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FEATURED ARTICLE

OSTEOLOGY OF A NEW GIANT BONY-TOOTHED BIRD FROM THE MIOCENE OF CHILE, WITH A REVISION OF THE TAXONOMY OF NEOGENE PELAGORNITHIDAE

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ABSTRACT—Bony-toothed birds (Pelagornithidae) were among the largest volant birds, but their representatives from the upper size range have so far been known only from very fragmentary fossils. Here we report an exceptionally well-preserved giant species from the late Miocene of the Bahía Inglesa Formation in northern Chile, in which most major limb bones are complete and uncrushed. The fossil has the longest wing skeleton of any bird, and its wingspan in life was at least 5.2 m. Mass estimates of 16–29 kg are, however, surprisingly low and within the range of large extant volant birds, or only moderately above. The fossil constitutes the most substantial record of the Pelagornithidae (bony-toothed birds), and is assigned to a new species, *Pelagornis chilensis*. It is one of the largest known pelagornithids and the three-dimensionally preserved bones allow recognition of many previously unknown osteological features, especially concerning the vertebrae, pectoral girdle, and limb elements. We revise the taxonomy of Neogene pelagornithids and propose classification of all Miocene and Pliocene species into a single genus, *Pelagornis*. Osteological features are highlighted in which giant Neogene Pelagornithidae differ from their smaller Palaeogene relatives.

INTRODUCTION

Pelagornithids or bony-toothed birds (Pelagornithidae) had a worldwide distribution and occur in Paleocene to Pliocene sediments. They are characterized by spiny projections along the tomia of the beak, termed pseudo- or bony-teeth, and some species reached a giant size with wingspans above 4 m. Earlier authors considered pelagornithids to be most closely related to either Procellariiformes (albatrosses, tubenoses, and allies) or the non-monophyletic "Pelecaniformes" (pelicans and allies; e.g., Howard, 1957; Harrison and Walker, 1976; Olson, 1985), but a phylogenetic analysis by Bourdon (2005) suggested sister-group relationship to the Anseriformes (waterfowl). The osteology of bony-toothed birds is, however, still poorly known, and most specimens consist of isolated fragments. Many species are further based on non-comparable skeletal elements so that pelagornithid taxonomy is confusing, which is especially true for the Neogene species (Olson, 1985; Warheit, 2002; Mayr, 2009a).

It has long been recognized that some of the Neogene pelagornithid species were among the largest known volant animals. However, although wingspans up to 6 m were assumed (Olson, 1985), virtually all remains of giant pelagornithids consist of fragmentary bones, so that reliable wingspan estimates were not possible and the anatomy of these birds remained very poorly known. Recently, however, a largely complete skeleton of a giant pelagornithid was discovered in Miocene marine sediments of the Bahía Inglesa Formation in northern Chile. The specimen was found by amateur collectors in the newly reported (Gutstein et al., 2007) "El Morro" site, approximately 10 km south of Bahía Inglesa town in the Atacama Region, in a thin layer of gray and fine sandstone with poorly consolidated mud grains and with abundant semiarticulated and well-preserved vertebrate fossils. This layer belongs to a transgressive-regressive marine sequence within the Bahía Inglesa Formation, Tortonian-Messinian in age (Gutstein et al., 2009), as indicated by Strontium isotope dating of 6.8 ± 1.3 million years at the top of the sequence (Achurra, 2004; Achurra et al., 2009).

The fossil was sold to a German fossil collector, who recognized its significance and in 2008 contacted one of the authors (G.M.). Through funds of the Senckenberg Nature Research Society, the specimen was acquired for repatriation into Chile and to ensure its permanent scientific availability. Details on the extent of its articulation in situ and the original position of the bones are unknown.

The Chilean species is in the uppermost size range of pelagornithids, and is remarkable not only for its very large size but also because all bones are three-dimensionally preserved. Its completeness and excellent preservation for the first time allows a detailed study of the osteology of a Neogene bony-toothed bird.

THE NEOGENE FOSSIL RECORD OF BONY-TOOTHED BIRDS

The comparatively rich fossil record of Palaeogene Pelagornithidae was summarized by Mayr (2009a). The first named Neogene bony-toothed bird is *Pelagornis miocaenus* Lartet, 1857, from the early and middle Miocene of France. This species is known from humeri and a tentatively referred sternum (Milne-Edwards, 1867–68; Harrison and Walker, 1976; Cheneval, 1996; Mourer-Chauviré and Geraads, 2008; Mayr et al., 2008), and its pelagornithid affinities went undetected for more than 100 years. Another possibly Neogene bony-toothed bird described in the early days of palaeornithology, *Pseudodontornis longirostris* Spulski, 1910, is based on a partial skull and was thus recognized as a bony-toothed bird from the beginning (Spulski, 1910; Lambrecht, 1930). According to Spulski (1910), the fossil was brought by a Brazilian sailor to Europe, but Lambrecht (1930) considered a Brazilian origin unlikely. The age of the specimen is likewise unknown, and the holotype seems to have been destroyed in the Second World War (Olson, 1985).

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Only few decades later, however, more substantial remains of Neogene pelagornithids were discovered. One of the best-known species is *Osteodontornis orri* Howard, 1957, from the late Miocene of California, whose holotype consists of a partial skeleton on a slab (Howard, 1957). Its total wingspan in life was estimated at 4.3–4.9 m (Howard, 1957), but few bone details can be observed in the crushed fossil. Additional material of *O. orri* was described by Howard and White (1962), Howard (1978), Olson (1985), and Stidham (2004). A further North American pelagornithid from the Pacific coast is *Cyphornis magnus* Cope, 1894, whose holotype and only known specimen is a proximal tarsometatarsus from an unknown horizon of Vancouver Island in Canada. The fossil was considered to be of Miocene age by earlier authors (Wetmore, 1928; Olson, 1985), but Goedert (1989) noted that it may actually be as old as late Eocene.

Pelagornithid remains from South Carolina, i.e., the North American Atlantic coast, were reported by Hopson (1964). He tentatively considered these specimens to be of early Miocene age, but according to Olson (1985) they probably came from late Oligocene deposits. The material includes a mandible fragment, which was referred to *Pseudodontornis longirostris* by Hopson (1964). A distal end of a tarsometatarsus was assigned to *Palaeochenoides mioceanus* Shufeldt, 1916, a species originally based on an incomplete femur from the same deposits, but Howard and Warter (1969) and Harrison and Walker (1976) considered this tarsometatarsus to be referable to *P. longirostris*. Identification and age of another, smaller distal tarsometatarsus, which was described as *Tympanonesiotes wetmorei* by Hopson (1964), were considered uncertain by Olson (1985). Olson (1984) figured remains of pelagornithids from the middle Miocene Calvert Formation of Maryland and Virginia. In addition to jaw fragments, the material includes a partial coracoid and an incomplete tibiotarsus. Olson and Rasmussen (2001) reported a number of fragmentary bones of bony-toothed birds from the Miocene or early Pliocene of the Lee Creek Mine in North Carolina, which were assigned to two unnamed species of *Pelagornis*.

Howard and Warter (1969) described a partial skull and an associated femur of a pelagornithid bird from New Zealand as *Pseudodontornis stirtoni*. Unfortunately, the exact age of the holotype is unknown and either Miocene or Pliocene (McKee, 1985). Without sufficient justification the species was transferred to the new taxon *Neodontornis* by Harrison and Walker (1976). A proximal humerus of a pelagornithid from the middle to late Miocene of New Zealand was identified by Scarlett (1972), and McKee (1985) reported an incomplete humerus and radius from Pliocene deposits. Pelagornithid remains were also found in the Miocene and early Pliocene of Japan, and include a well-preserved quadratum, a femur, and mandible fragments (Ono, 1980, 1989; Matsuoka et al., 1998).

There is no record of Neogene pelagornithids from Africa south of the Sahara, and these birds are absent in the rich marine avifauna of the early Pliocene locality Langebaanweg in South Africa (Rich, 1980; Olson, 1983). However, Mourer-Chauviré and Geraads (2008) described a pelagornithid from the latest Pliocene of Morocco as *Pelagornis mauretanicus*. This species is represented by a number of fragmentary cranial and postcranial bones of several individuals, and constitutes the latest fossil occurrence of the Pelagornithidae.

All previously published remains of South American bony-toothed birds consist of fragmentary remains. An incomplete rostrum was found in middle Miocene sediments of Venezuela (Rincón and Stucchi, 2003). Pelagornithidae further occur in the late Miocene and Pliocene of the Pisco Formation in Peru (Cheneval, 1993; Chávez et al., 2007), and Walsh and Hume (2001) and Chávez et al. (2007) described few bones from the late Miocene/early Pliocene of the Bahía Inglesa Formation in Chile.

MATERIALS AND METHODS

Osteological terminology follows Baumel and Witmer (1993) unless indicated otherwise.

Institutional Abbreviations—BMNH, The Natural History Museum, London; IRSNB, Institut royal des Sciences naturelles de Belgique, Belgium; MNHN, Museo Nacional de Historia Natural, Chile.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758
PELAGORNITHIDAE Fürbringer, 1888
PELAGORNIS Lartet, 1857

Emended Diagnosis—(1) Rostrum maxillare with transverse furrow just before tip; (2) carina sterni with marked cranial projection; (3) trabeculae laterales of sternum very long and massive; proximal end of humerus with (4) very small ventral portion, fossa pneumotricipitalis situated on ventral surface of bone, and (5) crista deltopectoralis situated far distally, with very little cranial deflection and bilobed margin; (6) ulna with very short olecranon; (7) ulna and radius with marked furrows along the cranial and caudal surfaces of the shaft; (8) carpometacarpus extremely long and narrow, with a very long and low os metacarpale alulare, spatium intermetacarpale very narrow and short; (9) femur with very shallow trochlea fibularis; (10) tibiotarsus with condylus lateralis smaller than condylus medialis; tarsometatarsus with (11) hypotarsus enclosing two bony canals, and (12) trochlea metatarsi II subequal in distal extent to trochlea metatarsi IV.

PELAGORNIS CHILENSIS, n. sp.

Holotype—MNHN SGO.PV 1061 (partial skeleton including the dorsal portion of the cranium and most of the beak, 11 presacral vertebrae, all elements of the pectoral girdle, fragments of the sternum, and most major bones of the forelimbs and hind limbs).

Type Locality—"El Morro" site, approximately 10 km south of Bahia Inglesa town, Atacama desert, northern Chile.

Type Horizon—Bahía Inglesa Formation; middle Miocene–early Pliocene, about 16–4.8 million years ago (Rojo, 1985; emended by Marquardt et al., 2000)

Differential Diagnosis—The new species is in the uppermost size range of the Pelagornithidae and distinctly larger than *Osteodontornis orri* Howard, 1957, *Pelagornis miocaenus* Lartet, 1857, *P. mauretanicus* Mourer-Chauviré and Geraads, 2008, and *Pseudodontornis stirtoni* Howard and Warter, 1969 (Tables 1–3). It is further distinguished from *Osteodontornis orri* in that the two rostral-most large pseudo-teeth are separated by only two smaller pseudo-teeth (six in *O. orri*; see Stidham, 2004). It differs from *Pseudodontornis stirtoni* in that the projection formed by the os spleniale at the intraramal joint is more ventrally directing (more caudally directed in *P. stirtoni*). It is distinguished from *Pseudodontornis longirostris* Spulski, 1910, in that the jaws have more than one pseudo-tooth between the largest pseudo-teeth, the caudal end of the mandible is vertically oriented, not slanting rostrocaudally (Fig. 1), and the os angulare forms a ventral projection caudal of the intraramal joint (Fig. 1A). In contrast to *Palaeochenoides mioceanus* Shufeldt, 1916, the trochlea fibularis of the femur lacks a sulcus.

Measurements—See Tables 1–3.

Etymology—The species name refers to the geographic origin of the new species.

Remarks—It is not possible to differentiate the Chilean pelagornithid from *Cyphornis magnus*, whose holotype and only

TABLE 1. Dimensions of the skull of pelagornithids in comparison (in mm).

	Skull, length	Upper beak, length	Upper beak, height at narial opening	Naso-frontal hinge, width	Quadratum, maximum height	Mandible, length	Mandible, height at angulus mandibulae
MNHN SGO.PV 1061	450	325	45.0	51.4	60.3	414	57.9
Pelagornis mauretanicus	—	—	—	—	48.4[a]	—	50.0
P. ("*Pseudodontornis*") *longirostris*	>400[b]	>260[c]	~38[c] (40.0[d])		~53–57[c]	—	~53[c]
P. ("*Pseudodontornis*") *stirtoni*	—	—	~29.0[d]	35.0[d]	—	—	—
P. ("*Osteodontornis*") *orri*	400[e]	300[e]	40[e]	27[e]	—	367[e]	56[f]
P. ("*Osteodontornis*") sp.[e]	—	—	—	—	44.6[f]	—	—

For the quadrate and mandible of MNHN SGO.PV 1061 measurements are from the left side.
[a]After Mourer-Chauviré and Geraads (2008).
[b]After Lambrecht (1930).
[c]Estimation based on Lambrecht (1930:fig. 1).
[d]After Howard and Warter (1969).
[e]After Howard (1957).
[f]Unnamed species from the Miocene of Japan; after Ono (1989).

known specimen is a badly damaged proximal tarsometatarsus (Cope, 1894). The latter fossil matches the proximal tarsometatarsus of the Chilean pelagornithid in size and overall morphology, but not enough details are visible for meaningful comparisons. The age of *C. magnus* is uncertain, and Goedert (1989) considered it possible that the species is conspecific with a very large pelagornithid from the late Eocene of Oregon. Because of the fragmentary nature of the holotype *C. magnus* and its uncertain age, we prefer to classify the Chilean pelagornithid in a new species. This is also justified by the large geographic distance of about 10,000 km between Vancouver Island in Canada, the type locality of *C. magnus*, and the Bahía Inglesa Formation in northern Chile.

