

NOTA PALEONTOLÓGICA

JAW-MUSCLE RECONSTRUCTION OF THE LATE PLIOCENE PSITTACIFORM *NANDAYUS VOROHUENSIS* FROM ARGENTINA

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PSITTACIFORMES is one of the most diverse clades of non-passeriform birds (Mayr, 2010). With a probable origin in the Australasian sector of Gondwana, they had a long and independent evolutionary history leading to their current pan-austral distribution (Homberger, 1991; Schweizer *et al.*, 2009). Despite their present diversity, Neotropical parrots (Arini) have a depauperate fossil record limited to the Pampean Region in Argentina. Two species of *Cyanoliseus* Bonaparte, 1854 (Acosta Hospitaleche and Tambussi, 2006) and *Nandayus vorohuensis* Tonni and Noriega, 1996, are the only known extinct species of Psittaciformes. The latter is an extinct relative of the Nanday Parakeet *Nandayus nenday* (Vieillot, 1823), and is the only fossil parrot represented by skull remains. It was found in Late Pliocene sediments (*Akodon (A.) lorenzini* Biozone in the Vorohué “Formation”) exposed in southeastern Buenos Aires Province (Cione and Tonni, 1995). Associated mammal material such as procyonids and echimyds indicate Chacoan (subtropical) environmental conditions (Cione and Tonni, 1995).

Parrot skull morphology is highly conservative across species (Tonni and Noriega, 1996). The well-marked naso-frontal hinge that separates the cranium from the conspicuously short beak, the wide interorbital part of the frontal bones (Mayr, 2013), large nostrils, large *ossa palatinum*, the robust and ventrally curved maxilla with sharp edges, and the pseudoprokinesis (Tokita, 2003) characterize all psittacid

skulls. This highly specialized type of cranial kinesis is distinguished by a bending-hinge involving secondary transformation of dermal bones located cranially to the nasal-frontal suture (Tokita, 2003). It differs from the standard prokinesis in its origin, as in the latter the naso-frontal suture itself becomes the bending area (Tokita, 2003) but in both cases the result is the same, producing a wide mouth-opening. The cranio-mandibular complexes of psittacids are derived among birds, featuring evolutionary novelties such as the presence of an *arcus suborbitalis* (SOA); and the *mm. ethmomandibularis* (EM) and *pseudomasseter* (PM) (see Zusi, 1993; Tokita, 2003, 2004).

The SOA is a parrot-specific bony structure ventrally bounding the orbit. It is formed by the ossification of the *ligamentum suborbitale* connecting the caudal extension of the *processus orbitalis* of the *os lacrimale* and the *processus postorbitalis* of the *os squamosum* (Zusi, 1993; Tokita, 2003). It has been considered essential as a muscle attachment site, and in strengthening the skull against the force exerted by the jaw muscles (Tokita, 2003). If the SOA is absent [*e.g.*, as in *Nandayus nenday* and *Myiopsitta monachus* (Boddaert, 1783)], a caudo-ventrally elongated *processus orbitalis* and a *ligamentum suborbitale* close the orbit.

The PM arises from the *m. adductor mandibulae externus superficialis*. It covers the lateral surface of the *arcus jugalis* and attaches to the SOA or to the elongate *processus orbitalis*

(Hofer, 1950, 1953; Zusi, 1993). The EM is derived from the *m. pterygoideus pars dorsalis* (Hofer, 1950; Burton, 1974). It is a large muscle originating in the cranio-dorsal portion of the orbit and attached to the medial aspect of the mandible. Both muscles help produce a strong adduction of the jaw (Burton, 1974; Tokita, 2003, 2004; Bhattacharyya, 2013).

The aim of this contribution is to verify the presence of osteological correlates for these apomorphies and to infer the absence/presence of other jaw muscles in the holotype of *Nandayus vorohuensis* Tonni and Noriega, 1996. This should provide new information shedding light on the evolution of these unique structures.

