



## **A *Haematopus*-like skull and other remains of Charadrii (Aves, Charadriiformes) from the Early Miocene of Saint-Gérard-le-Puy (Allier, France)**

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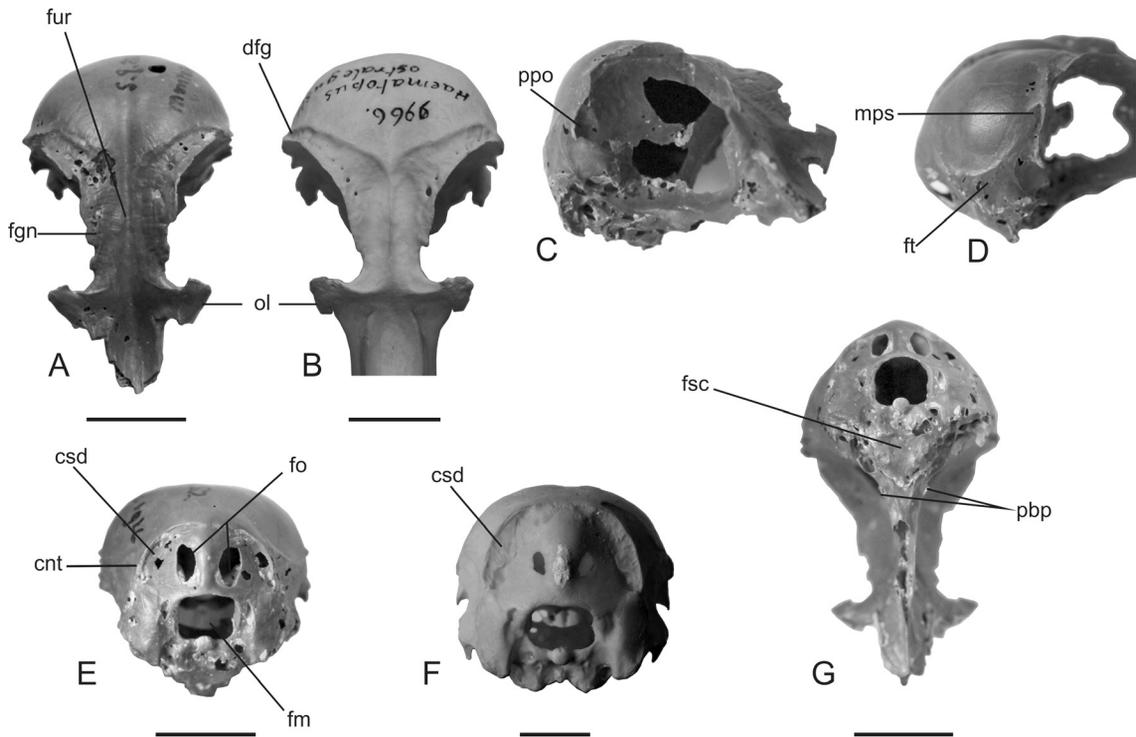
**Abstract** — Among Charadriiformes (shorebirds and allies), Charadrii (plovers and allies) have the poorest fossil record. The lacustrine, early Miocene deposits of Saint-Gérard-le-Puy in France have yielded several charadriiform birds, but so far no members of the Charadrii. We identified a *Haematopus* (oystercatcher)-like skull from the early Miocene locality of Montaigu-le-Blin, in the Saint-Gérard-le-Puy area. Affinities to extant Haematopodidae are, apart from an overall similarity, supported by two features of the occipital region not present in any other of the examined charadriiforms. The fossil nevertheless differs from recent oystercatchers in some osteological features, including much shallower temporal fossae. Additionally, we report two fossil remains of plover-like Charadrii, a humerus and a tarsometatarsus, which also represent the first record of this charadriiform clade in Saint-Gérard-le-Puy. The specimens resemble the corresponding bones of Charadriidae but a definitive assignment to that taxon is not possible.

**Key words:** Fossil birds, shorebirds, plovers, oystercatcher, Charadriidae

### **Introduction**

Most knowledge of early Miocene (Aquitanian, MN 1–2, 23–20.5 Ma) fossil avifaunas from Europe has been gleaned from few fossil rich localities, predominantly in France and Germany (MLÍKOVSKÝ 1992, 1996). Amongst these, the localities that make up Saint-Gérard-le-Puy are perhaps the best known and, being of lacustrine origin, it is not surprising that most fossil remains recovered from these localities can be referred to aquatic or semi-aquatic taxa. Despite relative abundant remains of Scolopaci and Lari (e.g., DE PIETRI *et al.* 2011; DE PIETRI & MAYR 2012), as yet no representatives of Charadrii (plovers, oystercatchers, thick-knees, and allies) have been described or mentioned.

