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A New Cormorant-like Bird (Aves: Phalacrocoracoidea) from the Early Miocene of Rauscheröd (Southern Germany)

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ABSTRACT. Presented here is a new species of a cormorant-like bird, assigned to ?*Borvocarbo tardatus* n.sp., from the Early Miocene of the locality Rauscheröd in Southern Germany. The preserved bones, a tibiotarsus, fragmentary ulna and radius, are compared in detail to those of fossil and extant taxa of phalacrocoracoids. Provided that the generic affiliation is confirmed when additional material is discovered, the new species is the stratigraphically youngest evidence and representative of the genus *Borvocarbo*.

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Cormorants are aquatic, piscivorous, diving birds of the Old and New World. Today they are most diversified in the Southern Hemisphere, where they inhabit both marine and freshwater environments. The fossil record of Phalacrocoracoidea (cormorants and anhingas, sensu Livezey & Zusi, 2007) dates back until the Early Oligocene of Europe (e.g., Mourer-Chauviré *et al*., 2004; Rasmussen *et al*., 1987; Roux, 2002), perhaps even to the Late Eocene (Mourer-Chauviré *et al*., 2004); however, the oldest systematically determinable genera/species are described from the Late Oligocene (Mayr, 2007; Mourer-Chauviré *et al*., 2004).

Tertiary taxa of European Phalacrocoracoidea belong to six genera: *Borvocarbo* Mourer-Chauviré, Berthet & Hugueney, 2004 (Late Oligocene and Early Miocene [this paper]), *Phalacrocorax* Brisson, 1760 (Early Miocene–Recent), *Oligocorax* Lambrecht, 1933 (Early Miocene), *Nectornis* Cheneval, 1984 (Miocene), and *Limicorallus* Kurochkin, 1968 (Late Oligocene and Early Miocene) and, as the single representative of darters, *Anhinga* Brisson, 1760 (Late Miocene–Recent). The fossil representatives of the genera *Phalacrocorax, Oligocorax, Nectornis* and *Limicorallus* are accepted as members of the Phalacrocoracidae (cormorants), whereas, following Mayr (2007), ?*Borvocarbo stoeffelensis*, and hence the entire genus, is probably phylogenetically positioned outside of the crown group (Phalacrocoracidae+Anhingidae), but still a Phalacrocoracoidea.

Hitherto, 11 species of cormorants and cormorant-like taxa are known during the Late Oligocene and Miocene in Europe (Table 1). Fossil darters are represented in Europe only by *Anhinga pannonica* (Lambrecht, 1916) from the Late Miocene of Romania (MN10) and Austria (MN9); this species has also been reported from the Late Miocene of Tunisia (Rich, 1972).

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Table 1. Valid fossil species of cormorants and its kin known from the Late Oligocene and Miocene in Europe.

Borvocarbo guilloti Mourer-Chauviré, Berthet & Hugueney, 2004	Late Oligocene	France
?*Borvocarbo stoeffelensis* Mayr, 2007	Late Oligocene (MP30)	Germany
Oligocorax littoralis (Milne-Edwards, 1863)	Early Miocene (MN1–3)	France, Germany, Czechia
Phalacrocorax intermedius (Milne-Edwards, 1867–1871a)	Early and Middle Miocene (MN3–5)	France, Germany, Czechia
Phalacrocorax ibericus Villalta, 1963	Late Miocene (MN9)	Spain
Phalacrocorax lautus Kurochkin & Ganea, 1972	Late Miocene (MN9?)	Moldova
Phalacrocorax serdicensis Burchak-Abramovic & Nikolov, 1984	Late Miocene (MN11–13)	Bulgaria
Phalacrocorax longipes (Tugarinov, 1940)	Late Miocene (MN11–13), Early Pliocene (MN15)	Ukraine
Nectornis miocaenus (Milne-Edwards, 1867)	Early Miocene (MN2–4)	France, Germany, Czechia
Nectornis anatolicus (Mourer-Chauviré, in Paicheler *et al*., 1978)	Miocene	Turkey
?*Limicorallus carbunculus* (Mayr, 2009)	Early Miocene	Germany

Oligocorax littoralis, P. intermedius, and *N. miocaenus* were originally described in the genus *Graculus* Koch, 1816, and were later referred to *Phalacrocorax*. The species *miocaenus* was moved to *Nectornis* by Cheneval (1984), while the species *littoralis* was only recently returned to the genus *Oligocorax* by Mayr (2001).

Here we describe a new species from the Lower Miocene of Rauscheröd, southern Germany.

Geology and stratigraphy of the locality. The locality of Rauscheröd, near Ortenburg, southwest of Passau, is situated in the North Alpine Foreland Basin, southeastern Germany (Lower Bavaria) (Fig. 1). The deposits at Rauscheröd represent the transition of brackish sediments of the Brackwater Molasse (Ottnangian) to the overlying limno-fluviatile sediments of the Upper Freshwater Molasse (Karpatian–Sarmatian). The bird bones come from the more brackish sediments outcropping in the basal part of the Rauscheröd gravel pit section. These sediments belong to the so-called "Ortenburger Schotter" (late Ottnangian–early Karpatian) (see Grimm, 1977; Lang, 2009), which are mostly interpreted as delta deposits (Schlickum & Strauch, 1968; Haas, 1987; Lang, 2009) that were discharged in the eastern part of the western Paratethys. The "Ortenburger Schotter" is composed of basal, fine-grained and brackish bottom-sets, overlaid by thick strata of coarse gravels and sands representing the delta fore-sets and topped by fine, limnic sediments of the top-sets, and can reach 20 to 40 m thickness (Lang, 2009). The "Ortenburger Schotter" is overlaid in the Rauscheröd gravel pit by an 18 m thick deposit of clays and marls (lacustrine sediments) of the limno-fluviatile Upper Freshwater Molasse (Ziegler & Fahlbusch, 1986).