MATERIALS AND METHODS

The holotype of *Nandayus vorohuensis* is housed in the Museo de La Plata (MLP 94-IV-1-1). The dorsal region of the skull and a small fragment of the left postarticular region of the mandible are not preserved (Fig. 1).

Muscle reconstruction was performed based on the presence of muscle attachment scars, which to a certain degree allows the inference of the muscle position and development (Bryant and Seymour, 1990). We assume that a few gross osteological features allow (limited) muscle reconstruction and extant close relatives can be used as comparative models. Accordingly, comparisons of muscular attachment points in *N. vorohuensis* were made on the basis of the jaw-muscle descriptions of the extant monk parakeet *Myiopsitta monachus*, recently reported by Carril *et al.* (2013). This specie was chosen for comparative purposes because of the highly conservative morphology across species and given that it represents the only taxon closely related to *N. vorohuensis* for which detailed anatomical data was available.

The extant phylogenetic bracket (EPB) represents a widely accepted method developed by Witmer (1995). Based on cladistic principles, comparative anatomy, and homology hypotheses, it allows inferring the presence or absence of soft tissues with some degree of certainty. However, in extant groups in which soft tissue structures are conservative in their presence-absence (*e.g.*, the jaw muscle of the *Neornithes*) and their osteological correlates are always present, EPB will always produce high levels of inference irrespectively of the extant groups chosen to bracket the fossil taxon. In these cases, the same set of conclusions can be obtained based on topological