The clade Charadrii encompasses the following families: Chionidae (sheathbills), Pluvianellidae (Magellanic Plover), Pluvianidae (Egyptian Plover) Charadriidae (plovers and allies), Haematopodidae (oystercatchers), Recurvirostridae (stilts and avocets), Ibidorhynchidae (Ibisbill), and Burhinidae (thick-knees). Although phylogenies based on molecular data (BAKER *et al.* 2007; FAIN & HOUDE 2007) have recovered a paraphyletic Charadriidae, with *Pluvialis* (golden plovers and the Grey Plover) in a clade together with Recurvirostridae, Haematopodidae, and Ibidorhynchidae, more recent phylogenies (BAKER *et al.* 2012) support a monophyletic Charadriidae, with *Pluvialis* occupying a basal position within the family.



**FIGURE 1.** The fossil skull NMB S.G.20252 (**A, C–E, G**) from the early Miocene of Saint-Gérard-le-Puy in comparison to the extant Eurasian Oystercatcher, *Haematopus ostralegus* (**B, F**). **A, B**, dorsal views; **C, D**, right lateral views; **E, F**, occipital views, and **G**, ventral view. **C** and **D** not to scale. Abbreviations: csd, crescent-shaped deep depression dorsal to the crista nuchalis transversa; cnt, crista nuchalis transversa; dfg, caudal portion of fossa glandulae nasalis; fgn, fossae glandularum nasales; fm, foramen magnum; fo, fonticuli occipitales; fsc, fossa subcondylaris; ft, fossa temporalis; fur, furrow at interorbital surface of the frontal bone; mps, scar marking the attachment for musculus pseudotemporalis superficialis; ol, os lacrimale; pbp, articulation facets for processus basipterygoidei; ppo, processus postorbitales. Scale bars equal 10 mm.

The fossil record of the Charadrii is very poor in comparison to that of other shorebirds (*i.e.*, Scolopaci and Lari), and the scarcity of Paleogene examples is particularly remarkable. Several specimens have been misassigned to this clade (OLSON 1985; MLÍKOVSKÝ 2002; MAYR 2009), whereas better supported records are mostly of dubious affinities. Paleogene remains of the Charadrii include an almost complete skeleton of uncertain affinities from the early Oligocene of France (BESSONAT & MICHOUT 1973) and *Jiliniornis huadianensis* HOU & ERICSON, 2002, from the middle Eocene of China, tentatively placed in the Charadriidae by the authors. A putative record of the Recurvirostridae, *Recurvirostra sanctaeneboulae* MOURER-CHAUVIRÉ, 1978, from the early Eocene of France, was based on the proximal end of an ulna, but genus level assignment of this specimen certainly needs to be corroborated by further material (see OLSON 1985). A yet unde-

scribed burhinid from Late Oligocene deposits in Australia was mentioned by BOLES (2001).

Miocene Charadrii are somewhat better represented than their Paleogene counterparts. The existence of Charadriidae from the Middle Miocene of France was briefly acknowledged by BALLMANN (1972), and further material was reported from the Early Miocene of the Czech Republic (MN 4b; MLÍKOVSKÝ 2002), although unfortunately it was neither described nor figured. A species of *Charadrius* from the Late Miocene-Early Pliocene of Arizona was noted by BICKART (1990), and from the same locality, this author also described members of the Recurvirostridae, notably the species *Himantopus olsoni*, as well as a species of *Recurvirostra*. A distal ulna from the Middle Miocene of California was assigned to the extant genus *Recurvirostra* by MILLER (1961), but because of the uninformative nature of the remains this assignment remains uncer-

tain (see OLSON 1985). The only known Miocene representative of the Burhinidae is *Burhinus lucorum*, from the Early Miocene of Nebraska (BICKART 1982), which was described on the basis of a humerus. Determining a well-resolved phylogenetic placement for most of these Miocene specimens is nevertheless likely to remain an elusive task, owing to the fragmentary nature of the material.

In this study we describe a skull of a putative oystercatcher collected from the locality of Montaigu, Allier, France, in the 1920s, which is housed in the Natural History Museum Basel, Switzerland. In addition, we describe a humerus of a plover-like bird and a tarsometatarsus, both of uncertain affinities within the Charadrii. Due to the rarity of Charadrii in early Neogene deposits, these remains contribute importantly to closing a vast gap in the fossil record of the group.

## Materials and methods

**Institutional abbreviations:** *MNHN*, Muséum National d'Histoire Naturelle, Paris, France; *NMB*, Natural History Museum Basel, Switzerland; *SMF*, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

Anatomical terminology follows BAUMEL & WITMER (1993); measurements are in millimetres (mm). The following species of extant Charadriiformes were used in comparisons (from NMB and SMF):