The vertebrate fauna of Rauscheröd is dominated by micromammals, based on which Ziegler & Fahlbusch (1986) referred it to the Mammalian Neogene Unit MN4b (Karpatian, Early Miocene). Large terrestrial mammals are represented by rhinoceroses (*Prosantorhinus* cf. *Pr. douvillei, Brachypotherium brachypus, Alicornops simorrensis* [pers. comm. K. Heissig, Munich]), proboscideans (*Gomphotherium, Prodeinotherium*) and cervids (*Procervulus dichotomus* [see Rössner, 1995]). The aquatic fauna is made up by freshwater elements, like beavers, crocodiles, turtles and fishes (perches), as well as marine vertebrates like sirenians (which might have been able also to live in brackish water) and sharks (Odontaspididae) (see Pfeil & Werner, 1991). In the middle part of the "Ortenburger Schotter", silicified wood (e.g., palm-trees) of great size (up to some meters) can be found (Selmeier, 1983; Ziegler & Fahlbusch, 1986). By means of the flora, especially the silicified wood fossils, Selmeier (1983) reconstructed a tropical to subtropical coastal forest along the eastern shores of the western Paratethys.

Figure 1. Geographical position of the locality Rauscheröd (southeastern Germany, Lower Bavaria).

Material and methods

The presented material is housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (Inventory number BSPG 1990 VI, collection R. Baumgartner).

The osteological terminology follows Baumel & Witmer (1993) and occasionally Ballmann (1969); measurements were taken after von den Driesch (1976).

Abbreviations: Collections: *BSPG*, Bayerische Staatssammlung für Paläontologie und Geologie, Munich; *MNHN*, Muséum national d'Histoire naturelle, Paris; *NHMW*, Naturhistorisches Museum Wien; *UCBL*, Université Claude Bernard-Lyon 1. Other abbreviations: *cmc*, carpometacarpus; *cor*., coracoid; *dist*., distal; *hum*., humerus; *L*, left; *mc*, metacarpal; *MN*, Mammal Neogene unit; *MP*, Mammal Paleogene unit; *prox*., proximal; *R*, right; *rad*., radius; *scap*., scapula; *tbt*, tibiotarsus; *tmt*, tarsometatarsus.

All of the extinct taxa of Phalacrocoracoidea cited above, as well as a selection of extant ones, have been considered for osteological comparisons with the fossils presented here.

The following taxa have been studied first hand: Fossil species: *O. littoralis* (MNHN, UCBL), *N. miocaenus* (MNHN, UCBL), *P. serdicensis* (casts at UCBL). Extant species: *P. carbo, P. aristotelis, P. (Microcarbo) melanoleucos, A. anhinga* (UCBL, NHMW).

Systematic paleontology

Order Pelecaniformes Sharpe, 1891

Phalacrocoracoidea *sensu* Livezey & Zusi, 2007

Borvocarbo Mourer-Chauviré, Berthet & Hugueney, 2004

Type species. *Borvocarbo guilloti* Mourer-Chauviré, Berthet & Hugueney, 2004, represented only by a coracoid from Créchy (Allier, France), Late Oligocene (MP30).

Additional species. ?*Borvocarbo stoeffelensis* Mayr, 2007, dissociated skeleton from Enspel (Germany), Late Oligocene (MP28).

?*Borvocarbo tardatus* n.sp.

Figs 2, 3

Holotype. Nearly complete left tibiotarsus (BSPG 1990 IV 16), figured also in Pfeil & Werner, 1991, pl. 5, fig. 2.

Paratypes. Proximal half of left ulna (BSPG 1990 IV 17), proximal third of right radius (BSPG 1990 IV 18).

Type locality. Gravel pit of the company “Sand- und Kieswerk Rauscheröd Ulrich Alex GmbH” in the village of Rauscheröd, near Passau (eastern Lower Bavaria, southeastern Germany), (topographic map 7445 Ortenburg, r: 4592970 h: 5380700). Early Miocene, MN4b, transition of upper Brackish Molasse to Upper Freshwater Molasse.

Etymology. From the Latin *tardatus*, meaning late; used in the sense that this species is the stratigraphically youngest (latest) of the genus *Borvocarbo* and that it retained primitive osteological characters up to the Early Miocene. All contemporaneous cormorant taxa show more derived osteological features.

Diagnosis. Largest species of *Borvocarbo*. Size between that of the extant cormorants *P. carbo* and *P. aristotelis*. Ulna with processus cotylaris dorsalis lacking hook-like distal end. Tibiotarsus with sulcus extensorius in almost central position along midline, with pons supratendineus proximodistally wide and almost horizontal, and condylus medialis extending only slightly further distally than condylus lateralis. These morphological characters also characterize ?*B. stoeffelensis*, but ?*B. tardatus* is distinctly larger.

