THE FIRST ITALIAN SPECIMEN OF *AUSTRIADACTYLUS CRISTATUS* (DIAPSIDA, PTEROSAURIA) FROM THE NORIAN (UPPER TRIASSIC) OF THE CARNIC PREALPS

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Abstract. The Triassic pterosaur *Austriadactylus cristatus* is reported for the first time from the Norian (Upper Triassic) of north-eastern Italy. It is only the second specimen of this taxon and provides new information on the mandibular dentition, cranium and postcranium (cervical vertebrae and the forelimb), not available in the holotype. A cladistic analysis shows that *Austriadactylus* is phylogenetically closer to *Preondactylus* than to *Eudimorphodon*.

Riassunto. Lo pterosauro triassico *Austriadactylus cristatus* è per la prima volta segnalato nel Norico (Triassico Superiore) dell'Italia nord-orientale. Si tratta del secondo esemplare riferibile a questo taxon e fornisce informazioni sulla dentatura mandibolare, su alcuni elementi cranici e postcraniali (soprattutto sulle vertebre cervicali e sugli arti anteriori) che non sono disponibili sull'olotipo. Un'analisi cladistica mostra che *Austriadactylus* è filogeneticamente più vicino a *Preondactylus* che a *Eudimorphodon*.

Introduction

The only specimen of the Triassic non-pterodactyloid pterosaur *Austriadactylus cristatus* Dalla Vecchia, Wild, Hopf & Reitner, 2002 is the holotype (SMNS 56342) that consists of a partial, articulated skeleton including the skull with lower jaw, from the Upper Triassic Seefeld Formation of Tyrol, Austria. It is preserved on one of two mirroring slabs obtained after the splitting of a layer of black dolostone (unfortunately the counter slab was lost) with many bones split sagittally. A second pterosaur specimen discovered in the Seefeld Formation comprises a partial, disarticulated skeleton (BSP 1994 I 51) attributed to *Eudimorphodon* cf. *ranzii*

Zambelli, 1973 by Wellnhofer (2003), but belongs to a new unnamed taxon (Dalla Vecchia 2009).

A pterosaur specimen (SC 332466) from the Upper Triassic of north-eastern Italy is reported here as a second example of *Austriadactylus cristatus* that shows skeletal features not seen in the holotype.

Institutional abbreviations. BMNH, The Natural History Museum, London, England; **BNM**, Bündner Naturmuseum, Chur, Switzerland; **BSP**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **GSM**, Geological Survey Museum, Keyworth, England; **MCSNB**, Museo Civico di Scienze Naturali di Bergamo, Italy; **MFSN**, Museo Friulano di Storia Naturale, Udine, Italy; **MPUM**, Museo di Paleontologia, Dipartimento of Scienze della Terra dell'Università di Milano, Italy; **PIMUZ**, Paläontologisches Institut und Museum der Universität Zürich, Switzerland; **SC**, Italian State collections; and **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **YPM**, Yale Peabody Museum, New Haven, USA.

Terminology and methods

The term 'non-pterodactyloid pterosaur' is used here for all genera included in the suborder Rhamphorhynchoidea of Linnean systematics (Wellnhofer 1978, 1991), which is paraphyletic according to phylogenetic systematics (e.g., Kellner 2003; Unwin 2003; Dalla Vecchia 2009). The use of single quotation marks in the following text indicates a taxon of doubtful validity.

According to Dalla Vecchia (2009), the new binomial *Carniadactylus rosenfeldi* is used for the campylognathoidid previously known as *Eudimorphodon rosenfeldi* Dalla Vecchia, 1995 and doubts are expressed about the generic distinction of *Raeticodactylus filisurensis* Stecher, 2008 relative to *Caviramus* Fröbisch & Fröbisch, 2006. Unlike Dalla Vecchia (2009), MCSNB 3359 is here considered as a specimen of *Peteinosaurus zambellii*, because its recent re-examination allowed the identification of a synapomorphy shared with one of the specimens referred to this species (MCSNB 3496; Dalla Vecchia 2003) and no substantial differences with the holotype (MCSNB 2886) were found.

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The forelimb bones are imagined as being oriented in their flight position. I follow the terminology used by Bennett (2001) for the orientation of the bones in space, but "cranial" and "caudal" are used in preference to "anterior" and "posterior". The terminology used for dentition is that suggested by Edmund (1969). The terms "cusps" and "cuspules" are used for topographically separate elevations present along the cutting margins of the tooth crowns when these elevations are low in number; a tooth is considered serrated when those elevations (now termed denticles) are closely spaced on the cutting margin and are similar in size. In order to identify and draw the skeletal elements, the margin of the bones and teeth, SC 332466 was wetted with alcohol and examined with a binocular microscope up to 144 X magnification.

Locality and stratigraphy

According to the discoverer, Mr. Elio Martinis, SC 332466 was found on a boulder in the bed of the Seazza Creek, close to the small church of Madonna Peraries, Preone Municipality, Udine Province, Friuli Venezia Giulia Region of north-eastern Italy. Geomorphologic and topographic constraints, as well as the local stratigraphy (Dalla Vecchia 1991, 2006), suggest that the specimen comes from the uppermost part of the lower member of the Dolomia di Forni Formation (sensu Dalla Vecchia 1991). This is the same locality and stratigraphic position as the holotype of *Preondactylus buffarinii* (see Wild 1984; Dalla Vecchia 2006), and corresponds to the stratigraphic section between outcrops F3 and F5 of Roghi et al. (1995).

A late Alaunian (late middle Norian) date for the Seefeld Formation and the fossiliferous portion of the Dolomia di Forni was proposed on the basis of the conodont assemblages by Roghi et al. (1995) and Donofrio et al. (2003), but an early late Norian (early Sevatian) age is indicated by a more recent conodont analysis (Moix et al. 2007).

Systematic palaeontology

Diapsida Osborn, 1903

Pterosauria Kaup, 1834

Austriadactylus Dalla Vecchia, Wild, Hopf & Reitner, 2002

Austriadactylus cristatus Dalla Vecchia, Wild, Hopf & Reitner, 2002

Figs 1-4

1994 *"Preondactylus" buffarinii* o una nuova forma di ?Dimorphodontidae Dalla Vecchia, pp. 89-93, figs. 1.29-1.31.

2002 *Austriadactylus cristatus* Dalla Vecchia, Wild, Hopf & Reitner, p. 196, figs. 1-3.

2003 *Preondactylus buffarinii* Dalla Vecchia, p. 25.

2006 A genus different from either *Eudimorphodon* and *Preondactylus* Dalla Vecchia, p. 439, fig. 12 right.

2008 un genere differente da *Eudimorphodon* and *Preondactylus* Dalla Vecchia, p. 186, fig. 183.

Holotype: SMNS 56342.

Referred specimens: SC 332466, in the Museo Geologico della Carnia, Ampezzo, Udine Province, Italy.

Distribution: Uppermost part of the lower member of Dolomia di Forni Formation (sensu Dalla Vecchia 1991), lower Sevatian (upper Norian), Udine Province, Friuli Venezia Giulia Region, Italy. The holotype comes from an abandoned mine near Ankerschlag, Tyrol, NW Austria, opened in the Seefeld Formation (lower Sevatian, upper Norian, following Moix et al. 2007).

