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Description of a new species of *Gastornis* (Aves, Gastornithiformes) from the early Eocene of La Borie, southwestern France ✡

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Abstract

The Early Eocene locality of La Borie is located near the village of Saint-Papoul, in southwestern France. It consists of clay deposits that have yielded numerous vertebrate fossils, including remains of the giant flightless bird *Gastornis*. These remains were initially attributed to the species *G. parisiensis*, which is otherwise recorded from the late Paleocene and earliest Eocene of the North Sea Basin. New fossil birds collected in the La Borie clay pit in 2018 include an almost complete mandible of *Gastornis*. We describe a new species of *Gastornis* based on this mandible and we show that the previously described remains from La Borie must be assigned to this new species. The new species differs from other species of *Gastornis* in the morphology of the mandible, maxilla and quadrate. The morphological diversity of the genus *Gastornis*, which existed in Europe for at least 17 million years, is emphasized.

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1. Introduction

The Early Eocene locality of La Borie is located near the village of Saint-Papoul, in the Carcassonne area, southwestern France. It consists of organic-rich clay deposits which have yielded fossils of plants and animals. These layers are occasionally covered by sandstone or conglomerate. All these deposits correspond to standing water bodies, suddenly invaded by sand and gravel during successive flood episodes. Analysis of the flora indicates a humid tropical climate, and a landscape of marshy wooded savanna in an alluvial plain (Laurent et al., 2010). The rich vertebrate fauna includes fishes, amphibians, chelonians, squamates, crocodiles, birds, and mammals. The study of mammals made it possible to assign the locality to the reference-level MP 8-9, early Eocene, middle Ypresian (Laurent et al., 2010; Danilo et al., 2013), with a numerical age of ca. 52 Ma (Escarguel et al., 1997).

Fossil birds from La Borie mainly include remains of the giant flightless groundbird *Gastornis*, which is known from the Paleocene to the middle Eocene of Europe (Martin, 1992; Buffetaut, 1997, 2008; Angst and Buffetaut, 2013; Hellmund, 2013) and early Eocene of North America (Andors, 1988, 1992; Eberle and Greenwood, 2012) and China (Hou, 1980; Buffetaut, 2013). The avian fossils from La Borie constitute the southernmost record of *Gastornis* in Europe and have been attributed to the species *Gastornis parisiensis* Hébert, 1855 (Buffetaut, 2008; Laurent et al., 2010; Bourdon et al., 2016). *Gastornis parisiensis* was previously known mainly in the late Paleocene (Thanetian) of the Reims area (Cernay-lès-Reims and Mont de Berru, northeastern France), and in the early Eocene (Ypresian) of the Paris area (Meudon and Passy) and London area (Croydon) (Hébert, 1855; Owen, 1856; Milne-Edwards, 1867-68; Lemoine, 1878, 1881; Newton, 1890; Martin, 1992; Angst and

Buffetaut, 2013). New fossil birds collected in the La Borie clay pit in 2018 include an almost complete mandible of *Gastornis*. We describe a new species of *Gastornis* based on the study of this mandible and we show that the previously described remains from La Borie must be assigned to this new species. Differences between the material from La Borie and the material from Cernay-lès-Reims and Mont de Berru have been reported previously, especially in the maxilla and quadrate (Bourdon et al., 2016).

2. Material and methods

The fossil material described here is deposited in the collection of the MHNT. The anatomical terminology follows Baumel et al. (1993), unless stated otherwise.

Institutional abbreviations: AMNH, American Museum of Natural History, New York, USA; APSO, Association des Paléontologues du Sud-Ouest, Toulouse, France; MDE, Musée des Dinosaures, Espéraza, Aude, France; MHNT, Muséum d'Histoire naturelle de Toulouse, France; MNHN, Muséum National d'Histoire Naturelle, Paris, France.

Other abbreviations: SP, fossiliferous sites in the quarry of La Borie (Laurent et al., 2010).

3. Systematic palaeontology

Class Aves Linnaeus, 1758

Order Gastornithiformes Stejneger, 1885

Family Gastornithidae Fürbringer, 1888

Genus ***Gastornis*** Hébert, 1855

Type species: *Gastornis parisiensis* Hébert, 1855 (« Conglomérat de Meudon », Ypresian, early Eocene, Meudon, Hauts-de-Seine, France).

Gastornis laurenti nov. sp.

Figs. 1, 2

LSID of new species: urn:lsid:zoobank.org:act:BAD679B2-1808-4512-B1FF-F9A136B32454

Derivation of the name: This species is dedicated to Yves Laurent, who directed the excavations in the quarry of La Borie from 2006 onwards, and discovered the mandible.

Holotype: MHNT.PAL.2018.20.1, almost complete mandible found in SP2.

Paratypes: MDE-A18, left tibiotarsus (Buffetaut, 2008, unknown SP); APSO.2006.SP1-62, right tibiotarsus; MHNT.PAL.2013.15.1, maxilla (SP5); MHNT.PAL.2013.15.2, right quadrate (SP5); MHNT.PAL.2013.15.3 to 8, six cervical vertebrae (SP1 and SP2); MHNT.PAL.2013.15.9, shaft of a left femur (SP2); MHNT.PAL.2013.15.10, left tibiotarsus (SP5) (Bourdon et al., 2016); all these bones are from the type locality.

Type locality: La Borie, Saint-Papoul, Department of Aude, southern France.

Type horizon: Middle Ypresian, early Eocene, close to reference level MP 8-9, age ca. 52-53 Ma (Danilo et al., 2013).

Referred material: The material also includes a series of postcranial gastornithid bones, partly from the same individual, which will be described in a subsequent publication.

Measurements: see Table 1.