Description

The left tibiotarsus (Fig. 2) is nearly complete, with only the cranial and proximal part of the crista cnemialis cranialis and the proximal ends of the crista patellaris and crista cnemialis lateralis broken off. However on the cranial face, in proximal view, the remaining part of the crista patellaris is roughly aligned mediolaterally and this indicates that the tip of the crista cnemialis lateralis was not offset cranially. In proximal view, the incisura tibialis is deeply marked. Two strong and projecting tubercles are situated on the proximal end, a smaller one on the area interarticularis and a larger one caudal to the facies articularis lateralis. In proximal view, the lateral margin of the facies articularis lateralis is somewhat flattened. The crista fibularis is strong and about 26 mm long. The shaft is oval in cross section and slightly compressed craniocaudally. The distal end is distinctly medially bent. The canalis extensorius is wide and runs obliquely from distomedially to proximolaterally and the sulcus extensorius extends along the midline of the shaft. Situated lateral to the pons supratendineus, the tuberositas retinaculi extensoris is developed as a moderate tuberculum, which is separated from the condylus lateralis by a weak sulcus. The tuberculum retinaculi m. fibularis is long and its proximal end merges smoothly into the shaft. Condyli medialis and lateralis are of almost equal size and are parallel and oriented vertically (in cranial view). The condylus medialis bears a deep indentation on its lateral side. The condylus medialis is only slightly longer in distal direction than the condylus lateralis and also exceeds the latter in craniocaudal direction. In distal view, the condylus medialis is tilted craniolaterally so that the distal trochlea tapers from the cranial end to the caudal one. For measurements, see Table 2.

Only the proximal half of the left ulna (Fig. 3) is preserved. The cotyla dorsalis is slightly narrower than the cotyla ventralis. The dorsal projection of the cotyla dorsalis (processus cotylaris dorsalis) is blade-like and does not form a distal hook. The olecranon is swollen proximally and caudally and projects ventrally. The impressio m.

Table 2. Measurements (in mm) of the tibiotarsus and ulna of ?*B. tardatus* and other available Tertiary taxa of phalacrocoracoids for comparison. *GL*, greatest length (including processus cnemialis); *L*, length (without processus cnemialis); *dWp*, proximal diagonal width; *WD*, smallest width of shaft; *Wd*, distal width; *Wp*, proximal width; *Dd*, distal depth; *Dp*, proximal depth; *Dgd*, largest diagonal distal. Asterisk * indicates type localities. Estimated measurements of slightly worn bones are given in parentheses.

tibiotarsus		GL	L	dWp	WD	Wd	Dd
?*Borvocarbo tardatus* n.sp.	*Rauscheröd (D)	ca. 112	107.1	20.1	7.3	13.7	12.5
?*Borvocarbo stoeffelensis*	*Enspel (D)	81.3	—	—	—	—	—
Oligocorax littoralis	*St-Gérand-le-Puy (F)	—	—	—	5.4	9.6–9.9	—
Nectornis miocaenus	*St-Gérand-le-Puy (F)	73	69.1	(12)	4.8	8.3	8.6
ulna		GL	Dp	Wp	WD	Dd	Dgd
?*Borvocarbo tardatus* n.sp.	*Rauscheröd (D)	—	16	13.5	7	—	—
?*Borvocarbo stoeffelensis*	*Enspel (D)	ca. 108	—	—	—	—	—
Oligocorax littoralis	*St-Gérand-le-Puy (F)	—	—	9.2	4.2	—	—
Nectornis miocaenus	*St-Gérand-le-Puy (F)	89.5–102	10–11	8–9	3.3–4.4	5.5–7.2	6.4–6.6