Emended diagnosis: Non-pterodactyloid pterosaur bearing a thin, sagittal cranial crest extending from the tip of the snout caudally to at least the middle of the orbit, highest rostral to the external naris and with radial ridges in the rostral, highest portion; short nasal with long premaxillary process. Peculiar heterodont dentition characterized by the apomorphic combination of tall, conical and slightly recurved tooth crowns in the premaxilla; triangular or lanceolate mesial maxillary tooth crowns that are higher apicobasally than long mesiodistally (like the subsequent teeth); some very large tooth crowns in the middle maxilla at the ascending process that are lanceolate, blade-like and serrated, followed by triangular, serrated tooth crowns in the distal part of the maxilla that decrease in size distally; mesialmost (symphyseal) mandibular teeth similar to the premaxillary teeth; subsequent tooth crowns small and not touching each other; mesial tooth crowns triangular, slightly curved caudally and higher apicobasally than long mesiodistally; mid-mesial tooth crowns bulbous and lanceolate, taller than long with 4-5 small denticles along each cutting margin; mid-distal tooth crowns slightly smaller, bulbous and triangular, lower apicobasally than long mesiodistally with 4-6 larger denticles along each cutting margin.

Description of SC 332466. The specimen is a partial, well-articulated skeleton preserved completely flattened on the surface of a dark grey dolostone bed (Fig. 1). Because of exposure to weathering, the bones and teeth have been partly eroded and are often cross-sectioned sagittally. It is therefore impossible to clearly distinguish single, overlapping skeletal elements, especially in the skull. Many elongate bones are crushed and broken longitudinally, appearing as two or more long, parallel elements. Weathering has completely eroded the thinner parts of some bones leaving just the thickest parts, which misleadingly appear as single bones.

The postcranial skeleton is preserved in dorsal view, with the wing metacarpal showing the dorsal distal condyle and the neural canal visible in some cervical vertebrae, the neural arch having worn away. The complete skull exposes the left side, but it is slightly deformed by crushing, and partly displays its dorsal surface. Both lower jaw rami are visible, displaced as in the holotype of *Preondactylus buffarinii* (cf. Dalla Vecchia 1998). The skull is articulated with the cervical vertebrae. The vertebral column is preserved articulated up to the distal third of its dorsal segment. The scapulocoracoids are preserved in what appears to be their anatomical position lateral to presacral vertebra 8 where the vertebral column is angled laterally 140°. The dorsal ribs are still connected to their corresponding vertebrae. The articulated left forelimb preserves traces of all the elements, except the distal half of wing phalanx 2 and wing phalanges 3 and 4. The radius and ulna are nearly completely flexed at the elbow and form angle of only 12°

Fig. 1 - *Austriadactylus cristatus*, SC 332466. Above, specimen; below, interpretative drawing. Abbreviations: aof = antorbital fenestra, ax = axis, bpt = basipterygoid process, c = carpus, ccr = cranial crest, cv3-7 = cervical vertebrae 3-7, d = dentary, dr = dorsal ribs, dr1 = first dorsal rib, dt = dentary teeth, dv1 = dorsal vertebra 1, ec = ectopterygoid, f = frontal, fe = femur, h = humerus, hy = ceratobranchial I (hyoid apparatus), itf = infratemporal fenestra, j = jugal, lc = lacrimal, ldc = large distal carpal, lj = lower jaw ramus, mcI-IV = metacarpals I-IV, mx = maxilla, mxt = maxillary teeth, n = nasal, na = external naris, or = orbit, p = parietal, pc = preaxial carpal, phI-1, phII-1, phII-2, phIII-2, and phIII-3 = manual phalanges I-1, II-1, II-2, III-2, and III-3, pmx = premaxilla, pmxt = premaxillary teeth, po = postorbital, prf = prefrontal, psc = proximal syncarpal, q = quadrate, ra = radius, sco = scapulocoracoid, sdc = small distal carpal, sdt = symphysial dentary tooth, se = sesamoid, so = supraorbital, sq = squamosal, ti = tibia, u = ulna, wph 1-2 = wing phalanges 1-2. Left elements are in parentheses. Scale bar = 20 mm.
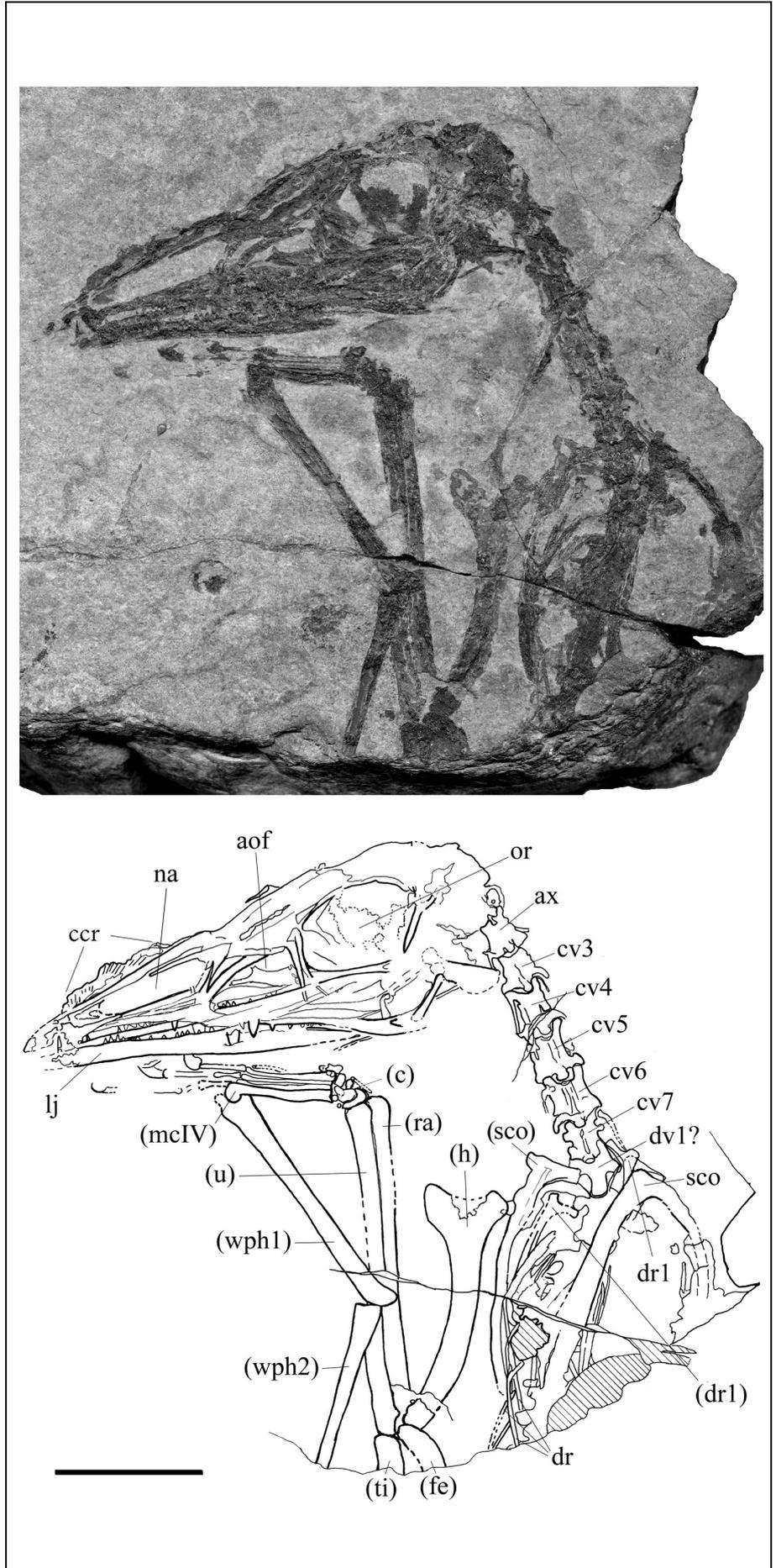
with the humerus. The metacarpus and the radius/ulna are nearly perpendicular to each other due to metacarpal flexion and a slight disarticulation of the carpus. Wing phalanx 1 is articulated proximally with the distal condyles of the wing metacarpal and is flexed, forming an angle of 50° with the metacarpus. Wing phalanx 1 still contacts wing phalanx 2, which is rotated preaxially by 52°. Of the hind limbs, only the distal part of the left femur and the proximal part of the left tibia are preserved. Measurements of the main skeletal elements are provided in Table 1.

