Skull identification key for Central European shorebirds (Aves: Charadriiformes: Scolopaci and Charadrii)

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Source: Stuttgarter Beiträge zur Naturkunde A, 9(1) : 267-282

Published By: Stuttgart State Museum of Natural History

URL: https://doi.org/10.18476/sbna.v9.a16

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Skull identification key for Central European shorebirds (Aves: Charadriiformes: Scolopaci and Charadrii)

Florian Schäfer & Gregor Schmitz

Abstract

Although the shorebirds (Charadriiformes: Scolopaci and Charadrii) are among the most thoroughly studied bird orders in Central Europe, no precise key for the identification of their skulls was available. This paper seeks to remedy this lack by presenting a dichotomous identification key for 38 species of shorebirds from Germany. Photographs and biometric measurements of the skulls are included to support the identification process.

Keywords: Aves, Charadriiformes, Charadriidae, Scolopacidae, Burhinidae, Haematopodidae, Recurvirostridae, skull morphology, identification key.

Zusammenfassung

Obwohl die Watvögel (Charadriiformes: Scolopaci und Charadrii) zu den viel beobachteten Vogelgruppen zählen, lag bisher kein präziser Bestimmungsschlüssel für die Schädel der mitteleuropäischen Arten vor. Mit der vorliegenden Arbeit wird diese Lücke geschlossen und ein dichotomer Schlüssel zur Bestimmung von 38 in Deutschland lebenden Watvogelarten vorgestellt. Zur Erleichterung der Bestimmung sind Fotos und Messdaten beigefügt.

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1 Introduction

Although the shorebirds (Charadriiformes: Charadriidae and Scolopacidae) are a special focus of ornithologists, an identification key for the skulls of this group still does not exist for Central Europe. As part of a graduate thesis project at the University of Konstanz (Schäfer 2014), the skulls of 38 German shorebird species were measured and analyzed in terms of functional anatomy and feeding behavior. Based on the underlying data and measurements, a distinction can even be made between skulls of closely related species. In this paper, we present a dichotomous identification key. In addition, we include supportive morphometric data and illustrations.

The skull of the Charadriiformes is characterised by the well-developed rhynchokinesis of its bill (Hoerschelmann 1970, Gussekloo et al. 2001). According to this the bill is schizorhinous or – rarely – secondary holorhinous (but in Pluvianidae and Burhinidae probably primary holorhinous) (Mickoleit 2004).

As mentioned in Ellrott & Schmitz (2010), the skull identification key presented in Brown et al. (2003) includes general skull types and the bill-cranium-ratio and was supplemented with illustrations and some basic morphometric data. Unfortunately, the number of specimens examined was not specified (except when only one specimen was available). The illustrations were not very detailed, not suited to comparing species, and some important species were missing.

Jansen & van Gestel (2009) present the following measurements on their "skullsite": total length, length, width and height of cranium, upper bill length, skull relation (total length/upper bill length). The photographs are clear and informative. Unfortunately, the measurements are taken from just one specimen in each case. In addition, despite the enormous number of species included, some Central European species are missing.

Because Germany has a good cross-section of the Central European fauna, we based our analysis on the species list in Barthel & Helbig (2005), but excluded very rare species in order to keep the identification key practical (see section 2 under "Species selection").

Acknowledgements

We are grateful to Dr. Doris Mörike and Christiane Zeitler (Stuttgart State Museum of Natural History), Dr. Elisabeth Stefan (Osteology Department of the Baden-Württemberg State Office for Monuments and Antiquities, Konstanz) for providing specimen. Dr. Bernd Leisler (Max Planck Institute for Ornithology, Radolfzell) helped us to define measurement methods and terminology. Finally, we would like to thank Esther Gollan (medicalart, Aachen) for the illustrations Figs. 1a and 1b.

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Tab. 1. Species included in the determination key. – Nomenclature according to Bauer et al. (2005), systematic order according to del Hoyo et al. (1992).

Scientific name	English name	German name
Charadrii		
Burhinidae		
Burhinus oedicnemus (Linnaeus, 1758)	Stone curlew	Triel
Haematopodidae		
Haematopus ostralegus Linnaeus, 1758	Eurasian oystercatcher	Austernfischer
Recurvirostridae		
Himantopus himantopus (Linnaeus, 1758)	Black-winged stilt, Common stilt	Stelzenläufer
Recurvirostra avosetta Linnaeus, 1758	Pied avocet, Eurasian avocet	Säbelschnäbler
Charadriidae		
Vanellus vanellus (Linnaeus, 1758)	Northern lapwing, Peewit	Kiebitz
Pluvialis squatarola (Linnaeus, 1758)	Grey plover, Black-bellied plover	Kiebitzregenpfeifer
Pluvialis apricaria (Linnaeus, 1758)	European golden plover	Goldregenpfeifer
Charadrius dubius Linnaeus, 1786	Little ringed plover	Flussregenpfeifer
Charadrius hiaticula (Linnaeus, 1758)	Common ringed plover	Sandregenpfeifer
Charadrius alexandrinus Linnaeus, 1758	Kentish plover	Seeregenpfeifer
Charadrius morinellus (Linnaeus, 1758)	Eurasian dotterel	Mornellregenpfeifer
Scolopaci		
Scolopacidae		
Numenius phaeopus (Linnaeus, 1758)	Whimbrel	Regenbrachvogel
Numenius arquata (Linnaeus, 1758)	Eurasian curlew	Großer Brachvogel
Limosa limosa (Linnaeus, 1758)	Black-tailed godwit	Uferschnepfe
Limosa lapponica (Linnaeus, 1758)	Bar-tailed godwit	Pfuhlschnepfe
Scolopax rusticola (Linnaeus, 1758)	Eurasian woodcock	Waldschnepfe
Lymnocryptes minimus (Brünnich, 1764)	Jack snipe	Zwergschnepfe
Gallinago gallinago (Linnaeus, 1758)	Common snipe	Bekassine
Phalaropus lobatus (Linnaeus, 1758)	Red-necked phalarope	Odinshühnchen
Phalaropus fulicarius (Linnaeus, 1758)	Red phalarope, Grey phalarope	Thorshühnchen
Actitis hypoleucos (Linnaeus, 1758)	Common sandpiper	Flussuferläufer
Tringa erythropus (Pallas, 1764)	Spotted redshank	Dunkler Wasserläufer
Tringa totanus (Linnaeus, 1758)	Common redshank	Rotschenkel
Tringa stagnatilis (Bechstein, 1803)	Marsh sandpiper	Teichwasserläufer
Tringa nebularia (Gunnerus, 1767)	Common greenshank	Grünschenkel
Tringa ochropus Linnaeus, 1758	Green sandpiper	Waldwasserläufer
Tringa glareola Linnaeus, 1758	Wood sandpiper	Bruchwasserläufer
Philomachus pugnax (Linnaeus, 1758)	Ruff	Kampfläufer
Arenaria interpres (Linnaeus, 1758)	Turnstone	Steinwälzer
Limicola falcinellus (Pontoppidan, 1763)	Broad-billed sandpiper	Sumpfläufer
Calidris canutus (Linnaeus, 1758)	Red knot	Knutt
Calidris alba (Pallas, 1764)	Sanderling	Sanderling
Calidris minuta (Leisler, 1812)	Little stint	Zwergstrandläufer
Calidris temminckii (Leisler, 1812)	Temminck's stint	Temminckstrandläufer
Calidris melanotos (Viellot, 1819)	Pectoral sandpiper	Graubrust-Strandläufer
Calidris ferruginea (Pontoppidan, 1763)	Curlew sandpiper	Sichelstrandläufer
Calidris maritima (Brünnich, 1764)	Purple sandpiper	Meerstrandläufer
Calidris alpina (Linnaeus, 1758)	Dunlin	Alpenstrandläufer

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2 Materials und Methods

Species selection

Species selection is based on BARTHEL & HELBIG (2005). From the 61 shorebird species listed in this paper, we included 38, because the others are classified as vagrants with an average of less than five records per year since 1980.

Materials

The skull material originates mainly from the NIKOLAUS Collection (Stuttgart State Museum of Natural History). We also used specimens from the SCHMITZ Collection (University of Konstanz) and the collection of the Osteology Department of the Baden-Württemberg State Office for Monuments and Antiquities (Landesdenkmalamt Baden-Württemberg – Arbeitsstelle Osteologie) in Konstanz (particularly for skulls of *Numenius phaeopus*). We requested thirteen other collections to send us specimens of shorebirds, however none were available.

Of the 38 species selected, we analyzed ten specimens each, all of which met the necessary condition, i. e. no damage that could prevent proper measuring. An effort was made to maintain a balanced sex ratio in selecting the skulls. In contrast to the Anseriformes (cf. ELLROTT & SCHMITZ 2010), shorebird skulls are less common in collections. For the following species, less than ten specimens could be included: *Burhinus oedicnemus* (9), *Numenius phaeopus* (9), *Tringa glareola* (9), *Himantopus himantopus* (8), *Calidris canutus* (8), *Actitis hypoleucos* (7), *Limicola falcinellus* (6), *Calidris temminckii* (5), *Lymnocryptes minimus* (4), *Calidris minuta* (4), *Tringa nebularia* (4), *Tringa ochropus* (4), *Phalaropus fulicarius* (3), *Tringa stagnatilis* (3), *Charadrius morinellus* (2), *Calidris melanotos* (1), *Phalaropus lobatus* (1), *Calidris maritima* (1) (see Tab. 1 for the nomenclature).