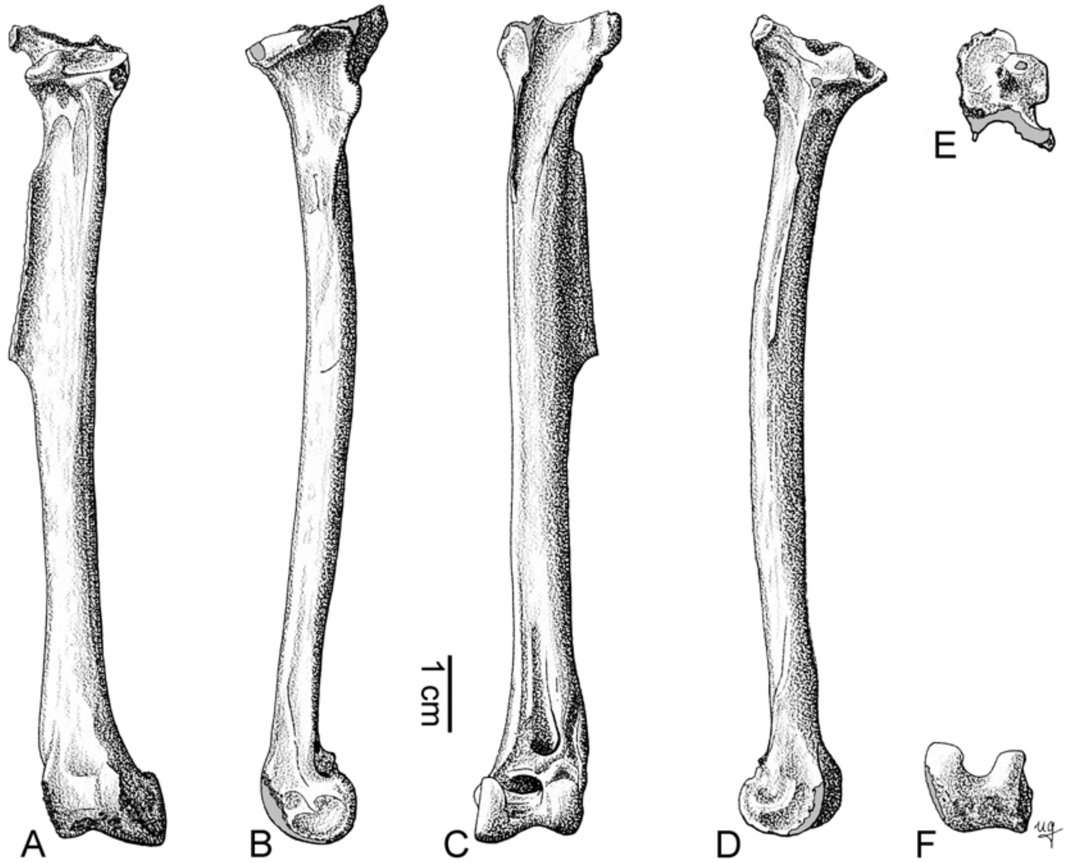

Figure 2. ?*Borvocarbo tardatus* n.sp. from the Early Miocene of Rauscheröd, left tibiotarsus (BSPG 1990 IV 16, holotype) in (*A*) caudal, (*B*) medial, (*C*) cranial, (*D*) lateral and (*E*) proximal, (*F*) distal aspects. Grey-shaded areas indicate damages.

scapulotricipitis on the dorsal side of the proximal end forms a small but distinctive pit; the impressio m. brachialis is well marked, about 3 cm long and becomes shallow distally. The insertion for the lig. collateralis ventralis on the ventral side of the proximal end is large and flat. The linea intermuscularis along the median cranial surface of the proximal shaft forms a prominent crest. The quill knobs (papillae remigales caudales) are weakly developed.

Only the proximal third of a right radius (Fig. 3) is preserved. The ventral margin of the cotyla humeralis is broken off. The caput radii on the proximal end is dorsally strongly swollen. The tuberculum bicipitale radii, situated ventrally somewhat distally to the proximal end, forms a short crest-like structure. The linea intermuscularis ventralis becomes more prominent distally.

Comparisons. Most of the Miocene cormorant taxa are created on, and are represented by, only scanty material, often a single bone, which makes comparisons, systematic determinations and phylogenetic discussions with these taxa difficult. For only a few species are a tibiotarsus, ulna and/or radius available for metrical and morphological comparisons (Table 3) with the material from Rauscheröd described here.

For comparison with extant taxa we consulted the only two European taxa, the Great Cormorant (*Phalacrocorax carbo*) and the European Shag (*P. aristotelis*, genus "*Stictocarbo*" after Siegel-Causey, 1988), and a representative of the microcormorants and the darters. The last are usually accepted to be a sister taxon of cormorants; for our comparisons, we selected an American Darter (*Anhinga anhinga*, North to South America).

The relationship of microcormorants (genus *Microcarbo* after Siegel-Causey, 1988) and other Phalacrocoracidae is still controversial. The osteological investigations of Siegel-Causey (1988) resulted in a position of the *Microcarbo* species within the taxon "Phalacrocoracinae" ("cormorants"), which itself is considered as a sister taxon of "Leucocarboninae" (shags). On the other hand, the analyses of mitochondrial sequence data by Kennedy *et al.* (2000) found that the microcormorants are the sister group of all other Phalacrocoracidae. Owing to the probable basal phylogenetic position of the microcormorants, we considered also the Little Pied Cormorant (*P. (M.) melanoleucos*, Australia, New Zealand, Tasmania, Indonesia, and some adjacent islands) for comparisons (hereafter *Microcarbo melanoleucos*).

Numbers in the following descriptions refer to features in Figs 4 and 5.

Comparison of tibiotarsus (Fig. 4). In comparison with the tibiotarsi of the extant taxa *Phalacrocorax carbo* and *P. aristotelis*, that of ?*B. tardatus* differs by having (1) higher and stronger protuberances proximal on the facies articularis. (2) thickening at the tip of the crista cnemialis lateralis, slightly more developed than in *Anhinga* and in *?B. stoeffelensis* (Mayr, 2007, fig. 6G), but less developed than in *Microcarbo*. Crista patellaris roughly aligned mediolaterally indicating that the tip of the crista cnemialis