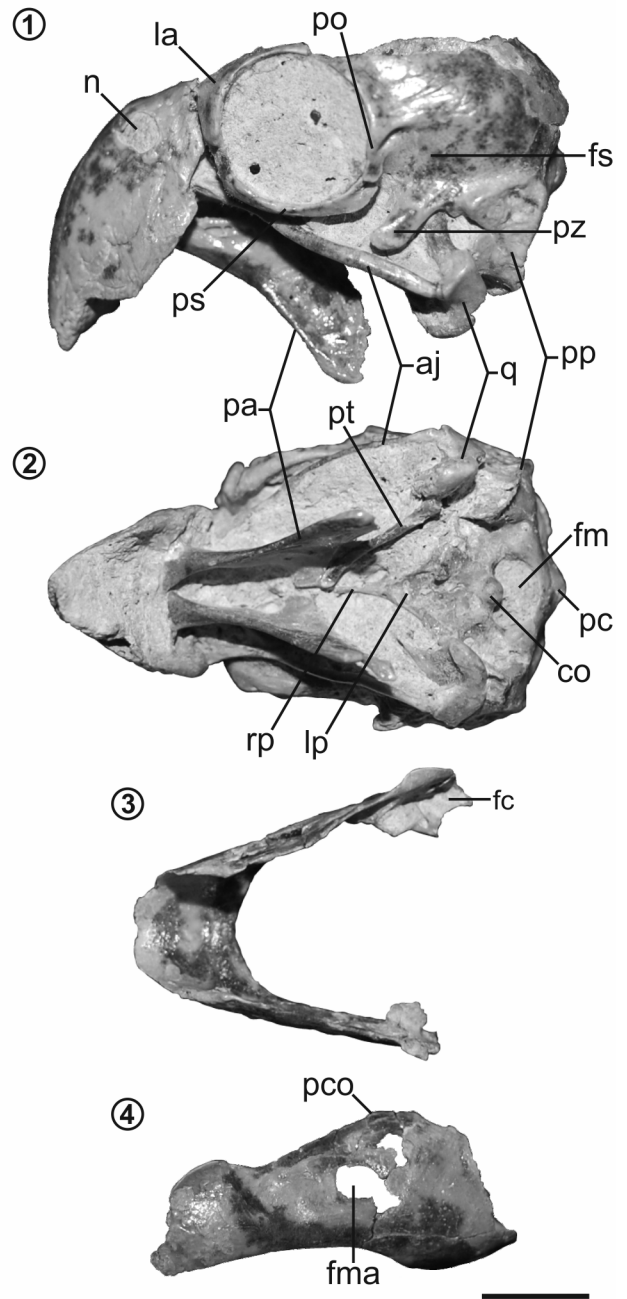


Figure 1. *Nandayus vorohuensis* Tonni and Noriega, 1996, holotype MLP 94-IV-1-1. **1–2**, skull; **1**, left lateral view, **2**, ventral view; **3–4**, mandible, **3**, dorsal view, **4**, right lateral view. Abbreviations: **aj**, arcus jugalis; **co**, condylus occipitalis; **fc**, fossa caudalis; **fm**, foramen magnum; **fma**, fenestra mandibulae; **fs**, fossa temporalis; **la**, os lacrimale; **lp**, lamina parasphenoidalis; **n**, nares; **pa**, os palatinum; **pc**, prominencia cerebellaris; **pco**, processus coronoideus; **po**, processus postorbitalis; **pp**, processus paroccipitalis; **ps**, processus orbitalis (os lacrimale); **pt**, os pterygoideum; **pz**, processus zygomaticus; **q**, os quadratum; **rp**, rostrum parasphenoidale. Scale bar= 1 cm.

criteria. In the case studied in this contribution, there are no reasons to doubt the presence of the inferred soft tissues

and therefore it is not necessary to use the EPB (Degrange, 2012), except for one case (see discussion).

The osteological nomenclature and anatomical orientations follow Baumel and Witmer (1993), whereas the myological terminology is that proposed by Holliday and Witmer (2007).

RESULTS

The *processus orbitalis* is elongated and almost contacts the *processus postorbitalis* (Tonni and Noriega, 1996); thus the SOA is considered absent (Fig. 1.1; 2.1, 3). The EM and the PM muscles are inferred to have been present. The osteological correlate for the insertion of the EM is a conspicuous bulge located on the cranio-medial aspect of the mandible (Fig. 2.7). A depression on the distal half of the lateral side of the *processus orbitalis* cranially delimited by a line indicates the origin of the PM (Fig. 2.1, 3). Also, the presence of the following adductor muscles could be inferred: *m. adductor mandibulae externus profundus* (AMEp), *m. adductor*

mandibulae externus superficialis (AMEs), *m. adductor mandibulae posterior* (AMP), *m. pterygoideus dorsalis* (Ptd), and *m. pterygoideus ventralis* (Ptv). The osteological correlates for the origin of AMEp are a shallow and cranio-caudally extended *fossa temporalis* and the dorsal surface of the *processus zygomaticus* (Fig. 2.1, 3). The AMEp has a wide insertion at the *processus coronoideus* on the mandible (Fig. 2.4). The osteological correlate of the origin of the AMEs is a rough scar on the caudo-ventral aspect of the *processus zygomaticus* (Fig. 2.1, 3). Although the development of the *processus zygomaticus* is similar in both the fossil and *M. monachus*, the origin of the muscle in the latter is restricted to the distal portion. In the extant *N. nenday* the process is longer, reaching the level of the *arcus jugalis*. In *M. monachus* this muscle inserts together with the PM on the lateral aspect of mandible, covering much of its surface. Limits of this muscle in the fossil are better marked in the caudal portion of the mandible (Fig. 2.4). The osteological correlate of the insertion of the AMP is on a concave subtriangular surface on the medial