Diagnosis: Mandibula: very elongate symphysis mandibulae; ventral outline of rostrum mandibulae strongly oriented craniodorsally (horizontal in *G. parisiensis* and slightly oriented craniodorsally in *G. giganteus*); canaliculi neurovasculares scarce and shallow (numerous and deep in the other species of *Gastornis*); internal surface of rostrum mandibulae smooth (presence of an inner ledge in *G. giganteus*); caudal edge of symphysis more rounded than in other species; articular part narrower than in other species; line linking the middle of the processus lateralis and medialis almost perpendicular to the long axis of the ramus mandibulae (obliquely oriented in *G. giganteus*); absence of crista intercotylaris between cotyla lateralis and cotyla medialis (crista intercotylaris present in *G. parisiensis* and *G. giganteus*). Os quadratum: tuberculum musculi adductor mandibulae oval in shape (prominent and hooked ventrally in *G. parisiensis*; large and rounded in *G. giganteus*); processus mandibularis lateromedially narrow (wider and shorter in *G. parisiensis* and *G. giganteus*); shallow sulcus intercotylaris (deeper in *G. parisiensis* and *G. giganteus*); shallow cotyla quadratojugalis, as in *G. giganteus* (deep, circular and surrounded by a thick ridge in *G. parisiensis*); slender processus orbitalis (very stout in *G. giganteus*). Maxilla: large apertura nasi ossea (smaller in *G. giganteus* and *G. geiselensis*); apertura nasi ossea more ventrally located than in *G. giganteus*; shallow sulcus nasi (deeper in *G. giganteus*); maxilla shorter than in *G. giganteus*; nasolacrimal process tall and prominent laterally (small and poorly developed in *G. giganteus*).

Description and comparisons:

Mandibula. The mandible MHNT.PAL.2018.20.1 is almost complete. It lacks the tip of the rostrum mandibulae, the extremities of the processus retroarticulares on both rami, and the tip of the processus medialis on the right ramus. The mandible from La Borie exhibits the general characteristics of the genus *Gastornis*, namely very large size, spout-shaped and very elongate rostrum mandibulae, robust rami mandibulae, strongly developed processus coronoideus, caudal part with very prominent processus mediales, laterales, and retroarticulares.

Pars symphysialis. The spout-shaped symphysis mandibulae forms a deep, narrow furrow which widens gradually in the caudal direction. Its internal margins are smooth and almost vertical. In the median part of the symphysis, a shallow, oval, barely distinguishable concavity corresponds to the insertion of the musculus genioglossus (Fig. 1(A: mg)). The smooth ventral surface of the symphysis exhibits a few canaliculi neurovasculares, and some small foramina neurovascularia. The bone is very thin at the level of the symphysis. The cristae tomiales are sharp from the tip of the rostrum mandibulae to the region just rostral to the processus coronoideus, and then widen slightly in the caudal direction. In lateral view, the ventral margin of the symphysis mandibulae is strongly oriented dorsally towards the tip of the rostrum, and the caudal part of the symphysis protrudes ventrally compared to the long axis of the mandibular ramus (Fig. 1(C)).

Pars intermedia. The upper part of the right mandibular ramus is somewhat twisted medially and the left ramus is not distorted. When the mandible lies on the caudal part of the symphysis on the one hand, and on the caudoventral angles of the articular part on the other hand, the cristae tomiales are straight, and slightly dorsally oriented towards the tip of the rostrum mandibulae. On the lateral side of the right ramus, the stout prominent processus coronoideus is prolonged cranioventrally by an oblique ridge, the crista coronoidea (Figs. 1(A: pc), 2(A: pc, cc)). The processus coronoideus and its crest correspond to the attachment of the musculus adductor mandibulae externus. This ridge ends at the level of a fracture zone that extends from the caudal part of the symphysis to the articular part. Ventral to this fracture, the bone exhibits a series of faint parallel crests that are visible under grazing light conditions. These crests are obliquely oriented from the dorsocaudal side to the cranioventral edge. In *Gastornis giganteus*, these parallel crests also correspond to external adductor muscle scars according to Witmer and Rose (1991: fig. 2). The left ramus of MHNT.PAL.2018.20.1 also shows a well-developed processus coronoideus, prolonged by a

crista coronoidea. A second parallel ridge is located caudal to the coronoid crest. This ridge is not preserved on the right ramus. Both ridges end at the level of a longitudinal ridge, located at approximately mid-height of the ramus, and which extends from the caudal extremity of the rostrum mandibulae to the articular part. Ventrally to this ridge, the bone exhibits a series of low parallel ridges, as on the right ramus. The height of the mandibular rami decreases progressively caudal to the coronoid processes. On the medial side of both rami is a large, elongate depression that extends to the caudoventral angle. This depression corresponds to the fossa aditus canalis mandibulae (Baumel and Witmer, 1993: fig. 4.1). This fossa exhibits a well-defined opening for the canalis mandibulae in *G. parisiensis* (Angst and Buffetaut, 2013: fig. 3(B1)). This opening is not visible in *G. laurenti* nov. sp.

Pars caudalis. As in other Galloanserae, the fossa articularis quadratica contains only two cotylae, the cotyla lateralis and the cotyla medialis, and the cotyla caudalis is absent (Zusi and Livezey, 2000). In *G. laurenti* nov. sp., the cotyla lateralis and the cotyla medialis are continuous and are not separated by a ridge. Caudal to these two cotylae is a tear-shaped concavity that ends at the lateral border of the fossa articularis quadratica, in the notch between the processus lateralis and the processus retroarticularis (Fig. 2(C: tc)). This concavity shows a small oblique crest situated caudal to the cotyla lateralis. Caudal to this depressed area, there is a triangular fossa, situated at the basis of the processus retroarticularis, visible on the right ramus. In dorsal view, a crista transversa, clearly visible on the left ramus, extends from the processus mandibulae medialis to the processus retroarticularis (Fig. 2(C: ctr)). On the right ramus the processus medialis mandibulae is crushed. On the left ramus this processus shows, on its dorsal face, a pneumatic foramen (Fig. 2(C: pf)) and a fossa for attachment of a ligament, possibly the ligamentum jugomandibulare mediale. A rounded fossa caudalis for insertion of the musculus depressor mandibulae is located on the caudal face of both processus mediales (Fig. 2(B: fc)). The processus retroarticulares consist of flattened blades, obliquely oriented compared to the long axis of each mandibular ramus. Their dorsal edge is sharp and their ventral edge is blunt (Fig. 2(B: pr)).