	SC 332466	SMNS 56342
Skull	72	110
Humerus	36	*70-75
Ulna	50	96.5
metacarpal I	13	-
metacarpal II	13.8	-
metacarpal III	14	-
metacarpal IV	15.7	-
wing phalanx 1	40	>79
wing phalanx 2	>24	101

Tab. 1 - Measurements in millimetres of some skeletal elements in SC 332466 and the holotype of *Austriadactylus cristatus* (SMNS 56342). * = uncertain measurement.

Skull

The skull (Fig. 2A-B) is elongated and low, and tapers rostrally. The rostrum has a straight dorsal outline and is not deep and convex like that of *Dimorphodon macronyx*. Dorsally, the skull is partially collapsed corresponding to the caudal part of the external naris and the rostral part of the antorbital fenestra. The collapse is shown by a notch along the skull margin and by the lateral exposure of elements of the skull roof. This was possibly caused by a traumatic event or by crushing after burial. The deformation has slightly reduced the caudal height of the external naris, and partly masks its original outline. Several elongated and narrow bones, more or less parallel to each other and to the main axis of the skull, are grouped along the ventral margin of the skull. They are the mandibular rami, the rostral (premaxillary) and caudal (jugal) processes of the maxillae, the jugal(s), and probably elements of the palate (palatines, vomers, pterygoids), exposed by crushing and by the slight skull deformation. Caudally, the ventral margin of the skull is probably straight.

The external naris is large, elongated rostrocaudally and with a trapezoidal outline. The antorbital fenestra is also large, approximately as long as high and with a triangular outline, although the deformation and slight displacement of the bones bordering it rostrally and dorsally masks its original shape. It probably lies level with the naris. The orbit is circular and is the widest skull opening. As in most other Triassic pterosaurs with a similar style of preservation, the outline of the infratemporal and supratemporal fenestrae cannot be discerned.

The prenarial portion of the premaxilla appears to be significantly longer than high and its dorsal margin is gently convex. The ventrocaudal (maxillary) process borders at least the ventrorostral margin of the external naris, possibly extending further caudally. The dorsocaudal (nasal or frontal) process seems to reach the frontal nearly at the level of mid-orbit. The traces of a very thin cranial crest are preserved along the dorsal edge of the premaxilla, perpendicular to the rostrum and crossed by subtle radial ridges. The maxilla is a slender, triradiate bone with long and low premaxillary and jugal processes. The premaxillary process tapers rostrally; the jugal process probably tapers too, but its border with the maxillary process of the jugal cannot be identified. The tall ascending (nasal) process is slightly arched and is inclined backwards. It is impossible to distinguish clearly the left from the right maxilla; their relative positions are indicated by the teeth. The nasal is a slender, V-shaped bone with a long premaxillary process bordering the caudal half of the dorsal margin of the external naris. The maxillary process seems to form the entire posterior margin of the external naris. The frontal (dorsocaudal) process seems to be shorter than in other non-pterodactyloid pterosaurs (e.g. Wellnhofer 1978; Unwin 2003; Sangster 2004).

The wide frontal is probably fragmented into several pieces by crushing and is slightly rotated toward the observer, partly exposing its dorsal surface. This is the case of its presumed rostral portion, which seems to reach the antorbital fenestra because of the shortness of the frontal process of the nasal. The orbital margin of the frontal is thickened. The outline of the other skull roof elements cannot be distinguished. A slender and apparently triradiate, Y-shaped bone along the posterior orbital margin is probably the right postorbital. If so, the supratemporal fenestra was very narrow, because of the shape and orientation of the squamosal and frontal processes of the postorbital.

A slender and sigmoidal bone, which is dorsally expanded with a short rostral process, could be a lacrimal (prefrontal of Wild 1979; interpreted as a lacrimal + prefrontal in *Dimorphodon macronyx* by Sangster 2004), because it is very similar in shape and position to the 'prefrontal' of *Eudimorphodon ranzii* (Wild 1979, fig. 1). A narrow bone just rostral to it could correspond to the 'adlacrymal' of Wellnhofer (1978), the 'lacrymal' of Wild (1979), or simply be the lacrimal of the other
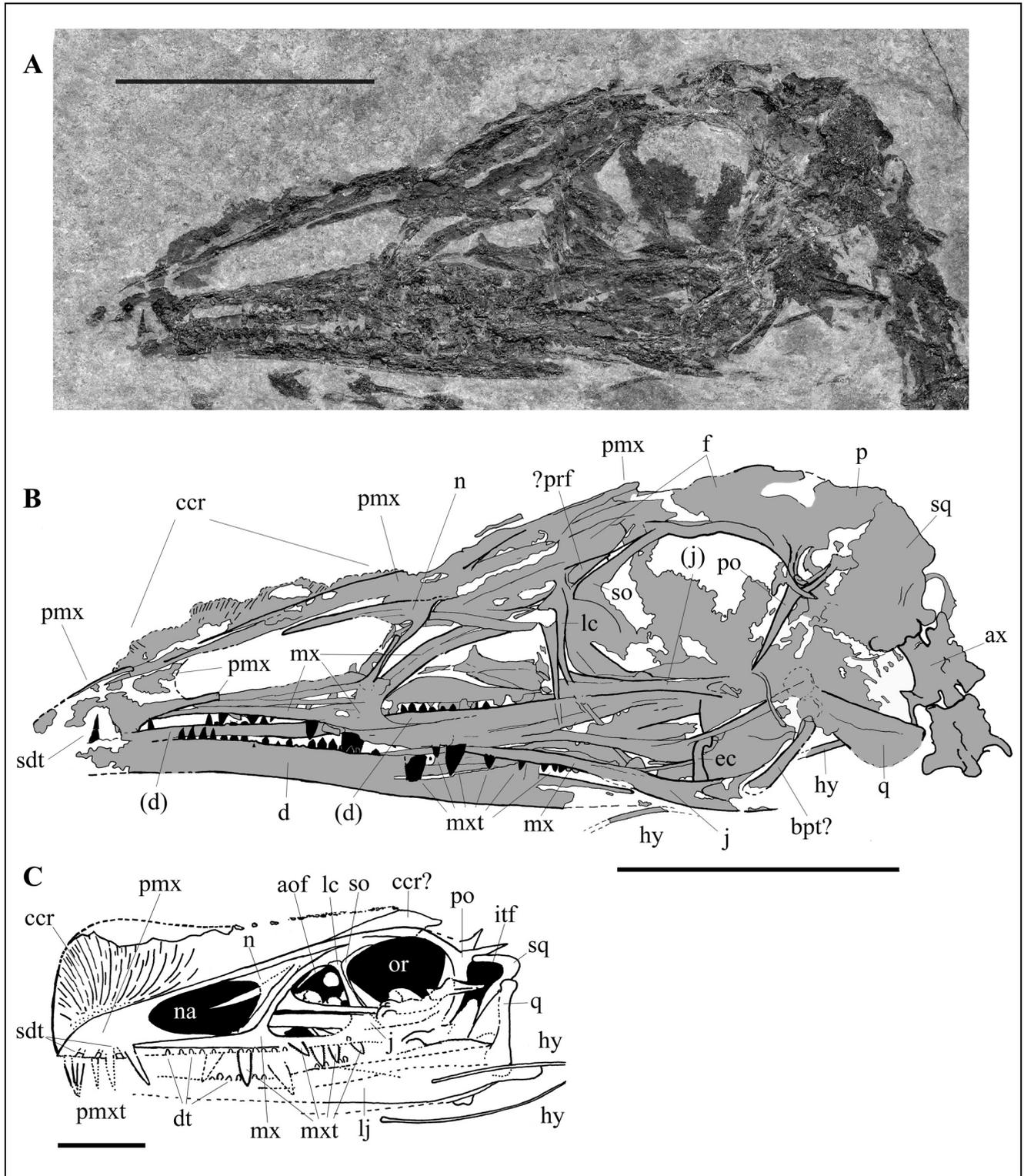
Fig. 2 - *Austriadactylus cristatus*, skull and lower jaws. A) The skull and lower jaws of SC 332466; B) interpretative drawing of SC 332466; C) the skull and lower jaw of the holotype, SMNS 56342 (from Dalla Vecchia et al. 2002, mirrored and modified). Abbreviations in figure 1. In B, teeth are emphasized with black and left elements are in parentheses. Scale bar = 20 mm.

