

Systematic reinterpretation of *Piksi barbarulna* Varricchio, 2002 from the Two Medicine Formation (Upper Cretaceous) of Western USA (Montana) as a pterosaur rather than a bird

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ABSTRACT

Varricchio (2002) described some forelimb bones from the Late Cretaceous (Campanian) Two Medicine Formation, Glacier County, Montana (USA), as the holotype of *Piksi barbarulna*, a supposed ornithothoracine bird. However reevaluation of *Piksi* Varricchio, 2002 instead recognizes this genus as belonging to Pterosauria Kaup, 1834 and not Aves Linnaeus, 1758. *Piksi* exhibits the following derived humeral traits of pterosaurs: 1) very large ectepicondyle; 2) large trochlea; 3) with a deep, wide and poorly delimited brachial depression that is proximodistally extended; 4) a wide and deep olecranal fossa not marked dorsally by a ridge; and 5) lacking a distal depression of the groove for the *m. humerotricipitalis*. Moreover, the putative Early Cretaceous birds *Eurolimnornis* Jurcsák & Kessler, 1986 and *Palaeocursornis* Jurcsák & Kessler, 1986, based on distal humeri, are also regarded as pterosaurs. The record of *Piksi* constitutes an important addition to the Latest Cretaceous pterosaurian record.

KEY WORDS
Pterosauria,
Late Cretaceous,
North America.

RÉSUMÉ

Réinterprétation de la position systématique de Piksi barbarulna Varricchio, 2002 (Formation Two Medicine, Crétacé supérieur, Montana, États-Unis): un ptérosaure plutôt qu'un oiseau.

Varricchio (2002) a décrit, du Crétacé supérieur (Campanien, Formation Two Medicine, Glacier County, Montana, USA), des os de pattes avant d'un oiseau supposé ornithothoraciné, comme l'holotype de *Piksi barbarulna*. La présente révision du genre *Piksi* le place plutôt chez les Pterosauria Kaup, 1834 que chez les Aves Linnaeus, 1758. Effet, l'humérus de *Piksi* Varricchio, 2002 porte des caractères dérivés de ptérosaures: 1) très grand ectepicondyle; 2) large trochlée; 3) avec une dépression brachiale profonde, large et peu délimitée qui est proximodistalement étendue; 4) une large et profonde fosse olécranienne non marquée dorsalement par un pont; et 5) l'absence de dépression distale sur le sillon du *m. humerotricipitalis*. Les citations de *Piksi* constituent donc d'importants ajouts au registre de ptérosaures du Crétacé le plus tardif. De plus, les genres du Crétacé inférieur *Eurolimnornis* Jurcsák & Kessler, 1986 et *Palaeocursornis* Jurcsák & Kessler, 1986, rapportés aux oiseaux sur la base de la partie distale des humérus, sont également considérés ici comme des ptérosaures.

MOTS CLÉS

Pterosauria,
Crétacé supérieur,
Amérique du Nord.

INTRODUCTION

Piksi barbarulna Varricchio, 2002 was originally described as a mid-sized Cretaceous bird. *Piksi* Varricchio, 2002 nested among basal ornithothoraces ornithurines, and but also displayed some similarities with a couple extant Galliformes (Varricchio 2002). The holotype and only known specimen consists of a right humerus and incomplete right ulna and radius. The specimen was found in outcrops from the Upper Cretaceous (Campanian) Two Medicine Formation of Montana, USA (Fig. 1). This formation has yielded the remains of a varied extinct fauna, including abundant ornithischian dinosaurs (see Varricchio 2002), the enantiornithine bird *Avisaurus gloriae* (Varricchio & Chiappe, 1995), and the azhdarchid pterosaur *Montanazhdarcho minor* (Padian, de Ricqlès & Horner, 1995). Some atypical features present in *Piksi*, such as the absence of quill feather knobs in the ulna and the conformation of the ulnar-humeral articulation were indicated by Varricchio (2002) as evidence of a probably ecologically distinct taxon. However, revision of the holotype of *Piksi* suggests that this peculiar specimen can be referred to the Pterosauria. Moreover, some features indicate that

Piksi belongs to the pterosaur clade Ornithocheiroidea (*sensu* Kellner 2003), thus constituting the second report of this group for North America, and one of the youngest ornithocheiroids known so far.

METHODS

We follow the main systematic arrangement of Kellner (2003). The term "Rhamphorhynchoidea" is here used as describing a paraphyletic group of all non-pterodactyloid pterosaurs (see Murry *et al.* 1991).