For photographic documentation, we chose those individuals that were most representative (i. e. with measurements close to mean values).

Abbreviations and measurements

The morphological terminology is based on BAUMEL & WITMER (1993), JOSEPH & STRAUCH (1978), KING & MCLELLAND (1978), and HUMMEL (2000). The skulls were measured as follows (see also Figs. 1a, 1b, Tab. 2):

Skull

TL	Total length (= upper bill length plus cranial length, i. e. the total length was not measured separately)
CL	Length of cranium: measured from a theoretical line between the occipital ends of the nostrils to the prominentia cerebellaris
UBL	Length of upper bill: measured from tip of upper bill to a theoretical line between the occipital ends of the nostrils

Cranium

CH	Height of cranium
CW	Width of cranium: measured behind postorbital process
OD	Diameter of orbita: measured from base of postorbital process to base of lacrimal
SG	Salt gland depressions: present ("yes") or absent ("no")
SOW	Width of supraorbital isthmus: measured at narrowest extent

Upper bill

BTS	Upper bill tip: protruding (cf. Fig. 6) "yes" or "no"
HC	Pits of Herbst corpuscles: present ("yes") or absent ("no")
NL	Length of nostril opening
PL	Length of premaxillar: measured from tip of upper bill to rostral end of nostril
UBS	Shape of upper bill (see lateral view): divided into three categories: "straight", "curved down" or "curved up"

Lower bill

LBH	Height of lower bill (in the region of the angulus mandibulae)
LBL	Length of lower bill

3 Identification key

The complete data set for all 38 species is presented in Tab. 2.

1 Upper bill length and cranial length almost equal (CL : UBL = max. 1 : 1.1). **2**
– Upper bill longer than cranium (CL < UBL). **10**
2 TL > 75 mm, no supraoccipital foramina, diameter of orbita > 22 mm (Fig. 48). ..... (Burhinidae) only ***Burhinus oedicnemus***
– TL < 75 mm, 2 supraoccipital foramina, diameter of orbita < 22 mm. **3**
3 Orbital edges at the supraorbital isthmus parallel (Fig. 2), orbit edge never enlarged (Fig. 37), without distinct depressions of the salt glands. ..... ***Arenaria interpres***
– Orbital edges at the supraorbital isthmus concave (dorsal view) and dorsally conspicuously enlarged (Fig. 3), often with distinct depressions of the salt glands. ...(Charadriidae) **4**
4 Supraorbital isthmus with 2 distinct depressions of the salt glands (Fig. 4). **5**
– Supraorbital isthmus without distinct depression of the salt glands (Figs. 3, 5). **9**
5 TL < 60 mm. **6**
– TL > 60 mm (Fig. 16). .. (Vanellinae) only ***Vanellus vanellus***
6 Prefrontale conspicuously separated from the frontale (dorsal orbit edge) (Figs. 3, 20). ..... ***Charadrius alexandrinus***
– Prefrontale and frontale fused (cf. Fig. 5). **7**
7 TL > 48 mm (Fig. 14). ..... ***Charadrius morinellus***
– TL < 45 mm. **8**
8 Dorsal orbit edge conspicuously enlarged, depression of the salt glands distinct, upper bill tip relatively solid, CW > 15mm, OD > 12 mm (Fig. 19). ..... ***Charadrius hiaticula***
– Dorsal orbit edge slightly enlarged, depression of the salt glands less distinct, upper bill tip slender, CW < 15mm, OD < 12 mm (Fig. 18). ..... ***Charadrius dubius***
9 Lateral edge of the prefrontale and frontale fused or at least in the same alignment (Fig. 5), UBL < 32 mm (Fig. 15). ..... ***Pluvialis apricaria***
– Lateral edge of the prefrontale separated from the frontale (cf. Fig. 3), UBL > 32 mm (Fig. 17). ..... ***Pluvialis squatarola***
10 Ventral orbit edge closed, i. e. fusion between lacrimal and postorbital process (Fig. 6). **11**
– Ventral orbit edge not closed (Fig. 7). **13**
11 Cranium massive (CH > 22 mm, CW > 22 mm, SOW > 9 mm), rostral part of upper bill laterally not enlarged (Fig. 25). ..... ***Scolopax rusticola***

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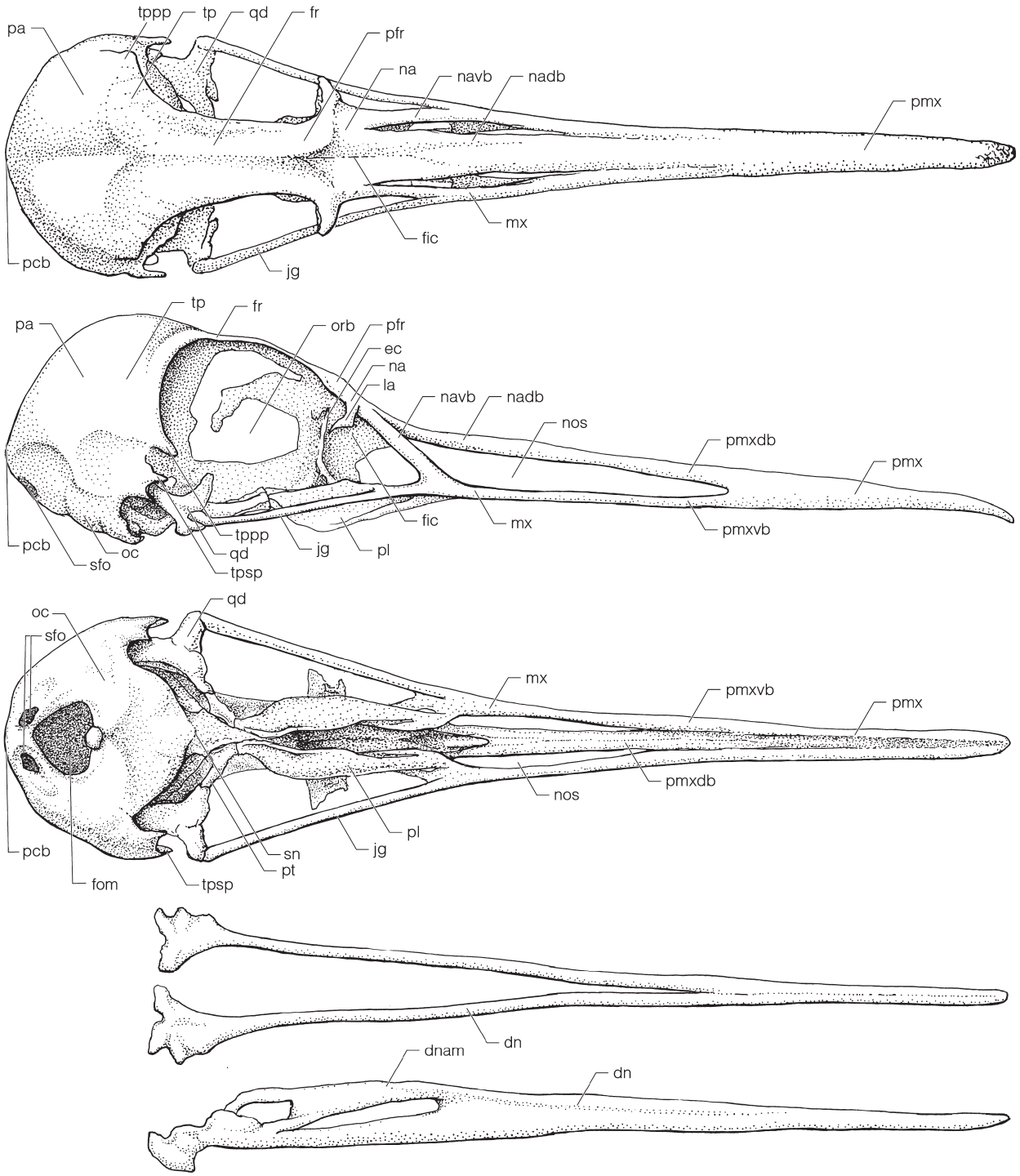

Fig. 1a. Detailed morphological terminology of a shorebird skull (*Tringa totanus*), in dorsal, lateral and ventral views (not all terms are used in the text). – [dn] dental/angular with [dnam] angulus mandibulae; [ec] ectethmoid; [fic] fissura craniofacialis; [fom] foramen magnum; [fr] frontal; [jq] jugal/quadratojugal; [la] lacrimal; [mx] maxillar; [na] nasal with [nadb] dorsal bar and [navb] ventral bar; [nos] nostril; [oc] occipital; [orb] orbita; [pcb] prominetia cerebellaris; [pfr] prefrontal; [pl] palatine; [pmx] premaxillar with [pmxdb] dorsal bar and [pmxvb] ventral bar; [pa] parietal; [pt] pterygoid; [qd] quadrate; [sn] sphenoidal; [sfo] supraoccipital foramina; [tp] temporal with [tppp] postorbital process and [tpsp] suprameatic process.