DESCRIPTION AND COMPARISONS

Skull—Cranium and rostrum of MNHN SGO.PV 1061 (Fig. 1) are distinctly larger than pelagornithid cranial remains from the Bahía Inglesa Formation described by Chávez et al. (2007). The rostrum maxillare is broken at the well-developed naso-frontal hinge and lacks the proximal section of the right tomium. It has slightly convex lateral surfaces and is mediolaterally constricted caudal of the narial openings (Fig. 1C). As in other pelagornithids, there is a longitudinal groove along each side of the rostrum, which begins from the tomium near the tip of the beak, and runs parallel to the culmen until its bends ventrally in the caudal third of the rostrum. The small, ovate narial openings are situated in this groove, just before the latter angles ventrally. The slightly down-turned and broadly rounded tip of the rostrum closely matches that of *O. orri* described by Stidham (2004). It is set apart from the rest of the beak by a transverse furrow ("anterior groove" of Stidham, 2004:fig. 2), which indicates that the compound ramphotheca consisted of four portions. Such a transverse furrow is a characteristic feature of Neogene bony-toothed birds, but is absent in the early Eocene *Odontopteryx* (Bourdon, 2005:Fig. 1a; Bourdon, 2006). The culmen forms a ridge from the transverse furrow to about 46 mm before the naso-frontal hinge, where the dorsal surface of the rostrum is flat as in *Pseudodontornis stirtoni*. In the early Eocene *Dasornis emuinus*, by contrast, the dorsal surface of the caudal rostrum is also roof-like (Mayr, 2008).

The formation of the pseudo-teeth is symmetrical in the left and right halves of the rostrum maxillare, with 22 of these projections being distributed over the rostral three fourths of the left tomium. As in the *O. orri* rostrum described by Stidham (2004), the rostral-most two pseudo-teeth, which border the rostral end of the longitudinal rostral groove, are less pointed than the other pseudo-teeth, and form more edge-like projections. Like in other Neogene Pelagornithidae (Mourer-Chauviré and Geraads, 2008), the pseudo-teeth are arranged in a regular pattern,

TABLE 2. Dimensions of wing and pectoral girdle bones in comparison (in mm).

	Coracoid, length[a]	Scapula, length	Humerus, length	Humerus, proximal width	Ulna, length	Ulna, proximal width	Carpometacarpus, length
MNHN SGO.PV 1061	143.3/144.5	—/>229.4	821.0/—	—/80.6	779.5/—	49.1/48.0	346.6/—
Pelagornis miocaenus	—	—	591–~710[b]	59.3–61.5[b]	—	—	—
P. mauretanicus	—	—	—	—	—	—	—
Pelagornis sp.[c]	—	—	—	65.3–70.1[c]	—	—	—
P. ("*Osteodontornis*") *orri*	—	—	>593[d]	—	650[d]	—	252[d]

For MNHN SGO.PV 1061 measurements from both sides are given (left/right).
[a]From tip of processus acrocoracoideus to angulus medialis.
[b]After Mourer-Chauviré and Geraads (2008).
[c]Unnamed species from the Pisco Formation (Peru); after Chávez et al. (2007).
[d]After Howard (1957).

TABLE 3. Dimensions of hind limb elements in comparison (in mm).

	Femur, length	Femur, proximal width	Femur, distal width	Tibiotarsus, length	Tibiotarsus, distal width	Tarsomet., length	Tarsomet., proximal width	Tarsomet., distal width
MNHN SGO.PV 1061	150.2/—	35.9/—	39.1/39.1	236.5/242.2	36.1/—	126.9/127.5	36.6/36.8	37.3/37.2
Pelagornis mauretanicus	133[a]	32.4[a]	34.5[a]	—	—	—	—	—
Pelagornis sp.[b]	—	29–30[b]	29.6–32.7[b]	—	—	—	—	—
Pelagornis sp.[c]	—	—	32.5[c]	—	—	—	—	—
P. ("*Pseudodontornis*") *stirtoni*	129.5[d]	—	~31[d]	—	—	—	—	—
P. ("*Osteodontornis*") *orri*	—	—	—	—	—	114[e]	—	—
Palaeochenoides mioceanus	—	—	40[a]	—	—	—	—	34.7[f]
Tympanonesiotes wetmorei	—	—	—	—	—	—	—	~24.5[f]
Cyphornis magnus	—	—	—	—	—	—	36.7[g]	—

For MNHN SGO.PV 1061 measurements from both sides are given (left/right).
[a]After Mourer-Chauviré and Geraads (2008).
[b]Unnamed species from the Miocene or Pliocene of North Carolina; after Olson and Rasmussen (2001).
[c]Unnamed species from the Pliocene of Japan; after Ono (1980).
[d]After Howard and Warter (1969).
[e]After Howard (1957).
[f]After Hopson (1964).
[g]After Wetmore (1928).

with very large pseudo-teeth being separated by three smaller ones, the central of which is again larger than the adjacent two. Next to some of the small spikes, there are rudimentary ridge-like pseudo-teeth. In MNHN SGO.PV 1061 the two rostral-most large pseudo-teeth are separated by only two smaller pseudo-teeth, whereas in *O. orri* there are six small pseudo-teeth between the two largest pseudo-teeth (Stidham, 2004), owing to the fact that one of the larger pseudo-teeth in *O. orri* is not a strongly developed as in MNHN SGO.PV 1061. The rostral-most pseudo-teeth are slightly caudally directed, whereas the central ones point ventrally, and the caudal-most are projecting rostrally.

These 'bony teeth' are very different from true avian teeth, which are covered by dentine and situated in alveoles (Lambrecht, 1930; Howard, 1957; Stidham, 2004), but resemble early developmental stages of first-generation archosaurian teeth, which likewise are mere outgrowths of the jaw bones (Harris et al., 2006; Westergaard and Ferguson, 1990). In chicken embryos the early odontogenic signaling pathways remain inducible (Harris et al., 2006; Sire et al., 2008), and we thus consider it well possible that 'bony teeth' indeed originated from tooth-specific developmental programs and are thus homologous to true avian teeth.

As in other Pelagornithidae, the ventral surface of the rostrum maxillare bears deep fossae for the reception of the mandibular pseudo-teeth (Lambrecht, 1930; Stidham, 2004). A palatal ridge ("Gaumenkamm" of Lambrecht, 1930) runs along the midline of the ventral surface; it forms a narrow ridge in the rostral half of the beak but is wider and with a more rounded surface in its caudal part. In the closed beak, the rami mandibulae were situated in the cavity of the rostrum, with the pseudo-teeth of the rostrum maxillare abutting their lateral surfaces (Zusi and Warheit, 1992).

Only the dorsal portion of the cranium is preserved. As far as comparisons are possible, its morphology corresponds well with the cranium of the early Eocene *Dasornis emuinus* reported by Mayr (2008), but the interorbital section of the ossa frontalia is wider. As in other Pelagornithidae (e.g., Bourdon, 2006; Mayr, 2008), the frontoparietal suture of the cranium is incompletely fused. The dorsal rim of the orbit is nearly perfectly semicircular. Only the base of the os praefrontale is preserved, which is fused with the os frontale in pelagornithids (Howard and Warter, 1969; Harrison and Walker, 1976; Mayr, 2008). As in early Eocene Pelagornithidae (Bourdon, 2005:Fig. 3a), there are deep depressions for the conchae caudales; the facies orbitales of the ossa frontalia bear shallow, elongate impressiones glandularum nasales, similar to those figured by Olson (1985:fig. 10). The processus postorbitalis is ventrally continuous with the straight ventrolateral margin of the os squamosum. There are no fossae temporales, and a processus zygomaticus is likewise absent. Details of the cotylae quadraticae cannot be discerned. The brain cavity is comparatively small and the cranial fossae for the two hemispheres of the telencephalon indicate that the latter had similar proportions to those of the early Eocene *Odontopteryx toliapica* (see Milner and Walsh, 2009); fossae for eminentiae sagittales are not visible. The dorsal surface of the cranium is perforated by irregularly sized and shaped holes, which are either post-mortem artifacts or indicate a pathologic condition of the bird; similar holes also occur on the right ramus mandibulae and some of the postcranial bones.

The morphology of the quadratum (Fig. 2E–H) corresponds well with other Neogene Pelagornithidae (Ono, 1989; Olson and Rasmussen, 2001; Mourer-Chauviré and Geraads, 2008). The processus oticus has two heads, but only on its caudal surface are these separated by an incisura intercapitularis. Rather than being convex, the articulation surface of the capitulum oticum is slightly concave; whether there was a second, cranially directed articulation facet as in *Pelagornis mauretanicus* (Mourer-Chauviré and Geraads, 2008:Fig. 6) cannot be clearly discerned because the corresponding area is eroded. An eminentia articularis, a derived feature of galloanserine birds (Weber and Hesse, 1995; Mayr and Clarke, 2003), is absent. As in the pelagornithid quadratum from the middle Miocene of Japan described by Ono (1989), the caudolateral edge of the quadratum of MNHN SGO.PV 1061 forms a sharp ridge, and the caudal surface is slanting rostrocaudally. The processus orbitalis is proportionally longer and with

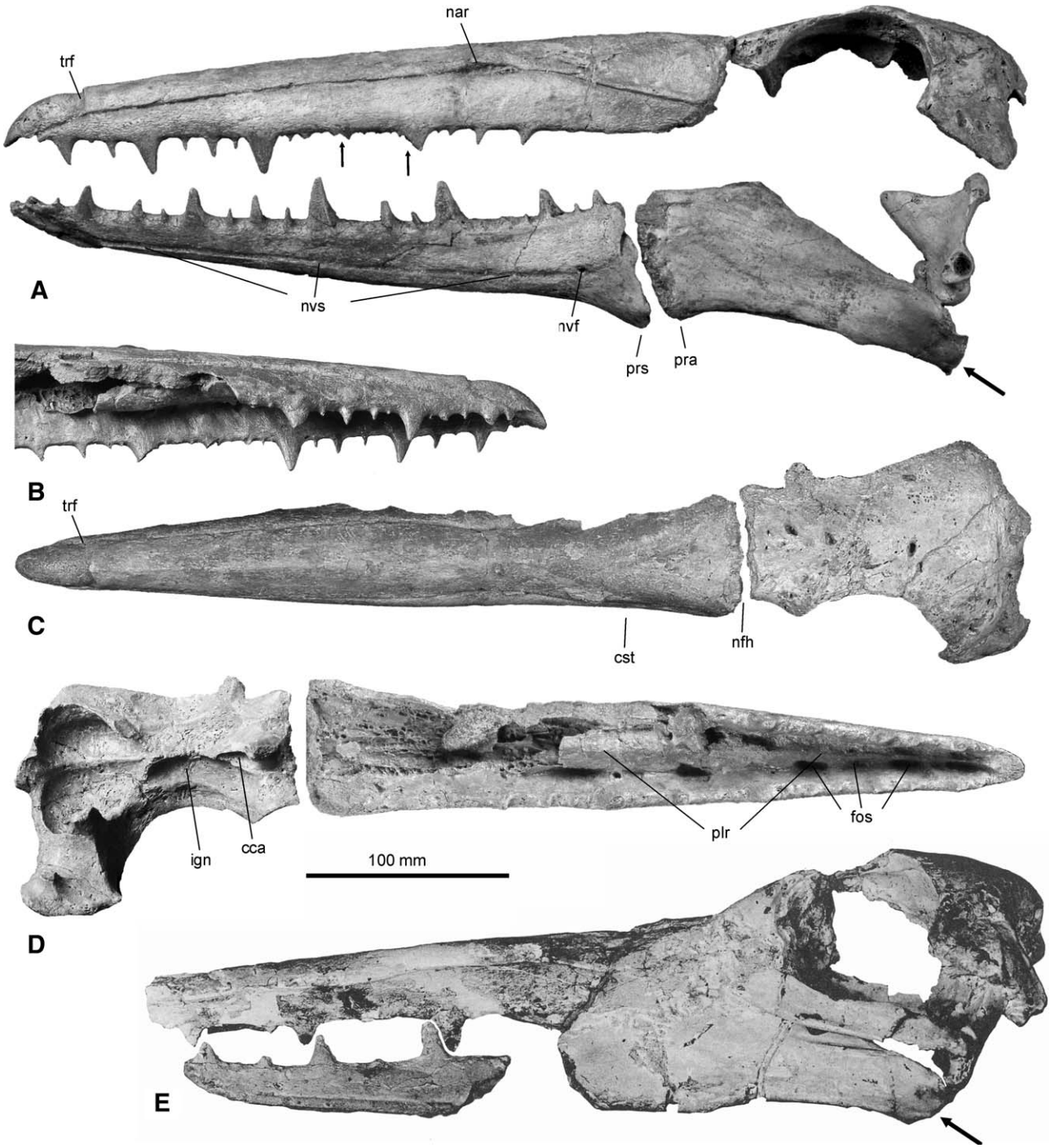

FIGURE 1. *Pelagornis chilensis*, n. sp., from the Miocene of the Bahía Inglesa Formation (holotype, MNHN SGO.PV 1061). **A**, skull in left lateral view. **B**, rostrum in right lateroventral view. **C**, **D**, cranium and rostrum in dorsal (**C**), and ventral (**D**) views. **E**, holotype skull of "*Pseudodontornis*" *longirostris* for comparison (from Lambrecht, 1930, reversed and with lettering removed). **Abbreviations**: **cca**, concha caudalis; **cst**, mediolateral constriction of beak; **fos**, fossae for reception of mandibular pseudo-teeth; **ign**, impressio glandulae nasalis; **nar**, narial opening; **nfh**, nasofrontal hinge; **nvf**, neurovascular foramen; **nvs**, neurovascular sulcus; **plr**, palatal ridge; **pra**, ventral projection formed by os angulare; **prs**, ventral projection formed by os spleniale; **trf**, transverse furrow. The small arrows point to two large broken pseudo-teeth; the large arrows indicate the caudal end of the mandible, which is more vertically oriented in *P. chilensis* than in *P. longirostris* (see text).