Charadrii: Burhinidae: *Burhinus oedicnemus*; “Charadriidae”: *Charadrius hiaticula*, *C. morinellus*, *Vanellus chilensis*, *V. coronatus*, *V. vanellus*, *Pluvialis apricaria*, *P. squatarola*; Chionidae: *Chionis minor*; Haematopodidae: *Haematopus moquini*, *H. ostralegus*; Pluvianidae: *Pluvianus aegyptius*; Recurvirostridae: *Recurvirostra avosetta*. Lari: Dromadidae: *Dromas ardeola*; Glareolidae: *Cursorius temminckii*, *Glareola pratincola*; “Sternidae”: *Anous stolidus*, *Chlidonias niger*, *Larosterna inca*, *Sterna paradisaea*, *S. saundersi*, *Thalasseus bergii*; Stercorariidae: *Catharacta skua*, *Stercorarius parasiticus*; Laridae: *Larus argentatus*, *L. canus*, *L. fuscus*, *L. hyperboreus*, *L. marinus*, *L. ridibundus*, *Rissa tridactyla*, *Xema sabini*,

*Rhodostethia rosea*. Scolopaci: Scolopacidae: *Actitis hypoleucos*, *Arenaria interpres*, *Calidris alpina*, *Limosa lapponica*, *L. limosa*, *Numenius arquata*, *N. phaeopus*, *Phalaropus fulicarius*, *Philomachus pugnax*, *Scolopax rusticola*, *Tringa erythropus*, *T. totanus*; Rostratulidae: *Rostratula benghalensis*, *R. semicollaris*; Jacanidae: *Actophilornis africanus*, *Hydrophasianus chirurgus*, *Jacana jacana*.

## Systematic Palaeontology

**Aves LINNAEUS, 1758**

**Charadriiformes HUXLEY, 1867**

**Charadrii sensu PATON *et al.* (2003)**

**Family incertae sedis, cf. Haematopodidae  
gen. et sp. indet.**

(Fig. 1)

**Material:** NMB S.G.20252 (cranium).

**Locality and age:** Montaigu, “Saint-Gérandle-Puy” area, Allier Basin; Early Miocene, MN2 (22.5–20.5 Ma).

**Measurements:** Maximum width of cranium across the widest part of the braincase (across processus postorbitales): 19.4 mm; maximum length as preserved: 34.5 mm; greatest diagonal diameter of foramen magnum: 5.2 mm; width across lacrimals: 14.4 mm; condylus occipitalis to ossa lacrimalia: 25.2 mm.

**Description and comparisons:** NMB S.G.20252 can be assigned to the Charadrii, and particularly a close relationship with Charadriidae, Recurvirostridae, and Haematopodidae can be presumed, based on the combination of the following characters: the presence of well developed, caudally extensive, fossae glandularum nasales, a distinct second opening caudal of foramen nervi maxillomandibularis, the presence of functional processus basipterygoidei, and the presence of well-developed fonticuli occipitales (see description and also MAYR 2011).

The specimen (NMB S.G.20252) is approximately the size of the Pied Avocet, *Recurvirostra avosetta*, and is smaller than all species of extant Haematopodidae. There is a close resemblance between NMB S.G.20252 (Fig. 1A) and the skull of *Haematopus ostralegus* (Fig. 1B). The fossae

glandularum nasales are distinct and separated by a midline furrow. As in most charadriiforms, the interorbital surface of the frontal bone displays a marked furrow between the fossae glandularum nasales (Fig. 1A), whereas in *Haematopus* there is a ridge (Fig. 1B), which is also present in members of the Lari, such as Stercorariidae, Alcidae, and Laridae. The presence of this ridge is likely to be related to the depth of the fossae glandularum nasales, which are deeper in *Haematopus* and the above mentioned taxa. Unlike in *Recurvirostra*, this frontal furrow is well marked. The supra-orbital rims of the fossae are not as wide or elevated as that of members of the Charadriidae, and most closely resembles the condition found in species of *Haematopus*. Contrary to the condition present in members of the Charadriidae, there is no marked circular incision or foramen formed by the duct of the nasal gland on the frontal (MAYR 2011). The lacrimals (Fig. 1A) are fused to the nasals, and are wide and dorsally projecting, similar to those of *Haematopus ostralegus* (Fig. 1B), but larger. Only a small portion of the descending process is preserved, which appears to have been mediolaterally compressed.

The processus postorbitales are short (Fig. 1C) and, unlike in oystercatchers, the fossae temporales (Fig. 1D) are weakly developed. The attachment for musculus pseudotemporalis superficialis (Fig. 1D) rostral to the processus postorbitales on the dorsocaudal rim of the orbit is very well marked, as in species of *Haematopus* and some charadriids (e.g., *Vanellus*), ending in a marked projection dorsal to the processus postorbitalis at the orbital rim. A processus zygomaticus is present, but whether it is shorter or approximately the same length as the processus suprameaticus (as in most members of the Scolopaci and Charadrii), cannot be established owing to the skull's preservation.