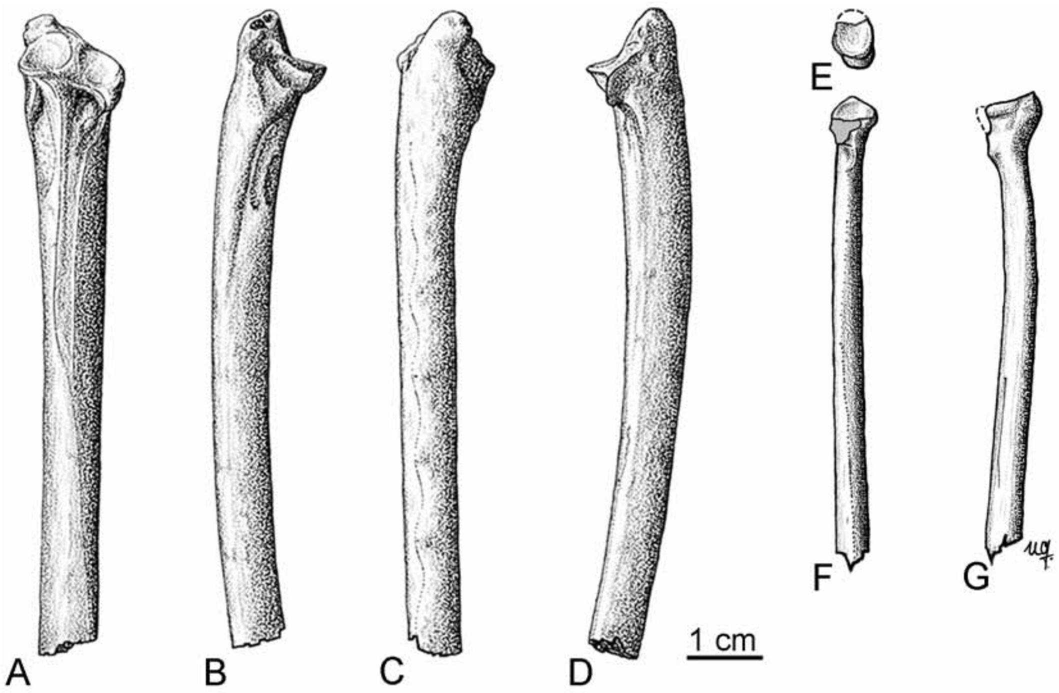

Figure 3. ?*Borvocarbo tardatus* n.sp. from the Early Miocene of Rauscheröd, left ulna (BSPG 1990 IV 17, paratype) in (*A*) cranial, (*B*) ventral, (*C*) caudal and (*D*) dorsal aspects, and right radius (BSPG 1990 IV 18, paratype) in (*E*) proximal, (*F*) ventral and (*G*) caudal aspects. Grey-shaded areas indicate damages.

Table 3. Availability of comparative material of fossil Oligocene and Miocene taxa of Phalacrocoracoidea from Europe and circum-Mediterranean regions.

fossil taxon	occurrence	tbt	prox. ulna	prox. radius	elements
Phalacrocorax					
P. intermedius	France, Germany, Austria, early Middle Miocene	—	—	—	humerus, coracoid, prox.cmc, vertebra
P. ibericus	Valles de Fuentiduena (Spain), Upper Miocene (MN9)	—	—	—	dist.humerus
P. lautus	Golboçica (Moldova), Upper Miocene (MN9?)	—	—	—	prox.femur, dist.ulna
P. serdicensis	Hrabarsko (Bulgaria), Late Miocene (MN11–13)	—	—	●	prox.humerus, prox.+dist. cmc, cran.+caud.coracoid, sternum, prox. scapula, prox.radius, dist.ulna
P. longipes	Ukraine, Late Miocene and Pliocene	—	—	—	prox.femur
Borvocarbo					
B. guilloti	Créchy, Allier (France), Late Oligocene, MP30	—	—	—	coracoid
?*B. stoeffelensis*	Enspel (Germany), Oligocene	●	●	●	partial skeleton
Oligocorax					
O. littoralis	France, Early Miocene	●	●	—	humerus, prox.ulna, femur, dist.tbt, prox.tmt
Nectornis					
N. miocaenus	France, Germany and Czechia, Lower Miocene	●	●	●	coracoid, scapula, ulna, radius, cmc, femur, tbt, tmt, sternum, furcula, pelvis
N. anatolicus	Turkey, Early/Middle Miocene	—	—	—	coracoid, prox.humerus, dist.ulna, dist.radius, cmc
Limicorallus					
?*L. carbunculus*	Probably Mainz-Weisenau (Germany), Lower Miocene	—	—	—	tmt
Anhinga					
A. pannonica	Tatarus-Brusturi (Romania) and Götzendorf (Austria), Late Miocene; Tunisia, Late Miocene	—	—	—	vertebra, humerus