a more pointed tip than that of the quadratum of the Japanese pelagornithid (Ono, 1989). On its medial surface there are two pneumatic openings, which correspond to the foramina pneumatica basiorbitale et rostromediale of Elzanowski and Stidham (2010; Fig. 2E). As in *P. mauretanicus* but in contrast to a pelagornithid quadratum from the Miocene or early Pliocene of North Carolina (Olson and Rasmussen, 2001:pl. 11f), there is no additional pneumatic foramen on the caudal surface of the

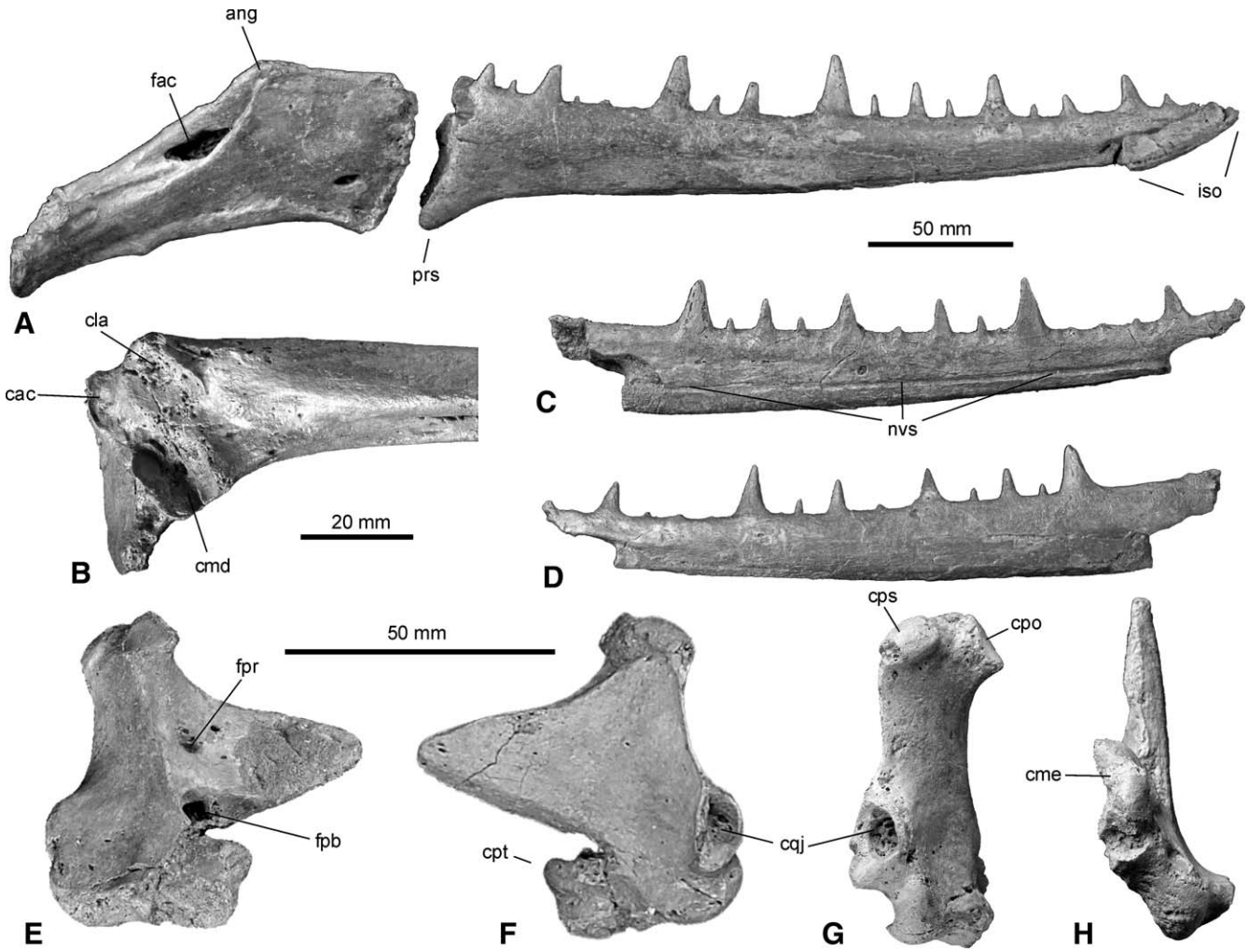

FIGURE 2. *Pelagornis chilensis*, n. sp., from the Miocene of the Bahía Inglesa Formation (holotype, MNHN SGO.PV 1061). **A**, left ramus mandibulae in medial view. **B**, proximal end of left ramus mandibulae in dorsal view. **C**, **D**, distal section of right ramus mandibulae in lateral (**C**) and medial (**D**) views. **E**–**H**, left quadratum in medial (**E**), lateral (**F**), caudal (**G**), and ventral (**H**) views. **Abbreviations**: **ang**, angulus mandibulae; **cac**, caudal cotyla (see text); **cla**, cotyla lateralis; **cmd**, cotyla medialis; **cme**, condylus medialis; **cpo**, capitulum oticum; **cps**, capitulum squamosum; **cpt**, condylus pterygoideus; **cqj**, cotyla quadratojugalis; **fac**, fossa aditus canalis neurovascularis; **fpb**, foramen pneumaticum basiorbitale; **fpr**, foramen pneumaticum rostromediale; **iso**, intersymphyseal ossification; **nvs**, neurovascular sulcus; **prs**, ventral projection formed by os spleniale. Same scale bars for **A**, **C**, and **D**, and for **E**–**H**.

processus mandibularis. Further as in *P. mauretanicus*, the rostrodorsal surface of the processus oticus forms a flat platform of subtriangular shape ("triangular shallow surface" of Mourer-Chauviré and Geraads, 2008:Fig. 6). The condylus lateralis is very short, and the deeply excavated and cup-like cotyla quadratojugalis is rostroventrally bordered by a distinct facies articularis quadratojugalis ventralis (terminology after Elzanowski and Stidham, 2010). The condylus pterygoideus is very prominent. As noted by Bourdon (2005, 2006), the configuration of the condyles of the processus mandibularis resembles that of extant Galloanseres. The condyli medialis et lateralis are very narrow and arranged nearly in line. In contrast to most extant neoavian taxa, but as in Galloanseres, the processus mandibularis lacks a condylus caudalis.

Earlier authors detailed that the mandible of pelagornithids is characterized by a synovial intraramal joint between the ossa spleniale et angulare, and by the absence of an ossified symphysis mandibulae (Howard and Warter, 1969; Harrison and Walker, 1976; Zusi and Warheit, 1992). With regard to these features it agrees with the late Cretaceous Ichthyornithidae and Hesperornithidae, which are genuinely toothed taxa outside crown group Aves (Zusi and Warheit, 1992). In MNHN SGO.PV 1061, the ventral portion of the tip of the ramus mandibulae forms a subrectangular notch (Fig. 2C), and the ventral margin of the ramus mandibulae caudal of this notch is very thin mediolaterally. This notch served for reception of an elongate intersymphyseal ossification, a feature previously only reported for hesperornithids (Martin, 1987). The ramus mandibulae has an irregular, somewhat undulated lateral surface; just rostral of the intraramal joint it becomes mediolaterally thicker. As in other Pelagornithidae (Matsuoka et al., 1998; Stidham, 2004; Mourer-Chauviré and Geraads, 2008), there is a longitudinal neurovascular sulcus along the lateral surface of the ramus mandibulae, which begins at a neurovascular foramen and runs in the ventral third of the ramus (Fig. 1A). A shorter and shallower sulcus also occurs on the medial surface of the ramus, in its distal third and also close to the ventral margin. The intraramal joint of pelagornithids was described in detail by Zusi and Warheit (1992), and the

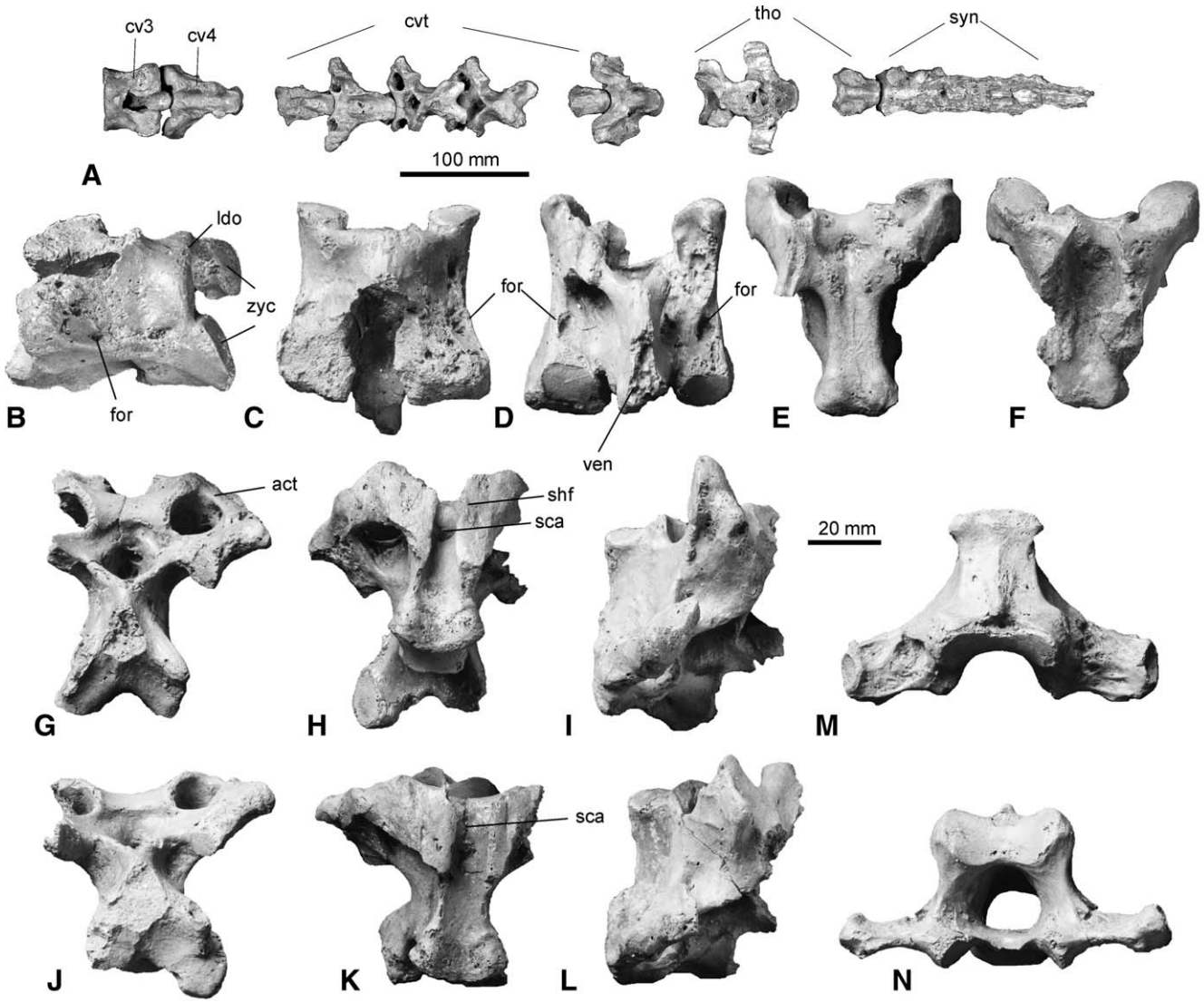

FIGURE 3. Vertebrae of *Pelagornis chilensis*, n. sp., from the Miocene of the Bahía Inglesa Formation (holotype, MNHN SGO.PV 1061). **A**, preserved parts of vertebral column (all vertebrae are isolated and were assembled for the figure). **B**–**D**, third cervical vertebra in dorsolateral (**B**), dorsal (**C**), and ventral (**D**) views. **E**, **F**, fourth cervical vertebra in ventral (**E**) and dorsal (**F**) views. **G**–**L**, two cervicothoracic vertebrae in dorsal (**G**, **J**), ventral (**H**, **K**), and left lateral (**I**, **L**) views. **M**, **N**, thoracic vertebra in ventral (**M**) and cranial (**N**) views. **Abbreviations**: **act**, ansa costotransversaria; **cv3**, third cervical vertebra; **cv4**, fourth cervical vertebra; **cvt**, cervicothoracic vertebrae; **for**, foramen enclosed by arcus interzygapophysialis; **ldo**, lamina dorsalis; **tho**, thoracic vertebrae; **sca**, sulcus caroticus; **shf**, bony shelf; **syn**, synsacrum; **ven**, processus ventralis; **zyc**, zygapophysis cranialis. Same scale bar for **B**–**N**.