For terminology of osteological features of the distal end of pterosaurian humerus we follow the paper of Averianov *et al.* (2005).

ABBREVIATION

MOR Museum of the Rockies, Montana State University, Bozeman, Montana, USA.

HORIZON AND LOCALITY

The holotype and only known specimen of *Piksi barbarulna* was collected on outcrops belonging

to the late Cretaceous Two Medicine Formation (Campanian; see Varricchio 2002). The fossiliferous MOR locality is TM-088, Bob's Vacation Site, Glacier County, Montana, USA and may represent a shallow floodplain depression or possibly ephemeral pond (Varricchio 2002).

THE SYSTEMATIC POSITION OF *PIKSI BARBARULNA*

Varricchio (2002) originally included *Piksi barbarulna* within Aves Linnaeus, 1758 and Ornithothoraces Chiappe & Calvo, 1994 on the basis of four derived traits: 1) radius diameter/ulna diameter less than 0.7; 2) well developed olecranal fossa on distal humerus; 3) distal condyles of humerus located anteriorly; and 4) semilunate distal articular surface of ulna. However, feature 1 is not unique to birds, as having the diameter of the radius smaller than that of the ulna is present in all but the most primitive pterosaurs (e.g., Kellner 2003). In the same way, traits 2, 3 and 4 are also present in most pterosaurs (Fig. 2), and thus no synapomorphy supports the ornithothoracine affinities of *Piksi*.

Although Varricchio (2002) only assigned *Piksi* to the Ornithothoraces, he did note some shared features with some less inclusive clades. For example, *Piksi* shares with Ornithurae a brachial depression (fossa) of the humerus, and with two galliforms a dorsal condyle (= capitulum herein) dorsoventrally broader than the ventral condyle (= trochlea herein). Both features are also a common trait among pterosaurs, particularly the most derived ones (e.g., *Pteranodon* Marsh, 1876, *Anhanguera* Campos & Kellner, 1985, *Quetzalcoatlus* Lawson, 1975; Eaton 1910; Averianov 2010) and consequently, challenge any potential galliform or ornithurine affinities of *Piksi* (Fig. 2).

More properly, *Piksi* is referable to the Pterosauria and distinguishable from Aves on the following features:

1) enlarged ectepicondyle and entepicondyle (Figs 2; 3). Varricchio (2002) interpreted that the large ectepicondyle, subequal in length to the capitulum, was an autapomorphic trait of *Piksi*, absent in any other known bird. Nevertheless, in pterosaurs,

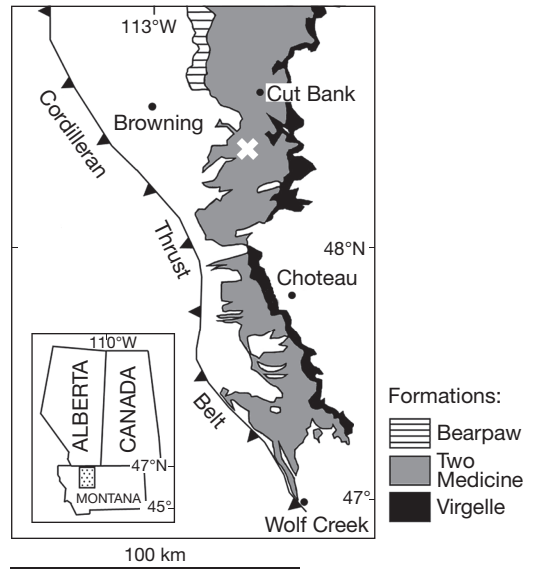


FIG. 1. — Locality map showing Bob's Vacation Site, TM-088 (white cross) in northwestern Montana within the Upper Cretaceous Two Medicine Formation and the locality for *Piksi barbarulna* Varricchio, 2002.

the distal end of the humerus exhibits two large distal condyles (i.e. capitulum and trochlea) as well as an enlarged ectepicondyle and a well-developed entepicondyle. As in birds, the capitulum (= radial condyle) and trochlea are bulbous and well developed. Contrasting with birds, in *Piksi* and remaining pterosaurs the ectepicondyle and entepicondyle are large and well developed, surrounding the radius and ulna, respectively (e.g., Wellnhofer 1991). In Pterosauria the large and subspherical ectepicondyle is apomorphic for the group, being absent in birds (see Murry *et al.* 1991; Kellner 2003);