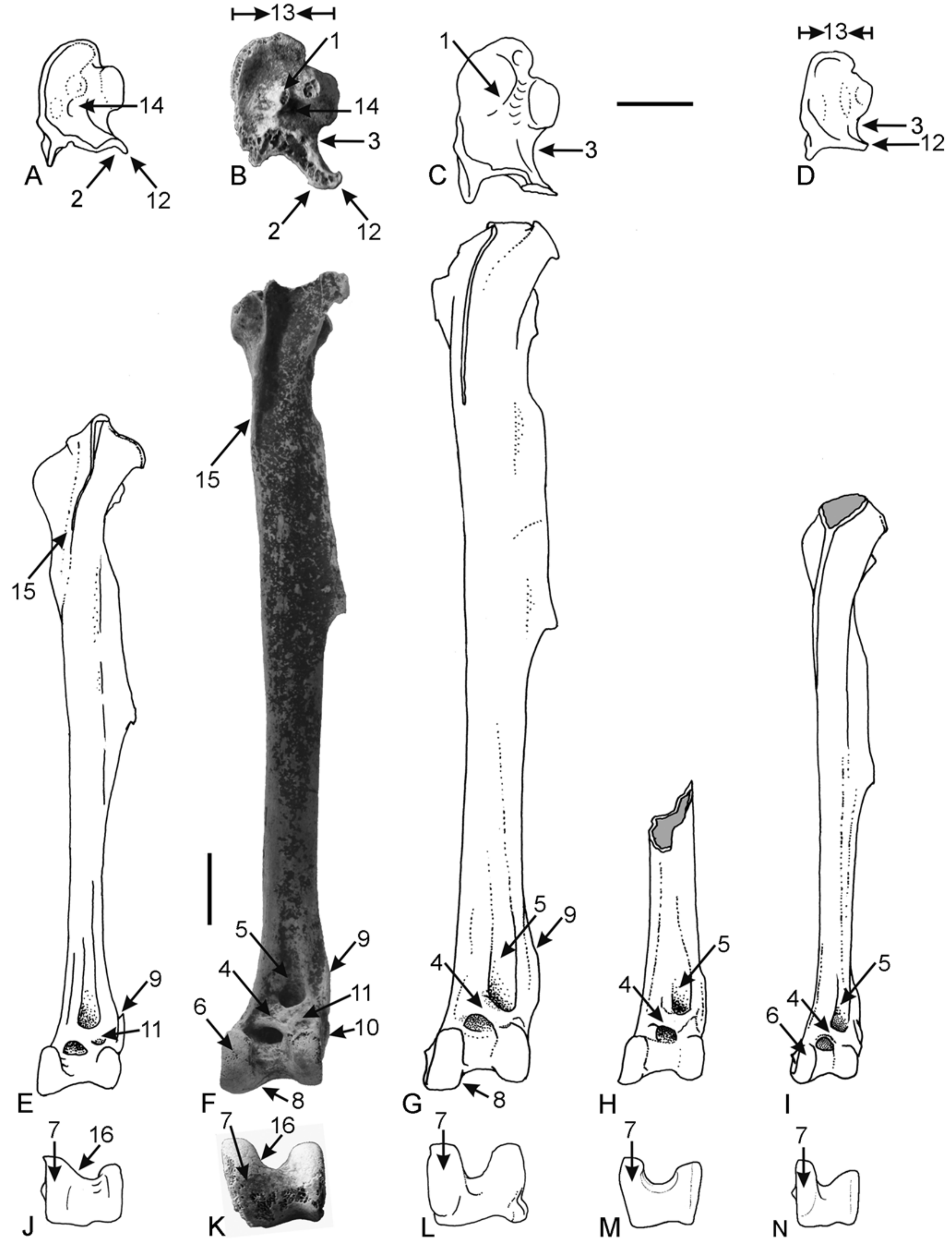

Figure 4. Distinguishing features of the tibiotarsi of (*A, E, J*) *Anhinga anhinga*, (*B, F, K*) ?*Borvocarbo tardatus* n.sp., (*C, G, L*) *Phalacrocorax carbo*, (*H, M*) *Oligocorax littoralis* (inverse, MNHN Av 9432), and (*D, I, N*) *Nectornis miocaenus* (MNHN Av 9411); in proximal (A–D), cranial (E–I), and distal (J–N) aspects.

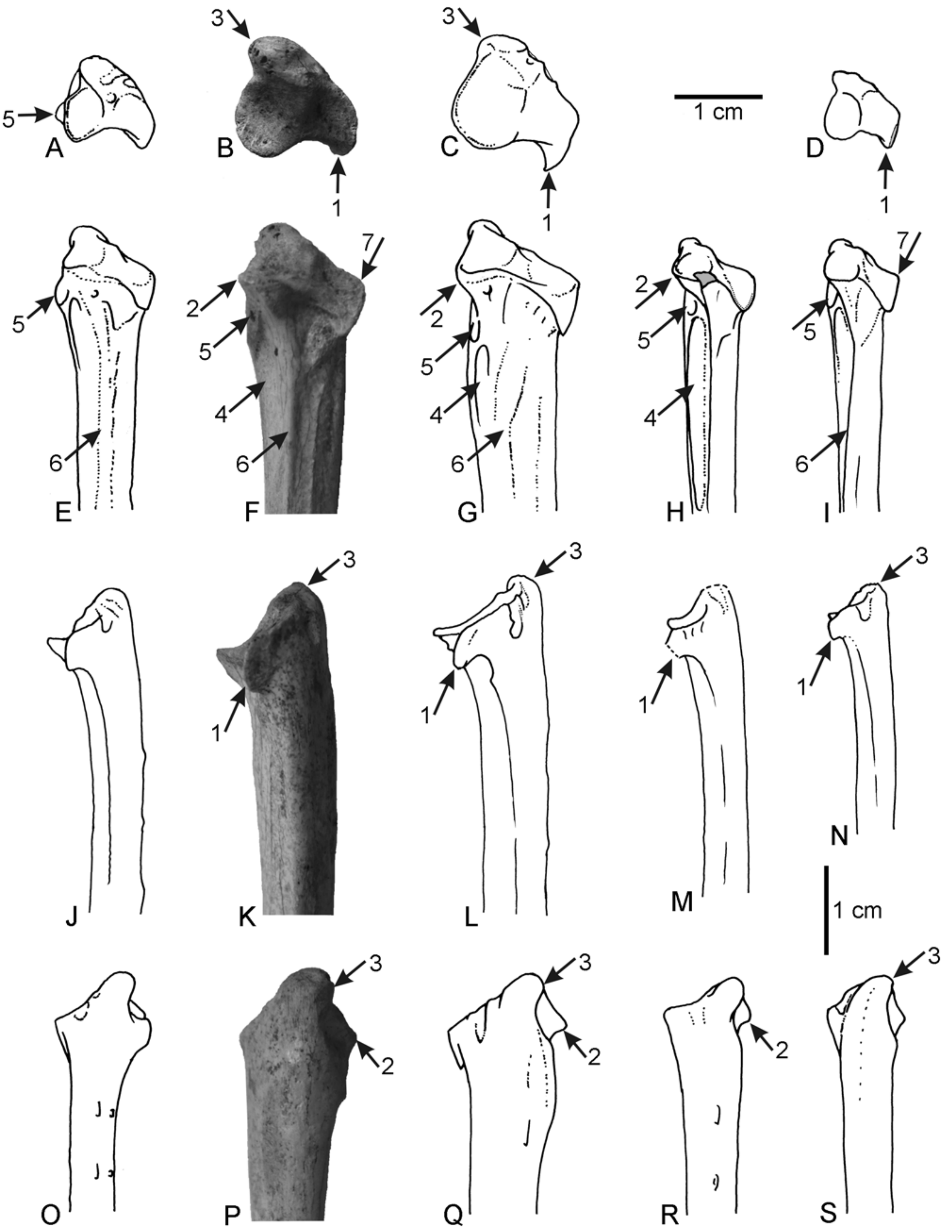

Figure 5. Distinguishing features of the ulnae of (*A, E, J, O*) *Anhinga anhinga*, (*B, F, K, P*) ?*Borvocarbo tardatus* n.sp., (*C, G, L, Q*) *Phalacrocorax carbo*, (*H, M, R*) *Oligocorax littoralis* (MNHN Av 9430) and (*D, I, N, S*) *Nectornis miocaenus* (MNHN Av 9375); in proximal (*A–D*), cranial (*E–I*), dorsal (*J–N*) and caudal (*O–S*) aspects.