morphology of MNHN SGO.PV 1061 confirms their observations. The left ramus mandibulae is separated at the joint, but the two halves were originally connected by a strap-like bony sheet of about 13 mm length in the dorsal part of the joint. In the ventral three fourths of the joint, however, the rostral and caudal portions of the mandibular ramus were completely separated. The articulation surface of the rostral portion forms a concave trough, that of the caudal portion is convex and unusually rugose. The rostral portion of the ramus mandibulae is dorsoventrally narrow over most of its length, but the os spleniale forms a marked protrusion on its caudoventral end (Fig. 2A). The caudal portion bears a very prominent angulus mandibulae; just caudal of it the depth of the ramus mandibulae declines towards the dorsoventrally low articular end. There is a marked fossa aditus canalis neurovascularis. A second, smaller foramen is located close to the rostroventral corner of the caudal mandibular portion, and has also been reported for *Pseudodontornis stirtoni* by Howard and Warter (1969). Mandibular fenestrae are absent. As in *Pseudodontornis longirostris* and *P. stirtoni* (see Howard and Warter, 1969), the caudal end of the mandible bears longitudinal furrows along its dorsal margin, both on the lateral and medial surfaces.

The mandibular tooth-like projections extend farther caudally than those of the rostrum. The completely preserved left ramus mandibulae bears 20 pseudo-teeth, and 17 can be counted on the incomplete right one. Howard (1957) estimated the presence of 19 pseudo-teeth on the mandible of the *O. orri* holotype. Arrangement of the mandibular pseudo-teeth is largely symmetrical in the left and right rami mandibulae; the largest, central one is broken in the right ramus mandibulae.

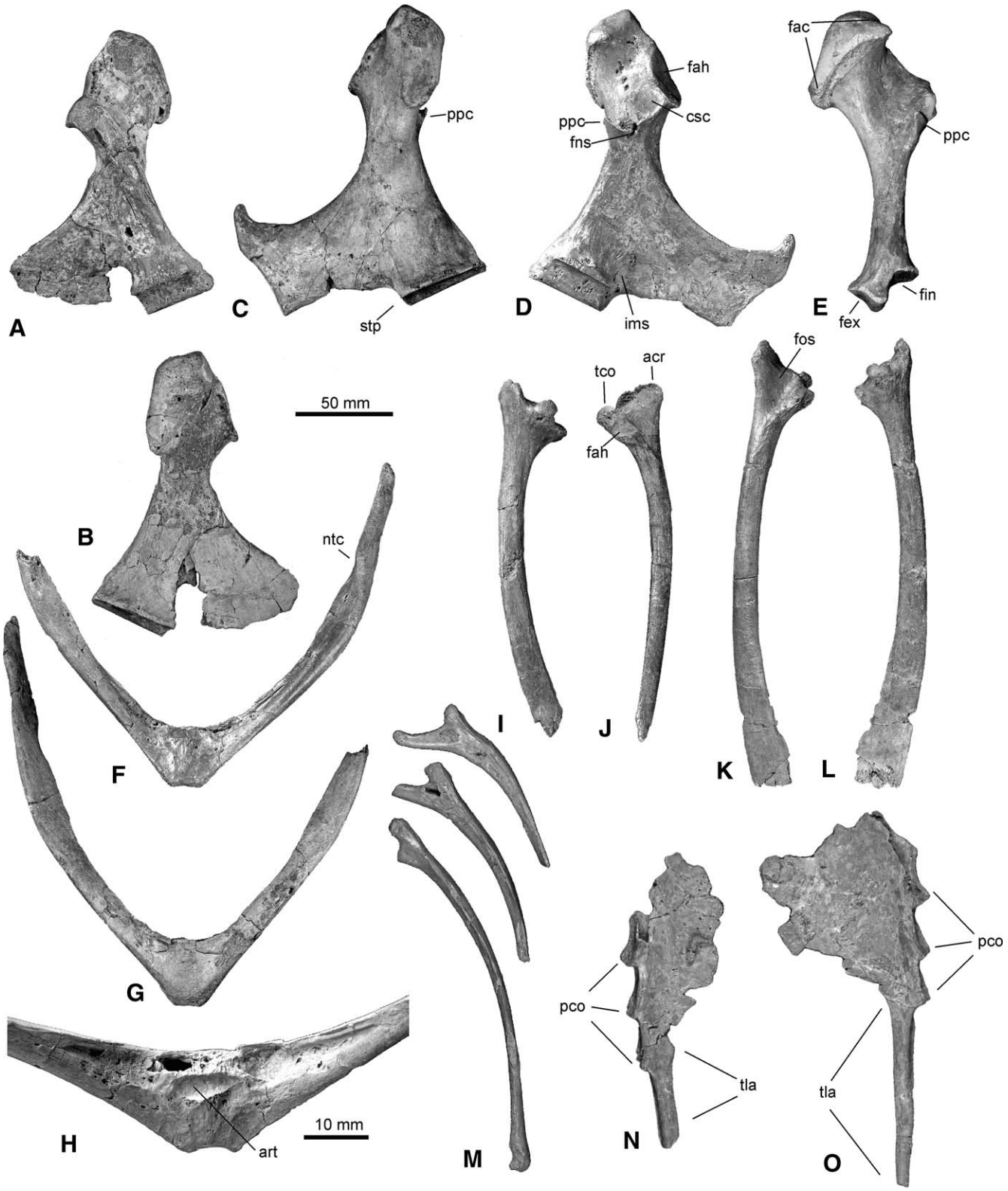

FIGURE 4. Pectoral girdle elements (**A**–**L**), ribs (**M**), and sternum (**N**, **O**) of *Pelagornis chilensis*, n. sp., from the Miocene of the Bahía Inglesa Formation (holotype, MNHN SGO.PV 1061). **A**–**E**, left (**A**, **B**) and right (**C**–**E**) coracoids in dorsal (**A**, **D**), ventral (**B**, **C**), and medial (**E**) views. **F**, **G**, furcula in caudal (**F**) and cranial (**G**) views. **H**, furcula, extremitas sternalis in caudodorsal view. **I**–**L**, left (**I**, **J**) and right (**K**, **L**) scapulae in medial (**I**, **L**) and lateral (**J**, **K**) views. **M**, ribs. **N**, **O**, sternum fragments in ventral view. **Abbreviations**: **acr**, acromion; **art**, articulation facet; **csc**, cotyla scapularis; **fac**, facies articularis clavicularis; **fah**, facies articularis humeralis; **fex**, facies externa of crista articularis sternalis; **fin**, facies interna of crista articularis sternalis; **fns**, foramen nervi supracoracoidei; **fos**, fossa between facies articularis humeralis and acromion; **ims**, impressio musculi sternocoracoidei; **ntc**, notch in scapus claviculae (see text); **ppc**, processus procoracoideus; **stp**, step in sternal margin of extremitas sternalis; **tco**, tuberculum coracoideum; **tla**, trabecula lateralis; **pco**, processus costalis. Same scale bars for **A**–**G** and for **I**–**O**.

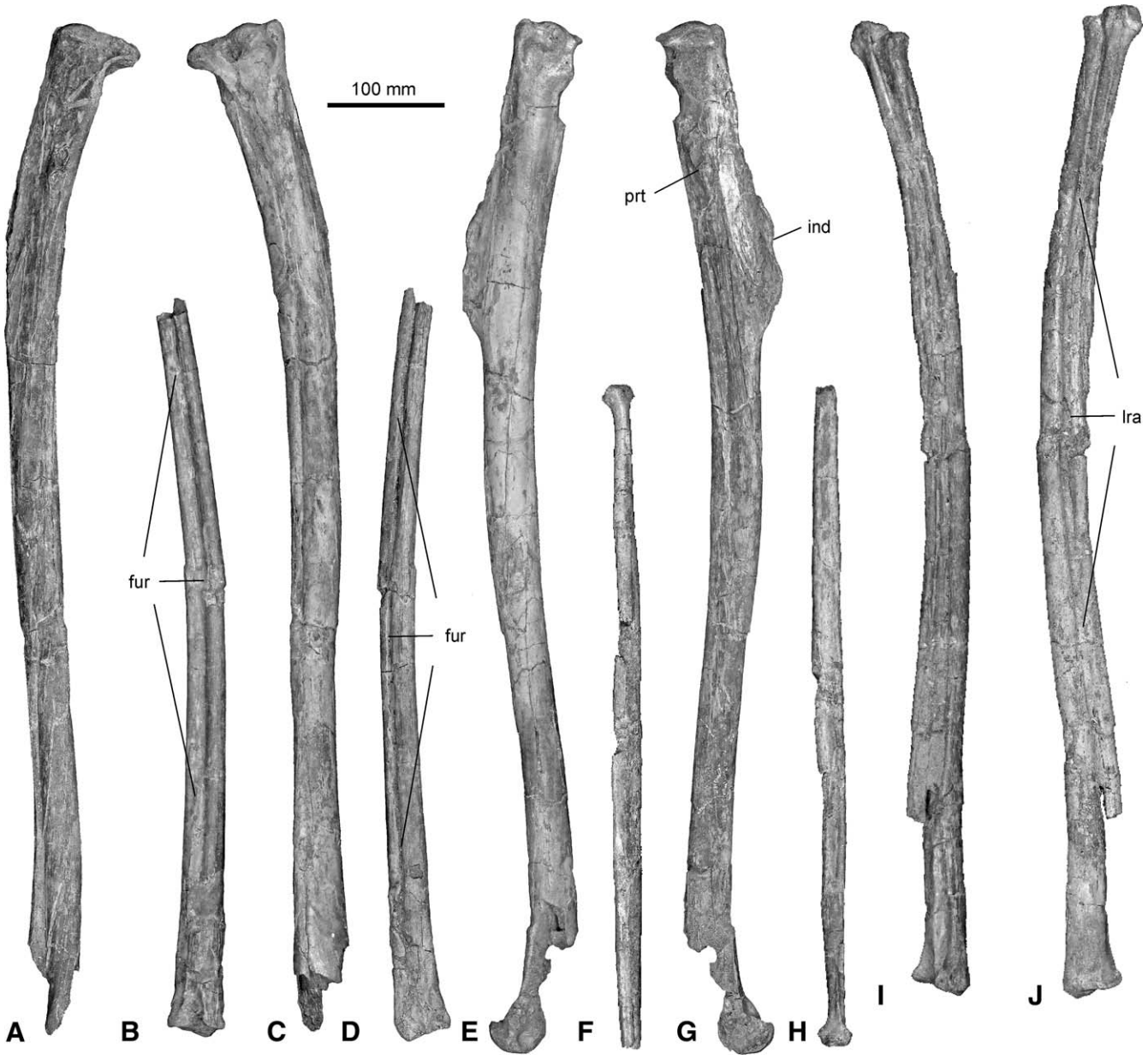

FIGURE 5. Humerus (**A**, **C**, **E**, **G**), ulna (**B**, **D**, **I**, **J**), and radius (**F**, **H**, **I**, **J**) of *Pelagornis chilensis*, n. sp., from the Miocene of the Bahía Inglesa Formation (holotype, MNHN SGO.PV 1061). **A**, **C**, right humerus in cranial (**A**) and caudal (**C**) views. **B**, **D**, right ulna in cranial (**B**) and caudal (**D**) views. **E**, **G**, left humerus in caudal (**E**) and cranial (**G**) views. **F**, **H**, right radius in cranial (**F**) and caudal (**H**) views. **I**, **J**, left ulna and radius in ventral (**I**) and dorsal (**J**) views. **Abbreviations**: **fur**, furrows along ulna and radius; **ind**, indentation in crista deltopectoralis; **lra**, left radius; **prt**, protuberance.