2) brachial depression proximodistally extended, wide, deep, and poorly delimited (Figs 2; 3). In the distal humerus of birds, the brachial depression (when present) is relatively small and well defined, being strongly dorsoventrally compressed, and clearly delimited by well-developed osseous edges (see Clarke & Chiappe 2001; Clarke & Norell 2002). In contrast, pterosaurs (e.g., Ornithocheiroidea, Azhdarchidae Nessov, 1984, Anhangueridae Campos & Kellner, 1985; Nessov 1991; Kellner & Tomida 2000; Averianov *et al.* 2005) present a

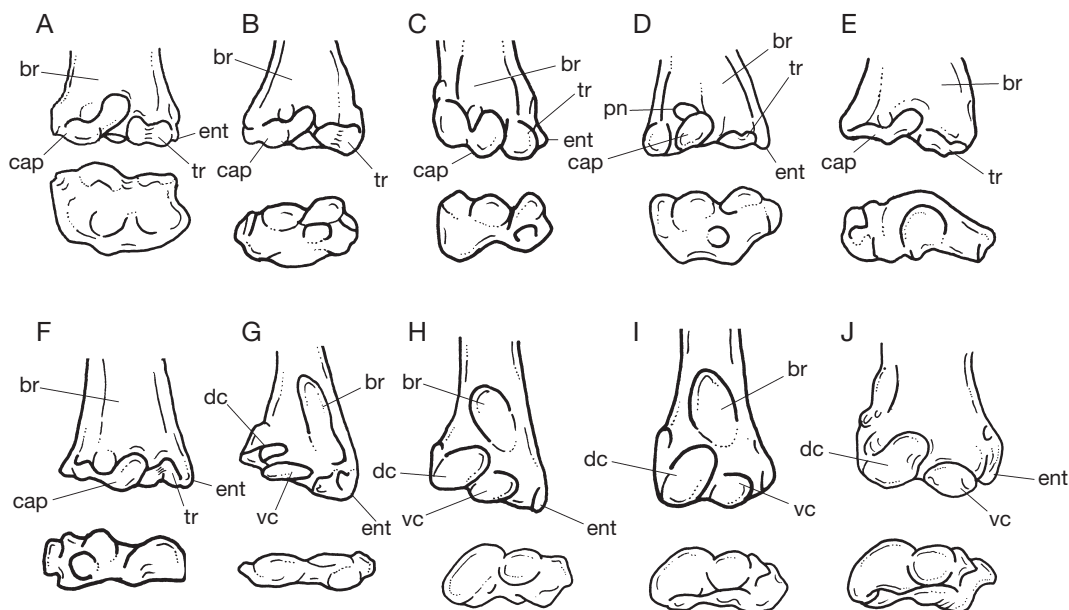


FIG. 2. — Right distal humerus of selected birds and pterosaurs in anterior (top), and distal (bottom) views: **A**, *Azhdarcho* Nessov, 1984 modified from Averianov (2010); **B**, *Dsungaripterus* Young, 1964 modified from Young (1964); **C**, *Piksi* Varricchio, 2002 modified from Varricchio (2002); **D**, Ornithocheiroidea indet., modified from Averianov *et al.* (2005); **E**, *Anhanguera* Campos & Kellner, 1985, modified from Veldmeijer (2003); **F**, *Montanahzdarcho* Padian, de Ricqles & Horner, 1995, modified from McGowen *et al.* (2002); **G**, *Enantiornithes* indet., modified from Hope (2002); **H**, *Ichthyornis dispar* Marsh, 1872, modified from Clarke (2004); **I**, *Anas platyrhynchos* Linnaeus, 1758; **J**, *Limenavis*, modified from Clarke & Chiappe (2001). Abbreviations: **br**, brachial depression; **cap**, capitulum; **dc**, dorsal condyle; **ent**, entepicondyle; **pn**, pneumatic foramen; **tr**, trochlea; **vc**, ventral condyle. Not to scale.