Comparison with G. parisiensis *Hébert, 1855*. A mandible of *G. parisiensis*, n° MHNT.PAL.2012.1.1, from the Paleocene of Mont de Berru, has been described by Angst and Buffetaut (2013: fig. 3). In this mandible, the crista tomialis slopes downwards in the cranial direction, but the tip of the symphysis is slightly bent upwards (Angst and Buffetaut, 2013:

fig. 3 (C)). In fact the cristae tomiales are incompletely preserved on both rami, and the real outline must have been straighter, with a small upwards tilt at the extremity (Fig. 3(C, D)). This differs considerably from *G. laurenti* nov. sp., in which the ventral side of the rostrum mandibulae slopes upwards in the cranial direction. In *G. parisiensis,* the mandible shows numerous deep canaliculi neurovasculares on the ventral side of the rostrum and on the lateral sides of the rami (Fig. 3(C: cn)), while these grooves are poorly developed in *G. laurenti* nov. sp. In *G. parisiensis,* a distinct foramen for the canalis mandibulae is present in the fossa aditus canalis mandibulae, whereas this foramen is not visible in *G. laurenti* nov. sp. In *G. parisiensis* the crista coronoidea extends to the ventral edge of the ramus mandibulae and ends in a rounded tubercle, with two smaller tubercles situated caudally (Angst and Buffetaut, 2013: fig. 3; Fig. 3(D)), while in *G. laurenti* nov. sp. this crest stops at the level of a longitudinal ridge located at mid-height of the ramus. In the mandible from La Borie a second ridge is situated caudally to the crista coronoidea. In *G. parisiensis,* a faint second ridge is also present. In *G. parisiensis* the processus lateralis projects only slightly laterally compared to the lateral side of the ramus (Fig. 3(A: pl)). In contrast, the processus lateralis strongly projects laterally in *G. laurenti* nov. sp. (Fig. 1(A: pl)). In *G. parisiensis* there is a distinct, although slightly eroded crista intercotylaris (Fig. 3(A: ci)), while both cotylae are continuous in *G. laurenti* nov. sp. In *G. parisiensis* the tear-shaped depression situated caudally to the cotylae is located at the base of the processus medialis and separated from the base of the processus retroarticularis by a distinct ridge. In contrast, in *G. laurenti* nov. sp.*,* the tear-shaped depression extends onto the notch between the lateral and retroarticular processes (Fig. 3(C: tc)). In *G. parisiensis* the crista transversa is much less developed than in *G. laurenti* nov. sp. In the former species, a large pneumatic foramen is present at the base of the processus medialis, whereas this pneumatic foramen is much smaller in *G. laurenti* nov. sp. (Figs. 2(C), 3(A: pf)). In *G. parisiensis*, there is no triangular fossa at the base of the retroarticular process but just a shallow depression. In *G. parisiensis*, the two mandibular branches make an angle of ca. 50° with one another, as in *G. laurenti* nov. sp., but the area where the branches meet is rather pointed, while it is more rounded in *G. laurenti* nov. sp.

Comparison with G. geiselensis *(Fischer, 1978)*. The material of *G. geiselensis* consists in the cranial part of a mandible (Dia 1; Fischer, 1962) and a complete one, the left branch of which is folded upon the ventral side (Dia 14; Fischer, 1978; Hellmund, 2013). The length of

the symphysis (156 mm) is comparable to that of *G. laurenti* nov. sp., but the mandibular branches are much stouter. At the level of the processus coronoideus, the dorsoventral height of the branches is 105-110 mm on the mandible Dia 1, and 96 mm on the mandible Dia 14, while in *G. laurenti* nov. sp. the height is only 76 mm. In *G. geiselensis*, the ventral surface of the symphysis shows deep canaliculi neurovasculares and very small foramina. These grooves are less developed and shallower in *G. laurenti* nov. sp. In *G. geiselensis*, the fossa articularis is damaged and it is not possible to see the cotylae. However, it can be observed that the line uniting the medial and lateral processes is perpendicular to the longitudinal axis of the ramus mandibulae, and that the lateral process projects slightly on the lateral side, as in *G. parisiensis*, and unlike in *G. laurenti* nov. sp. An opening for the canalis neurovascularis mandibulae (Fischer, 1978: fig. 3) is present on the left branch of the specimen Dia 14, whereas there is no visible opening in *G. laurenti* nov. sp. However, *G. geiselensis* is similar to *G. laurenti* nov. sp. in the fact that the ventral side of the rostrum mandibulae is craniodorsally oriented.

Comparison with G. giganteus *(Cope, 1876)*. In *G. giganteus* several complete mandibles have been described by Matthew and Granger (1917), Troxell (1931), Andors (1988, 1992) and Witmer and Rose (1991). In the specimen AMNH 6169, in lateral view, the crista tomialis slopes ventrally from the processus coronoideus, then slopes slightly upwards at the cranial extremity (Matthew and Granger, 1917: pl. XXI (1b); Angst and Buffetaut, 2013: fig. 4). However, this character is not constant since the outline of the tomium is straight in specimen USGS 21862, which is contemporaneous with AMNH 6169 (Witmer and Rose, 1991: fig. 2). Troxell (1931: p. 23) also reports some variation in the curvature of the tip of the symphysis, which is “either straight or slightly bent upward”. The canaliculi neurovasculares are well developed. In ventral aspect, both mandibular branches are swollen on either side of the symphysis (Fig. 4). The two mandibular rami make an angle of ca. 50° with one another, as in *G. laurenti* nov. sp. and *G. parisiensis*, but the area where the mandibular rami fuse is much more pointed. There is an “inner ledge” extending along the dorsomedial edge of the ramus, in the zone located between the angulus mandibulae and the processus coronoideus (Troxell, 1931: p. 21; Andors, 1988: p. 122). This inner ledge does not exist in *G. laurenti* nov. sp. The crista coronoidea extends to the ventral edge of the ramus mandibulae, and is much larger and stouter than in *G. laurenti* nov. sp. In USGS 21862 there is a strong ridge parallel to the crista coronoidea and situated caudal to it (Witmer and