In MNHN SGO.PV 1061, for the first time the caudal end of the mandible of a pelagornithid is well preserved (Fig. 2B). The processus medialis is dorsoventrally deep, with a rounded tip, and bears a small pneumatic foramen on the dorsal surface of its base. In contrast to extant Galloanseres, there is no processus retroarticularis. As in Galloanseres and the Mesozoic non-neornithine taxa *Ichthyornis* and *Hesperornis*, the cotylae lateralis et medialis are very shallow and not separated by a distinct crista intercotylaris (Fig. 2B). Caudal of the cotyla lateralis there is a further small cotyla, which does not articulate with the processus mandibularis of the quadratum (Fig. 2B), and whose functional significance is unknown.

Vertebrae—The morphology of the vertebrae of pelagornithids is poorly known. The atlas was described by Howard and White (1962), Harrison and Walker (1976), and Chávez et al. (2007); the axis by Olson and Rasmussen (2001). Chávez et al. (2007) further reported a cervicothoracic vertebra and another vertebral fragment from the Bahía Inglesa Formation, and four vertebrae are preserved in a recently described pelagornithid from the middle Eocene of Belgium (Mayr and Smith, 2010).

MNHN SGO.PV 1061 includes 11 vertebrae or fragments thereof (Fig. 3), which by comparison with extant birds constitute about half of the total number of the praesacral vertebrae. All vertebrae are heterocoelous, short, and very massive. The

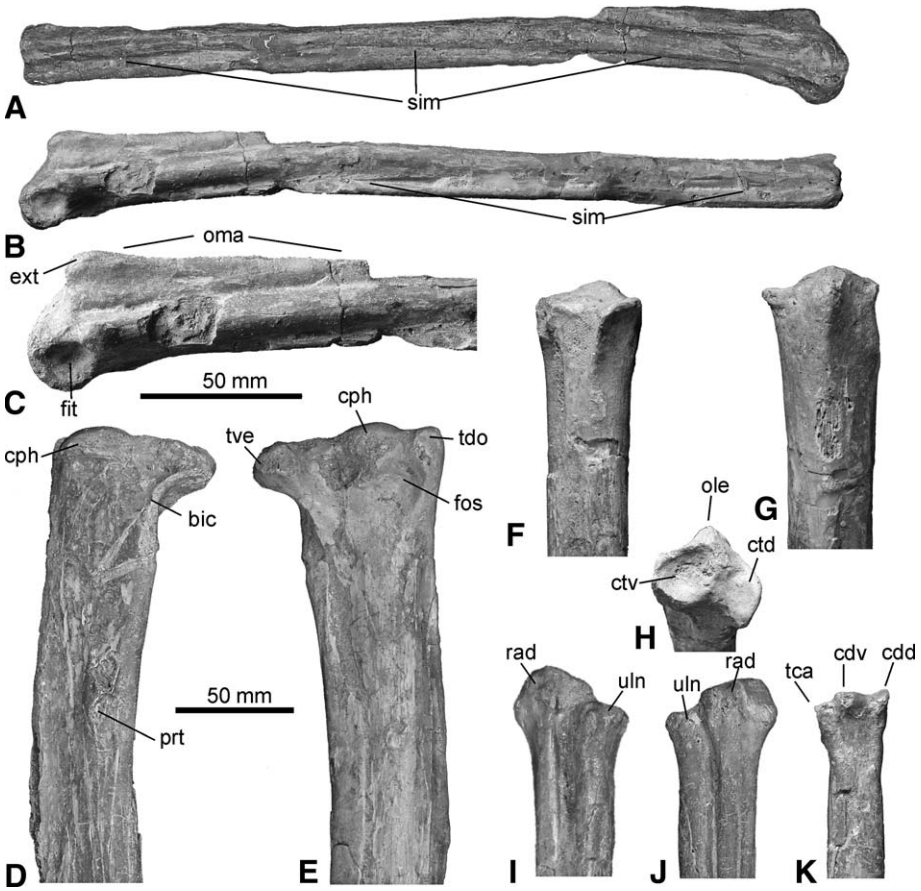

FIGURE 6. Wing elements of *Pelagornis chilensis*, n. sp., from the Miocene of the Bahía Inglesa Formation (holotype, MNHN SGO.PV 1061). **A**, **B**, left carpometacarpus in dorsal (**A**) and ventral (**B**) views. **C**, proximal end of left carpometacarpus in ventral view. **D**, **E** proximal end of right humerus in cranial (**D**) and caudal (**E**) views. **F**–**H**, proximal end of left ulna in cranial (**F**), caudal (**G**), and proximal (**H**) views. **I**, **J**, distal ends of left ulna and radius in cranial (**I**) and caudal (**J**) views. **K**, distal end of left ulna in dorsal view. **Abbreviations**: **bic**, crista bicipitalis; **cdd**, condylus dorsalis; **cdv**, condylus ventralis; **cph**, caput humeri; **ctd**, cotyla dorsalis; **ctv**, cotyla ventralis; **ext**, processus extensorius; **fit**, fossa infratrochlearis; **fos**, fossa between caput humeri and tuberculum dorsale; **ole**, olecranon; **oma**, os metacarpale alulare; **prt**, protuberance; **rad**, radius; **sim**, spatium intermetacarpale; **tca**, tuberculum carpale (broken); **tdo**, tuberculum dorsale; **tve**, tuberculum ventrale; **uln**, ulna. Same scale bars for **A** and **B** and for **D**–**K**.

series comprises two cervical vertebrae, which are identified as the third and fourth. The zygapophyses craniales of these two vertebrae are almost vertically oriented, which indicates that the skull was ventrally inclined rather than carried horizontally, possibly to aid skimming prey from the sea surface. This hypothesis is in concordance with data obtained from labyrinth morphology of pelagornithids (Milner and Walsh, 2009). The very thick cranial margin of the lamina dorsalis arcus of these two vertebrae (Fig. 3B) shows that the interlaminar ligaments were strongly developed. The arcus interzygapophysialis (terminology after Livezey and Zusi, 2006) of the third cervical vertebra encloses a small foramen. The third cervical vertebra further bears a processus ventralis, which is absent on the fourth cervical vertebra.

The six preserved cervicothoracic vertebrae have a very high arcus vertebrae, a corpus with a subrectangular cross-section, and small zygapophyses (Fig. 3). The long and narrow sulcus caroticus extends over the entire ventral surface of the corpus and is bordered by broad bony shelves (Fig. 3H); processus carotici are absent. The ansae costotransversariae are craniocaudally narrow. A very short processus costalis is preserved only on one of the cervicothoracic vertebrae; these processes are broken on the other vertebrae. The ventral surface of the caudal-most cervicothoracic and cranial-most thoracic vertebrae forms a marked step, just caudal of the facies articularis cranialis.

The three thoracic vertebrae are identified as the caudal-most and two cranial ones; the latter articulate with each other. Their corpi are dorsoventrally compressed and lack pleurocoels. In contrast to the pelagornithid from the middle Eocene of Belgium (Mayr and Smith, 2010), the corpus of the caudal-most thoracic vertebrae is not mediolaterally narrow but has a subrectangular cross-section, with a flat ventral surface and concave lateral surfaces. Also contrary to the Belgian pelagornithid, the corpi of the thoracic vertebrae of MNHN SGO.PV 1061 do not bear pneumatic openings on their lateral surfaces. The only thoracic vertebrae in which the processus transversi are preserved exhibits a large pneumatic opening on the cranioventral surface of the base of the latter. The processus spinosi of all thoracic vertebrae are broken. A processus ventralis is absent on the caudal-most thoracic vertebra, and the processus ventrales of the other thoracic vertebrae are very short, forming only a low ridge.

Ribs—MNHN SGO.PV 1061 includes three incomplete vertebral ribs from the right side of the body (Fig. 4M). One of these preserves the attachment site of a broken processus uncinatus at the beginning of its caudal third. The caudal surface of the extremitas dorsalis of the other two ribs exhibits a pneumatic opening between the capitulum and the tuberculum costae.

Furcula—The only previously described pelagornithid furcula belongs to a species from the middle Eocene Belgium (cf. *Macrodontopteryx*; Mayr and Smith, 2010). This specimen is fragmentary and in MNHN SGO.PV 1061 the pelagornithid furcula is for the first time nearly completely preserved (Fig. 4F–H). The bone is widely U-shaped and resembles that of the Diomedeidae (albatrosses) in its proportion. Contrary to the furcula of the latter and most extant birds, however, it lacks a craniocaudal curvature, which indicates a weakly developed cranial portion of the musculus deltopectoralis that supports humerus protraction (Stegmann, 1964). The extremitas omalis is simple and lacks a processus acromialis and a facies articularis acrocoracoidea; presence of the latter is a derived characteristic of most

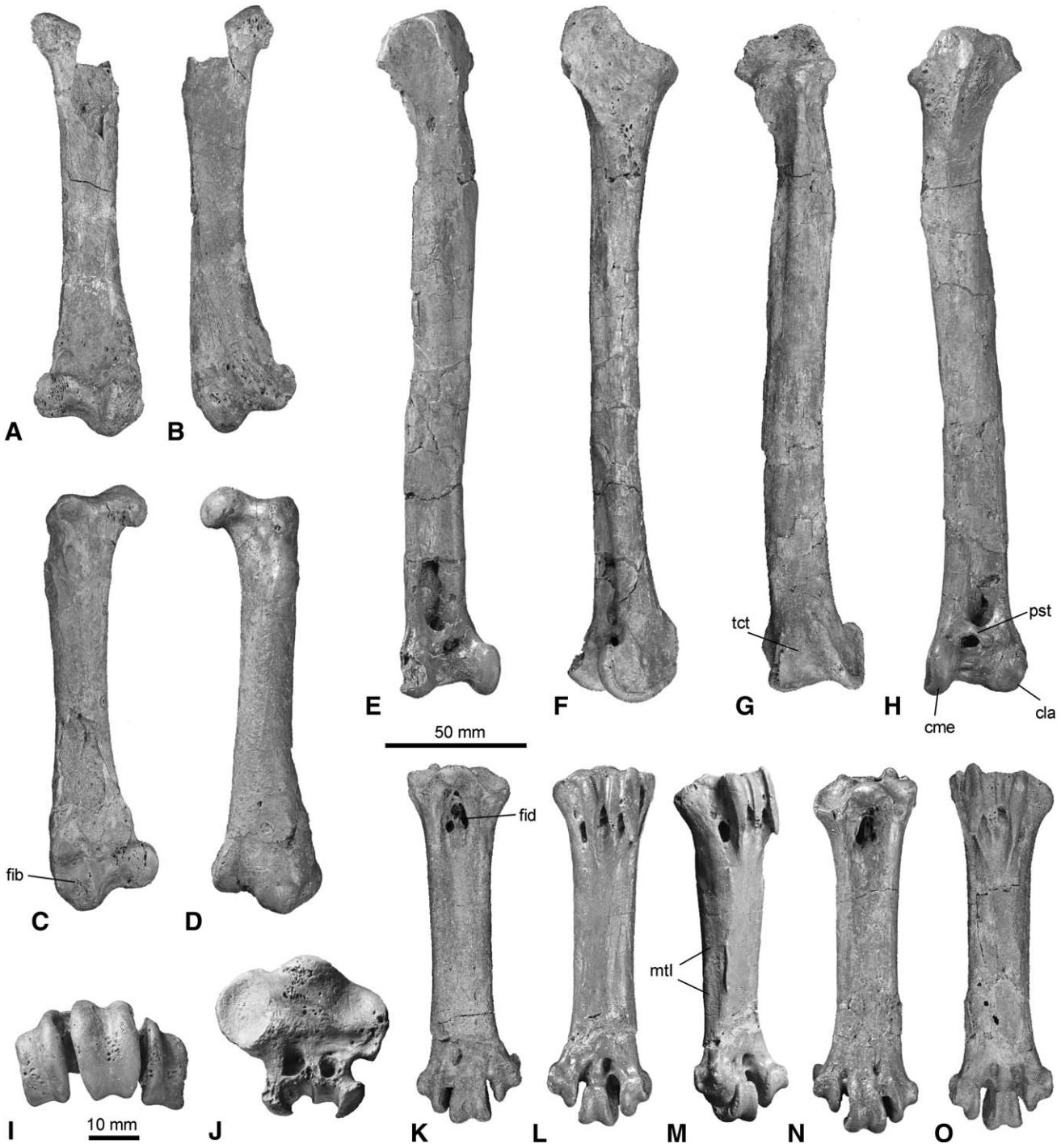

FIGURE 7. Hind limb elements of *Pelagornis chilensis*, n. sp., from the Miocene of the Bahía Inglesa Formation (holotype, MNHN SGO.PV 1061). **A**–**D**, right (**A**, **B**) and left (**C**, **D**) femurs in caudal (**A**, **C**) and cranial (**B**, **D**) views; **E**–**H**, right (**E**, **F**) and left (**G**, **H**) tibiotarsi in cranial (**E**, **H**), craniomedial (**F**), and caudal (**G**) views; **I**–**O**, right (**I**–**M**) and left (**N**, **O**) tarsometatarsi in distal (**I**), proximal (**J**), dorsal (**K**, **N**), plantar (**L**, **O**), and medioplantar (**M**) views. **Abbreviations**: **cla**, condylus lateralis; **cme**, condylus medialis; **fib**, trochlea fibularis; **fid**, fossa infracotylaris dorsalis; **fvd**, foramen vasculare distale; **mtI**, fossa metatarsi I; **pst**, pons supratendineus; **tct**, trochlea cartilaginis tibialis. Same scale bars for **A**–**H** and **K**–**O**, and for **I** and **J**.