wider and proximodistally extended bacial fossa. Furthermore, in pterosaurs this fossa shows a dorsoventral extension larger than its transversal width; whereas in birds the reverse condition is usually present (Clarke & Chiappe 2001). In the same way, pterosaur brachial fossa is transversely extended, covering most of the anterior surface of distal humeral shaft, whereas in birds it is more mediolaterally restricted; and 3) wide and deep olecranon fossa not delimited dorsally by a ridge. In birds the olecranon fossa, when it is present, is deep and dorsoventrally short, being proximally delimited by a transverse ridge, crest or step. In most pterosaurs (e.g., *Pteranodon*, *Anhanguera*, Ornithocheiroidea indet.; Eaton 1910; Hooley 1914; Veldmeijer 2003; Averianov *et al.* 2005) the olecranon fossa is represented by a very wide and dorsoventrally extended concavity, which lacks an osseous proximal limit. Moreover, in Aves this fossa is contigu-

ous with a distal depression of the groove for the *m. humerotricipitalis* (Clarke 2004) whereas in pterosaurs this structure is absent.

Among Pterosauria, *Piksi* can be included within the Pterodactyloidea due to the presence of: 1) distal condyles of humerus anteriorly directed. In “Rhamphorhynchoidea” (e.g., *Rhamphorhynchus* Von Meyer, 1846, *Nesodactylus* Clobert, 1969; Gross 1937; Colbert 1969) the condyles of the distal end of the humerus are anterodorsally oriented, showing a strongly upturned morphology in lateral view. Otherwise, in *Piksi*, as well as most pterodactyloids (e.g., *Pteranodon*, *Anhanguera*, *Montanahzdarcho* Padian, de Ricqles & Horner, 1995, *Pterodaustro* Bonaparte, 1979, *Dsungaripterus* Young, 1964, Ornithocheiroidea; Eaton 1910; Veldmeijer 2003; Padian *et al.* 1995; Bonaparte 1970; Young 1964; Averianov *et al.* 2005) the distal condyles lack dorsal orientation, and are only anteriorly directed. Additionally, *Piksi* lacks