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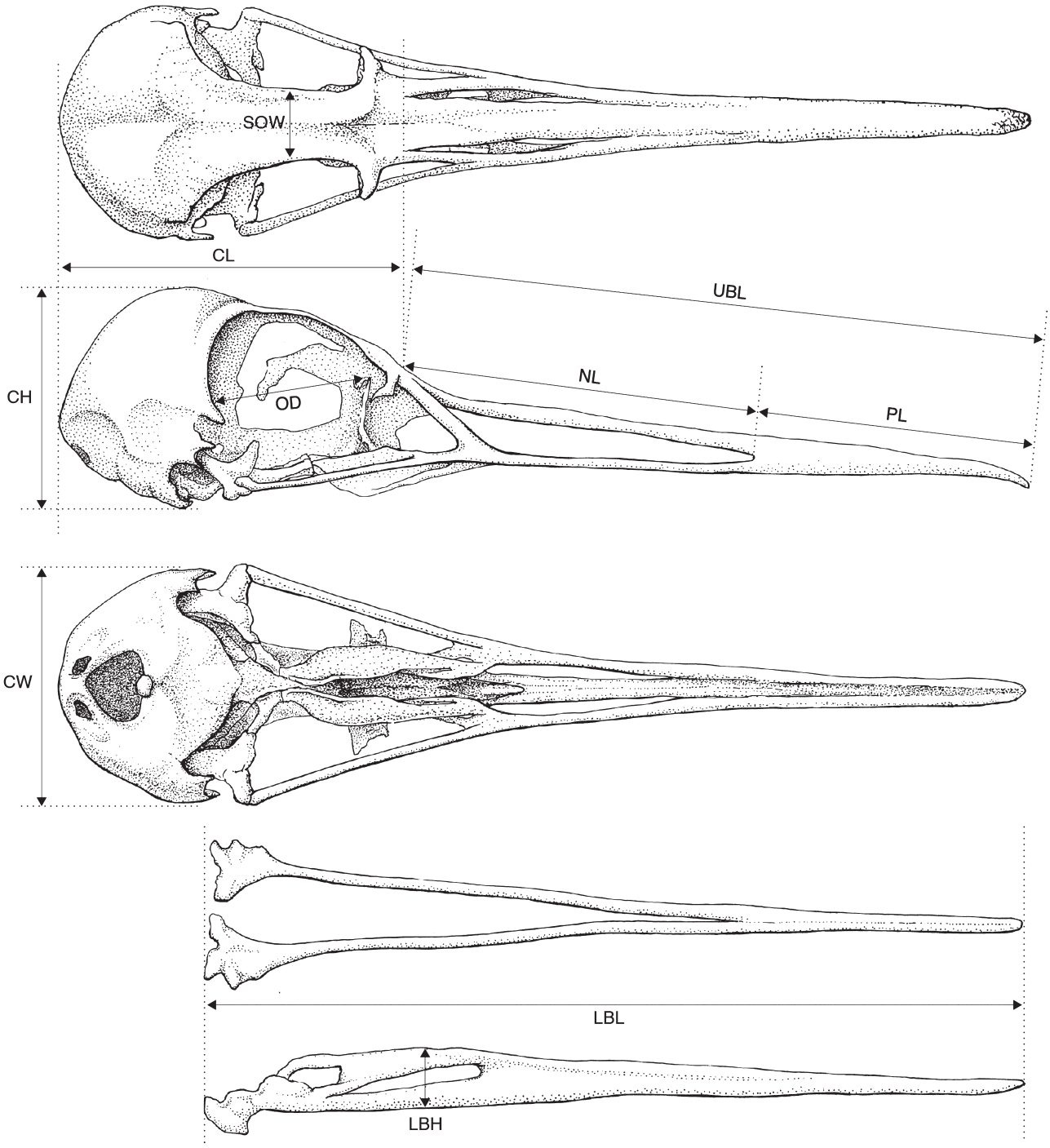

Fig. 1b. Measurements of a shorebird skull (*Tringa totanus*); definitions and abbreviations see section 2.

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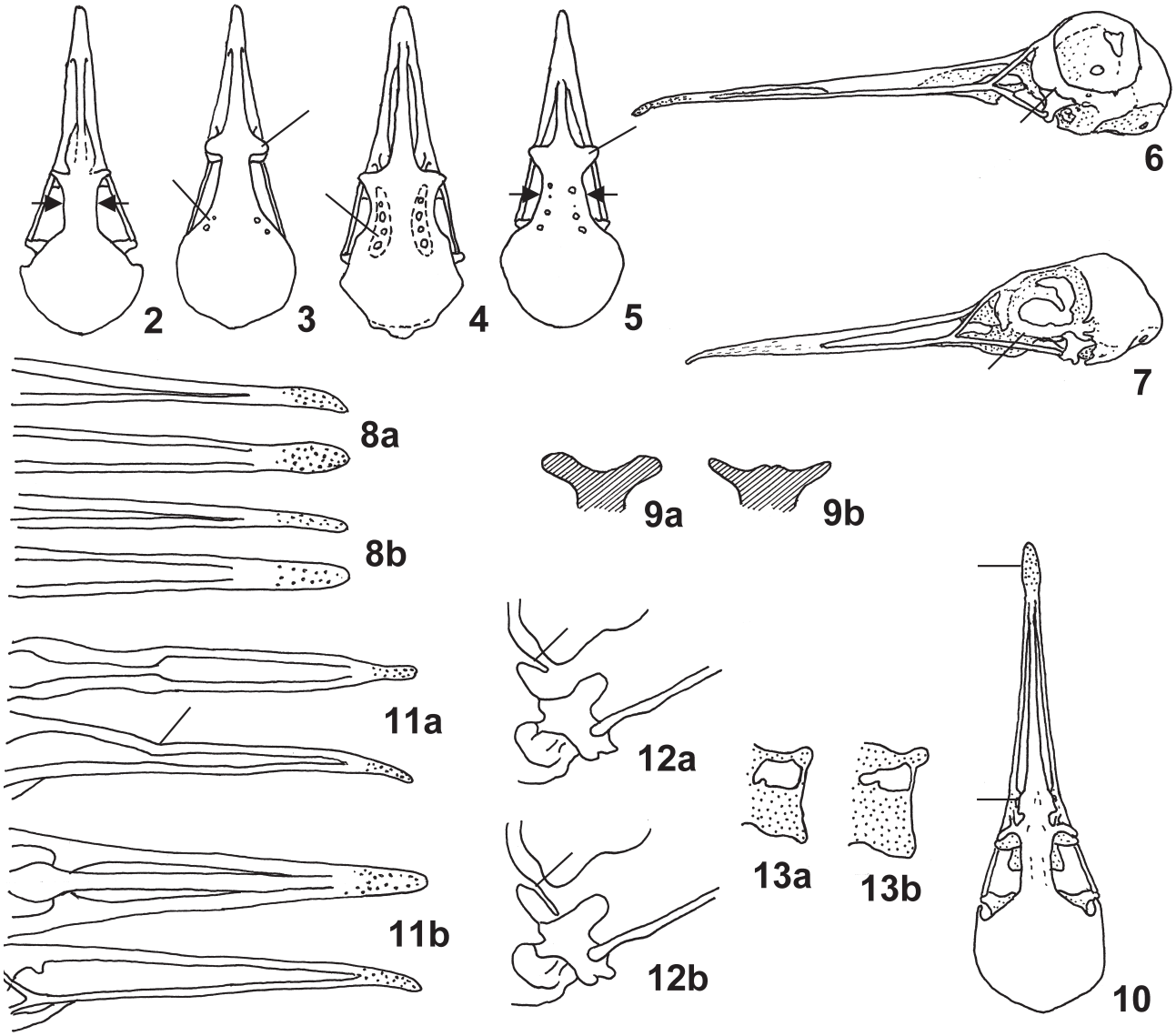

Figs. 2–13. Details of shorebird skulls. – **2**. *Arenaria interpres*, dorsal view. **3**. *Charadrius alexandrinus*, dorsal view. **4**. *Vanellus vanellus*, dorsal view. **5**. *Pluvialis apricaria*, dorsal view. **6**. *Scolopax rusticola*, lateral view. **7**. *Tringa totanus*, lateral view. **8**. Bill tips in lateral and dorsal views of (a) *Limosa limosa* and (b) *L. lapponica*. **9**. Transversal cross section of the supraorbital isthmus of (a) *Limosa limosa* and (b) *L. lapponica*. **10**. *Calidris canutus*, dorsal view. **11**. Bill in lateral and dorsal views of (a) *Limicola falcinellus* and (b) *Calidris* sp. **12**. Postorbital process in caudo-lateral view of (a) *Calidris maritima* and (b) *C. ferruginea*. **13**. Lacrimal, orbital view, of (a) *Tringa glareola* and (b) *T. ochropus*. – Arrows indicate important characteristics (see text).