Rose, 1991: fig. 2). This second ridge also exists in *G. laurenti* nov. sp. but is less prominent. In the caudal part, the line going through the processus lateralis and medialis is obliquely oriented compared to the axis of the ramus mandibulae, whereas it is perpendicular in the other species. In *G. giganteus* the processus lateralis slightly projects lateral to the external margin of the ramus, more so than in *G. parisiensis* and *G. geiselensis*, but less so than in *G. laurenti* nov. sp. (Fig. 4(A: pl)). On the articular fossa there is a crista intercotylaris between the cotylae medialis and lateralis (Andors, 1992: fig. 10(N); Fig. 4(A: ci)). A very small pneumatic foramen is situated on the dorsal face of the processus medialis, close to the caudal border of the cotyla medialis, while in *G. laurenti* nov. sp. the pneumatic foramen is situated more medially. In *G. giganteus*, as in *G. laurenti* nov. sp., there is a small, rounded depression for the attachment of the ligamentum jugomandibulare mediale on the medial part of the processus medialis.

Comparisons with other species of Gastornis. *G. russelli* Martin, 1992 is known by a tarsometatarsus and a fragment of maxilla, *G. sarasini* (Schaub, 1929) is known by an incomplete tarsometatarsus and one pedal phalanx (Angst et al., 2013), and *G. xichuanensis* (Hou, 1980) is known by a distal fragment of tibiotarsus (Buffetaut, 2013). *G. laurenti* nov. sp. differs from these species in size and morphology, based on the postcranial material associated with the mandible from La Borie.

Size comparison. The dimensions of *G. laurenti* nov. sp. are almost the same as those of *G. parisiensis*, and slightly below the mean values in *G. giganteus*, while *G. russelli* is smaller and *G. xichuanensis* is larger. The size of the mandible from La Borie, total length (as preserved) 338 mm, is comparable to that of *G. geiselensis*, 346 mm (Fischer, 1978), larger than that of *G. parisiensis*, 309 mm (Angst and Buffetaut, 2013), and smaller than that of *G. giganteus*, 384.7 mm (Andors, 1988) and 385 mm (Witmer and Rose, 1991).

Os quadratum. Among the elements previously found in La Borie and initially attributed to *G. parisiensis*, important morphological differences have been reported between the os quadratum MHNT.PAL.2013.15.2 and the quadrates from Cernay and Berru (Bourdon et al., 2016). These differences were attributed to intraspecific variation within *G. parisiensis*. The distinctive features of the quadrate from La Borie are now interpreted as autapomorphic characters of *G. laurenti* nov. sp. In the latter species, the tuberculum musculi adductor mandibulae is oval in shape and continuous with a sharp curved ridge that constitutes the rostral border of the processus oticus (Bourdon et al., 2016: fig. 2(A1-A2)). In

G. parisiensis, the tuberculum is very prominent and pointed, somewhat hooked ventrally (Bourdon et al., 2016: fig. 2(B, C)). The rostral margin of the processus oticus is not preserved in the quadrates from Cernay and Berru, therefore the presence or absence of ridge is not known in the latter species. In *G. giganteus*, the tuberculum musculi adductor mandibulae is large and rounded (Matthew and Granger 1917: pl. XXII (2a-b)), and there is no ridge at the rostral margin of the processus oticus. In *G. laurenti* nov. sp., the processus mandibularis is slender, lateromedially narrow, and the sulcus intercondylaris is shallow (Bourdon et al., 2016: fig. 2(A4)). In contrast, the processus mandibularis of *G. parisiensis* is markedly wider and shorter, and the condyli are more convex and separated by a deeper sulcus intercondylaris (Bourdon et al., 2016: fig. 2(B, C)). This latter feature is related to the presence of a crista intercotylaris in the mandible of *G. parisiensis* from Berru (Angst and Buffetaut, 2013), while this crista is absent in the mandible of *G. laurenti* nov. sp. The cotyla quadratojugalis of *G. laurenti* nov. sp. is shallow (Bourdon et al., 2016: fig. 2(A5)), as in *G. giganteus*. In contrast, the cotyla quadratojugalis is deep, circular, and surrounded by a thick edge in *G. parisiensis* (Bourdon et al., 2016: fig. 2(B, C)). In spite of the fact that the dorsal margin and the tip of the processus orbitalis are damaged in *G. laurenti* nov. sp. (Bourdon et al., 2016): fig. 2(A1)), it can be observed that this structure is much slenderer than in the North American species, which exhibits an extremely stout process (Matthew and Granger 1917: pl. XXII (2a)). A small opening located on the medial surface of the quadrate, dorsal to the processus mandibularis (Bourdon et al., 2016: fig. 2(A3)), has been interpreted as a foramen pneumaticum basiorbitale (Worthy et al., 2017). This opening actually corresponds to a small missing part of bone alongside a thin fracture. The foramen pneumaticum basiorbitale is absent in *G. laurenti* nov. sp., *G. parisiensis* and *G. giganteus*.

Maxilla. The maxilla MHNT.PAL.2013.15.1 from La Borie differs from that of *G. giganteus* in several features (Bourdon et al., 2016) which are now interpreted as distinctive characters of *G. laurenti* nov. sp. In the latter species, the apertura nasi ossea is distinctly larger and in more ventral position than in *G. giganteus* (Bourdon et al., 2016: fig. 1). In AMNH 6169, the maximum anteroposterior diameter of the apertura nasi ossea excluding the sulcus nasi is 28.0/29.5 mm (vs. 35.0 mm in *G. laurenti* nov. sp.) and the maximum dorsoventral diameter of the apertura nasi ossea is 12.4/16.0 mm (vs. 19.0 mm in *G. laurenti* nov. sp.) (Andors, 1988). In *G. laurenti* nov. sp., the sulcus nasi is shallower than in the North American species (Bourdon et al., 2016: fig. 1). Furthermore, the maxilla is much shorter in

G. laurenti nov. sp. than in *G. giganteus* (Bourdon et al., 2016: fig. 1), especially the portion located rostral to the apertura nasi ossea. In AMNH 6169, the length from the tip to the anterior end of the rostral socket for arcus jugalis is 241.8/242.9 mm (Andors, 1988). In *G. laurenti* nov. sp., the rostral socket for the arcus jugalis is not preserved, but we estimate the length of the maxilla to 170 mm. In *G. laurenti* nov. sp., the nasolacrimal process (Murray and Vickers-Rich, 2004) in the caudodorsal corner of the maxilla is very different from that of *G. giganteus* (Bourdon et al., 2016: fig. 1(A2, B)). In the specimen from La Borie, the nasolacrimal process is taller and more prominent laterally than in AMNH 6169. Furthermore, in *G. laurenti* nov. sp., on the ventral side of this nasolacrimal process, there is a flattened surface that may have articulated with a projection of os lacrimale. The nasolacrimal process is different in *G. giganteus* and probably formed part of the zona flexoria craniofacialis.