'pelecaniform' birds (except Phaethontidae and, possibly, Fregatidae; see Mayr, 2003). The scapus claviculae is twisted, being a craniocaudally narrow blade in its midsection, but more mediolaterally compressed in the dorsal part. Whereas its lateral margin is rounded, the medial one forms a sharp edge except for an area in about the dorsal fourth of the scapus claviculae, where it exhibits a notch and has a rounded medial surface (Fig. 4F).

The massive extremitas sternalis is very deep and craniocaudally wide, with a smoothly rounded cranial surface and a flat,

rugose caudal surface; close to the dorsal margin of the latter there is a concave, elongate articulation facet, which possibly contacted the cranial projection of the carina sterni characteristic for the sternum of *Pelagornis* (Fig. 4H; Mayr et al., 2008). The dorsal surface of the extremitas sternalis is damaged, and it cannot be said whether a large opening that is now exposed originally opened on the bone surface. The parts of the scapi clavicularum that attach to the extremitas sternalis bear a distinct fossa along their dorsal surface, which is cranially bordered by a ridge. The apophysis furculae forms two projections, which are separated by a concavity, whose surface does not indicate a direct articulation with the carina sterni.

The furcula of *Manu antiquus* Marples, 1946, from the Oligocene of New Zealand, which was considered to possibly stem from a pelagornithid (Mayr, 2009a), differs from MNHN SGO.PV 1061 in that the extremitas sternalis is less deep, the apophysis furculae more pointed, and the scapus claviculae mediolaterally compressed (Marples, 1946).

Coracoid—Only few coracoids of bony-toothed birds were previously described. Bourdon (2005, 2006) reported a fragmentary coracoid of *Odontopteryx toliapica* from the early Palaeogene of Morocco. Olson (1984) figured an incomplete coracoid from the Miocene of Maryland, and Olson and Rasmussen (2001) mentioned coracoid fragments from the Miocene or Pliocene of the Lee Creek Mine in North Carolina. The only nearly complete pelagornithid coracoid is from the middle Eocene of Belgium, and was described by Mayr and Smith (2010).

In MNHN SGO.PV 1061 both coracoids are preserved, and the right one is virtually complete (Fig. 4A–E). The massive processus acrocoracoideus is ventrally inflected. The facies articularis clavicularis does not overhang the sulcus supracoracoideus. In medial view, the boundary between the facies articularis clavicularis and the sulcus supracoracoideus forms a curved ridge; the adjacent surface of the sulcus supracoracoideus is irregularly textured. The facies articularis clavicularis passes into a marked protrusion on the ventral surface of the processus acrocoracoideus, and its dorsal edge forms a distinct, dorsally directed projection (Fig. 4E). The impressio ligamenti acrocoracohumeralis is narrow and shallow. The facies articularis humeralis has an ovate outline and a slightly concave, laterally facing surface. The sulcus supracoracoideus bears small pneumatic foramina in its dorsal section. The cotyla scapularis is small and positioned on an elevated socket; although it is still filled with matrix in both coracoids of MNHN SGO.PV 1061, it can be discerned that it was cup-like. The processus procoracoideus is short and pointed. The foramen nervi supracoracoidei is situated next to the base of the processus procoracoideus, close to the cotyla scapularis.

The very wide extremitas sternalis is completely preserved in the right coracoid of MNHN SGO.PV 1061 (Fig. 4C). Its dorsal surface bears many small foramina and a small but distinct impressio musculi sternocoracoidei. The crista articularis sternalis is short and very massive, with both the facies interna and the facies externa being very wide. The facies interna is not situated on the same level as the facies externa, but is more elevated. The sternal margin of the extremitas sternalis forms a marked step lateral of the facies externa, and the tip of the processus lateralis is pointed.

The coracoid of MNHN SGO.PV 1061 differs from the fragmentary coracoid figured by Olson (1984) in that the extremitas omalis is straighter and less medially angled. It is distinguished from the middle Eocene Belgian pelagornithid (Mayr and Smith, 2010) in the proportionally longer and narrower extremitas omalis and the smaller processus procoracoideus.

Scapula—Mayr and Smith (2010) described a largely complete scapula of a pelagornithid from the Middle Eocene of Belgium, and Olson and Rasmussen (2001) reported incomplete extremitates craniales of pelagornithid scapulae from the Miocene or early Pliocene of North Carolina.

Except for the caudal tip, the right scapula of MNHN SGO.PV 1061 is nearly complete, whereas the left one lacks the caudal third (Fig. 4I–L). Compared to the size of the bird, the bone is fairly small. The extremitas cranialis appears to be identical to that figured by Olson and Rasmussen (2001), in which the acromion is, however, broken. The mediolaterally wide and laterally upturned acromion of the Chilean pelagornithid is larger than that of the middle Eocene species described by Mayr and Smith (2010), whereas the facies articularis humeralis is smaller. The latter is separated from the acromion by a fossa on the lateral surface of the bone (Fig. 4K). The tuberculum coracoideum is marked. Caudal of the facies articularis humeralis, on the lateral surface of the bone, there is an elongated protrusion; a fossa is situated between this protrusion and the facies articularis humeralis, on the ventral surface of the bone. The corpus of the scapula is slightly curved and becomes very wide towards its caudal end; its cross-section is ovate in the cranial two thirds of the bone, whereas the caudal third is flattened and blade-like.

Sternum—The single previously described sternum of a Neogene pelagornithid is a specimen from the Miocene of Portugal, which was assigned to *Pelagornis miocaenus* by Mayr et al. (2008). MNHN SGO.PV 1061 includes only the caudolateral parts of the bone (Fig. 4N, O). On each of the two fragments three processus costales and a long rod-like trabecula lateralis are preserved. The latter has a subtriangular cross-section, with a sharp medial edge. The preserved parts of the corpus sterni form a flat and very thin sheet and do not exhibit any noteworthy curvature.

Humerus—Humerus morphology of Neogene pelagornithids is comparatively well known, and apart from its larger size (Table 2), the humerus of MNHN SGO.PV 1061 (Fig. 5) resembles that of *Pelagornis miocaenus* and other Neogene Pelagornithidae (note that the cranial and caudal surfaces of the fragmentary proximal humerus were mistaken by Olson and Rasmussen, 2001:pl. 11, and the specimen is actually from the left side). The ventral portion of the proximal end of the bone is very small and narrow. The fossa pneumotricipitalis is also very small and situated on the ventral, rather than caudal, surface of the bone; whether there are pneumatic openings on the base of this fossa cannot be discerned as the area is still filled with matrix. The sulcus transversus is short and shallow. As in other pelagornithids, the caput humeri forms a overhang on the cranial surface of the bone (Fig. 6D); on the caudal surface, it is bordered dorsally by a marked fossa (Fig. 6E). The tuberculum dorsale is caudally prominent and has a convex surface. The well-developed tuberculum ventrale bears a pit on its tip. The crista bicipitalis is markedly concave, with a cranially raised proximal section. As noted by Olson (1985), the crista deltopectoralis is situated far distally, and in contrast to virtually all extant birds it has very little cranial deflection. The crista deltopectoralis further has an unusual shape in that its bears a concave indentation, so that its outline is bilobed, with a more prominent distal lobe; such an indentation is absent in an early Eocene pelagornithid described by Mayr and Smith (2010). On the cranial surface of bone, there is an elongate fossa at the base of the crista deltopectoralis.

There is a prominent protuberance on the cranial surface of the shaft, on the level of the proximal end of the crista deltopectoralis, which Olson (1985:200) identified as the attachment site of either the musculus coracobrachialis cranialis or the caput humerale of musculus biceps brachii. Such a protuberance is also present in a large pelagornithid from the middle Eocene of Belgium, which was referred to *Dasornis emuinus* by Mayr and Smith (2010).

The humerus shaft is sigmoidally curved and craniocaudally flattened. The distal end of the right humerus is broken, and of the left humerus only the dorsal portion with the condylus dorsalis is preserved.

Ulna—The left ulna of MNHN SGO.PV 1061 is complete and preserved in association with the radius; the isolated right one

lacks the distal fourth of the bone (Fig. 5). Proximal ulnae of large pelagornithids from the Miocene of Peru and Chile were described by Chávez et al. (2007), and the proximal ulna of MNHN SGO.PV 1061 closely corresponds to these specimens. Apart from being larger, the proximal ulna of MNHN SGO.PV 1061 also resembles that of a large pelagornithid from the late Eocene of Oregon (Goedert, 1989). The bone is shorter than the humerus and becomes very narrow towards its distal end. The olecranon is very short and proximally hardly protrudes beyond the plane of the cotylae (Fig. 6F, G). The shallow cotylae themselves are positioned on the proximal surface of the bone, with their surfaces being oriented perpendicular to the long axis of the ulna. Between the tuberculum ligamenti collateralis ventralis and the rim of the cotyla ventralis there is a marked depression on the ventral side of the proximal end; the tuberculum ligamenti collateralis ventralis itself is not as prominent and elongated as in *Odontopteryx* (see Bourdon 2005:character 65). The processus cotylaris dorsalis is small. The incisura radialis and the impressio brachialis are marked. The shaft is craniocaudally compressed and exhibits a unique morphology in that there are two marked furrows, on its cranial and caudal surfaces, respectively, which begin about 100 mm distal of the proximal end and extend over at least 500 mm (because the distal portion of the shaft of the left ulna is crushed, the distal end of the furrow is not clearly discernible). Papillae remigales for the attachment of the secondaries are not visible. The distal end of the bone corresponds with the distal ulna of *Pelagornis mauretanicus* (Mourer-Chauviré and Geraads, 2008). As in the latter, the condylus dorsalis is very small and seems to have been exceeded by the tuberculum carpale in size (Fig. 6K).

Radius—Both radii of MNHN SGO.PV 1061 are incomplete, and whereas the left one lacks the proximal portion, the distal part is absent on the right radius. As in *Pelagornis mauretanicus* (Mourer-Chauviré and Geraads, 2008), the cotyla humeralis on the proximal end of the bone is ovate, proximodorsally elongated, and bordered dorsally and ventrally by a well-developed tuberculum bicipitale radii. The ventral tuberculum bicipitale radii proceeds into a marked ridge on the caudal surface of the proximal radius. The proximal part of the shaft has a circular cross-section, but its midsection is craniocaudally flattened and exhibits a marked sulcus along its caudal surface. The distal end of the bone is wider than the distal ulna, and as in *P. mauretanicus* it bears a marked excavation that encompasses the distal end of the ulna.

Carpometacarpus—Bourdon (2006) described pelagornithid carpometacarpi from the early Palaeogene of Morocco, but carpometacarpus morphology of Neogene Pelagornithidae is poorly known. The bone is crushed in the holotype of *Osteodontornis orri*, and the only other specimens are incomplete proximal carpometacarpi of *O. orri* and *Pelagornis mauretanicus* (Howard, 1978; Mourer-Chauviré and Geraads, 2008).

The left carpometacarpus of MNHN SGO.PV 1061 is nearly complete and three-dimensionally preserved, but a small portion in its distal third has been restored and the distal part of the bone shows some displacement relative to the proximal part. The bone is very long and slender, and its morphology is not matched by any extant bird. The bone offered little support for attachment of the primaries, which must have been either very short or strongly inclined towards the axis of the bone, so that the hand-wing of *Pelagornis* was exceptionally narrow. The proximal end is curved caudally and closely resembles the specimen of *O. orri* described by Howard (1978). The cranial portion of the trochlea carpalis is unusually steep, so that the caudal end of the carpometacarpus is beveled. The ventral rim of the trochlea carpalis bears a notch in its caudal portion and thus appears bipartite, with the small distal part of this trochlea forming an elongate protrusion caudal of the processus pisiformis. There is a marked fossa infratrochlearis proximocaudal of the processus pisiformis. The latter is very bulky, with a particularly massive caudal portion; distally it gradually merges into the os metacarpale majus. A fovea carpalis cranialis is absent, but as in *O. orri* (see Howard, 1978) there are two pneumatic openings craniodistally of the processus pisiformis. The larger distal one of these has an elongate ovate shape. The dorsal and ventral rims of the trochlea carpalis have about equal caudal extent. The os metacarpale alulare is greatly elongated and measures about one fourth of the entire length of the carpometacarpus. The processus extensorius is very low, so that the cranial margin of the os metacarpale alulare is straight and distally declining; in extant birds, an equally low and elongated os metacarpale alulare only occurs in Gaviiformes (loons) and Sphenisciformes (penguins). The dorsal and ventral surfaces of the os metacarpale alulare are essentially flat; most of the dorsal surface of the bone and the distal half of its ventral surface are separated from the os metacarpale majus by a sulcus. The distal articulation facet for the phalanx digiti alulae is craniocaudally narrow and has only a slightly convex surface.