The general shape of the occipital region of NMB S.G.20252 (Fig. 1E) is also very similar to that of *Haematopus ostralegus* (Fig. 1F). Contrary to the condition in all other examined charadriiforms (except some members of the Alcidae), there is a deep crescent-shaped depression dorsal to the crista nuchalis transversa (Fig. 1E). In addition, the foramen magnum, in occipital view, displays a subsquare shape, with a straight dorsal rim (Fig. 1E); among extant charadriiforms

these features are only observed in species of *Haematopus* and NMB S.G.20252. The fossa subcondylaris is deep and wide (Fig. 1G). The fonticuli occipitales (Fig. 1E) are much larger than those of most examined Recent Charadriiformes, but similar to those of some charadriids (e.g., *Charadrius hiaticula*, *C. morinellus*). The presence of functional but weakly developed processus basiptyergoidei is demonstrated by the marked articulation surface on the base of the skull (Fig. 1G). Basiptyergoid processes are present in most members of the Scolopaci and Charadrii (see STRAUCH 1978).

**Family incertae sedis, gen. et sp. indet.**

(Fig. 2, Table 1)

**Material:** MNHN Av. 4102 (left tarsometatarsus).

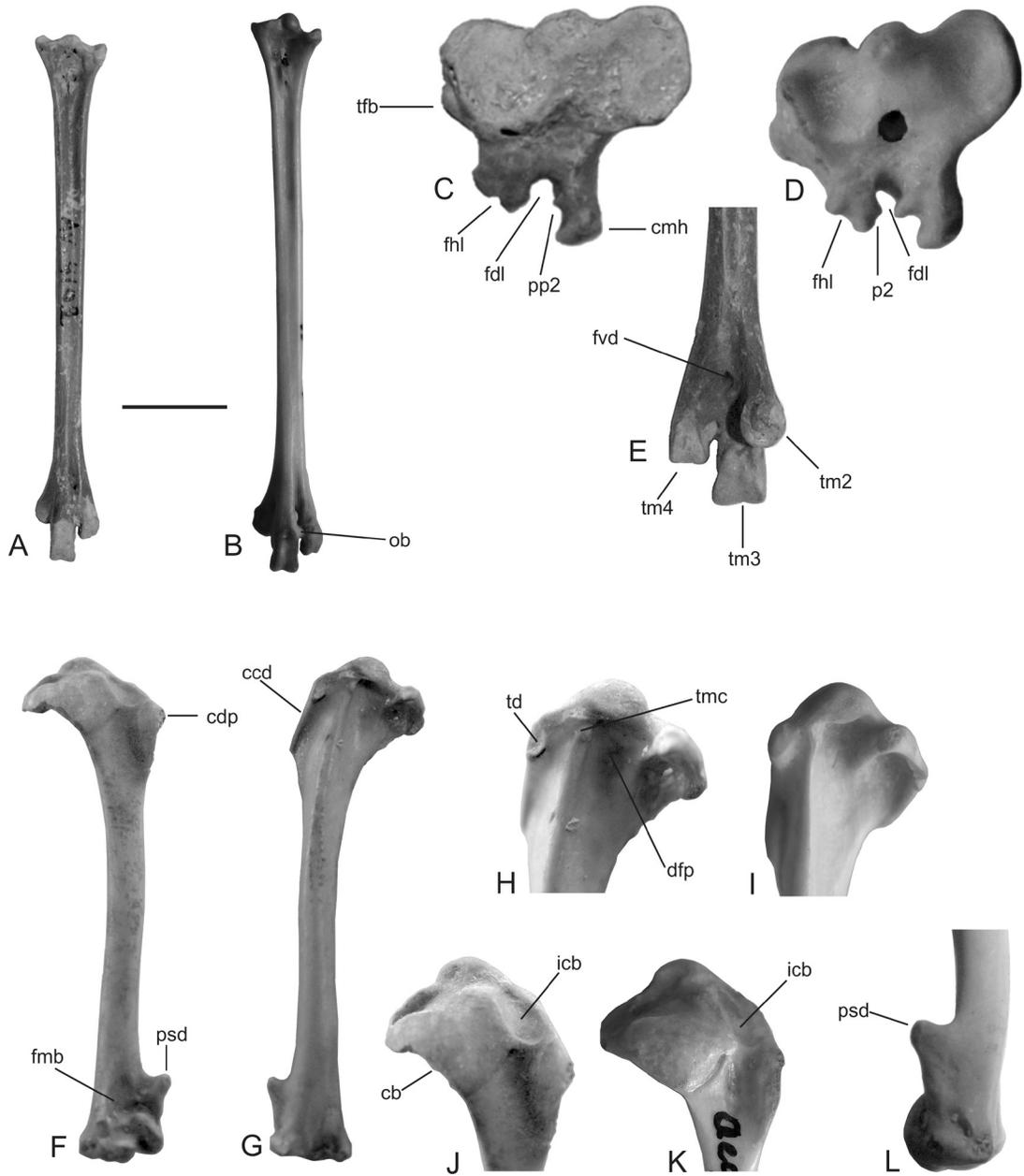
**Locality and age:** “Saint-Gérard-le-Puy”, possibly Langy or Montaigu; Early Miocene, MN2 (22.5–20.5 Ma).