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– Cranium smaller (CH < 17 mm, CW < 17 mm, SOW < 7 mm), rostral part of upper bill lateral slightly enlarged laterally. **12**
12 TL > 75 mm, UBL > 55 mm (Fig. 26). ...***Gallinago gallinago***
– TL < 75 mm, UBL < 55 mm (Fig. 27). ....***Lymnocryptes minimus***
13 TL > 100 mm. **14**
– TL < 100 mm. **17**
14 Rostral half of bill curved down. .....(*Numenius*) **15**
– Bill straight or slightly curved up. ..... (*Limosa*) **16**
15 TL > 150 mm (Fig. 21). .....***Numenius arquata***
– TL < 150 mm (Fig. 22). .....***Numenius phaeopus***
16 Bill straight, bill tip cap-shaped (Fig. 8a), supraorbital isthmus V-shaped (Figs. 9a, 23). .....***Limosa limosa***
– Bill straight or slightly curved up, tip of bill flat (Fig. 8b), supraorbital isthmus W-shaped (Figs. 9b, 24)..... .....***Limosa lapponica***
17 CW < 22 mm.....**18**
– CW > 22 mm (Fig. 45). ....(Haematopodidae) only ***Haematopus ostralegus***
18 Lacrimal pin- or bow-shaped.....(Recurvirostridae) **19**
– Lacrimal planar, 2-dimensional..... **20**
19 Bill conspicuously up-curved, distinct processsus prefrontale (Fig. 46)..... ***Recurvirostra avosetta***
– Bill straight, no distinct processsus prefrontale, prefrontale and frontale fused (Fig. 47). .....***Himantopus himantopus***
20 Basal end of the fronto-nasal hinge with lateral extensions (Figs. 10, 11b), bill tip short (PL < 0.25 UBL), distinct Herbst corpuscles.....**21**
– Other combination of characters..... **30**
21 Rostral half of nostrils differing from apical half by narrow slit shape, center of frontal-nasal hinge with a distinct transversal dorsal indentation (Figs. 11a, 38)..... .....***Limicola falcinellus***
– Nostrals consistently tapering towards bill tip, no distinct transversal dorsal indentation in center of frontal hinge (Fig. 11b). **22**
22 CL > 23 mm, prominetia cerebellaris salient/prominent (Fig. 36).....***Philomachus pugnax***
– CL < 23 mm, prominetia cerebellaris not salient/prominent (Figs. 28–35). .....(*Calidris*) **23**
23 TL < 40 mm. **24**
– TL > 40 mm. **25**
24 Bill tip slightly spoon-shaped (cf. Fig. 10) (Fig. 30)..... .....***Calidris minuta***
– Bill tip not widened, consistently tapering towards bill tip (Fig. 31). .....***Calidris temminckii***
25 Bill straight (Figs. 28, 29, 35). **26**
– Bill slightly curved down (Figs. 32–34). [The bill tip distal of the rostral bending-zone can be shaped up or down; therefore it is helpful to take the lower bill shape also into consideration]..... **28**
26 CW > 15 mm, CH > 14 mm, OD > 11 mm (Fig. 28)..... ..... ***Calidris canutus***
– CW < 15 mm, CH < 14 mm, OD < 10 mm. **27**
27 UBL > 35 mm (Fig. 35). ..... ***Calidris alpina***
– UBL < 32 mm (Fig. 29). .....***Calidris alba***
28 NL < 30 mm (Fig. 32).....***Calidris melanotos***
– NL > 32 mm. **29**
29 Postorbital process elongated (Figs. 12a, 34)..... ..... ***Calidris maritima***
– Postorbital process relatively short (Figs. 12b, 33). ....***Calidris ferruginea***
30 TL > 50 mm, bill tip elongated and solid (PL > 11 mm). .... (*Tringa*) **31**
– TL < 50 mm, bill tip usually short, if elongated upper bill conspicuously dorso-ventrally flattened. **36**
31 TL > 81 mm. **32**
– TL < 74 mm. **33**
32 Rostral fourth of bill tip (PL) conspicuously curved down, PL > 0.6 UBL (Fig. 39).....***Tringa erythropus***
– Rostral bill slightly curved up, PL ± 0.5 UBL (Fig. 42). ....***Tringa nebularia***
33 TL > 66 mm. **34**
– TL < 63 mm. **35**
34 CW > 16 mm, dorsal edge of lower bill extremely straight (Fig. 40).....***Tringa totanus***
– CW < 15 mm, dorsal edge of lower bill slightly up-curved (Fig. 41). .....***Tringa stagnatilis***
35 NL < 19 mm, interspace between lacrimal and processus prefrontale ± oval (Figs. 13a, 44). ..... ***Tringa glareola***
– NL > 23 mm, interspace between lacrimal and processus prefrontale slit-shaped (Figs. 13b, 43). .....***Tringa ochropus***
36 Bill broad, conspicuously flattened (Fig. 50)..... ..... ***Phalaropus fulicarius***
– Bill narrow, not flattened.....**37**
37 Skull tiny (TL < 43 mm, CL < 17 mm), bill tip extremely pointed (Fig. 49).....***Phalaropus lobatus***
– Skull larger (TL > 46 mm, CL > 18 mm), bill tip not extremely pointed (Fig. 51).....***Actitis hypoleucos***

4 Discussion

If indicated for a given specimen, an effort was made to maintain a balanced sex ratio in selecting the skulls. One noticeable sexual dimorphism in skulls has been identified for the genus *Numenius* (cf. Glutz von Blotzheim et al. 1986). In this case, the crania of the females are larger on average (CW and CH), and they tend to have longer bills (UBL) than the males. However, because the smallest skull of the larger species (*Numenius arquata*) was still larger than the largest skull of the smaller species (*Numenius phaeopus*), this sexual dimorphism was irrelevant in terms of identification. A sexual dimorphism has likewise been reported for the related genus *Limosa* (Glutz von Blotzheim et al. 1986), but is less pronounced. Although the skulls of *Limosa limosa* and *L. lapponica* overlap morphometrically, other characteristics can be used to distinguish between these two species.

Species in the genera *Calidris* and *Charadrius* are not easily distinguishable. The smaller *Calidris* species, as well as *Charadrius dubius* and *Ch. hiaticula* can best be distinguished using a combination of morphometric data. Skulls of *Ch. dubius* are generally larger than those of *Ch. hiaticula*, but a more precise distinction still is difficult.

Lateral extensions on the basal end of the fronto-nasal hinge were identified as taxonomically relevant structures. However, their morphological function has yet to be determined. This characteristic appears in all the *Calidris* species included in this study, but also in *Philomachus* and

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Limicola. The idea that *Limicola* is closely related to *Calidris* is further evidenced by the similarities in the behaviour and habits of the two genera. Our morphological analysis of the skulls supports the theory (Glutz von Blotzheim et al. 1999, Joseph & Strauch 1978) that even though *Philomachus* is similar in its habits to the shanks and tattlers (*Tringa*), it more probably is related to *Calidris*.

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Tab. 2. Skull measurements (in mm) of 38 Central European shorebird species (max = maximum, Ø = mean, min = minimum, SD = standard deviation). For abbreviations see section 2 and Fig. 1b.