side of the skull. A V-shaped element at the dorsorostral margin of the orbit could be the supraorbital, by analogy with the skull reconstruction of *Dimorphodon macronyx* produced by Sangster (2004, fig. 2.1A). A small prefrontal possibly occurs between the rostrodorsal part of the supraorbital and the frontal. Although the complete outline of the jugals cannot be discerned, those bones are undoubtedly low and long, unlike the deep jugal of *Dimorphodon macronyx* and *Eudimorphodon ranzii* (e.g., Wellnhofer 1978; Unwin 2003). In fact, all the bones preserved in the zone where jugals occur in articulated skulls are low and elongated. Two of these show a hint of a caudal notch and dorsal (postorbital) and caudal (quadratojugal) processes, suggesting that they could be the jugals. A small, hook-like bone below the level of the orbit could be an ectopterygoid. A probable right quadrate is slightly displaced from its position of articulation with the squamosal and the mandible.

Lower jaw

The mandibular ramus is low, slender and with straight, parallel margins, at least in its mid-rostral portion (Fig. 2A-B). Most of the rostral ends of both mandibular rami were worn away. The caudal portion, bearing the 'coronoid' process and the articular cotyle for the quadrate, cannot be distinguished. The mandibular rami are unfused at the symphysis and the rostral termination is slightly downturned and unexpanded. No large foramina are present on the laterodorsal margin of the dentary. The retroarticular process could not be significantly inclined with respect to the axis of the ramus, because there is no trace of a bone directed caudoventrally.

Filiform bones preserved along the ventrocaudal margin of the skull are probably ceratobranchials I of the hyoid apparatus.

Dentition

No traces of the premaxillary teeth are preserved. At least 12 maxillary teeth can be counted. Two occur midway along the premaxillary process of the maxilla. They appear to be lanceolate and approximately the same size as the maxillary teeth occurring midway along the jugal process (Fig. 2B), but denticles cannot be detected along their cutting margins. A larger tooth, (1.5 mm high), occurs just rostral to the ascending process; it is lanceolate, much higher apicobasally than long mesiodistally, with its distal cutting edge finely serrated. Three very large teeth follow, occurring below the ascending process or just caudal to it. It is likely that they do not all belong to the same maxilla, but it is impossible to state which maxilla bears each of them. They are lanceolate, much higher apicobasally than long mesiodistally, flat labially and with serrated mesial

and distal margins (Fig. 3A1-2). The first two are the largest and are partially concealed. The distal cutting margin of the second bears 9 or 10 small denticles in a segment of the cutting margin 1.35 mm long; denticles along the cutting edges have a similar size (Fig. 3A1). The third large tooth crown is 2.5 mm high apicobasally. Only the apical part (1.5 mm high) is preserved as dentine, the remaining part is represented by an impression only. The serration pattern is the same as in the preceding large tooth; at least 6-7 small denticles are identifiable along the mesial margin (Fig. 3A2). Distal to this tooth, the maxillary crowns are triangular and decrease in size; the first following crown is only 1 mm high (Fig. 3A3), and the last is 0.65 mm high. They have serrated cutting edges with up to six small denticles approximately the same size along both edges. The smallest, distal maxillary teeth resemble the mid-distal mandibular teeth, which however occur in a more mesial position.

The mesialmost and mid-mesial mandibular teeth are preserved mainly in the right ramus where there are traces of at least 18 teeth. Three mesial and possibly eight mid-distal teeth are identifiable in the left mandibular ramus. The dentition here is strongly heterodont. The impression of a right tooth at least 1.65 mm apicobasally high indicates that the first (symphyseal) mandibular teeth were large, slender, straight, pointed and probably conical (Fig. 3A4). Subsequent teeth change shape along the mandible, but all are smaller and of a similar size. The first four non-symphyseal crowns identifiable along the right ramus have a triangular outline in labial view and are slightly curved caudally (Fig. 3A5). They are higher apicobasally than long mesiodistally (height ranges 0.87-0.88 mm; mesiodistal length is 0.60 mm), and appear labiolingually flattened, but this could be the result of weathering and compression. No denticles are visible along the cutting margins at a magnification of 144 X. The three subsequent crowns are of similar size but are poorly preserved, possibly showing an inflated 'root'. This row of seven teeth is 5.35 mm long and the crowns do not contact each other basally. A toothless segment follows, where an erupting tooth still within the dentary possibly occurs. Subsequently, a sequence of mid-mesial teeth is observed: a tooth like the preceding ones but also showing an inflated, barrel-like 'root' separated from the crown by a slight constriction is present (Fig. 3A6), as is the apical part of an erupting tooth, another tooth showing an inflated, barrel-like 'root' (the three teeth are regularly spaced and do not contact each other), an empty alveolus, and the deep impressions of three lanceolate crowns that are bulbous (Fig. 3A7), at least labially, and are more closely appressed than the preceding ones. The possible presence of small denticles along the cutting margins of the latter crowns cannot be determined. Three sub-