The maxilla is partially preserved in *G. geiselensis* (Fischer, 1978), including the apertura nasi ossea on the right hand side (not visible in Fischer, 1978: fig. 2). The apertura nasi ossea is distinctly smaller and the sulcus nasi is shorter than in *G. giganteus* and *G. laurenti* nov. sp. The diagonal diameter of the apertura nasi ossea is only 16 mm and the length of the sulcus nasi is 17 mm (Fischer, 1978).

Presently, no comparison can be made between *G. laurenti* nov. sp. and *G. parisiensis* concerning the morphology of the maxilla. It was stated previously that the maxilla from Cernay (Martin, 1992: fig. 1) is too large to fit with the tarsometatarsus described as the type specimen of *G. russelli* (Martin, 1992: fig. 6), and that it might belong to a juvenile individual of *G. parisiensis*, as suggested by open suturae and very large apertura nasi ossea (Bourdon et al., 2016). However, we now think that the maxilla from Cernay may actually belong to *G. russelli*, because the dimensions of the tarsometatarsus of *G. russelli* provided by Martin (1992) are erroneous. The length of this tarsometatarsus is 164 mm (CMC, pers. obs.) instead of 129 mm (Mourer-Chauviré and Bourdon, 2016). In this condition, the dimensions of the maxilla from Cernay are compatible with those of the holotype of *G. russelli*, which implies that the maxilla is unknown in *G. parisiensis*.

4. Discussion

The genus *Gastornis* includes several species that succeed each other in time, from *Gastornis sp*. from Walbeck and Maret, which are relatively small forms, to *G. geiselensis*

that represents the last member of this genus. *Gastornis sp*. from Walbeck and Maret are dated as middle Paleocene, early to middle Selandian, reference level MP 1-5, ca. 61 Ma (De Bast et al., 2013; Mayr and Smith, 2019), and *G. geiselensis* is present in the early Eocene of Messel, Ypresian, reference level MP 10, and in the middle Eocene of Geiseltal, Lutetian, reference levels MP 11, 12, and 13, ca. 44 Ma for the reference level MP 13 (Escarguel et al., 1997). This means that some representatives of the genus *Gastornis* existed for at least 17 myr. In *Gastornis sp*. from Walbeck, the lack of fusion between the coracoid and the scapula is considered as a primitive feature (Mayr, 2007). However unfused coracoid and scapula are also known in the material of *G. parisiensis*, but they may belong to juvenile individuals. Several species are recorded after the late Paleocene: *G. russelli*, late Thanetian; *G. parisiensis*, late Thanetian and early Ypresian; *G. laurenti* nov. sp., middle Ypresian; *G. sarasini*, late Ypresian; *G. geiselensis*, late Ypresian and Lutetian (Angst, 2014; Buffetaut and Angst, 2014). The sexually dimorphic *Gastornis* sp. from Louvois is coeval with *G. russelli* and *G. parisiensis*, but differs from these two species in several features (Mourer-Chauviré and Bourdon, 2016). The Louvois locality is very close to Cernay-lès-Reims and Mont de Berru, where *G. parisiensis* and *G. russelli* have been found. This means that three different forms of large groundbirds coexisted in a relatively small area.

The different species of *Gastornis* show great morphological variability. In the oldest species, *G. parisiensis* and *G. russelli*, the tarsometatarsus has parallel medial and lateral sides. In contrast, the tarsometatarsus of the most recent species *G. geiselensis* is strongly constricted at mid-shaft. A slight constriction is visible in *G. sarasini*, which is intermediate in age between the previous ones, but its tarsometatarsus is incomplete. In *G. giganteus*, which is also intermediate in age, “the proximal and the distal extremities [of the tarsometatarsus] are widely expanded with respect to the shaft, which is narrowly constricted towards its middle” (Andors, 1988: p. 235). In *G. laurenti* nov. sp., the mandible differs from the more ancient form, *G. parisiensis*, and also from *G. giganteus* and the more recent form *G. geiselensis*. There are also morphological differences in the cranial and postcranial skeleton. In the North American gastornithids several species have been described, some of them based on pedal phalanges, but all these species have been put in synonymy with *G. giganteus*. However, these pedal phalanges seem to be quite different from those of *G. giganteus*, and it is possible that several coeval species were also present in

North America. In addition, the measurements of *G. giganteus* (Andors, 1988) show considerable size variation and this could also point to the presence of several species.