		Skull			Cranium					Upper bill					Lower bill	
Species		**TL**	**CL**	**UBL**	**CH**	**CW**	**OD**	**SOW**	**SG**	**NL**	**PL**	**UBS**	**BTS**	**HC**	**LBL**	**LBH**
Burhinus	max	86.6	42.1	44.8	26.3	30.5	25.7	15.2	yes	24.9	22.2	straight	no	no	70.0	7.2
oedicnemus	**Ø**	**82.5**	**41.0**	**41.5**	**24.4**	**29.5**	**24.3**	**13.6**		**22.4**	**19.1**				**65.9**	**6.8**
n = 9	min	76.5	38.7	37.8	22.7	28.2	21.9	12.1		19.4	14.6				63.4	6.1
	SD	11.0	1.6	5.8	1.2	0.6	1.6	0.9		3.0	4.6				6.5	0.2
Pluvialis	max	68.9	32.1	37.4	21.2	22.6	20.1	11.2	yes	24.6	13.8	straight	no	no	53.7	5.8
squatarola	**Ø**	**66.7**	**31.3**	**35.4**	**20.5**	**22.0**	**19.6**	**9.1**		**22.8**	**12.6**				**51.1**	**5.5**
n = 10	min	63.8	30.5	32.9	19.9	21.1	19.1	7.8		20.2	10.1				47.7	5.1
	SD	2.7	0.4	2.4	0.2	0.2	0.1	1.0		1.7	1.4				3.3	0.1
Vanellus	max	67.9	31.5	36.4	20.6	22.0	18.6	12.5	yes	28.9	9.1	straight	no	no	47.9	5.8
vanellus	**Ø**	**63.3**	**29.7**	**33.6**	**20.1**	**21.1**	**18.3**	**11.1**		**25.9**	**7.7**				**46.1**	**5.1**
n = 10	min	60.7	29.1	31.4	19.5	20.4	17.5	9.3		24.4	6.1				44.3	4.7
	SD	3.8	0.6	1.9	0.1	0.3	0.1	1.2		1.9	0.7				1.8	0.1
Pluvialis	max	61.9	30.8	31.1	20.1	21.6	19.7	11.0	yes	23.3	10.8	straight	no	no	46.5	5.2
apricaria	**Ø**	**59.1**	**29.2**	**29.9**	**19.5**	**20.7**	**18.9**	**9.8**		**21.9**	**8.0**				**43.9**	**4.5**
n = 10	min	57.4	28.1	29.0	18.6	19.6	17.9	8.8		19.1	6.7				40.9	3.7
	SD	1.9	0.7	0.4	0.2	0.6	0.3	0.5		2.5	2.1				2.7	0.2
Charadrius	max	51.1	26.7	25.7	17.5	17.6	16.0	8.3	yes	19.0	6.7	straight	no	no	36.0	3.3
morinellus	**Ø**	**50.5**	**26.2**	**24.3**	**17.4**	**17.5**	**15.4**	**7.7**		**17.8**	**6.5**				**35.5**	**3.3**
n = 2	min	49.5	25.7	22.8	17.3	17.4	14.8	7.0		16.6	6.2				35.0	3.3
	SD	1.8	0.5	4.2	0.0	0.0	0.7	0.8		2.9	0.1				0.5	0.0
Charadrius	max	43.8	22.7	21.1	14.9	16.6	13.8	8.0	yes	16.2	5.0	straight	no	no	31.2	3.1
hiaticula	**Ø**	**40.0**	**21.5**	**18.5**	**14.1**	**15.9**	**13.2**	**6.6**		**13.8**	**4.7**				**28.1**	**2.7**
n = 10	min	37.2	20.1	17.1	13.6	15.0	12.2	5.5		12.4	4.0				26.0	2.5
	SD	3.9	0.7	1.6	0.2	0.2	0.3	0.7		1.5	0.1				2.5	0.0
Charadrius	max	40.9	21.3	20.0	13.7	15.7	14.0	5.4	yes	14.7	6.0	straight	no	no	29.8	3.0
alexandrinus	**Ø**	**39.6**	**20.5**	**19.1**	**13.2**	**15.3**	**13.3**	**4.6**		**13.7**	**5.4**				**28.6**	**2.5**
n = 10	min	38.6	19.7	18.5	12.9	14.7	12.0	3.7		12.6	4.7				27.1	2.3
	SD	0.6	0.2	0.3	0.1	0.1	0.3	0.4		0.5	0.2				0.6	0.0
Charadrius	max	37.8	19.8	18.4	13.0	14.2	11.6	6.4	yes	14.0	6.5	straight	no	no	26.8	2.8
dubius	**Ø**	**36.9**	**19.2**	**17.7**	**12.5**	**13.7**	**11.2**	**4.8**		**12.9**	**4.8**				**25.5**	**2.7**
n = 10	min	36.0	18.0	16.8	12.0	13.1	10.5	3.6		11.6	4.0				24.0	2.5
	SD	0.4	0.3	0.3	0.1	0.2	0.1	0.6		0.6	0.6				0.9	0.0
Recurvirostra	max	115.6	27.3	89.4	19.5	20.5	14.5	10.0	yes	36.3	53.7	curved	no	no	104.0	4.7
avosetta	**Ø**	**109.1**	**26.1**	**83.0**	**18.1**	**19.1**	**13.6**	**7.5**		**34.8**	**48.2**	up			**97.7**	**4.3**
n = 10	min	102.9	25.3	77.6	17.2	18.0	12.5	5.4		32.0	42.3				90.1	4.0
	SD	18.3	0.5	14.5	0.4	0.5	0.3	1.9		2.4	13.2				17.8	0.1
Haematopus	max	115.0	35.6	82.5	25.7	26.3	19.7	12.1	yes	52.5	30.0	slightly	no	no	101.0	8.0
ostralegus	**Ø**	**106.1**	**33.4**	**72.7**	**24.6**	**24.7**	**19.0**	**10.5**		**46.4**	**26.3**	curved			**91.2**	**7.5**
n = 10	min	95.0	32.0	61.8	23.3	23.7	18.5	9.4		34.9	19.6	up			78.6	6.5
	SD	35.9	1.5	36.7	0.6	0.7	0.1	0.8		25.6	8.8				42.7	0.2

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		Skull			Cranium					Upper bill					Lower bill	
Species		**TL**	**CL**	**UBL**	**CH**	**CW**	**OD**	**SOW**	**SG**	**NL**	**PL**	**UBS**	**BTS**	**HC**	**LBL**	**LBH**
Himantopus	max	104.2	29.0	75.5	19.2	20.3	17.5	9.5	yes	39.4	36.7	straight	no	no	90.6	4.3
himantopus	**Ø**	**97.5**	**27.8**	**69.7**	**18.3**	**19.8**	**16.5**	**8.9**		**36.9**	**32.8**				**85.8**	**4.1**
n = 8	min	91.0	26.2	63.3	17.4	18.9	15.7	8.2		33.1	25.6				82.5	3.9
	SD	17.1	1.0	17.2	0.4	0.2	0.4	0.2		4.4	15.0				7.5	0.0
Numenius	max	219.0	38.5	181.0	26.8	26.2	21.7	14.0	yes	168.0	30.0	curved	yes	yes	196.0	9.4
arquata	**Ø**	**195.9**	**36.5**	**159.4**	**25.5**	**25.1**	**19.4**	**11.1**		**141.5**	**17.9**	down			**173.8**	**8.1**
n = 10	min	164.2	31.2	133.0	21.0	20.5	15.1	6.3		118.0	13.0				146.0	3.0
	SD	240.9	4.8	188.5	2.8	2.9	3.3	4.4		263.2	33.4				183.3	3.5
Limosa	max	142.4	29.9	113.0	19.6	21.5	16.6	7.1	no	105.0	10.0	straight	yes	yes	124.0	5.1
lapponica	**Ø**	**129.5**	**28.5**	**101.0**	**18.6**	**20.5**	**15.4**	**6.5**		**93.5**	**7.5**				**114.2**	**4.7**
n = 10	min	111.5	26.5	85.0	17.9	19.5	13.8	5.1		70.0	4.0				98.0	4.3
	SD	121.2	0.9	107.5	0.3	0.4	0.6	0.5		116.3	2.3				93.3	0.1
Limosa	max	149.1	30.5	121.0	20.1	20.5	15.1	8.2	no	114.0	9.0	slightly	slightly	yes	129.0	5.4
limosa	**Ø**	**129.3**	**28.3**	**101.0**	**19.2**	**19.8**	**14.5**	**7.6**		**94.2**	**6.8**	curved			**111.8**	**4.9**
n = 10	min	115.3	27.3	87.5	18.1	18.8	13.4	7.1		81.1	5.2	up			100.4	4.1
	SD	89.2	1.0	90.8	0.4	0.3	0.3	0.1		90.6	1.3				88.9	0.1
Numenius	max	131.3	34.1	97.0	24.5	23.6	20.2	7.1	yes	85.2	12.6	curved	yes	yes	117.5	7.6
phaeopus	**Ø**	**127.4**	**33.4**	**94.0**	**22.2**	**22.2**	**19.3**	**6.5**		**82.3**	**11.7**	down			**99.4**	**6.7**
n = 9	min	122.3	32.6	89.7	21.2	20.6	18.7	5.8		79.6	10.1				88.1	6.0
	SD	18.1	0.4	13.3	2.4	1.5	0.5	0.3		9.7	1.2				163.8	0.6
Scolopax	max	119.6	30.6	89.0	24.3	23.9	17.9	12.5	no	78.0	13.0	straight	yes	yes	94.0	5.2
rusticola	**Ø**	**112.9**	**28.9**	**84.0**	**23.3**	**23.0**	**17.0**	**10.6**		**72.7**	**11.3**				**88.4**	**4.6**
n = 10	min	104.5	27.7	76.0	22.0	22.2	15.9	9.3		66.0	10.0				82.0	4.2
	SD	17.9	0.8	16.0	0.5	0.3	0.5	1.0		13.1	0.9				14.9	0.1
Gallinago	max	100.3	23.1	78.7	16.6	16.9	12.2	6.4	no	65.3	13.6	straight	yes	yes	87.4	3.0
gallinago	**Ø**	**94.8**	**22.2**	**72.6**	**15.7**	**16.4**	**11.4**	**5.5**		**61.5**	**11.1**				**79.5**	**2.7**
n = 10	min	87.6	21.6	65.6	15.2	15.9	10.7	5.0		57.4	8.2				69.3.2	2.5
	SD	18.6	0.3	17.9	0.2	0.1	0.2	0.2		9.6	3.4				4.6	0.0
Lymnocryptes	max	69.6	20.9	49.0	14.4	15.0	10.1	4.5	no	42.4	8.4	straight	yes	yes	54.7	3.2
minimus	**Ø**	**68.2**	**19.8**	**48.4**	**13.9**	**14.3**	**9.8**	**3.8**		**41.1**	**7.3**				**52.2**	**3.0**
n = 4	min	66.5	18.6	47.9	13.4	13.5	9.4	3.2		39.9	5.5				50.9	2.7
	SD	2.1	1.2	0.2	0.3	0.5	0.1	0.3		1.4	1.7				2.9	0.0
Actitis	max	49.8	20.9	29.9	13.6	13.9	11.7	3.4	no	25.4	6.9	straight	yes	yes	39.2	3.0
hypoleucos	**Ø**	**48.7**	**19.8**	**28.9**	**13.0**	**13.3**	**10.7**	**2.8**		**23.7**	**5.2**				**38.4**	**2.7**
n = 7	min	47.9	18.9	28.0	12.5	12.9	10.0	2.4		22.0	3.2				36.6	2.4
	SD	0.5	0.5	0.3	0.2	0.1	0.3	0.2		2.1	2.2				0.8	0.0
Phalaropus	max	47.2	18.0	29.8	12.0	12.0	9.6	2.6	no	25.1	5.3	straight	no	yes	38.7	2.7
fulicarius	**Ø**	**45.7**	**17.7**	**28.0**	**11.6**	**11.8**	**9.4**	**2.5**		**23.3**	**4.7**				**36.4**	**2.6**
n = 3	min	44.8	17.4	27.1	11.3	11.4	9.2	2.5		21.8	4.1				34.6	2.6
	SD	1.7	0.1	2.3	0.1	0.1	0.0	0.0		2.8	0.4				4.4	0.0
Phalaropus									no			straight	no	yes		
lobatus	**Ø**	**41.4**	**15.4**	**26.0**	**10.6**	**10.9**	**8.2**	**1.5**		**22.0**	**4.0**				**33.5**	**1.8**
n = 1																
Tringa	max	94.5	26.0	68.6	16.9	17.8	13.9	6.2	no	25.4	45.2	straight	no	yes	82.6	4.5
erythropus	**Ø**	**88.7**	**25.3**	**63.4**	**16.3**	**16.9**	**13.3**	**5.4**		**23.3**	**40.1**				**77.2**	**4.1**
n = 10	min	82.8	24.2	57.0	15.6	16.4	12.2	4.5		21.8	34.4				71.0	3.4
	SD	13.9	0.3	12.2	0.1	0.2	0.2	0.2		1.4	9.3				12.2	0.1
Tringa	max	92.0	27.5	64.5	18.0	18.6	15.7	5.7	no	35.6	33.3	slightly	no	yes	79.3	5.2
nebularia	**Ø**	**87.0**	**27.1**	**59.9**	**17.5**	**18.2**	**15.2**	**5.1**		**30.6**	**29.3**	curved			**75.4**	**5.0**
n = 4	min	81.9	26.5	55.4	17.0	17.7	14.6	4.4		25.4	22.8	up			72.7	4.8
	SD	18.2	0.2	15.3	0.2	0.1	0.2	0.4		17.6	21.0				9.0	0.0
Tringa	max	73.7	25.2	48.7	16.9	17.2	14.0	4.7	no	29.1	21.4	straight	no	yes	62.0	4.4
totanus	**Ø**	**71.4**	**24.5**	**46.9**	**16.3**	**16.8**	**13.1**	**4.2**		**27.0**	**19.9**				**59.4**	**4.0**
n = 10	min	67.3	22.3	44.7	14.7	16.2	12.3	3.9		25.0	17.7				57.8	3.6
	SD	3.6	0.7	2.0	0.4	0.1	0.3	0.1		1.8	1.3				1.8	0.1