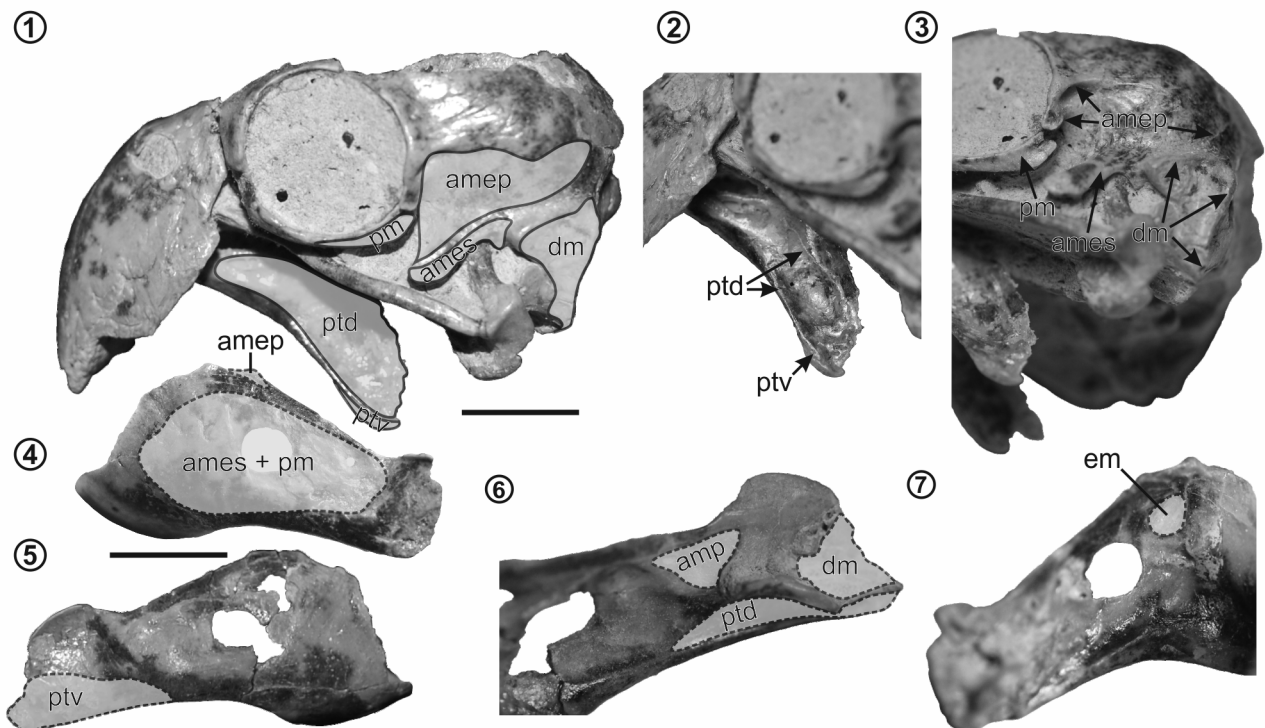


Figure 2. Jaw muscle reconstruction in *Nandayus vorohuensis*, holotype MLP 94-IV-1-1. 1–3, skull. 1, lateral view; 2, details of *os palatinum*, 3, detail of the temporal region. 4–7, jaw; 4, left lateral view; 5, right lateral view; 6, right caudo-medial view of the mandible; 7, left cranio-medial view of the mandible. Muscle origins are indicated in continuous lines, meanwhile discontinuous lines indicate muscle insertion. Arrows in 2 and 3 indicate osseous features and muscles origins discussed in the main text. Abbreviations: **amep**, *m. adductor mandibulae externus profundus*; **ames**, *m. adductor mandibulae externus superficialis*; **amp**, *m. adductor mandibulae posterior*; **dm**, *m. depressor mandibulae*; **em**, *m. ethmo-mandibularis*; **pm**, *m. pseudomasseter*; **ptd**, *m. pterygoideus dorsalis*; **ptv**, *m. pterygoideus ventralis*. Scale bar= 1 cm. 2, 3, 6 and 7 are not at scale for comparison.

and caudal aspect of the mandible, between the *processus coronoideus* and the *fossa articularis quadrati* (Fig. 2.6). The origin of the Ptd is on the *ossa palatinum* and the *ossa pterygoideum*. The origin on the palatine portion of the muscle occupies the entire dorsal aspect of the large *ossa palatinum* and consists of a shallow depression that is well-delimited cranio-ventrally by the *crista lateralis* and caudo-dorsally by a thick ridge (Fig. 2.1, 2). The insertion is located on a concave surface without ridges placed on the medial and caudal surface of the mandible, ventral to the insertion of the AMP (Fig. 2.6). The origin of the Ptv is noticeable by a scar restricted to the distal lateral tip on the ventro-medial aspect of the *ossa palatinum* (Fig. 2.1, 2). The insertion of this muscle on the latero-ventral aspect of the mandible is poorly marked, contrary to the condition of *M. monachus*, which allows its reconstruction (Fig. 2.5).