Fig. 3 - *Austriadactylus cristatus*, teeth. A1-8) teeth of SC 332466: A1) large maxillary tooth crown below or just distal to the ascending process, A2) large maxillary tooth crown below or just distal to the ascending process, A3) distal maxillary tooth crown, A4) symphysial dentary tooth, A5) mesial dentary tooth crowns, A6) mesial dentary tooth showing also the base, A7) impression of a mid-mesial dentary tooth crown, A8) distal dentary tooth crowns. B) Teeth of the holotype, SMNS 56342 (distal direction to the left). Abbreviations in figure 1. Scale bar = 1 mm in A; B, scale in millimetres.
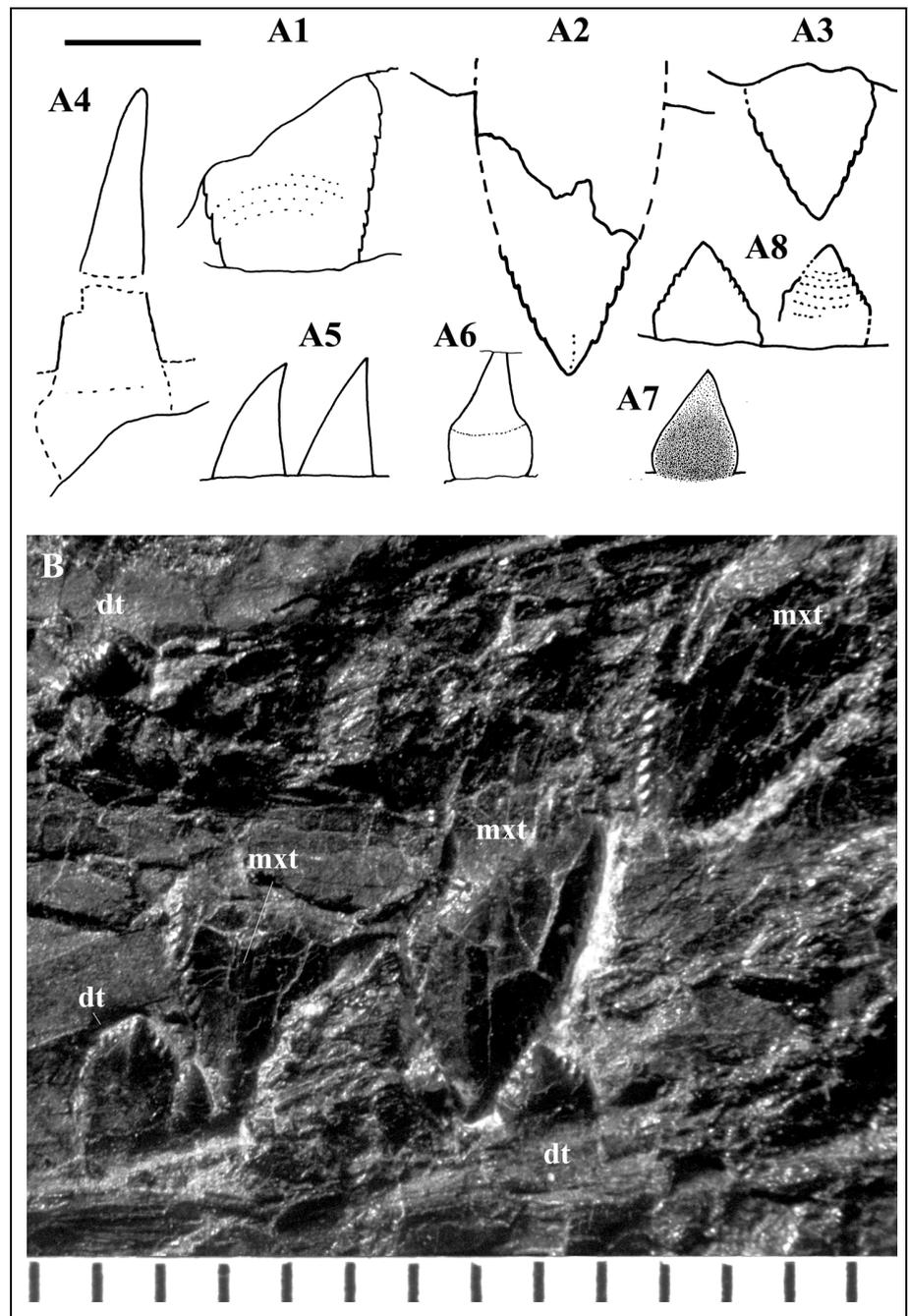
sequent, poorly preserved crowns are tentatively identified in correspondence of the overlap of one of the largest maxillary teeth. A triangular, mid-distal crown follows: this is as long mesiodistally as high apicobasally and bears at least four small denticles along the distal cutting edge. It resembles the mid-distal teeth of the left ramus, which occur in a slightly more distal position, beneath the antorbital fenestra. Traces of at least eight consecutive mid-distal teeth are identifiable in the left ramus. The better preserved (the most mesial of the row, which are heavily weathered) have triangular crowns as high apicobasally as long mesiodistally or just slightly higher (0.80 mm) than long (0.70 mm), bearing serrated cutting margins (Fig. 3A8). The max-

imum denticle count is 5-6 per margin. The 'root' is visible in cross-section in another tooth of the row and is long (more than twice the crown height) and tapers basally.

Axial skeleton

The first identifiable vertebra seems to contact the skull, and its position indicates that it is the axis, although it differs from the axis of *Eudimorphodon ranzii* (see Wild 1979, pl. 1). The atlas cannot be recognized. Six procoelous vertebrae follow caudally. Presacral vertebra 8 is similar in morphology to the preceding vertebrae, but the first dorsal ribs are close and were possibly articulated with it. Bennett (2007) defined the

first dorsal vertebra as the first vertebra that bore a long rib that articulated with the sternum. Therefore, presacral vertebra 8 may be the first dorsal vertebra in which case the cervical segment is formed by seven elements, unlike the nine cervical vertebrae present in pterosaurs according to Bennett (2007). The cervical vertebrae have a quadrangular outline in ventrodorsal view, with prezygapophyses projecting forward beyond the cotyle of the centrum, as in other Triassic pterosaurs. The condyle of the centrum appears small compared to that in the holotypes of *Eudimorphodon ranzii* and *Carniadactylus rosenfeldi* (Dalla Vecchia, 1995) where, however, the vertebrae are exposed in ventral view. A narrow and deep groove is present longitudinally in a medial position on the centrum, and probably represents the neural canal. The remains of articulated cervical ribs are preserved. The vertebral column is angled between the presacral vertebrae 8 and 9. No details are recognizable of the following dorsal vertebrae. Several dorsal ribs are preserved in the thoracic region. The most cranial (the two first dorsal ribs) are robust and have a dicephalous head with a long capitulum and a short tuberculum.

Pectoral girdle

The scapula and coracoid are fused forming a scapulocoracoid. The scapula seems to be much longer than the coracoid, although the state of preservation suggests caution for this feature. The shaft of the right coracoid seems to be narrow and slightly flared ventrally. The proximal portion of the coracoid is slightly curved caudally as in *Peteinosaurus zambellii* (MCSNB 3359; Wild 1979). No clear evidence of a sternal plate can be identified, but such a thin bone was probably completely worn away, if present.

Limbs

The humerus has a relatively long and slightly arched shaft and a relatively small proximal, expanded part. The deltopectoral crest is subtriangular with the apex directed proximally. The radius and ulna are paired without a spatium interosseum and are slightly sigmoidal. The ulna has a well-developed olecranon-like process and is less than 1.5 times the length of the humerus (Tab. 1).