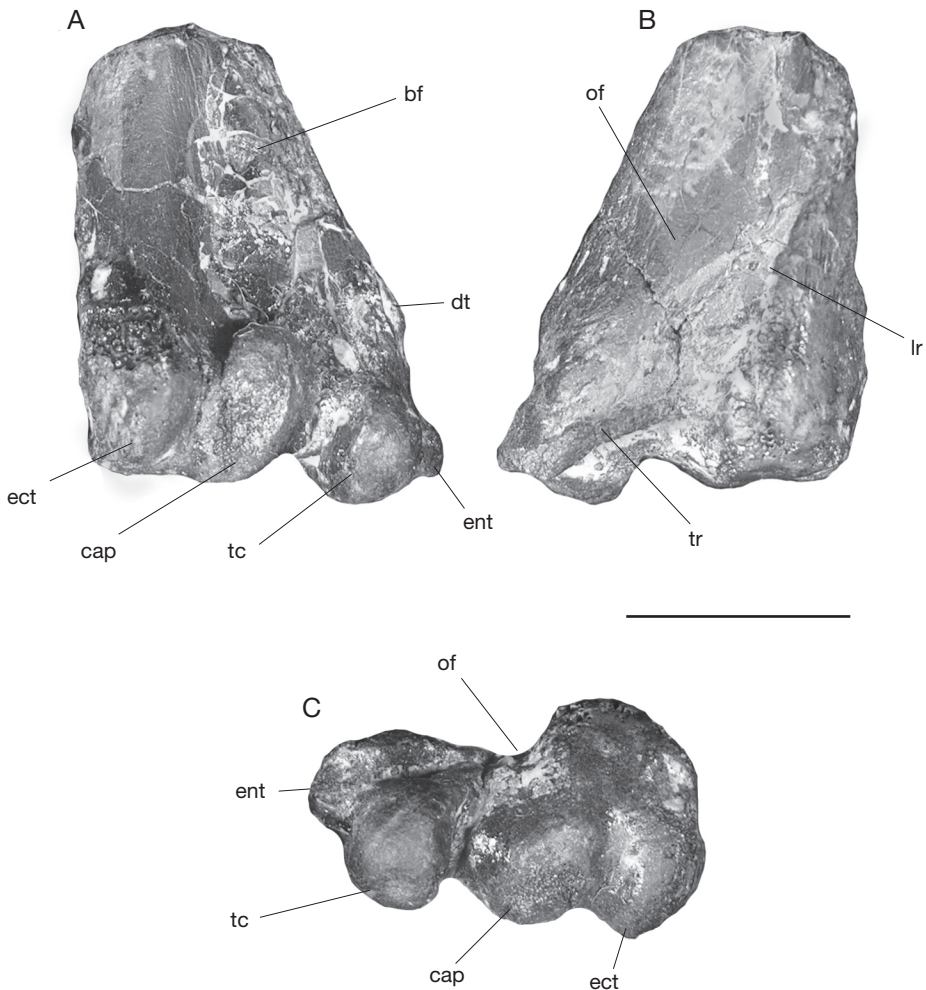


FIG. 3. — *Piksi barbarulna* Varricchio, 2002 (holotype, MOR 1113). Distal end of right humerus in (A) anterior, (B) posterior, and (C) distal views. Abbreviations: **bf**, brachial depression; **cap**, capitulum; **dt**, dorsal tubercle; **ect**, ectepicondyle; **ent**, entepicondyle; **lr**, lateral ridge; **of**, olecranal fossa; **tr**, transverse ridge; **tc**, trochlea. Scale bar: 5 mm.

the peculiar curvature of the lateral margin of the capitulum characteristic of “Rhamphorhynchoidea” (Murry *et al.* 1991); and 2) distal end of ulna well expanded in transverse width (Kellner *et al.* 2003). In *Piksi*, as occurs in pterodactyloids, the ulna shows a very transversely expanded and anteroposteriorly compressed distal end, a condition that, distinguishes derived pterosaurs from plesiomorphic Archaeoptero-dactyloidea.

In addition, *Piksi* is reminiscent to Ornithocheiroidea by having the distal end of the humerus with

external margin anteroposteriorly larger than the internal one in distal view (Figs 2; 3). This morphology is considered diagnostic of Ornithocheiroidea by several authors (Bennett 1989; Kellner 2003). In *Piksi* the humerus is subtriangular in distal view, with its external margin anteroposteriorly larger than the internal one. The anterior margin of the bone is nearly straight (in contrast with the strongly convex condition of *Dsungaripterus* and Azhdarchidae for example) and is transversely shorter than the posterior one. This morphology is

characteristic of ornithocheiroid pterosaurs (Bennett 1989; Unwin & Lü 1997). On the contrary, in Dsungaripteridae and Azhdarchidae, the distal end of the humerus is D-shaped in distal view, showing external and internal margins subequal in anteroposterior extension and the anterior margin strongly convex (Young 1964; Bennett 1989; Murry *et al.* 1991; Averianov 2010).

Moreover, in derived anhanguerids the distal end of the humerus is strongly compressed anteroposteriorly, and is well expanded transversely (Kellner & Tomida 2000; Veldmeijer 2003). Anhanguerids also present a distal end with its posterior margin much larger than the others, whereas in the ornithocheiroid-like specimen of Averianov *et al.* (2005) and *Piksi* the reverse condition is present (Fig. 2). In this way, the outline of the distal end of the humerus in *Piksi* is very similar to that of the Ornithocheiroidea indet. reported by Averianov *et al.* (2005). Thus, although incompletely preserved, *Piksi* probably belongs to an ornithocheiroid pterosaur.

SYSTEMATIC PALEONTOLOGY

Order PTEROSAURIA Kaup, 1834

Suborder PTERODACTYLOIDEA

Plieninger, 1901

Super Family ORNITHOCHEIROIDEA Seeley, 1870
(*sensu* Kellner, 2003)

Genus *Piksi* Varricchio, 2002

Piksi barbarulna Varricchio, 2002

HOLOTYPE. — MOR 1113; distal end of right humerus, proximal half of right radius, proximal half and distal end of right ulna. The bones have some distortions due to compression; however, main anatomical details of the specimens are clearly discernible (for detailed discussion of pterosaurian taphonomical bias see Kellner 2010).

EMENDED DIAGNOSIS. — *Piksi barbarulna* is a minute pterosaur diagnosable by the following autapomorphies: 1) distal margin of humerus oblique relative to the main axis of the shaft, with trochlea strongly distally extended; 2) trochlea bulbous and subspherical; 3) acute and well defined transverse crest connecting the entepicondyle and the lateral ridge that delimitates the olecranal fossa, in posterior view.

COMMENTS

The only named pterosaur from the Two Medicine Formation is *Montanazhdarcho minor* Padian, de Ricqlès & Horner, 1995 (Padian *et al.* 1995; McGowan *et al.* 2002). *Piksi* differs from the latter in having a less distally expanded humerus, a more anteroposteriorly compressed humerus, distal end of the humerus with its external margin longer than the internal one (diagnostic trait of Ornithocheiroidea), more bulbous and larger ectepicondyle, and capitulum shorter and smaller (see additional features in *Piksi*'s generic diagnosis) (Fig. 2).

