiate them. In addition, the jaw morphology of 'dromatheriid' cynodonts differs significantly from that of *Caviramus* in having a high coronoid process, an abbreviated postdentary region, and an upward curvature of the anterior and posterior ends of the ramus.

Very thin walls of the bones and a conspicuous pneumaticity can be observed in cross-sectional view of PIMUZ A/III 1225. Extremely thin bone walls and pneumaticity are means of light construction of the skeleton, which is well known for pterosaurs as a possible adaptation for flight (de Ricqlès *et al.* 2000), but is not reported

for the terrestrial cynodonts or 'prolacertiforms' such as *Tanystropheus* and *Langobardisaurus*. Moreover, the distinct V-shape form of the aperture of the large foramina positioned along the shelf, parallel to the tooth row of PI-MUZ A/III 1225, is a feature that is commonly found in archosaurs and, in combination with the aforementioned characters, offers further support for the affinity of this specimen to the Pterosauria.

Despite the strong similarities of the dentition of *Caviramus schesaplanensis* to that of the basal pterosaur *Eudimorphodon*, these two taxa can be clearly differentiated on the basis of a number of characters of the jaw morphology, which also explicitly characterize the newly described taxon. *Caviramus schesaplanensis* differs from *Eudimorphodon* in having a mandibular ramus of constant height, teeth that are rather small in relation to the ramus, only being one-third of the height of the ramus, a blunt, round symphyseal region, and a peculiar ventral notch with a large number of foramina and small pits anterior to it. Moreover, the postcoronoid process has a strong, ventrally directed angle of about 30 degress to the horizontal, which is similar to that of *Eudimorphodon* specimens with an angle of about 20 degrees (BSP 1994I 51, Text-fig. 5). Thanks to the good preservation of the cast of the fossa aductoria and the imprint of the ramus, the possibility that this strong angle in *Caviramus* is attributable to distortion can be ruled out. Also characteristic is the row of foramina paralleling the tooth row, with the foramina being posteriorly embedded in a shelf and anteriorly possessing a cup-shaped structure. The overall appearance of the ramus of *Caviramus schesaplanensis* is that of a robust, stout element, but its internal structure is very thin and fragile with thin bone walls and individual jaw elements with strong pneumaticity.

In addition to *Eudimorphodon* and *Austriadactylus*, *Caviramus schesaplanensis* therefore represents a third basal pterosaur possessing a multicusped dentition very similar to that of *Eudimorphodon*. As already suggested by Dalla Vecchia *et al.* (2002), this reflects early radiation and diversity of pterosaurs in the Late Triassic shortly after their first recorded appearance in the fossil record. Furthermore, it indicates that multicuspid dentition was a common feature in basal pterosaurs.

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