Five main elements are tentatively identifiable in the carpal region, but other ossifications may be present (Fig. 4). The proximal syncarpal is 4.5 mm wide craniocaudally and 2.5 mm long proximodistally. It has a broad, concave distal surface articulated with a large, quadrangular distal carpal possibly bearing a distal process (Fig. 4). Alternatively, the latter could be a smaller, overlapping distal carpal. Two smaller, quadrangular, distal carpals occur along the preaxial margin, probably originally articulated with metacarpals I-II. The preaxial carpal lays close to the proximocranial part of metacar-

pal I. It has a distal depression for a sesamoid, whose traces are possibly present close by. Along the postaxial margin, a small rounded ossification seems to contact the proximal articular surface of the wing metacarpal. Another smaller element could be present proximally. It is not possible to state whether they are single separated bones, parts of a same element, or even parts of the largest distal carpal. Two small and rounded depressions on the proximal end of metacarpal I could be the traces of two further small ossifications. The pteroid cannot be unambiguously identified, although traces of two apparently rod-like bones are preserved near the distal end of metacarpal I and just cranial to the carpus respectively (Fig. 4).

Metacarpal I is slightly shorter than metacarpal II, which is nearly as long as metacarpal III (Fig. 4; Tab. 1). The distal terminations of metacarpals I and II are asymmetrically expanded, with a more prominent cranial portion. Metacarpal IV is slightly longer than metacarpal III. A large and asymmetrically developed dorsal condyle articulates with the corresponding cotyle of wing phalanx 1. The preserved remnants of digits I-III show that the phalanges were still in anatomical articulation and that digital elongation was progressive from digit I to digit III. Digit I has a single, slender and long (7.2 mm) non-ungual phalanx, whereas digit II has a significantly shorter (~3.8 mm) first phalanx. Wing phalanx 1 is slightly longer than the humerus, significantly shorter than the ulna and over twice the length of metacarpal IV (Tab. 1). Wing phalanx 1 is sectioned longitudinally, showing that at least the distal third has a spongy inner structure and possibly was not hollow inside, which may be plesiomorphic. However, the bone walls could have been crushed together, eliminating the medullary cavity. Only the proximal half of the gracile wing phalanx 2 is preserved; it was presumably as long as wing phalanx 1 or longer.

The left femur and tibia are articulated with each other at the knee and the tibia is probably flexed.

Discussion. The co-ossification of the scapula and coracoid and the presence of a proximal syncarpal sug-
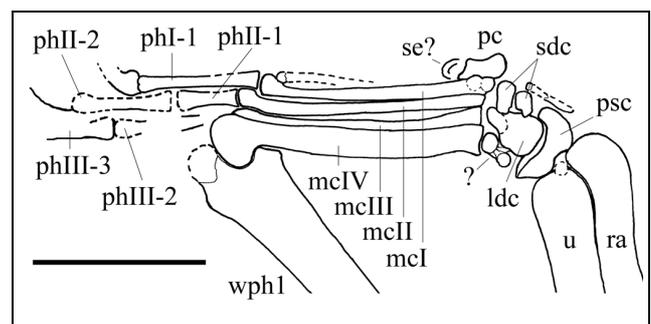

Fig. 4 - *Austriadactylus cristatus*, interpretative drawing of the manus of SC 332466. Abbreviations in figure 1. Scale bar = 10 mm.

gest that SC 332466 is not a juvenile, but osteological maturity cannot be confirmed because of the poor state of preservation and the absence of the pelvis, sacrum and tibiotarsus (Bennett 1993, 1995). The presence of more than a single, large distal carpal cannot be considered an unambiguous feature of osteological immaturity, because the distal carpus is poorly known in non-pterodactyloid pterosaurs. The absence of a distal syncarpal is the condition in all presumed pterosaur outgroups and could be plesiomorphic for Triassic pterosaurs (Dalla Vecchia 2009).

The only Triassic pterosaurs with a cranial crest are *Austriadactylus cristatus* and '*Raeticodactylus*' *filisurensis* Stecher, 2008. Marked differences exist between SC 332466 and '*Raeticodactylus*' *filisurensis* suggesting no strict relationships: in SC 332466, the cranial crest is thinner and with radial ridges present basally; there is no mandibular crest; the mandibular ramus is much more slender; there are no cup-shaped structures (large foramina) on the dorsolateral side of the dorsoventrally deep rostral part of the dentary; large oval foramina every 2-3 teeth, in a row parallel to the tooth row along the laterodorsal margin of the dentary are not observed; there is no long and narrow retroarticular process directed posteroventrally, making with the dentary axis an angle of about 35°; the dentition is distinctive ('*Raeticodactylus*' *filisurensis* has multicusped lateral teeth in both lower and upper jaw); and the ulna is longer than the wing phalanx 1 (it is shorter in '*Raeticodactylus*' *filisurensis*).

SC 332466 shares with the holotype of *Austriadactylus cristatus* (SMNS 56342) a thin cranial crest with ridges diverging radially from a point close to the tip of the snout. The mid-distal maxillary dentition has the same peculiar features in SC 332466 and SMNS 56342 (Figs. 2B-C, 3A1-3, B; Dalla Vecchia et al. 2002), shared only with *Preondactylus buffarinii* (Dalla Vecchia 2003, work in prep.). The mid-mesial mandibular teeth have the same unique morphology (cf. Dalla Vecchia et al. 2002, fig. 3D), although diminutive serrations cannot be observed in SC 332466 because of the poor preservation. The crowns of the mid-distal mandibular teeth have a similar shape and bear 4-6 denticles per cutting margin in both cases (Fig. 3A8, B). The mid-mesial to distal mandibular teeth of SMNS 56342 were defined as "multicusped" by Dalla Vecchia et al. (2002), but following the terminology adopted here they can be considered serrated. Their morphology does not correspond to that of the distal mandibular teeth of any other pterosaur (Dalla Vecchia et al. 2002; Dalla Vecchia 2003, 2004). Only *Peteinosaurus zambellii* has small denticles on the distalmost mandibular teeth (Dalla Vecchia 2003), but the cutting margins of those teeth are crenulated, rather than serrated as in *Austriadactylus*. SC 332466 and SMNS 56342 also share in common the

general outline of the skull (low, with a tapering rostrum) and the outline and proportions of the external naris, the antorbital fenestra and the orbit (Fig. 2B-C). The premaxillary process of the nasal borders the caudal half of the dorsal margin of the external naris, and the frontal process is short in both specimens.

The Friulian specimen is significantly smaller than the holotype of *Austriadactylus cristatus* (Tab. 1), possibly because it represents a younger individual. However, the body size cannot be indicative *per sé* of immaturity or taxonomic separation. In fact, the two specimens obviously belonged to different populations, possibly being slightly different in geological age and inhabiting separate islands (see the late Norian palaeogeographic map of western Tethys in Gaetani et al. 2000). Adult body size can be highly variable in a same species because of ecological factors, mainly in insular settings (e.g., Wikelski 2005). The premaxillary process of the nasal is shorter in the holotype and the maxillary process of the premaxilla is longer. The frontal and squamosal processes of the postorbital are more divergent, but the bone is poorly preserved in both specimens. As the two specimens belonged to different populations, some differences may be present because of intraspecific variability. Alternatively, they may represent two closely related, but separate, species. This might be because they lived in a palaeogeographic context favouring speciation, but this could only be ascertained with new material. Pending the discovery of additional specimens that might shed light on this subject, SMNS 56342 and SC 332466 are here considered to be conspecific.