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Table and Figure captions

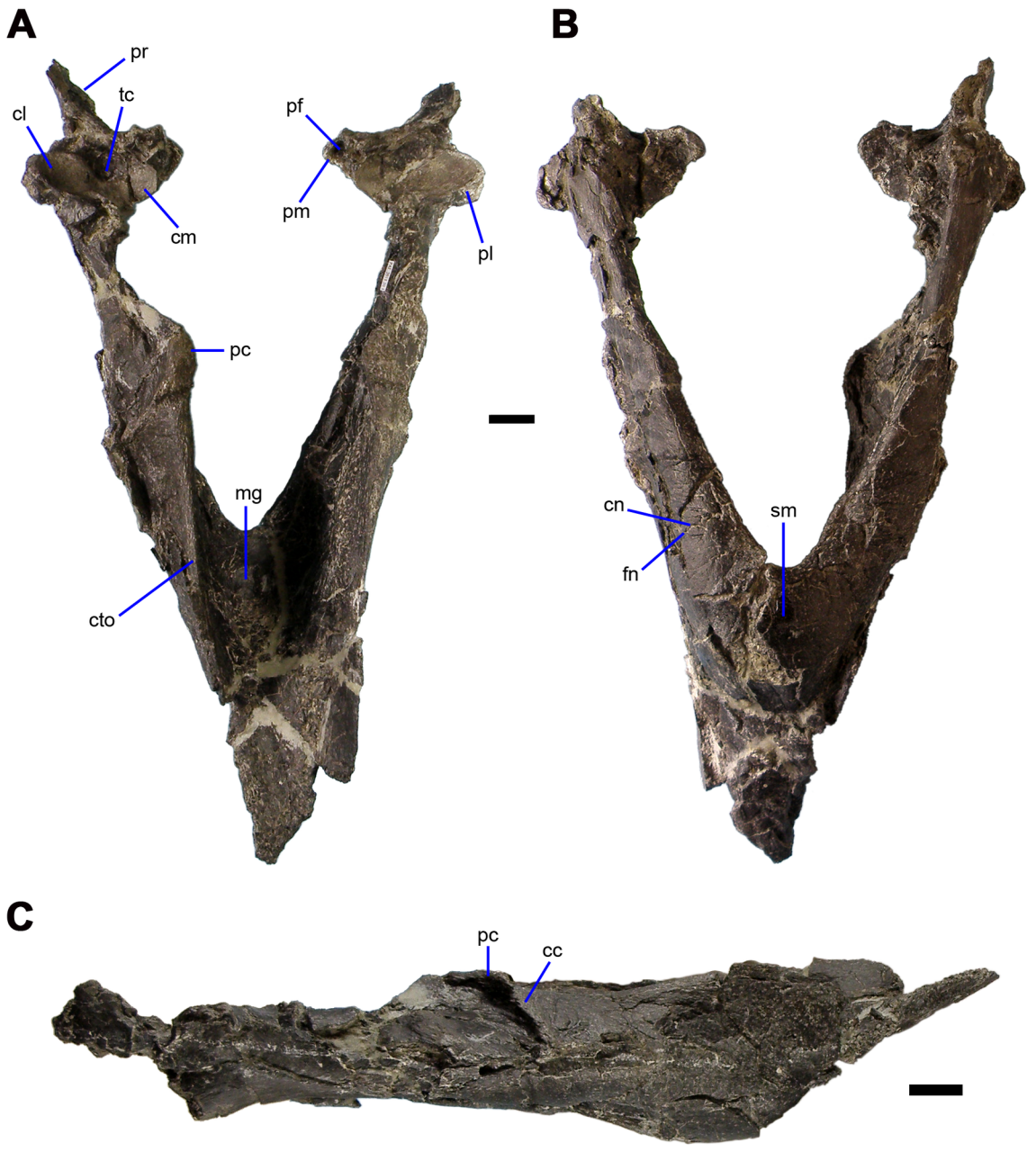
Table 1. Measurements of the holotype mandible MHNT.PAL.2018.20.1, as preserved, in mm. Measurements of the paratypes are provided in Buffetaut (2008) and Bourdon et al. (2016).

Fig. 1. *Gastornis laurenti* nov. sp., holotype mandible MHNT.PAL.2018.20.1 in dorsal (**A**), ventral (**B**) and caudal (**C**) views. Abbreviations: cc, crista coronoidea; cl, cotyla lateralis; cm, cotyla medialis; cn, canaliculi neurovasculares; cto, crista tomialis; fn, foramina neurovascularia; mg, insertion of musculus genioglossus; pc, processus coronoideus; pf, pneumatic foramen; pl, processus lateralis; pm, processus medialis; pr, processus retroarticularis; sm, symphysis mandibulae; tc, tear-shaped concavity. Scale bars: 2 cm.

Fig. 2. *Gastornis laurenti* nov. sp., holotype mandible MHNT.PAL.2018.20.1 in left dorsolateral (**A**), caudal (**B**) and dorsal (**C**) views. Abbreviations: cc, crista coronoidea; cl, cotyla lateralis; cm, cotyla medialis; ctr, crista transversa; fc, fossa caudalis; pc, processus coronoideus; pf, pneumatic foramen; pl, processus lateralis; pm, processus medialis; pr, processus retroarticularis; tc, tear-shaped concavity. Scale bars: 2 cm.

Fig. 3. *Gastornis parisiensis* Hébert, 1855, mandible MHNT.PAL.2012.1.1 in ventral (**A**), dorsal (**B**), right lateral (**C**) and left lateral (**D**) views. Abbreviations: ci, crista intercotylaris; cl, cotyla lateralis; cm, cotyla medialis; cn, canaliculi neurovasculares; fn, foramina neurovascularia; pc, processus coronoideus; pf, pneumatic foramen; pl, processus lateralis; pm, processus medialis; sm, symphysis mandibulae; tc, tear-shaped concavity. Scale bars: 2 cm.