The abductor *m. depressor mandibulae* (DM) has a broad origin in the exoccipital region marked by a subtriangular depression located caudo-ventrally to that of the AMEp (Fig. 2.1, 3) and its insertion is located in the caudal portion of the mandible, in the *fossa caudalis* (Fig. 2.6). This fossa is located in the posterior portion of the *processus retroarticularis* of the jaw, which is short in its caudal extension in the fossil and *M. monachus*, but very long in the extant *N. nenday*.

Finally, sediment covers the orbit region where the origin of the muscles *mm. protractor pterygoideus et quadrati*, *pseudotemporalis superficialis* and *profundus* were confined. This is also the case with the *m. adductor mandibulae externus medialis* that would be located on the medial facet of the *ossa quadratum*. None of these four muscles could be reconstructed.

DISCUSSION

Jaw muscles could be only partially reconstructed because of the fragmentary condition of the specimen. However, we found evidence of two psittaciform muscle novelties, *i.e.*, the EM and the PM muscles. The huge EM insertion could be associated with a large and powerful muscle for mandible closure. The elongated *processus orbitalis* provides a cranially positioned PM attachment that assists in generating strong bite forces. This process is shorter in the related extant *N. nenday*. We also found evidence of five of the seven common jaw muscles of birds (Bhattacharyya, 2013) in addition to the PM and the EM that are characteristic of psittaciforms. Some

authors (Hofer, 1950; Burton, 1974; Carril *et al.*, 2013) found that the *m. pseudotemporalis profundus* (which originates on the *processus orbitalis* of the *os quadratum* and inserts on the inner dorsal aspect of the mandible) is absent in extant Psittaciformes. Attached sediment prevented confirmation of this condition in the specimen studied here.

The highly developed jaw adductor musculature of Psittaciformes enables them to exert strong bite forces (Burton, 1974; Tokita, 2003, 2004; Bhattacharyya, 2013). These jaw muscles move in coordination with the strong muscular tongue, and the specialized hooked bill allows parrots to crack and eat a wide variety of seeds and nuts. The beak also helps during arboreal locomotion, which involves a variety of movements and postures including perching, climbing, hanging, and moving easily among trees. All these activities imply the use of the upper jaw, powerful jaw muscles, strong grip exerted by both jaws, and even intricate movements of the head resulting from the action of neck muscles. Cranial features found in *N. vorobuensis* are similar to those of living parrots so we can infer the diet and locomotion of the extinct taxon to be at least similar to that of extant species.

Zusi (1993) stated that the SOA and the PM work as an integrated morphological and functional system, but their occurrence varies among parrots. For example, some extant species (*e.g.*, *Strigops* Gray, 1854; *Ara* Lacépède, 1799) do not have a PM despite possessing a well-developed SOA. In this sense, the use of EPB would indicate a level I or II of inference, depending of the phylogenetic frame used (*e.g.*, Wright *et al.*, 2008; Mayr, 2010). However, our results indicate that in *N. vorobuensis*, the SOA is absent but the PM is present, a condition shared with the Neotropical *Pionites* and *Myiopsitta*. The heterogeneous distribution of these characters reaffirms the idea that the direction of the evolutionary changes may have varied independently in the crown group Psittaciformes more than once (Tokita, 2003; Carril *et al.*, 2013). Assuming that the trophic habits of psittaciforms are similar, we cannot find a plausible explanation for the relationship between cranio-mandibular complex capabilities and the presence or absence of these muscles.

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