SC 332466 provides information on the skull, lower jaw, dentition and postcranial skeleton of *Austriadactylus cristatus* that is unknown in the holotype and is utilized here in a revised diagnosis and the phylogenetic analysis of the taxon. In particular, the new specimen shows that the lower jaw ramus is slender and slightly downturned rostrally, and that the mid-mesial dentary crowns differ in morphology from the inflated subsequent crowns. In addition, the shape of the teeth along the premaxillary process of maxilla is unknown in the holotype. The deltopectoral crest of the humerus has the same shape as in *Preondactylus buffarinii*, *Peteinosaurus zambellii* (MCSNB 3359) and *Dimorphodon macronyx* (see Dalla Vecchia, 1998), but is unlike the square deltopectoral crest of *Eudimorphodon ranzii* and other campylognathoidids. The long bone length ratios show that wing phalanx 1 of SC 332466 is comparatively short, as in *Preondactylus buffarinii*, *Peteinosaurus zambellii* and *Dimorphodon macronyx*, and unlike the campylognathoidids (Tab. 2).

Phylogenetic remarks. *Austriadactylus* was ignored in most previous phylogenetic analyses (Kellner

	1	2	3	4	5	6	7	8	9	10	11	12	13
h	18.15	26	26.3	28	47	40	42	82	70-75*	**36**	32	38.5	63-91
u/h	1.11	1.29	1.37	1.36	1.38	-	1.31	1.29	1.38-1.29*	**1.39**	1.31	1.30	1.29
h/mcIV	2.16	2.89	2.50	--	1.62	-	1.93	-	-	**2.29**	2.25	2.29	1.95-2.36
u/mcIV	2.39	3.72	3.43	--	2.24	-	2.62	-	-	**3.18**	2.95	2.91	3.00
h/fe	0.92	1.33	1.42	1.32	1.14	-	1.13	1.46	-	**-**	0.98	1.05	1.04-1.09
h/ti	0.88*	1.04	-	0.98	0.94*	0.69	0.77	0.98	-	-	0.73	0.81	0.71-0.76
u/fe	1.02	1.71	1.95	1.79	1.58	-	1.49	1.89	-	-	1.29	1.34	1.34-1.40
u/ti	0.98*	1.34	-	1.33	1.30	-	1.02	1.26	-	-	0.95	1.03	0.97-0.98
ti/fe	1.04*	1.27	-	1.34	1.22*	-	1.46	1.50	-	-	1.35	1.30	1.39-1.46
fe/mcIV	2.34	2.18	1.76	-	1.41	-	1.76	-	-	-	2.28	2.18	1.87-2.23
ti/mcIV	2.44*	2.78	-	-	1.72*	-	2.58	-	-	-	3.09	3.12-2.82	2.74-3.15
wph1/h	0.97*	1.31	1.43	1.43*	1.70*	1.32	1.52	1.38	-	**1.11**	1.11	1.09	1.06-1.20
wph1/u	0.90*	1.01	1.04	1.05*	1.23*	-	1.16	1.07	-	**0.80**	0.85	0.86	0.82-0.90
wph1/mcIV	2.14*	3.78	3.57	--	2.75*	-	3.05	-	-	**2.55**	2.49	2.57-2.50	2.35-2.70
wph1/fe	0.91*	1.73	2.03	1.89*	1.95*	-	1.73	2.02	-	-	1.09	1.15	1.10-1.26
wph1/ti	0.89*	1.36	-	1.40*	1.60*	0.92	1.18	1.34	-	-	0.81	0.82-0.88	0.80-0.88
wph2/wph1	1.14*	1.04	0.88	0.91*	-	-	0.91	0.96	-	-	1.10	0.96*-1.00	1.03-1.15
wph3/wph2	1.00*	1.02	1.10*	-	-	-	1.09	1.07*	1.02	-	1.00	1.09	1.08-1.12
wph3/wph4	-	1.12	1.06	-	-	-	1.23	1.41*		-	1.39	1.33	1.25
wph3/wph1	1.14*	1.06	0.96*	-	-	-	0.99	1.03*	1.21	-	1.08	1.09	1.24-1.29

Tab. 2   - Ratios of long bone lengths in Triassic pterosaurs and *Dimorphodon macronyx*. Ratios of SC 332466 are highlighted in bold. The humerus length (in mm) is reported as general indicator of size. Legend: 1 = MGUH VP 3393 (holotype of '*Eudimorphodon*' *cromptonellus*; from Jenkins et al. 2001), 2 = MCSNB 8950 (indeterminate campylognathoidid, see Dalla Vecchia, 2009), 3 = MPUM 6009 (*Carniadactylus rosenfeldi*, see Dalla Vecchia, 2009), 4 = MCSNB 2887 (indeterminate campylognathoidid, see Dalla Vecchia 2009), 5 = MCSNB 2888 (holotype of *Eudimorphodon ranzii*), 6 = BSP1994 I 51 (unnamed taxon, see Dalla Vecchia 2009), 7 = MFSN 1797 (holotype of *Carniadactylus rosenfeldi*, from Dalla Vecchia 2009), 8 = BNM 14524 ('*Raeticodactylus*' *filisurensis*, from Stecher 2008), 9 = SMNS 56342 (holotype of *Austriadactylus cristatus*), 10) SC 332466 (*Austriadactylus cristatus*), 11 = MFSN 1770 (holotype of *Preondactylus buffarinii*), 12 = *Peteinosaurus zambellii* (MCSNB 2886, holotype, and MCSNB 3359), 13 = *Dimorphodon macronyx* (specimens YPM 350 and YPM 9182 from Padian 1983, GSM 1546 and BMNH R.1034 [holotype] from Unwin 1988, BMNH 41212 from Wellnhofer 1978). * = based on estimated or approximate measurements.

2003, 2004; Sangster 2004; Lü & Ji 2006; Wang et al. 2005, 2008), but it belongs within Campylognathoididae according to Unwin (2003, 2004).

The phylogenetic position of *Austriadactylus cristatus* was investigated using the data matrix of Dalla Vecchia (2009) that contains 73 characters (Appendix 1), three outgroup taxa (*Macrocnemus bassanii*, *Ticinosuchus ferox* and *Herrerasaurus ischigualastensis*), and 23 ingroup taxa. Unlike Dalla Vecchia (2009), the character state codings of MCSNB 3359 were added to those of *Peteinosaurus zambellii* and one was modified (see Appendix 1). The new information provided by SC 332466 allowed the coding of 11 characters previously unknown in *Austriadactylus cristatus* (see Appendix 1).

Character 4 appears to be polymorphic (see Appendix 1). The phylogenetic analysis by parsimony was performed using PAUP* 4.0b10 for Microsoft Windows (Swofford 2002) and the ACCTRAN setting. The analysis produced six equally parsimonious trees with a length of 209 steps, consistency index = 0.5742, homoplasy index = 0.4928, retention index = 0.7335, and rescaled consistency index = 0.4212. The Strict Consensus Tree topology is unchanged with respect to that obtained by Dalla Vecchia (2009), excluding the deletion of MCSNB 3359. *Austriadactylus cristatus* forms a clade with *Preondactylus buffarinii*, which is basal within the Pterosauria (Fig. 5). They share four unambiguous synapomorphies:

1) Jugal and premaxillary processes of the maxilla are subequal in shape and size, low, long, tapering and pointed. Although the caudal part of the jugal process is poorly preserved in both *Austriadactylus cristatus* specimens, it is undoubtedly low, long and, as far as it is preserved, similar to the premaxillary process in shape and size. In *Eudimorphodon ranzii*, the premaxillary process is shorter, higher and with a dorsal notch (Wild 1979). In *Carniadactylus rosenfeldi* (MPUM 6009), the premaxillary process is also shorter and higher, and the jugal process only tapers at its caudal termination (Wild 1979). In '*Raeticodactylus*' *filisurensis*, the premaxillary process is also deep (Stecher 2008). In *Dimorphodon macronyx*, the premaxillary process has a pointed termination, but it is parallel sided for most of its length, and is relatively short (Sangster 2004). In *Campylognathoides* spp., the premaxillary process is parallel sided with a square termination, and the jugal process is also parallel sided (Padian 2008b). In *Dorygnathus banthensis*, both processes do not taper all their length long like in *Austriadactylus* and the premaxillary process is much deeper than the jugal process (Padian 2008a).