Fig. 4. *Gastornis giganteus* (Cope, 1876), mandible AMNH 6169 in ventral (**A**) and dorsal (**B**) views. Abbreviations: ci, crista intercotylaris; cl, cotyla lateralis; cm, cotyla medialis; cto, crista tomialis; pc, processus coronoideus; pl, processus lateralis; pm, processus medialis; pr, processus retroarticularis; sm, symphysis mandibulae; tc, tear-shaped concavity. Scale bar: 2 cm.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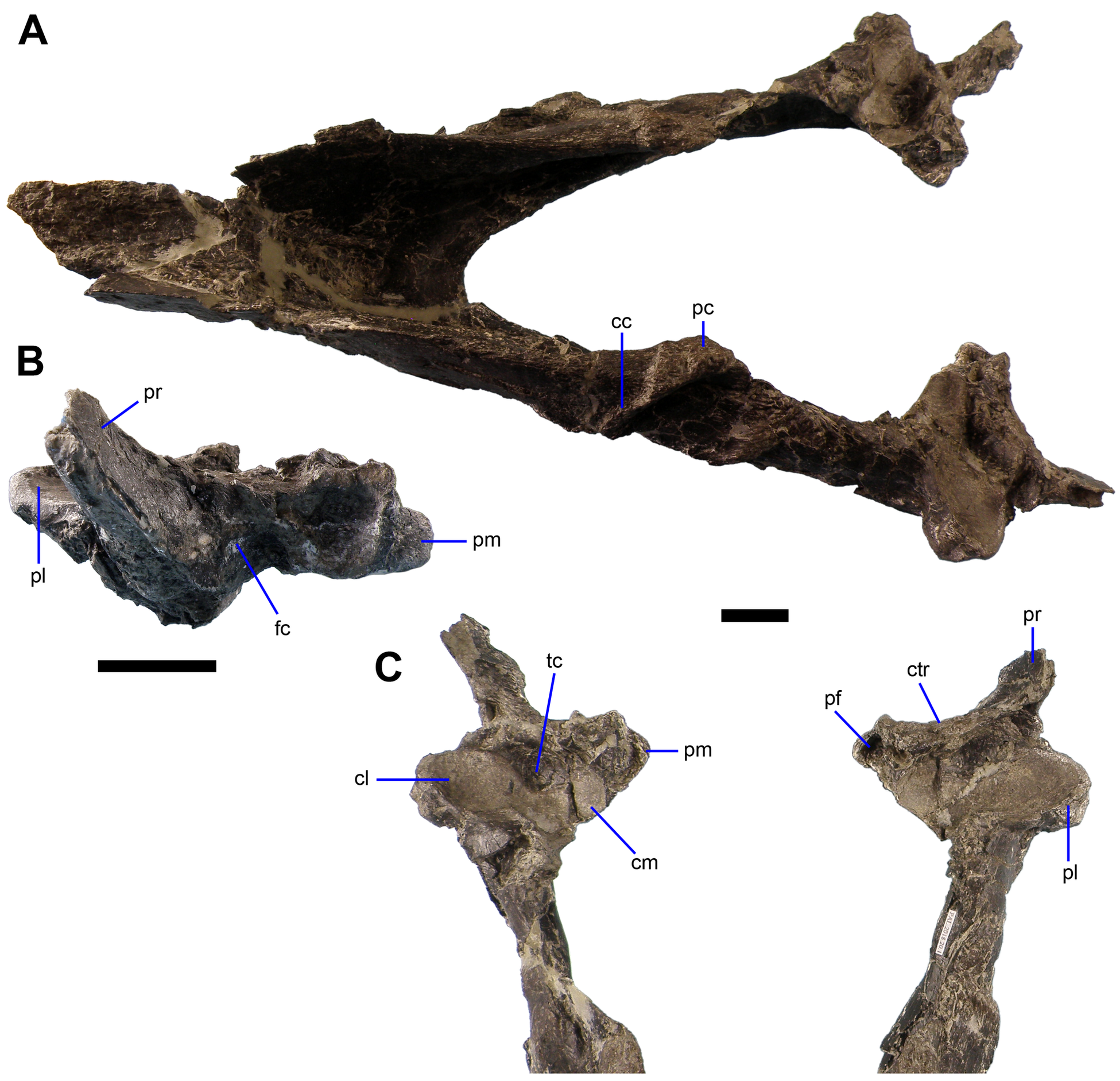
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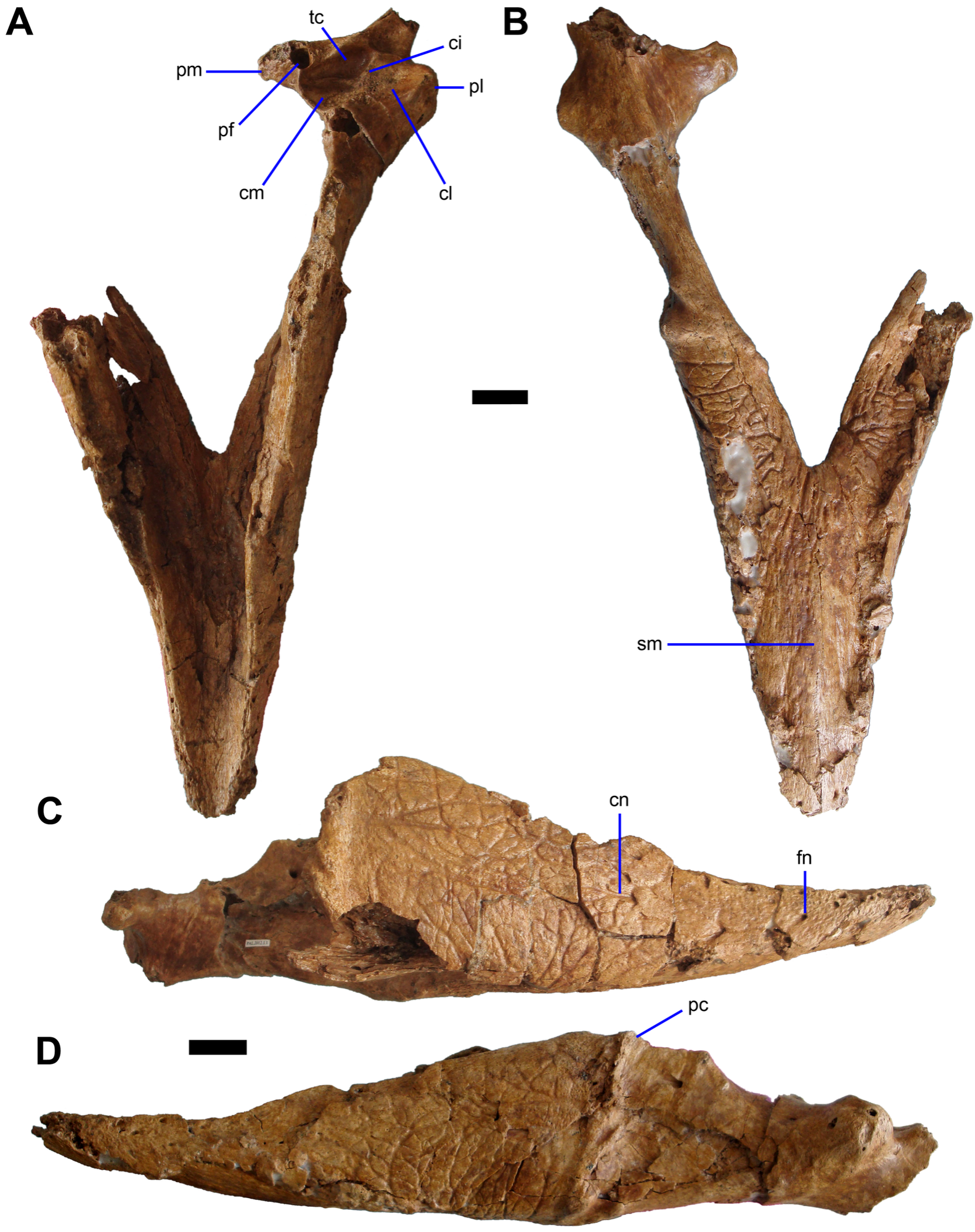
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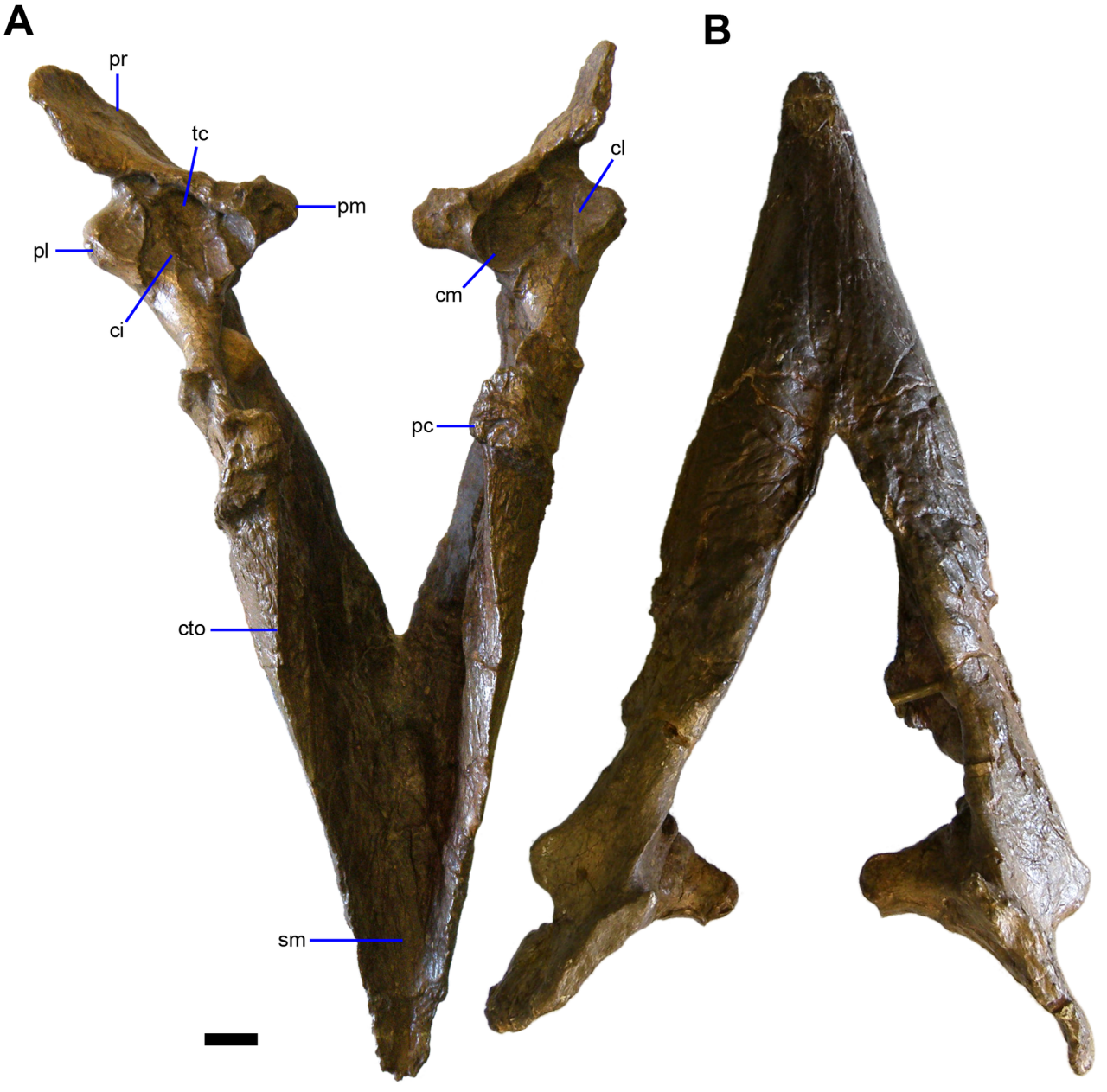
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Table 1.