**Measurements:** see Table 1.

**Remarks:** MNHN Av. 4102 (Fig. 2A) is about the size of the Grey Plover, *Pluvialis squatarola*, which is the largest member of the Charadriidae. This bone was found in MNHN among the material attributed to *Laricola desnoyersii* (MILNE-EDWARDS, 1868; see also DE PIETRI *et al.* 2011), but was neither figured nor mentioned by Milne-Edwards (1867–1868).

**Description and comparison:** MNHN Av. 4102 can be assigned to the Charadrii based on the shape of the hypotarsus (Fig. 2C), in which the sulcus for the tendon of musculus flexor digitorum longus is centrally positioned (Fig. 2C, D). This configuration is characteristic for representatives of the Charadrii, and differs from most representatives of the Scolopaci in which there is a canal for the tendon of musculus flexor digitorum longus (MAYR 2011).

The proximal end of MNHN Av. 4102, although appreciably worn, displays a very prominent tuberculum m. fibularis brevis (Fig. 2C), which also characterizes most members of the Charadrii. At the distal end, the foramen vasculare distale (Fig. 2E) is proportionally smaller than in *Pluvianus aegypticus* and members of the Charadriidae, but resembles the condition found in representatives of the genus *Pluvialis*. The osseous bridge (Fig. 2B) between the foramen



**FIGURE 2.** Left tarsometatarsus (MNHN Av. 4102) and left humerus (MNHN SG 13754) of plover-like birds from the early Miocene of Saint-Gérard-le-Puy in comparison with extant Charadriidae. **A, B**, dorsal view of tarsometatarsus MNHN Av. 4102 (**A**), and of *Vanellus vanellus* (**B**); **C, D**, hypotarsi of MNHN Av. 4102 (**C**), and *Pluvialis squatarola* (**D**, mirrored); **E**, plantar view of distal end of MNHN Av. 4102. **F, G**, humerus MNHN SG 13754 in cranial (**F**) and caudal (**G**) views; **H, I**, caudal views of the proximal end of humeri of MNHN SG 13754 (**H**), and *Vanellus vanellus* (**I**); **J, K**, cranial view of proximal end of MNHN SG 13754 (**J**), and *Charadrius hiaticula* (**K**); **L**, dorsal view of distal humerus MNHN SG 13754. Abbreviations: ob, osseous bridge; cb, crista bicipitalis; ccd, craniodorsal margin of crista deltopectoralis; cdp, crista deltopectoralis; cmh, crista medialis hypotarsi; dfp, dorsal fossa pneumotricipitalis; fdl, canal/sulcus for musculus flexor digitorum longus; fh1, sulcus for musculus flexor hallucis longus; fmb, fossa musculi brachialis; fvd, foramen vasculare distale; icb, impressio coracobrachialis; p2, sulcus for tendon of musculus flexor perforatus digiti II; pp2, sulcus for tendon of musculus flexor perforans et perforatus digiti II; psd, processus supracondylaris dorsalis; sps, scar on processus supracondylaris dorsalis; td, tuberculum dorsale; tfb, tuberculum musculus fibularis brevis; tm2, trochlea metatarsi II; tm3, trochlea metatarsi III; tm4, trochlea metatarsi IV; tmc, tubercle on proximal-most end of margo caudalis. Scale bars equal 10 mm. C–E and H–L not to scale.

vasculare distale and the incisura intertrochlearis lateralis is broader in MNHN Av. 4102 than in members of the Charadriidae, and again, this feature is also found in members of the extant genus *Pluvialis*, but also in *Recurvirostra*.

MNHN Av. 4102 is slightly larger than the tarsometatarsus of most specimens of the fossil laromorph *Laricola desnoyersii* (see DE PIETRI *et al.* 2011); its distal end clearly differs from that of members of the Lari in the more elongated trochlea metatarsi III (as in the clades Charadrii and Scolopaci). Most importantly, as in all taxa in the Charadrii with the exception of the Chionidae, a fossa metatarsi I is absent.

Overall, MNHN Av. 4102 differs from the tarsometatarsus of *Haematopus ostralegus* in that it is more slender, with a proportionally longer shaft and relatively more narrow articular ends, and from the corresponding bone of *Recurvirostra* (Avocets, Recurvirostridae) in that it is not as long or slender. Thus, MNHN Av. 4102 displays plover-like proportions (Fig. 2A). No other postcranial elements that can be attributed to the Charadrii have been found in the collections housed in NMB and MNHN to match this tarsometatarsus in size, although it would agree with the oystercatcher-like skull described above (see discussion).