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		Skull			Cranium					Upper bill					Lower bill	
Species		**TL**	**CL**	**UBL**	**CH**	**CW**	**OD**	**SOW**	**SG**	**NL**	**PL**	**UBS**	**BTS**	**HC**	**LBL**	**LBH**
Tringa	max	72.5	20.8	51.8	13.9	14.4	11.2	3.3	no	28.8	23.0	straight	no	yes	61.0	2.8
stagnatilis	**Ø**	**68.6**	**20.7**	**47.9**	**13.6**	**14.1**	**11.0**	**3.0**		**27.1**	**20.8**				**57.9**	**2.7**
n = 3	min	66.0	20.6	45.2	13.2	14.0	10.9	2.6		24.9	17.5				55.3	2.6
	SD	11.7	0.0	11.9	0.1	0.1	0.0	0.1		4.0	8.5				8.4	0.0
Tringa	max	62.4	21.8	40.6	14.3	14.6	12.1	4.0	no	26.3	14.3	straight	no	yes	53.2	3.2
ochropus	**Ø**	**59.5**	**21.1**	**38.4**	**13.9**	**14.4**	**11.5**	**3.8**		**25.3**	**13.1**				**49.0**	**2.9**
n = 4	min	56.5	20.7	35.5	13.2	14.2	11.2	3.6		23.8	11.7				45.6	2.6
	SD	6.0	0.2	4.7	0.2	0.0	0.2	0.0		1.3	1.1				9.9	0.1
Tringa	max	56.5	22.0	34.5	14.4	15.0	12.7	4.5	no	18.3	16.7	straight	no	yes	46.1	3.2
glareola	**Ø**	**54.4**	**21.5**	**33.0**	**14.0**	**14.4**	**11.8**	**3.9**		**17.4**	**15.6**				**44.5**	**2.9**
n = 9	min	51.8	21.1	30.6	13.4	13.8	10.7	3.0		16.4	13.2				42.6	2.7
	SD	2.5	0.1	2.0	0.1	0.2	0.6	0.2		0.5	1.2				1.5	0.0
Philomachus	max	70.5	26.8	44.0	17.1	18.0	14.3	5.6	no	35.8	9.4	slightly	yes	yes	58.3	4.8
pugnax	**Ø**	**65.9**	**25.3**	**40.6**	**16.2**	**17.0**	**13.0**	**4.4**		**32.6**	**8.0**	curved			**54.1**	**3.9**
n = 10	min	58.9	23.0	35.7	15.1	15.8	11.8	3.3		28.2	6.00	down			46.6	3.3
	SD	21.3	2.9	9.2	0.4	0.8	0.7	0.7		6.0	1.0				20.3	0.2
Calidris									no			curved	yes	yes		
maritima	**Ø**	**62.9**	**21.5**	**41.4**	**14.0**	**15.2**	**10.2**	**2.8**		**34.1**	**7.3**	down			**51.0**	**2.9**
n = 1																
Calidris	max	65.5	19.5	46.3	13.3	14.6	10.2	4.0	no	40.5	7.0	curved	yes	yes	53.5	3.4
ferruginea	**Ø**	**61.3**	**18.9**	**42.4**	**12.8**	**14.1**	**9.9**	**3.2**		**36.9**	**5.5**	down			**49.6**	**3.1**
n = 10	min	55.1	18.2	36.2	12.2	13.6	9.3	2.4		32.1	4.1				44.1	2.8
	SD	9.3	0.2	9.0	0.1	0.1	0.1	0.2		7.9	0.6				7.8	0.1
Calidris	max	62.1	23.2	40.2	15.5	16.7	12.7	4.2	no	34.2	6.4	straight	yes	yes	52.0	3.9
canutus	**Ø**	**60.3**	**22.5**	**37.8**	**15.1**	**16.5**	**12.1**	**3.8**		**32.1**	**5.7**				**47.8**	**3.6**
n = 8	min	54.5	21.9	32.0	14.7	16.0	11.4	3.3		26.0	5.1				42.9	3.4
	SD	6.3	0.2	7.3	0.1	0.1	0.2	0.1		7.7	0.2				9.4	0.0
Calidris	max	60.4	19.2	41.6	13.2	14.4	9.5	3.3	no	36.6	5.5	straight	yes	yes	49.1	3.2
alpina	**Ø**	**57.4**	**18.7**	**38.7**	**12.7**	**14.0**	**9.1**	**3.0**		**34.0**	**4.7**				**45.3**	**2.8**
n = 10	min	55.5	17.7	36.6	12.3	13.8	8.5	2.5		32.2	4.1				43.2	2.5
	SD	2.5	0.2	2.6	0.1	0.0	0.1	0.1		2.9	0.2				3.7	0.1
Calidris									no			curved	yes	yes		
melanotos	**Ø**	**56.6**	**21.5**	**35.1**	**14.4**	**15.0**	**10.0**	**2.9**		**29.6**	**5.5**	down			**44.4**	**3.0**
n = 1																
Limicola	max	56.1	18.4	38.3	12.1	13.6	10.3	2.9	no	34.1	4.2	straight	yes	yes	47.1	3.4
falcinellus	**Ø**	**52.6**	**17.6**	**35.0**	**11.7**	**13.1**	**9.3**	**2.7**		**31.8**	**3.2**				**43.8**	**3.2**
n = 6	min	50.3	16.9	32.8	11.2	12.5	8.5	2.5		29.7	2.5				41.0	2.5
	SD	5.4	0.3	4.0	0.1	0.2	0.4	0.0		3.0	0.4				5.3	0.4
Calidris	max	50.7	20.2	31.4	13.2	14.9	11.1	3.2	no	25.2	6.7	straight	yes	yes	39.8	3.4
alba	**Ø**	**48.6**	**19.0**	**29.6**	**12.8**	**14.6**	**10.4**	**2.9**		**23.6**	**6.0**				**38.4**	**2.9**
n = 10	min	46.8	18.4	28.1	12.6	14.1	10.0	2.6		22.2	5.5				36.5	2.6
	SD	1.9	0.2	1.1	0.1	0.1	0.2	0.0		0.8	0.1				1.6	0.1
Arenaria	max	49.0	23.6	25.9	15.9	17.2	13.2	4.5	no	17.7	9.4	straight	yes	no	37.6	4.1
interpres	**Ø**	**46.9**	**23.0**	**23.9**	**15.3**	**16.9**	**12.6**	**4.0**		**15.5**	**8.4**				**36.3**	**3.8**
n = 10	min	44.8	22.3	22.0	15.0	16.7	11.7	3.5		14.2	7.8				33.4	3.2
	SD	1.7	0.2	1.3	0.1	0.0	0.2	0.1		1.2	0.2				1.6	0.1
Calidris	max	39.1	16.7	22.5	10.9	11.9	8.4	2.4	no	18.8	4.5	straight	yes	yes	28.8	2.2
temminckii	**Ø**	**37.9**	**16.3**	**21.6**	**10.6**	**11.5**	**8.1**	**2.2**		**17.7**	**3.9**				**27.6**	**2.0**
n = 5	min	35.8	15.6	20.2	10.3	10.7	7.8	2.0		16.3	3.2				26.0	1.8
	SD	2.5	0.2	1.5	0.1	0.2	0.1	0.0		1.0	0.3				1.4	0.0
Calidris	max	39.8	16.1	23.9	10.7	12.0	8.9	2.4	no	20.0	4.7	straight	yes	yes	30.9	2.3
minuta	**Ø**	**37.7**	**15.7**	**22.0**	**10.6**	**11.7**	**8.2**	**2.0**		**17.8**	**4.2**				**28.6**	**2.2**
n = 4	min	36.8	15.5	20.8	10.4	11.2	7.4	1.8		16.1	3.9				27.5	2.2
	SD	2.0	0.1	1.9	0.0	0.1	0.4	0.1		2.7	0.1				2.5	0.0