lateralis was not offset cranially. (3) incisura tibialis deeply expressed, as for example in *Anhinga*, while in *P. carbo, P. aristotelis* and *Microcarbo* it makes a shallow curve. (4) a less oblique (almost horizontal) and proximodistally wide pons supratendineus and (5) a sulcus extensorius that runs almost in the midline of the shaft (more laterally in *Phalacrocorax*, meaning in *P. carbo* and *P. aristotelis* also in the following text). (6) The condylus medialis is stronger (about same size as condylus lateralis) than in *Phalacrocorax* and, in distal view, (7) is tilted slightly obliquely in the mediocranial direction so that the distal trochlea tapers slightly caudally, whereas in *Phalacrocorax* the condyles and their medial and lateral margins are almost parallel. In cranial view, (8) the condylus medialis is distally shorter than in *Phalacrocorax*, only slightly distally surpassing the lateral one. (9) The tuberculum retinaculi m. fibularis is less prominent and proximally ends less abruptly than in extant *Phalacrocorax*. (10) The epicondyli medialis and lateralis are stronger than in extant *Phalacrocorax*. (9) The apophysis externa ligamenti obliqui (Ballmann, 1969) is stronger and more individualised.

The microcormorant *Microcarbo melanoleucos* is almost half of the size of ?*B. tardatus* and furthermore differs in its tibiotarsus in the aforementioned mentioned features (3) (4), (5), (6), (7), (10), and (11). In *M. melanoleucos*, (2) the crista patellaris is roughly flat and aligned lateromedially and joins the caudal side of the thickened tip of the crista cnemialis lateralis, (4) the pons supratendineus is more oblique, (5) the sulcus extensorius runs more laterally, (6) the condylus medialis is more slender (in cranial and distal views) than the lateral one and, in cranial view, is tilted distomedially (almost vertical in ?*B. tardatus*), and (10) the epicondyli medialis and lateralis and (11) the apophysis externa ligamenti obliqui are weaker. Furthermore, in proximal view, the lateral prominence for the contact with the caput fibulae is more pointed in *M. melanoleucos*.

No tibiotarsus of *P. intermedius* is known so far. Metrical comparisons of other skeletal elements suggest that *P. intermedius* and ?*B. tardatus* might have been of similar size. On the other hand, *N. miocaenus, N. anatolicus* and *O. littoralis* are all distinctly smaller than the new Rauscheröd cormorant.

Unlike the tibiotarsus of *O. littoralis* from Saint-Gérand-le-Puy (MN2, France) (Milne-Edwards 1867–1871b, pl. 42, figs 9–12) that of ?*B. tardatus* differs by the aforementioned features (4) and (5): (4) the pons supratendineus is less oblique in transversal direction in comparison to that of *O. littoralis*. In distal view, (7) the distal condyles of both taxa are similar in tapering slightly caudally, but in *P. littoralis*, the condyles are oriented more parallel, whereas in ?*B. tardatus* the condylus medialis is slightly oblique.

The tibiotarsus of ?*B. tardatus* differs from that of *Nectornis* by its more cranially projecting crista cnemialis cranialis (in medial view) and by (12) a much more projecting and craniolaterally oriented crista cnemialis lateralis (in proximal view). (13) The proximal end is mediolaterally wider (in relation to depth) and the lateral margin of the facies articularis lateralis projects more laterally. (5) The sulcus extensorius runs almost along the midline of the shaft (situated more laterally in *Nectornis*) and (4) the pons supratendineus is less oblique in transversal and cranial directions than in *Nectornis*. (6) The condylus medialis is broader and (7) tapers slightly caudally (in distal view) in ?*B. tardatus*, whereas the medial and lateral margins are parallel in *Nectornis*.

In contrast to the conditions in *A. anhinga*, in ?*B. tardatus* (14) the fossa synovialis externa (Ballmann, 1969) on the proximal end of the tibiotarsus is deeper and (12) the crista cnemialis lateralis projects further craniolaterally (in proximal view). (15) The crista cnemialis cranialis is cranially convex at its distal base (in medial view) (concave in *Anhinga*). (9) The tuberculum retinaculi m. fibularis is situated more proximally on the distal end and (11) the apophysis externa ligamenti obliqui forms a strong tubercle proximal to the condylus lateralis, whereas in *A. anhinga* it forms a deep fossa. In distal view, (16) the incisura intercondylaris in ?*B. tardatus* is less asymmetric. ?*B. tardatus* and *A. anhinga* agree well in the presence of strong protuberances on the proximal articular surface, the shape of the incisura tibialis, the position of the sulcus extensorius and the orientation of the pons supratendineus.

As in ?*B. stoeffelensis*, the condylus medialis of the distal tibiotarsus of ?*B. tardatus* protrudes only slightly further distally than the condylus lateralis (Mayr 2007). Unfortunately, the second diagnostic feature of the tibiotarsus of ?*B. stoeffelensis*, the crista patellaris without lateral proximal projection, cannot be ascertained because of the incomplete preservation of the Rauscheröd tibiotarsus.