**Family incertae sedis**

**cf. Charadriidae gen. et sp. indet.**

(Fig. 2, Table 1)

**Material:** MNHN SG 13754 (left humerus).

**Locality and age:** “Saint-Gérard-le-Puy”, possibly Langy or Montaigu; Early Miocene, MN2 (22.5–20.5 Ma).

**Measurements:** see Table 1.

**TABLE 1.** Measurements (in mm) of humerus MNHN SG 13754 and tarsometatarsus MNHN Av. 4102.

	Humerus		Tarsometatarsus	
	MNHN SG 13754	MNHN Av. 4102	MNHN SG 13754	MNHN Av. 4102
Greatest length	28.1	49.5		
Proximal width	6.9	6.8		
Distal width	4.3	6.2		
Min. width of shaft	1.9	2.7		

**Remarks:** MNHN SG 13754 (Fig. 2F, G) is very small, approximately the size of humeri of the Common Ringed Plover, *Charadrius hiaticula* (Charadriidae).

**Description and comparisons:** MNHN SG 13754 can be assigned to the Charadrii based on the combination of the following features: well-developed dorsal fossa pneumotricipitalis, concave crista deltopectoralis (absent in most Scolopaci), absence of transverse ridge across incisura capitis (present in Scolopaci), wide impressio coracobrachialis (narrow in Laromorphae).

On the caudal surface of the proximal end, a well-developed second fossa pneumotricipitalis is present (Fig. 2H), a homoplastic trait within charadriiform birds, but nevertheless present in all representatives of the Charadrii except Burhinidae and absent from most members of the Scolopaci with the exception of taxa in the Thinocoridae (seedsnipes) and some Scolopaciidae. This trait is also variable within Lari, and is absent in Turnicidae, Glareolidae, Dromadidae and Stercorariidae (MAYR 2011), *Anous* (noddies), the fossil family Laricolidae (DE PIETRI *et al.* 2011), and many Pan-Alcidae (SMITH 2011). There is a well-marked tubercle on the proximal-most end of the margo caudalis (Fig. 2H), which among some of the examined Charadrii is also developed, albeit not as a tubercle but as an enlarged surface, as in the lapwing *Vanellus vanellus* (Fig. 2I). Contrary to the condition in most members of the Scolopaci, the dorsal surface of the crista deltopectoralis is concave (Fig. 2A, B), and its craniodorsal margin is slender. The tuberculum dorsale is well defined, but it does not protrude as strongly dorsally as in the laromorph genus from the same locality, *Laricola* (see DE PIETRI *et al.* 2011). The ventral rim of the crista bicipitalis (Fig. 2J) is slightly damaged. The cranial surface of the proximal humerus displays a wide impressio coracobrachialis (Fig. 2J), with a distinctly rounded dorsal margin of the intumescencia humeri, which distinguishes this humerus from that of the Laromorphae (see DE PIETRI *et al.* 2011). At the distal end, the processus supracondylaris dorsalis does not display the proximodistally elongated scar present in the plover genus *Vanellus* (Fig. 2L).

MNHN SG 13754 differs from *Pluvianus aegyptius* in the better developed, *i.e.*, further dorsally projecting, processus supracondylaris dorsalis, in that the shaft of the bone is not as curved, and in that the proximal and distal ends are not as dorsoventrally compressed as in *Pluvianus*. MNHN SG 13754 can also be differentiated from the corresponding bone of *Haematopus* in that the processus supracondylaris dorsalis projects further dorsally, and in that the fossa m. brachialis is proportionally larger in the fossil. It differs from the plover genus *Pluvialis* in that the second (dorsal) fossa pneumotricipitalis extends entirely under the caput humeri, and in that the impressio coracobrachialis is broader than in *Pluvialis*, thus resembling that of other charadriids in its proportions (Fig. 2K).

## Discussion

Most members of the Charadrii are not associated with lacustrine environments, and therefore would not have constituted a significant component of the avifauna of Saint-Gérand-le-Puy. Consequently it is not surprising that the fossil Charadrii here described represent the first record of this group from these Early Miocene localities.

As already mentioned, several features suggest an assignment of NMB S.G.20252 to the Charadrii, and more specifically to a clade including the Charadriidae, Recurvirostridae, and Haematopodidae (a clade including these families and Ibidorhynchidae was recovered by BAKER *et al.* (2007), BAKER *et al.* (2012), and MAYR (2011)). NMB S.G.20252 shares with species of *Haematopus* two derived features of the occipital region, absent from all other examined charadriiform taxa, namely the well-marked crescent shaped-depressions caudal to the crista nuchalis transversa and the subsquare shape of the foramen magnum. Despite a remarkable resemblance between *Haematopus* and NMB S.G.20252, both can be differentiated on the basis of distinctive features, such as the presence of a furrow at the interorbital region of the frontal of the fossil (as opposed to the presence of a ridge in *Haematopus*); also much shallower fossae temporales and larger fonticuli occipitales are present in the fossil skull. Establishing how NMB S.G.20252

relates to extant species of Haematopodidae and other Charadrii awaits the discovery of additional material.