Based on the transversal expansion of the distal humerus of *Piksi*, compared with that of *Anhanguera spielbergi* Veldmeijer, 2003 and *A. piscator* Kellner & Tomida, 2000 (Kellner & Tomida 2000; Veldmeijer 2003) we calculated a wing span of approximately one metre, which posits *Piksi* as a very small pterodactyloid pterosaur (see also Costa & Kellner 2009).

DESCRIPTION AND COMPARISONS

HUMERUS (FIG. 3)

The distal end of the right humerus is preserved. It is poorly expanded, and lacks the typical anteroposteriorly compressed outline present in other pterosaurs, such as *Anhanguera* and *Pteranodon* (Bennett 2001; Veldmeijer 2003). The distal margin of the bone is oblique with respect to the main axis of the humeral shaft, with its medial portion more distally projected than the lateral one, thus contrasting with other pterosaurs in which the distal margin of the bone is perpendicular to its main axis (e.g., *Anhanguera*, *Montanazhdarcho*, *Pterodaustro*; Bonaparte 1970; McGowan *et al.* 2002; Veldmeijer 2003). As in pterosaurs, the brachial fossa is transversely wide and proximodistally deep, with poorly defined margins. The capitulum is large and bulbous, being subequal in size with the trochlea. The groove that separates the trochlea from the capitulum is deep and narrow. The trochlea is subspherical and strongly distally projected, showing its main axis oblique to the major humeral axis. Otherwise, in most other pterosaurs this condyle is transversely extended and its main axis is nearly perpendicular to the major axis of the bone (e.g., Azhdarchidae, *Pteranodon*; Eaton



FIG. 4. — *Piksi barbarulina* Varricchio, 2002 (holotype, MOR 1113), right proximal ulna in ventral (A) and dorsal (B) views, proximal half of right radius in posterior (C) and anterior (D) views. Scale bar: 10 mm.

1910; Nessov 1991). Pneumatic foramina are present proximolaterally to the trochlea. The entepicondyle projects distally to the level of the trochlea, and is separated from the trochlea by a deep and narrow groove. The capitulum is more distally positioned than the ectepicondyle and is separated from the latter by a shallow groove. The ectepicondyle is large and suboval in contour, showing its main axis subparallel to the long axis of the humerus.

The dorsal tubercle is present but poorly developed. In posterior view the entepicondyle is connected by a well-developed transverse crest to the large lateral ridge that delimitates the olecranal fossa, contrasting with remaining pterosaurs. The olecranal fossa is wide and deep, being well delimited by lateral and medial ridges.

In distal view the humerus shows its external margin anteroposteriorly larger than the internal one.

The anterior margin of the bone is nearly straight (in contrast with the strongly convex condition of *Dsungaripterus* and the Azhdarchidae, for example) and is transversally shorter than the posterior one. This morphology is diagnostic of ornithocheiroid pterosaurs (cited as as subtriangular distal end of the humerus in distal view by Kellner [2003] and Averianov *et al.* [2005]).

RIGHT ULNA (FIGS 4; 5)

This element was originally considered by Varricchio (2002) as very different from that of birds. In fact, the specimen differs from theropod ulnae (including birds), but resembles that of pterosaurs in lacking a well-defined “olecranon process”, in having a strongly concave caudal edge of the shaft, and in having an anteroposteriorly extended and lateromedially compressed proximal bone epiphysis (Varricchio 2002; Clarke 2004).

The distal end of ulna consists on a badly broken weathered portion of bone. Varricchio (2002) identified a semilunar dorsal condyle and a large ventral condyle, as typical of ornithothoracine birds.

However, this element does not fit with an ornithothoracine distal ulna because it lacks a carpal tuberosity, the “ventral condyle” is dorsoventrally elongated but transversely compressed, the intercondylar groove is extremely deep and wide, and the distal end of the bone in distal view is strongly compressed transversely. Moreover, in the putative posterior view, there is only a wide and shallow median groove, without signs of condyles, and thus, lacking the typical ulnar trochlea present in most birds (Clarke & Norell 2002; Clarke 2004). On the other hand, the element is confidently identified as pterosaurian on the basis of the typically hemispherically convex tuberculum (Wiffen & Molnar 1988).