Comparison of ulna (Fig. 5). The proximal ulna of ?*B. tardatus* is distinguished from those *P. carbo* and *P. aristotelis* by having (1) a less prominent and less projecting processus cotylaris dorsalis without a hook-like distal end; (2) the ventral edge of the cotyla ventralis projecting less ventrally; (3) the olecranon more swollen and projecting more proximally (best observed in caudal view, difference in elevation between proximal end of cotyla ventralis and of olecranon); (4) the impressio brachialis shallower proximally; (5) the tuberculum lig. collateralis ventralis situated more proximally, just below the margin of the cotyla ventralis (more distally in *P. carbo* and *P. aristotelis*); (6) the linea intermuscularis forming a more prominent crest along the midline of the cranial surface of the proximal shaft.

Several of these aforementioned distinguishing features between the ulna of ?*B. tardatus* and those *P. carbo* and *P. aristotelis* do not distinguish between ?*B. tardatus* and the microcormorant *M. melanoleucos*. However, beside the distinctly smaller size of the *M. melanoleucos*, the species also clearly differs from ?*B. tardatus* by having (1) a well-developed hook-like projecting processus cotylaris, (3) a less swollen and less proximoventrally projecting olecranon, and a less cranially projecting margin of the cotyla ventralis.

Unlike in *O. littoralis* (Milne-Edwards, 1867–1871b, pl. 44, figs 6–8), in ?*B. tardatus* (1) the processus cotylaris dorsalis is less prominent and less projecting, without a hook-like distal end (even if a little broken in *O. littoralis*); (5) the tuberculum lig. collateralis ventralis is situated more proximally; (2) the ventral edge of the cotyla ventralis projects less ventrally, and (4) the impressio brachialis is shallower (also in its distal extent).

In contrast to that of *N. miocaenus*, the ulna of ?*B. tardatus* has (1) the processus cotylaris dorsalis without the hook-like distal end, (3) the olecranon more swollen and projecting slightly more proximally, (5) the tuberculum lig. collateralis ventralis projecting slightly less ventrally, (7) the dorsocaudal border of the cotyla dorsalis rounded (in *Nectornis* it forms an angle) and (6) the crest-like linea intermuscularis along the proximal part of the cranial surface of the shaft more prominent than in *Nectornis*.

Unlike that of *A. anhinga*, the tuberculum lig. collateralis ventralis of ?*B. tardatus* is (5) weaker and less projecting ventrally and (6) the crest-like linea intermuscularis is more prominent.

Unlike in members of the compared fossil and extant Phalacrocoracidae (inclusive also *M. melanoleucos*), but similar to *Borvocarbo*, species of the Anhingidae have the distal hook-like process of the cotyla dorsalis less developed.

Comparison of radius. The proximal end of the radius of ?*B. tardatus* is more similar to that of *Anhinga* than to those of extant cormorants, in which the tubercle-like caput radii is more prominent and projects further dorsally than in the Rauscheröd specimen.

Discussion and results

The detailed osteological comparisons above exclude an affiliation of the present material to the taxa *Phalacrocorax* (represented by *P. carbo* and *P. aristotelis*), the microcormorants (represented by *M. melanoleucos*), *Nectornis*, and *Oligocorax*. Furthermore, ?*L. carbunculus* differs from the Rauscheröd form by its diminutive size. Even if there are some morphological resemblances to *Anhinga*, the cormorant from Rauscheröd shows best correspondence with *Borvocarbo*.

The original description and diagnosis of the genus *Borvocarbo* (Mourer-Chauviré *et al*., 2004) is based on only a coracoid of *B. guilloti* from the Late Oligocene of Créchy (France). Recently, Mayr (2007) described the new cormorant species ?*B. stoeffelensis*, based on a partial skeleton from the Late Oligocene of Enspel (Germany), which he tentatively referred to *Borvocarbo*. A definite generic assignment was not possible because the type species was itself described from only a coracoid, which in the Enspel fossil is very poorly preserved.

In the case of the Rauscheröd cormorant material, the coracoid is also unknown, but the ulna and tibiotarsus share some characteristic features with ?*B. stoeffelensis*. Another reason to assign the Rauscheröd form to ?*Borvocarbo* is its possession of primitive osteological characters compared to those of the Neogene forms.

The new species ?*B. tardatus* from Rauscheröd is distinctly larger than both ?*B. stoeffelensis* and *B. guilloti* and is thus the largest representative of *Borvocarbo*. The estimated size of ?*B. tardatus* is between the *P. carbo* and *P. aristotelis*; the greatest length of the tibiotarsus is about 27% longer than that of ?*B. stoeffelensis*. According to Mayr (2007), the absences of a hook-like distal projection of the processus cotylaris dorsalis on the ulna and of a proximal process on the crista cnemialis lateralis on the proximal tibiotarsus are plesiomorphic features within Phalacrocoracoidea (Mayr, 2007). Unfortunately, the latter character is not preserved in the ?*B. tardatus* material. Mayr (2007) concluded that ?*B stoeffelensis* is positioned outside the crown group Phalacrocoracidae + Anhingidae. All the characters described here for the tibiotarsus, ulna, and radius of ?*B. tardatus* are plesiomorphic in comparison with the Recent Phalacrocoracidae.

If the attribution to the genus *Borvocarbo* were to be correct, this new record extends the stratigraphical range of *Borvocarbo* from the Late Oligocene into the Early Miocene of Europe.

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