The earliest unambiguous records of oystercatchers date from the Early and middle Pliocene, and come from North America. Two humeri from the Lower Pliocene of Lee Creek, North Carolina, lacking the proximal end and significantly differing in size, were referred to the extant genus *Haematopus* (OLSON & STEADMAN 1979; OLSON & RASMUSSEN 2001). A further specimen that can be classified within Haematopodidae is *Haematopus sulcatus* (BRODKORB, 1955), from the middle Pliocene of the Bone Valley formation of Florida and known from the distal end of a tibiotarsus. Although originally this specimen was assigned its own genus (*Palostralegus*) within Haematopodidae, it was later referred to the extant genus *Haematopus* by OLSON & STEADMAN (1979). All other fossil remains that have been classified within this family are from Pleistocene and Holocene sites (*e.g.*, BRODKORB 1967; TYRBERG 1998). Given the poor fossil history of oystercatchers, NMB S.G.20252 would not only represent the first Neogene European record of the family, but the earliest record worldwide.

Few species of extant Haematopodidae are present in inland environments; *Haematopus ostralegus* and *H. finschi* are found during the breeding season in inland habitats. The presence of an oystercatcher-like bird in lacustrine deposits therefore indicates that, similarly to *Haematopus ostralegus* and unlike most other oystercatchers, the species from Saint-Gérand-le-Puy was not restricted to coastal environments. The lake system of Saint-Gérand-le-Puy is notable for having functioned as breeding grounds for the very abundant laromorph *Laricola* (DE PIETRI *et al.* 2011). Whether it was also visited for this purpose by the above-described oystercatcher-like bird can, however, not be said based on the available material.

As already noted in the introduction, Neogene Charadriidae have been recorded as early as the Middle Miocene (MN 4b, MLÍKOVSKÝ 2002), although in most instances the phylogenetic affinities of these findings have not been formally assessed. The tarsometatarsus (MNHN Av. 4102) and the humerus (MNHN SG 13754) described herein represent the first records of

plover-like birds from Saint-Gérand-le-Puy. The tarsometatarsus displays plover-like proportions, and agrees with the tarsometatarsus of species of *Pluvialis* in the relatively smaller foramen vasculare distale, and in the broad osseous bridge between the foramen vasculare distale and incisura intertrochlearis lateralis. A potential close relationship with this genus, however, which in molecular phylogenies was recently recovered as a basal charadriid (BAKER *et al.* 2012), is only hypothetical, supported by overall resemblance and size, and the specimen can only be tentatively referred to the Charadriidae. It is also possible, that MNHN Av. 4102 and the oystercatcher-like skull NMB S.G.20252 represent the same taxon, as they do match in size. This would suggest that the morphology of the described tarsometatarsus is plesiomorphic for the Charadriidae/Haematopodidae/Recurvirostridae clade, a claim that can only be substantiated with further fossil finds. Similarly, and in the absence of derived humeral features supporting its referral to the Charadriidae, the small humerus MNHN SG 13754 can only be tentatively referred to as a member of this family, despite its overall resemblance to charadriid plovers. If future evidence supports a more confident placement within Charadriidae, both MNHN Av. 4102 and MNHN SG 13754 would become the earliest records of the family.

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### References

- BAKER, A. J., PEREIRA, S. L. & PATON, T. A. (2007): Phylogenetic relationships and divergence times of Charadriiformes genera: multigene evidence for the Cretaceous origin of at least 14 clades of shorebirds. *Biology Letters*, **3**: 205–209.
- BAKER, A. J., YATSENKO, Y., TAVARES, E.S. (2012): Eight independent nuclear genes support monophyly of the plovers: the role of mutational variance in gene trees. *Molecular Phylogenetics and Evolution*, **65**: 631–641.
- BALLMANN, P. (1972): Les oiseaux miocènes de Vieux-Collonges (Rhône). – *Documents des Laboratoires de Géologie de Lyon*, **50**: 94–101.
- BAUMEL, J. J., & WITMER, L. M. (1993): Osteologia. – In: BAUMEL, J. J., KING, A. S., BREAZILE, J. E., EVANS, H. E., & VANDEN BERGE, J. C. (eds.). Handbook of avian anatomy: Nomina Anatomica Avium, 2<sup>nd</sup> Edition. *Publications of the Nuttall Ornithological Club*, **23**: 45–132.
- BESSONAT, G. & MICHAUT, A. (1973): Découverte d'un squelette complet d'échassier dans le Stampien provençal. – *Bulletin du Museum d'Histoire Naturelle Marseille*, **33**: 143–145.
- BICKART, K. J. (1982): A new Thick-Knee, *Burhinus*, from the Miocene of Nebraska, with comments on the habitat requirements of the Burhinidae (Aves, Charadriiformes). – *Journal of Vertebrate Paleontology*, **1/3–4**: 273–277.
- BICKART, K. J. (1990): The birds of the late Miocene-early Pliocene Big Sandy Formation, Mohave County, Arizona. – *Ornithological Monographs*, **44**: 1–72.
- BOLES, W.E. (2001): A new emu (*Dromaiinae*) from the Late Oligocene Etadunna Formation. – *Emu*, **101**: 317–321.
- BRODKORB, P. (1955): The avifauna of the Bone Valley Formation. – *Florida Geological Survey, Report of Investigations*, **14**: 1–57.
- BRODKORB, P. (1967): Catalogue of fossil birds: Part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). – *Bulletin of the Florida State Museum*, **11**: 99–220.
- DE PIETRI, V. L., & MAYR, G. (2012): An assessment of the diversity of early Miocene Scolopaci (Aves, Charadriiformes) from Saint-Gérand-le-Puy (Allier, France). – *Palaeontology*, **55**: 1177–1197.
- DE PIETRI, V. L., COSTEUR, L., GÜNTERT, M., & MAYR, G. (2011): A revision of the Lari (Aves, Charadriiformes) from the early Miocene of Saint-Gérand-le-Puy (Allier, France). – *Journal of Vertebrate Paleontology*, **31**: 812–828.