Rather than being flattened, the os metacarpale minus has a subovate cross-section and a convex caudal surface; it becomes dorsoventrally and craniocaudally wider towards the distal end of the bone. It is separated by a furrow from the os metacarpale majus, but the two bones are fused over most of the length of the carpometacarpus and the symphyses metacarpalis proximalis et distalis are very long. In fact, ossa metacarpalia minus et majus are separated by a very narrow spatium intermetacarpale only in the middle third of the carpometacarpus, over a length of about 80 mm. Parts of the spatium intermetacarpale are still filled with matrix and obscured by artificial resin that was used to stabilize the bone; the sulcus between the ossa metacarpalia minus et majus in the distal third of the carpometacarpus exhibits many small pits. The facies articularis digitalis major on the distal end of the carpometacarpus has a flat surface; distally, the facies articularis digitalis minor is on level with the facies articularis digitalis major. A sulcus tendinosus is only visible in the distal sixth of the dorsal surface of the distal end.

Pelvis—The morphology of the pelvis of pelagornithid birds is unknown, and in MNHN SGO.PV 1061 only the cranioventral portion of the synsacrum and a small fragment of the crista spinosa synsacri are preserved. The cranial-most synsacral vertebra bears articulation facets for ribs, and its facies articularis cranialis is dorsoventrally narrow.

Femur—Femora are known from *Palaeochenoides mioceanus*, *Pseudodontornis stirtoni*, an undescribed species of *Pelagornis* from North Carolina, an unnamed pelagornithid from Japan that was originally assigned to the Procellariiformes, and *Pelagornis mauretanicus* (Hopson, 1964; Howard and Warter, 1969; Ono, 1980; Olson, 1984; Olson and Rasmussen, 2001; Mourer-Chauviré and Geraads, 2008). In MNHN SGO.PV 1061 both femora are preserved, the left one is nearly complete, whereas the right lacks the lateroproximal portion (Fig. 7A–D). The bone closely corresponds with other femora assigned to *Pelagornis*, and has similar overall proportions to the femur of Pelecanidae (pelicans). The caput femoris is slightly proximally directed and the laterodistal portion of the facies articularis acetabularis is well delimited from the femur shaft. The crista trochanteris is short and low. The area of the impressiones musculares trochanteris on the craniolateral surface of the proximal end and that of the impressiones obturatoriae on its caudal surface form marked embossments. The shaft gradually widens distally and the cranial surface of the condylus lateralis slants laterally. On the distal end of the bone, the fossa poplitea is shallow, as is the sulcus patellaris. In contrast to the femur of *Palaeochenoides mioceanus* the trochlea fibularis does not bear a sulcus. In both femora of MNHN SGO.PV 1061, the shaft is damaged, and medullary bone, indicative of breeding females, cannot be discerned.

Tibiotarsus—The tibiotarsus of Neogene bony-toothed birds has not been described so far, but Olson (1984) figured an incomplete specimen from the middle Miocene of Virginia. Bourdon (2005, 2006) reported pelagornithid tibiotarsi from the early Palaeogene of Morocco.

In MNHN SGO.PV 1061 both tibiotarsi are nearly complete (Fig. 7E–H). In craniocaudal view, the shaft of the bone is sigmoidally curved, with the proximal end being laterally inflected and the distal end medially bent. The cristae cnemiales are proximally protruding beyond the facies articulares. The crista cnemialis cranialis is not completely preserved in both specimens, but is cranially prominent. With regard to the proportions of the cristae cnemiales, the proximal tibiotarsus is more similar to that of the Pelecanidae than to the Diomedeidae, in which they are much better developed. The fossa flexoria on the caudal surface of the proximal end is well developed and marked. The crista fibularis is low and indistinct; opposite of it, on the medial side of the proximal end, the impressio ligamenti collateralis ventralis forms an elongate ridge-like prominence. The narrow pons supratendineus bridges a marked sulcus extensorius; its lateral section bears a low tubercle. The condyli of the distal end are widely spaced and narrow. In contrast to early Palaeogene Pelagornithidae (Bourdon, 2005:Fig. 3u) but as in extant Pelecanidae, the condylus lateralis is smaller than the condylus medialis. Contrary to the Diomedeidae and several other extant taxa, the rim of the condylus medialis does not exhibit a notch in its distal section. The medial surface of the condylus medialis is essentially flat, and condylus medialis and condylus lateralis have about equal distal extent. The trochlea cartilaginis tibialis is proximodistally deep.

Tarsometatarsus—The tarsometatarsus (Fig. 7I–O) is larger than an otherwise similar pelagornithid tarsometatarsus from the Bahía Inglesa Formation, which was described by Walsh and Hume (2001) (length 127 mm versus 105 mm). The hypotarsus includes two bony canals, presumably for the tendons of musculus flexor digitorum longus and m. flexor hallucis longus, whereas it does not enclose bony canals in Eocene pelagornithids (Mayr and Smith, 2010). On the plantar hypotarsal surface there are three sulci, which are bordered by well-developed cristae lateralis et medialis hypotarsi. Two further sulci are situated lateral to the crista lateralis hypotarsi. The fossa infracotylaris dorsalis exhibits a large pneumatic foramen as in *Cyphornis magnus*; the large foramina vascularia proximalia are also situated within this fossa. The shaft of the bone has a subrectangular cross-section. The very shallow fossa metatarsi I is situated far proximally on the medial surface of the bone (Fig. 7M), its plantar margin is bordered by a distinct ridge. This fossa indicates the presence of a hind toe, whose existence in Neogene pelagornithids was contentious (Howard, 1957; Hopson, 1964; see, however, Bourdon, 2005:character 23, concerning the possible absence of a hallux in the early Eocene *Odontopteryx*).

In size and morphology, the distal end closely matches the distal tarsometatarsus from the late Oligocene of South Carolina that was assigned to *Palaeochenoides mioceanus* by Hopson (1964). The foramen vasculare distale is large and on the plantar side of the bone opens close to the canalis interosseus distalis. The trochlea metatarsi II is shorter than the trochlea metatarsi IV; the proximomedial edge of its plantar surface forms a plantar projection. In its shape and orientation this trochlea differs from that of early Eocene Pelagornithidae, in which the trochlea metatarsi II is much shorter and more plantarly deflected (Fig. 8I). The trochlea metatarsi III is slightly laterally directed.

Compared to extant birds, the bone resembles the tarsometatarsus of the Pelecanidae in its proportions and in the presence of a large pneumatic opening in the fossa infracotylaris dorsalis, but differs in, e.g., the less prominent medial hypotarsal crest and the shorter trochlea metatarsi II.

DISCUSSION

Taxonomy of Neogene Pelagornithidae

Olson (1985) classified Miocene and Pliocene Pelagornithidae in three genera, *Pelagornis*, *Osteodontornis*, and *Pseudodontornis*, and some authors also accepted validity of the taxon *Neodontornis* (e.g., Matsuoka et al., 2003); depending on the age of the holotype, *Cyphornis* may be another Neogene bony-toothed bird.

Of the type species of these taxa, only *Osteodontornis orri* is represented by a partial skeleton, whose bones are, however, badly crushed. *Pelagornis miocaenus* is known from humeri and a tentatively referred sternum, the holotype of *Pseudodontornis longirostris* is a skull, and of *Neodontornis* (*Pseudodontornis*) *stirtoni* only a partial skull and a tentatively referred femur were described. The holotype and only known specimen of *Cyphornis magnus* is a proximal tarsometatarsus. Direct comparisons are thus only possible between the type species of *Pseudodontornis*, *Neodontornis*, and *Osteodontornis*.

The characters listed by Harrison and Walker (1976:22) to diagnose *Neodontornis* are either also present in *Pseudodontornis* ("zygoma deep and stout," "rounded, posterior portion of palatine large," "lateral longitudinal sulcus of lower mandible not continued posteriorly as far as mandibular suture"), or cannot be assessed in either *Pseudodontornis* and *Osteodontornis* owing to the quality of the known fossil material ("ventral portion of prefrontals broad," "small ovate foramen on internal side of lower mandible"). In all of these features, *Neodontornis stirtoni* agrees with the Chilean pelagornithid.

Olson (1985) already has considered it possible that *Pelagornis* and *Pseudodontornis* are synonymous. Howard (1957) listed seven features in order to distinguish *Osteodontornis* from *Pseudodontornis*: (1) the proportions of the cranium (longer in *Pseudodontornis*), (2) the proportions of the rostrum relative to the cranium (lower in *Pseudodontornis*), (3) the proportions of the os quadratojugale (higher in *Pseudodontornis*), (4) the rostral extent of the ossa palatina (greater in *Pseudodontornis*), (5) the shape of external narial openings (rounder in *Osteodontornis*), (6) the caudal extent of the mandible (greater in *Osteodontornis*), and (7) the number of pseudo-teeth between the largest projections (lower in *Pseudodontornis*). Some of these differences may well be artifacts of the poor preservation of the *O. orri* holotype, whose skull is flattened and crushed. Because the cranium is incomplete and the morphologies of the os quadratojugale and os palatinum are unknown, the condition of characters 1, 3, and 4 cannot be assessed in MNHN SGO.PV 1061. We also found it difficult to discern the exact shape of the narial openings in the published photographs of the lost holotype of *P. longirostris*. In the caudal extent of the mandible, MNHN SGO.PV 1061 agrees with *Pseudodontornis*, whereas it corresponds with *Osteodontornis* in the presence of more than one small pseudo-tooth between the largest ones. Intraspecific variability of the pseudo-teeth of pelagornithids is, however, poorly known, and the low number of small pseudo-teeth in the holotype of *P. longirostris* and other specimens assigned to *Pseudodontornis* (Hopson, 1964; Chávez et al., 2007) may also be due to different ages of the individuals.

Howard (1957) did not compare *Osteodontornis orri* with *Pelagornis miocaenus*, whose pelagornithid affinities were first recognized by Brodkorb (1963). The sternum of *O. orri* is unknown and no well-preserved humeri were described, so that the taxon *Osteodontornis* currently cannot be differentiated from *Pelagornis*. The length of the humerus of *O. orri* was estimated at about 600 mm by Howard (1957), whereas that of *P. miocaenus* has a length of 591—ca. 710 mm (Mourer-Chauviré and Geraads, 2008:Table 3). Because of this overlap in size, it is not even possible to conclusively show distinctness of *O. orri* and *P. miocaenus* on the species level with the material at hand. Harrison and Walker's (1976) non-comparative diagnoses of Neogene

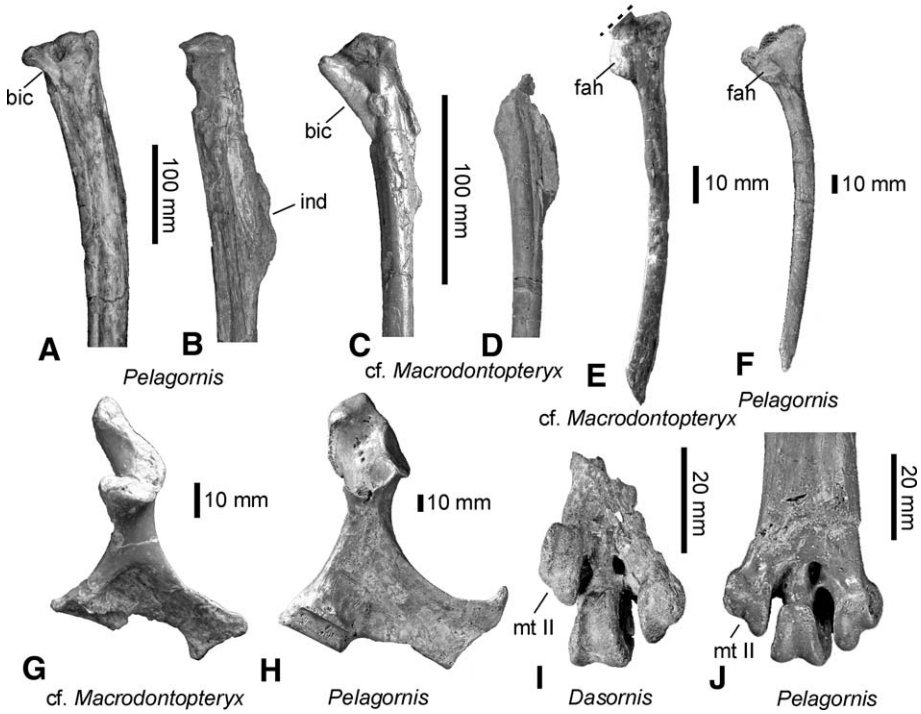

FIGURE 8. Selected postcranial bones of *Pelagornis chilensis*, n. sp., in comparison to Eocene Pelagornithidae. **A**–**D**, proximal ends of the right (**A**, caudal view) and left (**B**, cranial view) humerus of *P. chilensis* (holotype, MNHN SGO.PV 1061) and proximal humeri of cf. *Macrodontopteryx oweni* from the middle Eocene of Belgium (**C**, left humerus of IRSNB Av 86 in caudal view, reversed to facilitate comparisons; **D**, right humerus of IRSNB Av 87 in caudal view). **E**, **F**, left scapulae of **E**, cf. *M. oweni* from the middle Eocene of Belgium (IRSNB Av 86; attached portion of acromion of coracoid digitally removed at dashed line) and **F**, *P. chilensis* (holotype, MNHN SGO.PV 1061). **G**, **H**, coracoids of **G**, cf. *M. oweni* from the middle Eocene of Belgium (IRSNB Av 86; left coracoid, reversed to facilitate comparisons) and **H**, *P. chilensis* (right coracoid of holotype, MNHN SGO.PV 1061). **I**, **J**, distal ends of right tarsometatarsi of **I**, *Dasornis emuinus* from the early Eocene London Clay in England (BMNH A 894) and **J**, *P. chilensis* (holotype, MNHN SGO.PV 1061). **Abbreviations**: **bic**, crista bicipitalis; **fah**, facies articularis humeralis; **ind**, indentation in crista deltopectoralis; **mt II**, trochlea metatarsi II.

pelagornithid genera are likewise insufficient to justify distinctness of the latter.