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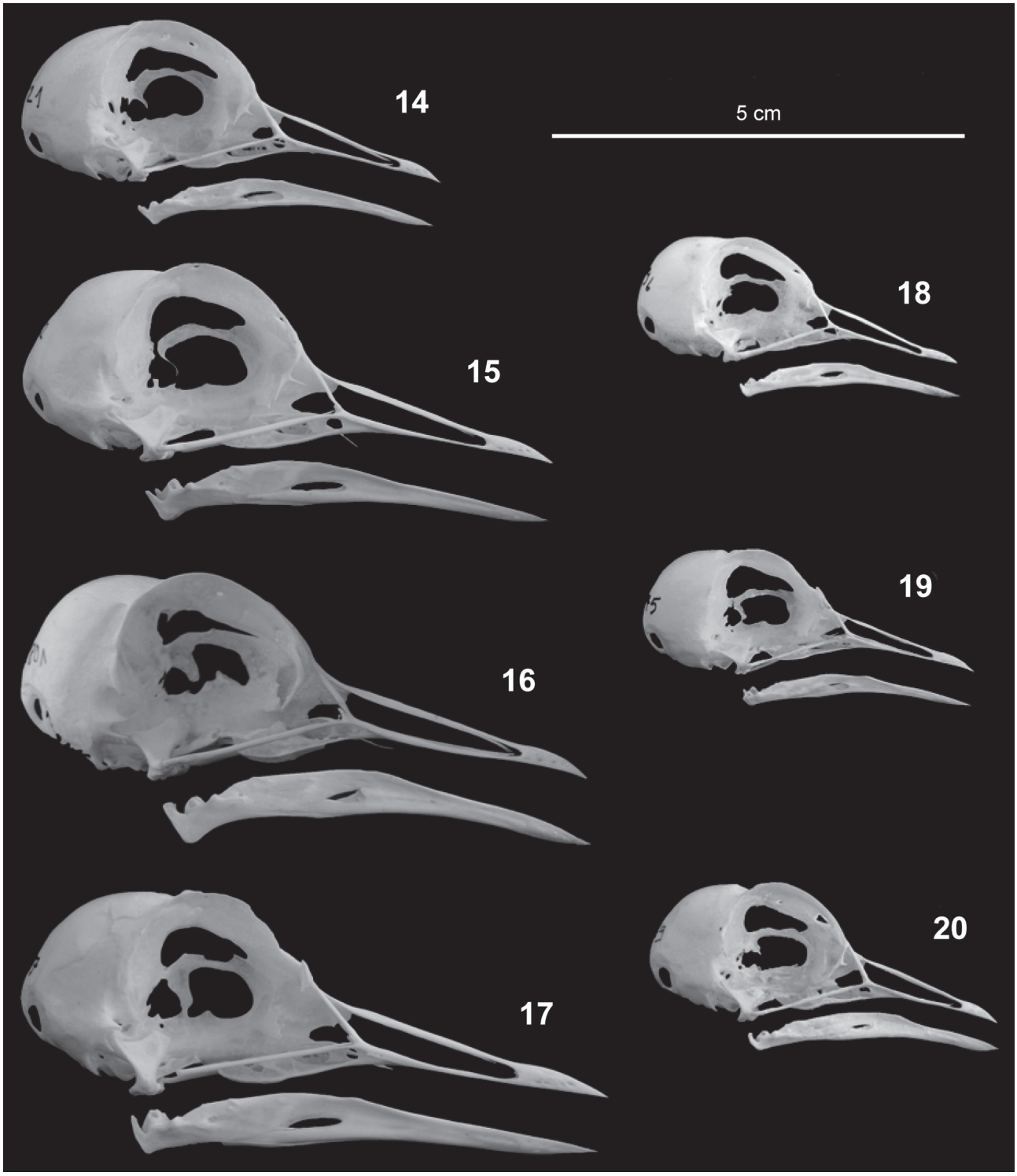

Figs. 14–20. Skulls of Charadriidae, lateral view. – **14**. *Charadrius morinellus*. **15**. *Pluvialis apricaria*. **16**. *Vanellus vanellus*. **17**. *Pluvialis squatarola*. **18**. *Charadrius dubius*. **19**. *Ch. hiaticula*. **20**. *Ch. alexandrinus*.

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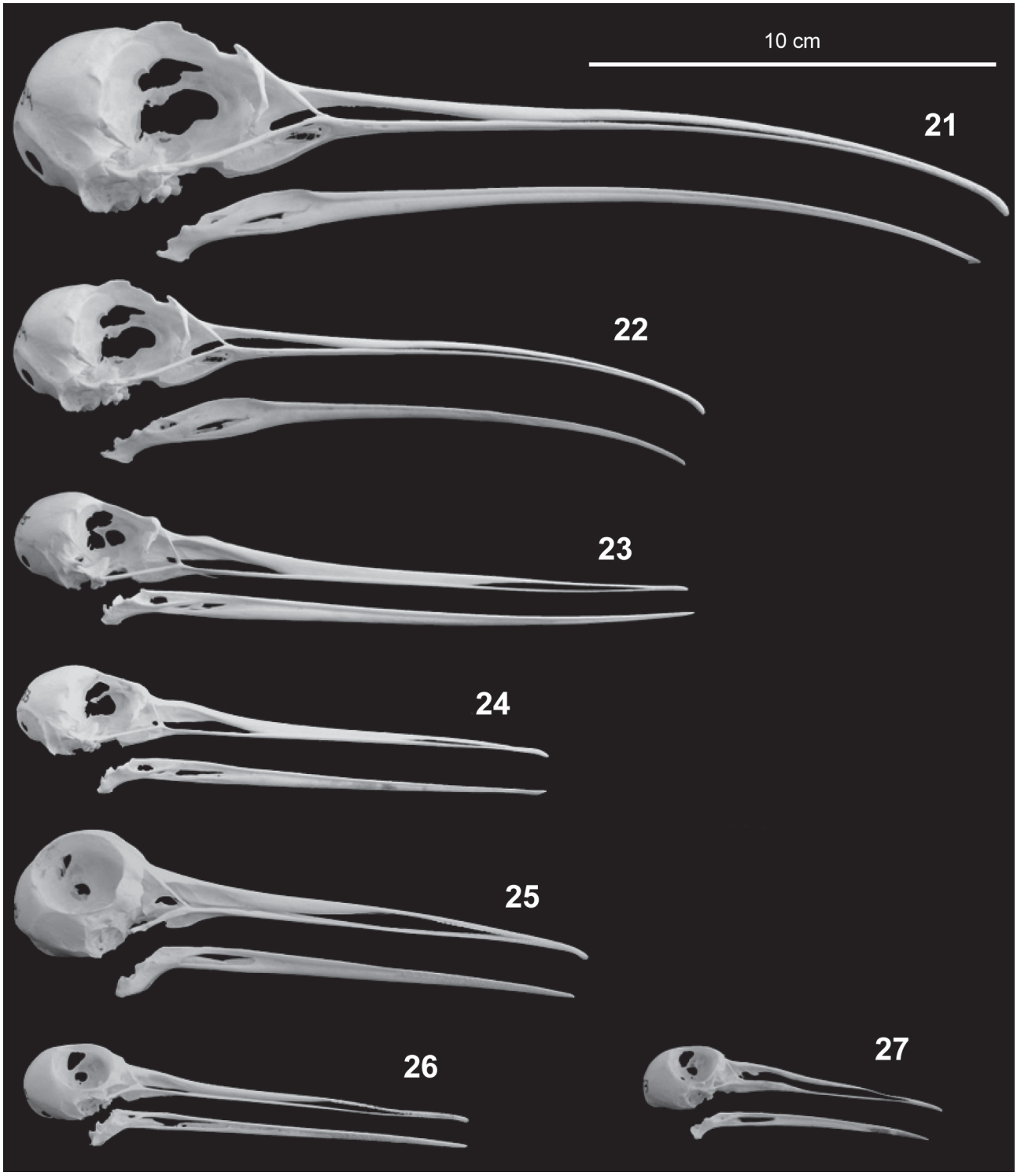

Figs. 21–27. Skulls of *Numenius*, *Limosa* and snipes, lateral view. – **21**. *Numenius arquata*. **22**. *N. phaeopus*. **23**. *Limosa limosa*. **24**. *L. lapponica*. **25**. *Scolopax rusticola*. **26**. *Gallinago gallinago*. **27**. *Lymnocryptes minimus*.