- DEL HOYO, J., ELLIOTT, J. A., & SARGATAL, J. (eds). (1996): Handbook of the Birds of the World Volume 3. Barcelona (Lynx Edicions).
- FAIN, M.G., & HOUDE, P. (2007): Multilocus perspectives on the monophyly and phylogeny of the order Charadriiformes (Aves). – *BMC Evolutionary Biology*, **7**: 35.
- HOU, L., & ERICSON, P.G. (2002): A middle Eocene shorebird from China. – *Condor*, **104**: 896–899.
- HUXLEY, T.H. (1867): On the classification of birds; and on the taxonomic value of the modifications of certain of the cranial bones observable in that class. – *Proceedings of the Zoological Society of London*, **1867**: 415–472.
- LINNAEUS, C. (1758): Systema Naturae per Regna Tria Naturae. Tenth edition, two volumes. – 824 pp. Stockholm (L. Salvii).
- MAYR, G. (2009): Paleogene fossil birds. – 262 pp. Heidelberg (Springer).
- MAYR, G. (2011): The phylogeny of charadriiform birds (shorebirds and allies) – reassessing the conflict between morphology and molecules. – *Zoological Journal of the Linnean Society*, **161**: 916–943.
- MILLER, L.H. (1961): Birds from the Miocene of Sharktooth Hill, California. – *Condor*, **63**: 399–402.
- MILNE-EDWARDS, A. (1867–68): Recherches anatomiques et paléontologiques pour servir à l’histoire des oiseaux fossiles de la France, vol. 1. – 474 pp. Paris (Victor Masson et fils)
- MLÍKOVSKÝ, J. (1992): The present state of knowledge of the Tertiary birds of Central Europe. – In: CAMPBELL, K.E. (ed.): Papers in avian paleontology honouring Pierce Brodkorb. – *Natural History Museum of Los Angeles County (Science Series)*, **36**: 433–458.
- MLÍKOVSKÝ, J. (1996): Tertiary Avian Faunas of Europe. – *Acta Universitatis Carolinae, Geologica*, **39**: 777–818.
- MLÍKOVSKÝ, J. (2002): Cenozoic birds of the world. Part 1: Europe. – 417 pp. Praha (Ninox Press).
- MOURER-CHAUVIRÉ, C. (1978): La poche à phosphate de Sainte-Néboule (Lot) et sa faune de Vertébrés du Ludien supérieur. 6. Oiseaux. – *Palaeovertebrata*, **8**: 217–229.
- OLSON, S.L. (1985): The fossil record of birds. – In: FARNER, D.S., KING, J.R., & PARKES, K.C. (eds.): *Avian Biology*, Vol. 8. – pp. 79–238. New York (Academic Press).
- OLSON, S.L. & STEADMAN, D.W. (1979): The fossil record of the Glareolidae and Haematopodidae (Aves: Charadriiformes). – *Proceedings of the Biological Society of Washington*, **91**: 972–981.
- OLSON, S.L. & RASMUSSEN, P. (2001): Miocene and Pliocene birds from the Lee Creek Mine, North Carolina. – *Smithsonian Contributions to Paleobiology*, **90**: 233–365.
- PATON, T.A., BAKER, A.J., GROTH, J.G., & BARROW-CLOUGH, G.F. (2003): RAG-1 sequences resolve phylogenetic relationships within Charadriiform birds. – *Molecular Phylogenetics and Evolution*, **29**: 268–278.
- SMITH, N.A. (2011). Taxonomic revision and phylogenetic analysis of the flightless Mancallinae (Aves, Pan-Alcidae). – *ZooKeys*, **91**: 1–116.
- STRAUCH, J.G. (1978). The phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatibility analysis. – *Transactions of the Zoological Society of London*, **34**: 263–345.
- TYRBERG, T. (1998). Pleistocene birds of the Palearctic: A catalogue. – Nuttall Ornithological Club, Vol. 27. – 720 pp. Cambridge, Massachusetts.