Future studies may support classification of Neogene Pelagornithidae into different genera, but current evidence does not. Separation of poorly known Neogene pelagornithids into different genera contributes to taxonomic confusion rather than clarity and aggravates any studies of new material. We thus propose to classify all Neogene Pelagornithidae into a single genus, *Pelagornis*, with the currently recognized species within this taxon being *Pelagornis miocaenus* Lartet, 1857, from the Miocene of Europe, *P. mauretanicus* Mourer-Chauviré and Geraads, 2008, from the Pliocene of North Africa, *P. stirtoni* (Howard and Warter, 1969) from the Miocene or Pliocene of New Zealand, *P. orri* (Howard, 1957) from the Miocene of California, *P. longirostris* (Spulski, 1910) whose age and occurrence are unknown, and *P. chilensis*, n. sp., from the Miocene of Chile.

Wingspan and Weight

The new fossil for the first time allows a reliable assessment of the wingspan of one of the largest pelagornithids. Because the carpometacarpus is 1.4 times longer than that of *Osteodontornis orri* (Table 2), we assume a length of 20 cm for the two missing distal wing phalanges, which measure 15 cm in *O. orri* (see Howard, 1957). The length of one wing skeleton was thus ~210 cm, i.e., twice that of the Wandering Albatross, *Diomedea exulans*, which has the largest wingspan of extant birds. With a body width of 25 cm, inferred from the dimensions of the furcula, the skeleton alone spanned 445 cm (Fig. 9).

Isolated primaries of the holotype of *O. orri* measure 30 and 40 cm, but it is unknown whether these quite short feathers are indeed the longest primaries (Howard, 1957). A primary length of 40 cm leads to a conservative wingspan estimate of 525 cm for the Chilean pelagornithid. However, if the hand-wing had a similar length to that of albatrosses, reaching 1.7 times the ulna length (Howard, 1957), a wingspan up to 610 cm would have been possible. Because the new fossil is distinctly larger than *O. orri* (Tables 1–3), previous wingspan estimates of 6 m for this latter species (Olson, 1985) are exaggerated, and the Chilean pelagornithid provides the first uncontroversial evidence for a wingspan above 5 m in a bony-toothed bird.

Among volant birds, only the Miocene teratorn *Argentavis magnificens* (Teratornithidae) may have rivaled the size of giant pelagornithids (Campbell and Tonni, 1980; Chatterjee et al., 2007). Wingspan estimates for this vulture-like bird, which is represented by few incomplete bones, range from 570 to 830 cm, but were only indirectly derived from its hypothetical mass and wing area, and extrapolations of bone dimensions of related species (Campbell and Tonni, 1983). With a length of ~57 cm (Campbell and Tonni, 1980), the humerus of *A. magnificens* is, however, significantly shorter than that of the Chilean pelagornithid (Table 2). Isometric scaling with the mean humerus and wing-skeleton lengths of the well-known smaller teratorn *Teratornis merriami*, which are 31.7 and 102 cm, respectively (Campbell and Tonni, 1983), yields a wing skeleton length of 183 cm for *Argentavis*, which is also less than in the Chilean fossil. Hence, if *Argentavis* had a larger wingspan, this must have been due to much longer primaries, whose size is unknown for either of the fossil species. We thus conclude that *P. chilensis* exhibits the largest well-established avian wingspan.

There exists a correlation between the mass of a bird and the least circumferences of the femur and tibiotarsus, with $\log M = 2.411 \cdot \log C_F - 0.065$ and $\log M = 2.424 \cdot \log C_T + 0.076$, where M is the body mass in gram, C_F the least femur circumference, and C_T the least tibiotarsus circumference (Campbell and Marcus, 1992). With least shaft circumferences of 58.4 and 64.1 mm for the femur and tibiotarsus of the Chilean pelagornithid, this results in mass estimates of 15.6 and 28.6 kg, respectively. Even the larger of these values is much less than the estimated mass of 71.9 kg for *A. magnificens* (Campbell and Marcus, 1992), and not significantly above the mass of the heaviest extant volant bird, the Mute Swan, *Cygnus olor*, whose males can reach ~20 kg. These low values are nevertheless plausible, because the bones of pelagornithids were exceedingly thin-walled, and the hind limbs, which

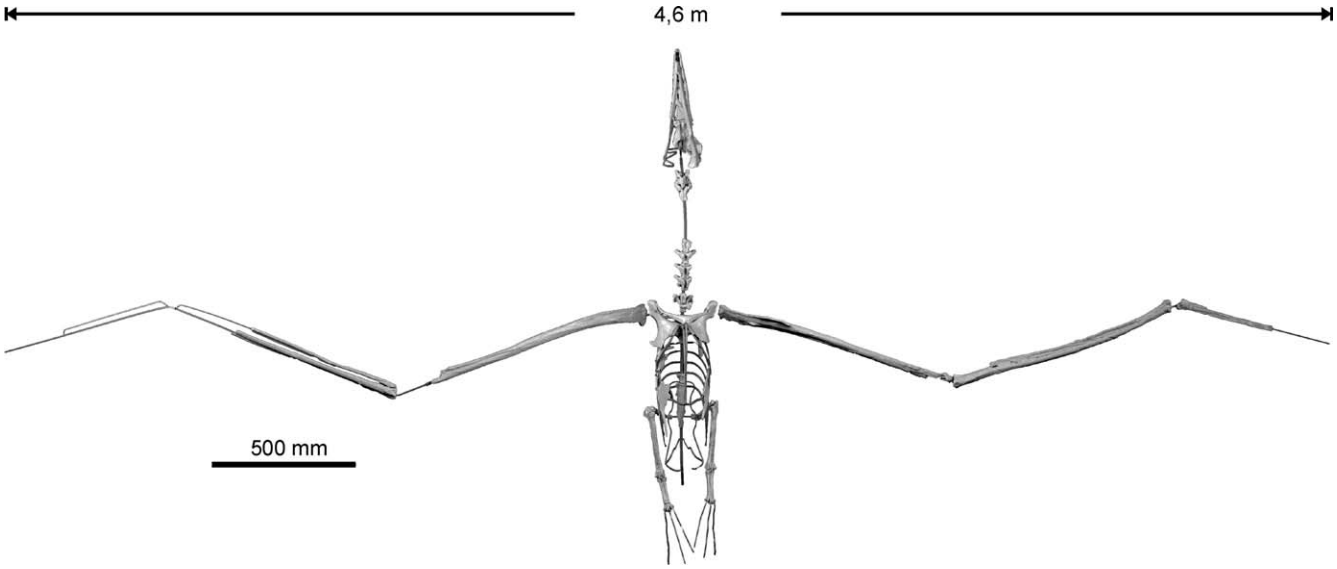

FIGURE 9. Life-size reconstruction of the holotype skeleton of *Pelagornis chilensis*, n. sp., in ventral view, based on casts of the bones. Missing skeletal elements (vertebral column, ribs, some wing bones, pelvis, and pedal phalanges) are indicated by metal bars. Reconstruction by Regina Ellenbracht.

had to bear the weight of the bird, are very small. In combination with the very narrow wings, these low weight estimates testify highly efficient soaring abilities of pelagornithids, which appear to have been among the most proficient avian long-distance soarers.

Evolution

Bourdon (2006) already listed some of the profound osteological differences between the giant Neogene Pelagornithidae and their early Palaeogene relatives such as *Odontopteryx*, and the well-preserved holotype of *P. chilensis* allows recognition of additional features (Fig. 8). Some of the most distinct differences are found in the morphology of the proximal humerus, which in Neogene pelagornithids has a much smaller and narrower ventral portion, a concave rather than convex crista bicipitalis, and a concave indentation in the crista deltopectoralis (Fig. 8B). Olson (1985) detailed that the unique morphology of the proximal humerus of giant pelagornithids did not allow rotation of the bone, and that these birds were therefore not capable of flapping flight. The very low and elongated os metacarpale alulare, which has a narrow and only weakly convex distal articulation facet, indicates that the digitus alulae could not be spread to a great extent. Probably, thus, pelagornithids did not have a functional alula, which in extant birds serves to prevent stalling in flight with a high angle of attack, particularly during takeoff and landing (Nachtigall and Kempf, 1971). Because rotation of the humerus of pelagornithids was restricted, takeoff may have been by simple spread of the wings against headwinds. The wings were probably also held in a horizontal position during landing, in which case a functional alula would have been dispensable.

Compared to the early Eocene *Odontopteryx*, the olecranon of the ulna is more strongly reduced in Neogene Pelagornithidae, and the carpometacarpus is much more elongated and narrower, with the latter feature indicating that Neogene pelagornithids had a more slender wing than their Palaeogene relatives. Differences in the pectoral girdle elements of Neogene and Palaeogene Pelagornithidae concern the more massive processus acrocoracoideus of the coracoid of *Pelagornis* and the larger acromion of the scapula (Fig. 8F). The caudal margin of the sternum of *Pelagornis* has much longer trabeculae laterales, and instead of an articulation facet for the furcula on the apex carina, there is a marked rostral projection, which may have acted as a bearing for the furcula (Mayr et al., 2008; Mayr and Smith, 2010).

Pelagornis also differs from early Palaeogene pelagornithids in features of the hind limbs. Contrary to the Eocene species, the hypotarsus of Neogene Pelagornithidae includes bony canals, and on the distal tarsometatarsus the trochlea metatarsi II reaches farther distally and is less plantarly deflected. These characters also distinguish the tarsometatarsus of *Pelagornis* from that of the large early Eocene *Dasornis* (Fig. 8I), which indicates that they are not primarily size-related. The pedal phalanges are only preserved in the holotype of *Pelagornis* ("*Osteodontornis*") *orri*, and it has not been noted before that the phalanges of the second and third toes are unusually wide (Howard, 1957:Fig. 8). Because the distal phalanges of the fourth toe show usual proportions, this is unlikely to be a mere result of the flattening of the skeleton. In some fossil and extant Procellariiformes with flattened pedal phalanges, the feet are used as an anchor or break (Mayr, 2009b). Although the legs of these procellariiform species are very long in comparison to those of *Pelagornis*, we consider it possible that, immersed into the water, the feet of *Pelagornis* may have also assisted in flight control, once prey was located on the sea surface.

With records from South America, North Africa, Japan, and New Zealand, pelagornithids were widely distributed in the Pliocene, and the reasons for their extinction remain enigmatic. Environmental changes as well as predation or interference competition at breeding sites are factors that may have played a role, and it is notable that the latest record, from the late Pliocene of North Africa (about 2.5 Ma; Mourer-Chauviré and Geraads, 2008), temporally coincides with the final closure of the Isthmus of Panama about 2.7 Ma, which not only allowed carnivorous placental mammals to enter South America, but is also assumed to have had profound effects on oceanic circulation systems (e.g., Keigwin, 1982; Haug and Tiedemann, 1998).

We finally note that the phylogenetic affinities of bony-toothed birds still have not been convincingly resolved. Pelagornithids share with galloanserine birds a derived morphology of the basipterygoid articulation, a bicondylar processus mandibularis of the quadratum (Bourdon, 2005), and, probably functionally

correlated therewith, very shallow mandibular cotylae, which are not separated by a distinct crista intercotylaris. Whereas these features may support a sister-group relationship to Galloanseres, a position within crown group Galloanseres conflicts with the absence of synapomorphies of the latter, such as well-developed, blade-like processus retroarticulares and an eminentia articularis on the quadratum (contra Bourdon, 2005).

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