Because of the thin premaxillary process of the maxilla, the external naris of *Preondactylus* and *Austriadactylus* is very large and elongated dorsocaudally to ventrorostrally.

2) Teeth in the maxilla distal to the ascending (dorsal) process are large, triangular, serrated and decrease in size distally. In *Eudimorphodon ranzii*, maxillary teeth are of uniform size and multicusped, excluding two much larger, unserrated teeth below the ascending process (Wild 1979). They are also all the same size and multicusped in '*Eudimorphodon*' *cromptonellus* (see Jenkins et al. 2001) and *Carniadactylus rosenfeldi* (MPUM 6009; Wild 1979). In '*Raeticodactylus*' *schesaplanensis*, they are all the same size, multicusped and similar to those of the lower jaw, although more bulbous (Stecher 2008). In *Dimorphodon macronyx*, the teeth are mesiodistally narrower, recurved and unserrated (Sangster 2004). In *Campylognathoides* spp., the teeth are relatively small, do not decrease much in size distally and are unserrated (Padian 2008b). In *Dorygnathus banthensis*, they are relatively small, conical and unserrated (Padian 2008a).
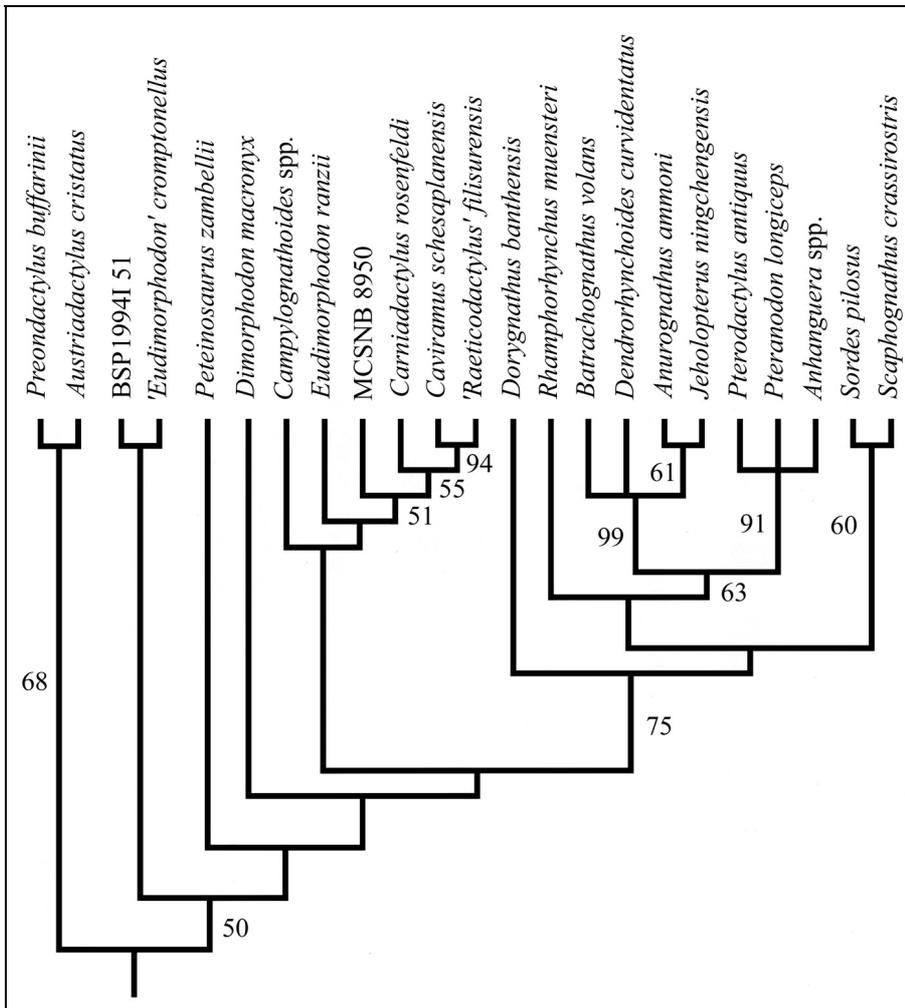

Fig. 5 - Strict Consensus Tree of six most parsimonious trees resulting from a maximum parsimony analysis of 23 pterosaur taxa. Numbers refer to bootstrap values. Outgroup taxa are omitted.

3) Mandibular teeth are much smaller than maxillary teeth. This is convergently present in *Dimorphodon macronyx*. They are of similar size and shape in the other Triassic pterosaurs ('*Eudimorphodon*' *cromptonellus*, *Eudimorphodon ranzii*, *Carniadactylus rosenfeldi*, and '*Raeticodactylus*' *schesaplanensis*; unknown in *Peteinosaurus zambellii*) and in Jurassic non-pterodactyloid pterosaurs.

4) Maxillary teeth below the ascending (dorsal) process of maxilla are much enlarged. This is convergently present in BSP 1994 I 51 (unnamed taxon, see Dalla Vecchia, 2009; deduced from an isolated tooth), and in *Eudimorphodon ranzii*. It is also the condition in one of the outgroups (*Herrerasaurus ischigualastensis*).

The bootstrap values (1000 replicates) show that the clade *Austriadactylus cristatus* + *Preondactylus buffarinii* is slightly less supported than in the previous analysis by Dalla Vecchia (2009) (bootstrap value 68 vs 70; Fig. 5).

The relationships between *Austriadactylus cristatus* and *Preondactylus buffarinii* is the subject of a paper (in preparation) describing an undescribed specimen of *Preondactylus* (MFSN 25161).

Conclusions

The crested, non-pterodactyloid pterosaur *Austriadactylus cristatus* is now known from the Norian of north-eastern Italy as well as Austria. This pterosaur species differs markedly from the only other known Triassic pterosaur with a cranial crest, '*Raeticodactylus*'

filisurensis. The dentition, shape of the deltopectoral crest of the humerus and relative size of wing phalanx 1 (see long bone ratios in Tab. 2) cast doubts about on the supposed close phylogenetic relationships between *Austriadactylus* and *Eudimorphodon* suggested by Unwin (2003, 2004). Instead, the results of a phylogenetic analysis confirm a close relationship with *Preondactylus buffarinii*.

Appendix 1

Character states of *Austriadactylus cristatus* and *Peteinosaurus zambellii*.

For characters, character state descriptions and codings of the other pterosaurs, see Dalla Vecchia (2009). Characters states coded for the first time in this paper are highlighted in bold.

Austriadactylus cristatus
1000/1100100 100000000? 1000000011 0001000000 ?00?????01 0??01???11 ??111????0 ???

Peteinosaurus zambellii
?0??????? ?????????1 10000?0??? 000?0000?? 0010100101 0140110001 1111110010 011

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