Total length	338.0
Right ramus mandibulae, length, from tip to caudal end of processus retroarticularis	355.0
Left ramus mandibulae, length, from tip to caudal end of processus retroarticularis	343.0
Maximal width at external edge of cotylae laterales	199.0
Craniocaudal length of symphysis mandibulae	146.0
Height of ramus mandibulae at caudal extremity of symphysis	76.0
Dorsoventral height at left processus coronoideus	57.3
Right processus coronoideus, length of crista coronoidea	43.0
Right ramus mandibulae, minimal dorsoventral heigth just cranial to fossa articularis	30.5
Right pars caudalis, width from tip of processus lateralis to tip of processus medialis	72.2
Left pars caudalis, width from tip of processus lateralis to tip of processus medialis	72.5
Right fossa articularis quadratica, width	59.0
Left fossa articularis quadratica, width	58.0
Right cotyla medialis, width	29.8
Left cotyla medialis, width	28.3
Right cotyla lateralis, width	31.0
Left cotyla lateralis, width	30.6
Right processus retroarticularis, length	39.6
Left processus retroarticularis, length	30.0
Estimated angle between the two branches of the mandible measured at the putative tip of the rostrum	30°
Angle between the two lines joining the extremities of processus retroarticulares and the caudal edge of the symphysis	50°