Although badly weathered and poorly preserved, the distal end of ulna of *Piksi* shows some interesting traits. Its distal end is well expanded in transverse width, a feature that distinguishes it from the plesiomorphic Archaeoptero-dactyloidea (Kellner *et al.* 2003). The presence of a well-developed and proximodistally extended ventral ridge is reminiscent to that of Ornithocheiroidea (e.g., *Anhanguera*; Kellner *et al.* 2003), and the absence of a pneumatic

foramen on the posterior face of the bone differentiates it from *Pteranodon* (Bennett 2001). Because of its poor preservation, no more features can be discerned in this specimen.

RADIUS (FIG. 4)

The proximal half of the bone is preserved. This element is indistinguishable from that of other pterosaurs, and shows a very well developed biceps tubercle.

DISCUSSION

BRIEF COMMENTS ON THE STATUS OF THE PUTATIVE EARLY CRETACEOUS BIRDS *EUROLIMNORNIS* AND *PALAEOCURSORNIS*

Early Cretaceous (Berriasian) sediments from the Cornet fossiliferous locality have yielded a large amount of vertebrate remains (see Dyke *et al.* 2011), including several bones putatively referred to birds. Jurcsák & Kessler (1986) described these fossils as belonging to the derived neornithine bird genera and species *Eurolimnornis corneti* Jurcsák & Kessler, 1986, *Palaeocursornis biharicus* Jurcsák & Kessler, 1986. They suggested neognathan affinities for *Eurolimnornis* Jurcsák & Kessler, 1986 and palaeognathan affinities for *Palaeocursornis* Jurcsák & Kessler, 1986. Most latter authors followed Jurcsák & Kessler (1986) in considering both taxa as belonging to birds (Hope 2002; Dyke *et al.* 2011). If the phylogenetic position proposed by Jurcsák and Kessler (1986) is followed, *Palaeocursornis* and *Eurolimnornis* may represent the oldest examples of crown group birds (see Hope 2002). However, an overview of published available information suggests that both *Palaeocursornis* and *Eurolimnornis* belong to Pterosauria, rather than Aves.

Palaeocursornis biharicus Jurcsák & Kessler, 1986 was described as the distal end of an avian femur, an identification followed by Dyke *et al.* (2011). However, these authors did not report any trait in order to sustain its avian affinities or even the identification of the specimen as a femur. However, the holotype of *Palaeocursornis* resembles a pterosaurian humerus and differs from

avian (or dinosaurian) femora in having a deep pneumatic foramen above the distal condyles, only two distal condyles (lacking a tibiofibular crest; Rauhut 2003), medial condyle (trochlea herein) with a dorsoventral sulcus (= intertrochlear sulcus; Costa & Kellner 2009), medially displaced posterior groove (patellar sulcus of Dyke *et al.* 2011), and a convexity (ulnar tubercle) that separates two concavities on the distal surface of the bone (see Averianov 2010). This combination of character indicates the element as a distal pterosaurian humerus. Moreover, the specimen shares with pterosaurs a proximodistally extended brachial depression that is wide, deep, and poorly delimited; and a wide and deep olecranal fossa not delimited dorsally by a ridge. Although the distal end of the bone is poorly preserved, some features suggest Azhdarchid affinities for *Palaecursornis*. The specimen importantly shares with *Azhdarcho* Nessel, 1984 a D-shaped distal humerus, capitulum with a very deep *fovea supratrochlearis ventralis*, and a well-developed and deep trochlear groove (Averianov *et al.* 2005; Averianov 2010).

Eurolimnornis corneti Jurcsák & Kessler, 1986 was described by Jurcsák & Kessler (1986) on the basis of the distal end of a humerus as belonging from a grebe-like neornithine bird, whereas Dyke *et al.* (2011) identified it as an indeterminate avialan. However, the distal end of the humerus of *Eurolimnornis* may be referred to Pterosauria, rather than Avialae on the basis of the following combination of features: brachial depression proximodistally extended, wide, deep, and poorly delimited; wide and deep olecranal fossa not delimited dorsally by a ridge; deep pneumatic foramen above distal condyles; a wide pneumatic foramen behind distal condyles in distal view; and trochlea with a dorsoventral sulcus (see above). Although fragmentary, *Eurolimnornis* differs from Azhdarchoidea and Ornithocheiroidea in lacking a D-shaped distal humerus, and from the former in lacking a deep *fovea supratrochlearis ventralis* (see above). The incomplete nature of holotype of *Eurolimnornis* does not allow referral of this bone beyond Pterosauria indet.

Moreover, Dyke *et al.* (2011) reported the presence of some additional bird bones from the

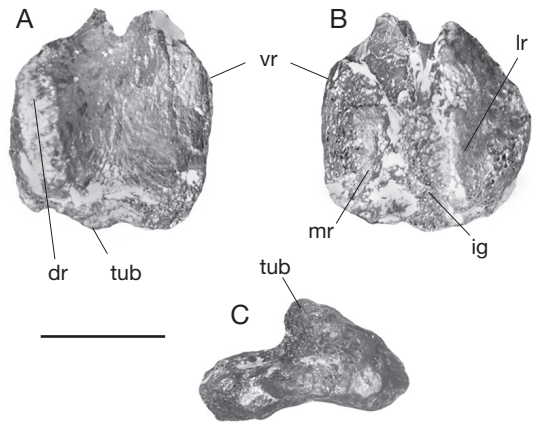


FIG. 5. — *Piksi barbarulna* Varricchio, 2002 (holotype, MOR 1113). Distal end of left ulna in anterior (A), posterior (B), and distal views (C). Abbreviations: ig, intercondylar groove; lr, lateral ridge; mr, medial ridge; tub, tuberculum; vr, ventral ridge. Scale bar: 5 mm.

Cornet fossil locality. Among them, they reported an incomplete furcula, proximal radius shaft, and distal femora. Regarding the putative “furcula” and “radius”, Dyke *et al.* (2011) did not cite a single feature in order to sustain its avian or even bone identity. Distal femora are rather different from that present in other birds in having very small and widely separated distal condyles, a very wide, opened and pneumatized popliteal groove, and in lacking an anterior extensor groove. These characters suggest that these bones do not belong to avian femora. In overall morphology these fragmentary specimens are very similar to proximal radius of the pterosaurian *Azhdarcho* (Averianov 2010). However, these specimens, together with the putative furcula and radius reported by Dyke *et al.* (2011) may be regarded as indeterminate until more detailed studies may be carried out. As pointed out by Dyke *et al.* (2011) very few avialans are known globally from the Early Cretaceous, and thus, the exclusion of both *Eurolimnornis* and *Palaecursornis* from birds is of great significance.

PIKSI AND ITS SIGNIFICANCE FOR LATE CRETACEOUS PTEROSAURIAN FAUNAS

A reevaluation of the putative bird *Piksi barbarulna* Varricchio, 2002 demonstrates that this genus

belongs to the Pterosauria. Among pterosaurs, its peculiar distal humeral morphology excludes *Piksi* from the Azhdarchidae, the latest surviving clade of pterosaurs, and the dominant group of post-Campanian flying reptiles currently represented in the fossil record (Company *et al.* 1999).

Piksi probably belongs to the Ornithocheiroidea, a clade of toothed pterosaurs abundant in Early Cretaceous outcrops of Europe, South America, and Asia (Wang & Zhou 2006). The Latest Cretaceous record of pterosaurs is mainly restricted to the Azhdarchidae, a group found almost around the world, excluding Antarctica (Bennett 1989; Nessonov 1991; Bennett & Long 1991; Padian *et al.* 1995; Kellner & Langston 1996; Buffetaut *et al.* 1996, 2002; Pereda Suberbiola *et al.* 2003; Osi *et al.* 2005). The Campanian-Maastrichtian dominance of azhdarchids, lead some authors to suggest that post-Campanian pterosaur faunas were relatively uniform (McGowan *et al.* 2002). However, Campanian-Maastrichtian beds of Europe yielded isolated remains referable to *Ornithocheirus* (Ornithocheiroidea; see Wellnhofer 1991) and other non-azhdarchid taxa (Jianu *et al.* 1997; Barrett *et al.* 2008), and Campanian-Maastrichtian beds of USA and Brazil yielded fragmentary specimens of pteranodontid-like taxa and Nyctosauridae, respectively (see Company *et al.* 1999). Additionally, a nearly complete rostrum from the Maastrichtian of USA was recently assigned to the Tapejaridae (Kellner 2004). To these reports, here we add the non-azhdarchid *Piksi barbarulna*, also from USA. In conclusion, the current record of the Pterosauria is suggestive of a large diversity of Late Cretaceous pterosaurs, probably comparable to that of Early Cretaceous times and contrasting with previous claims of poor diversity for this time.

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