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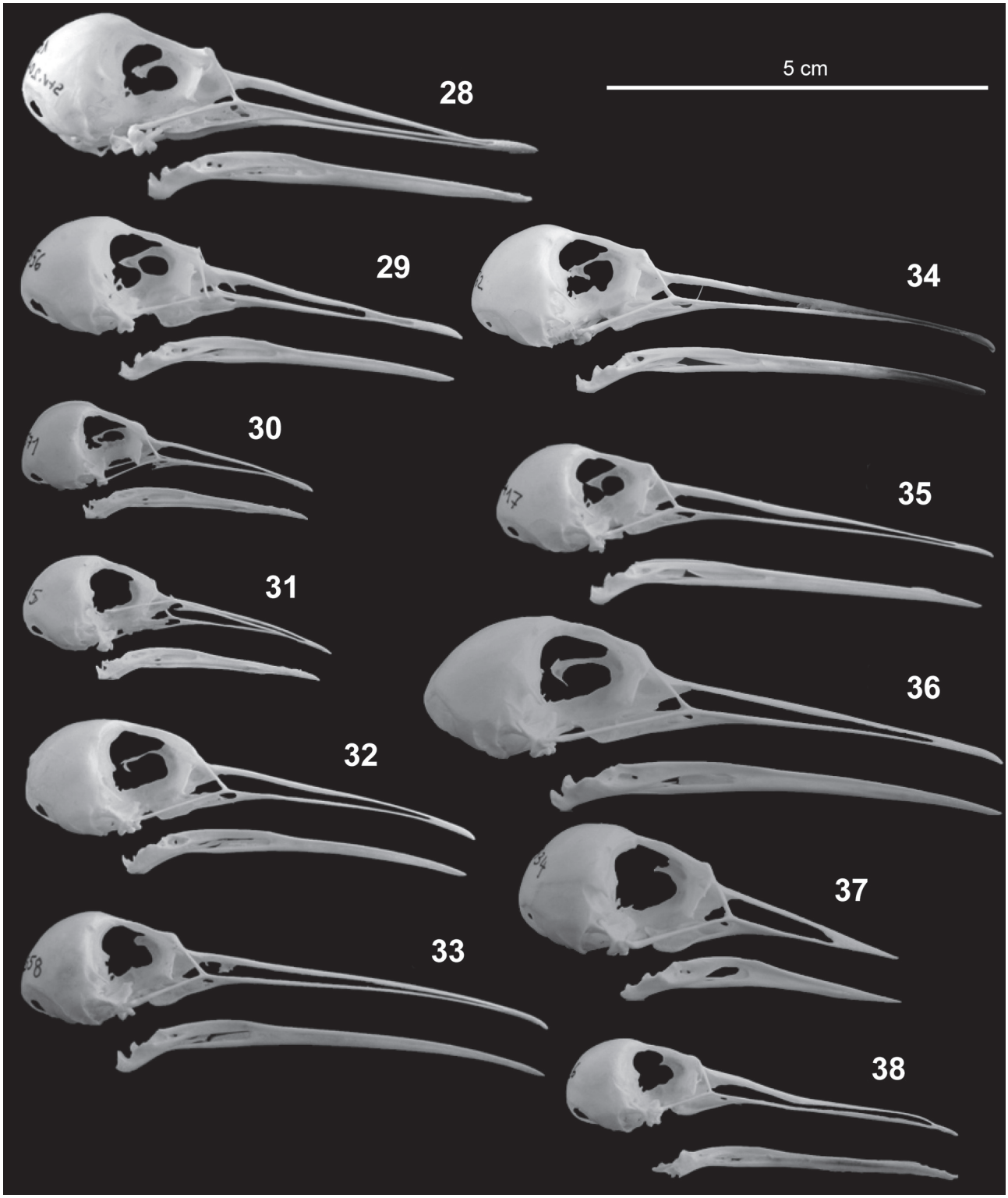

Figs. 28–38. Skulls of various sandpipers, lateral view. – **28**. *Calidris canutus*. **29**. *C. alba*. **30**. *C. minuta*. **31**. *C. temminckii*. **32**. *C. melanotus*. **33**. *C. ferruginea*. **34**. *C. maritima*. **35**. *C. alpina*. **36**. *Philomachus pugnax*. **37**. *Arenaria interpres*. **38**. *Limicola falcinellus*.

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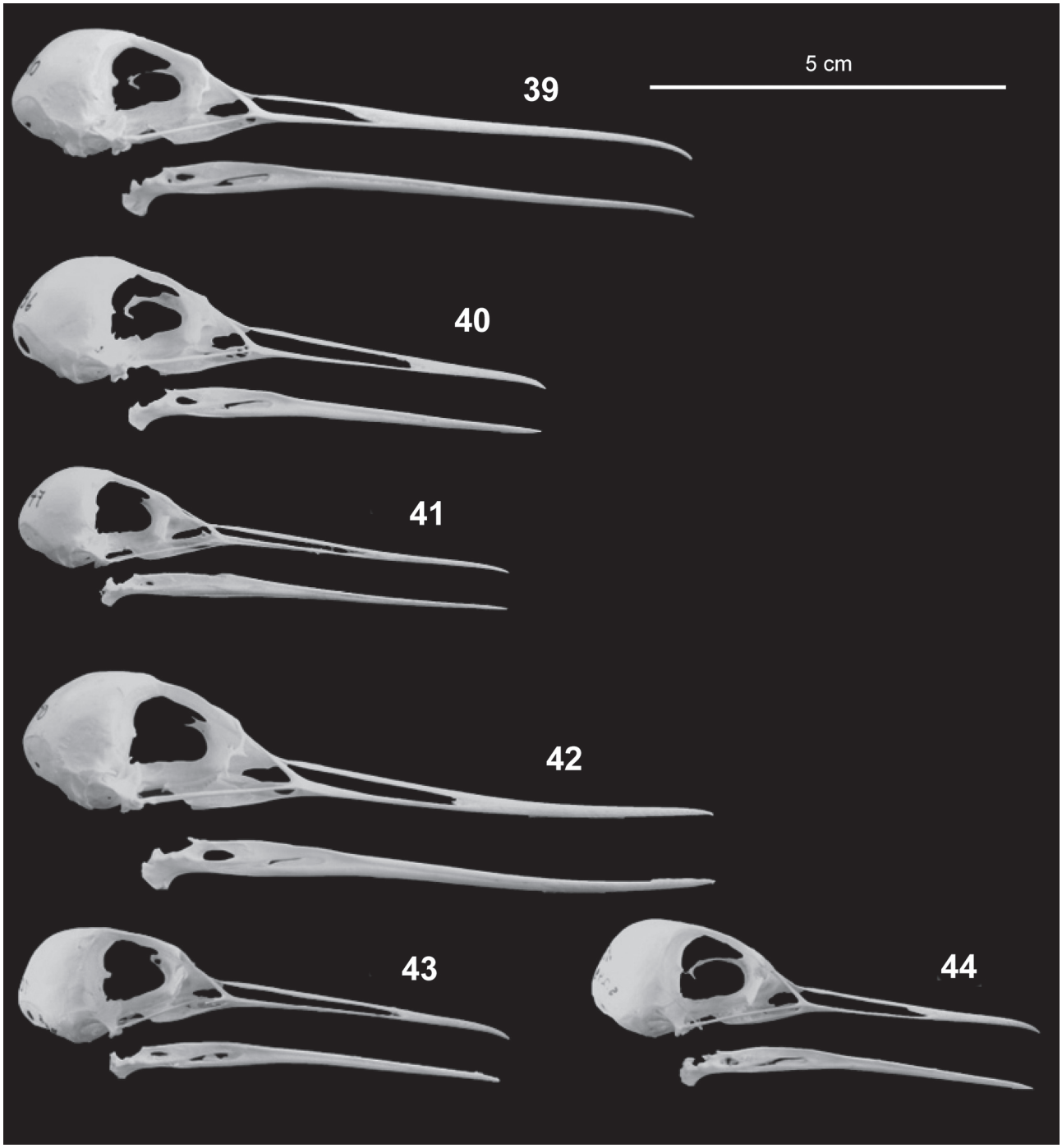

Figs. 39–44. Skulls of *Tringa*, lateral view. – **39**. *Tringa erythropus*. **40**. *T. totanus*. **41**. *T. stagnatilis*. **42**. *T. nebularia*. **43**. *T. ochropus*. **44**. *T. glareola*.

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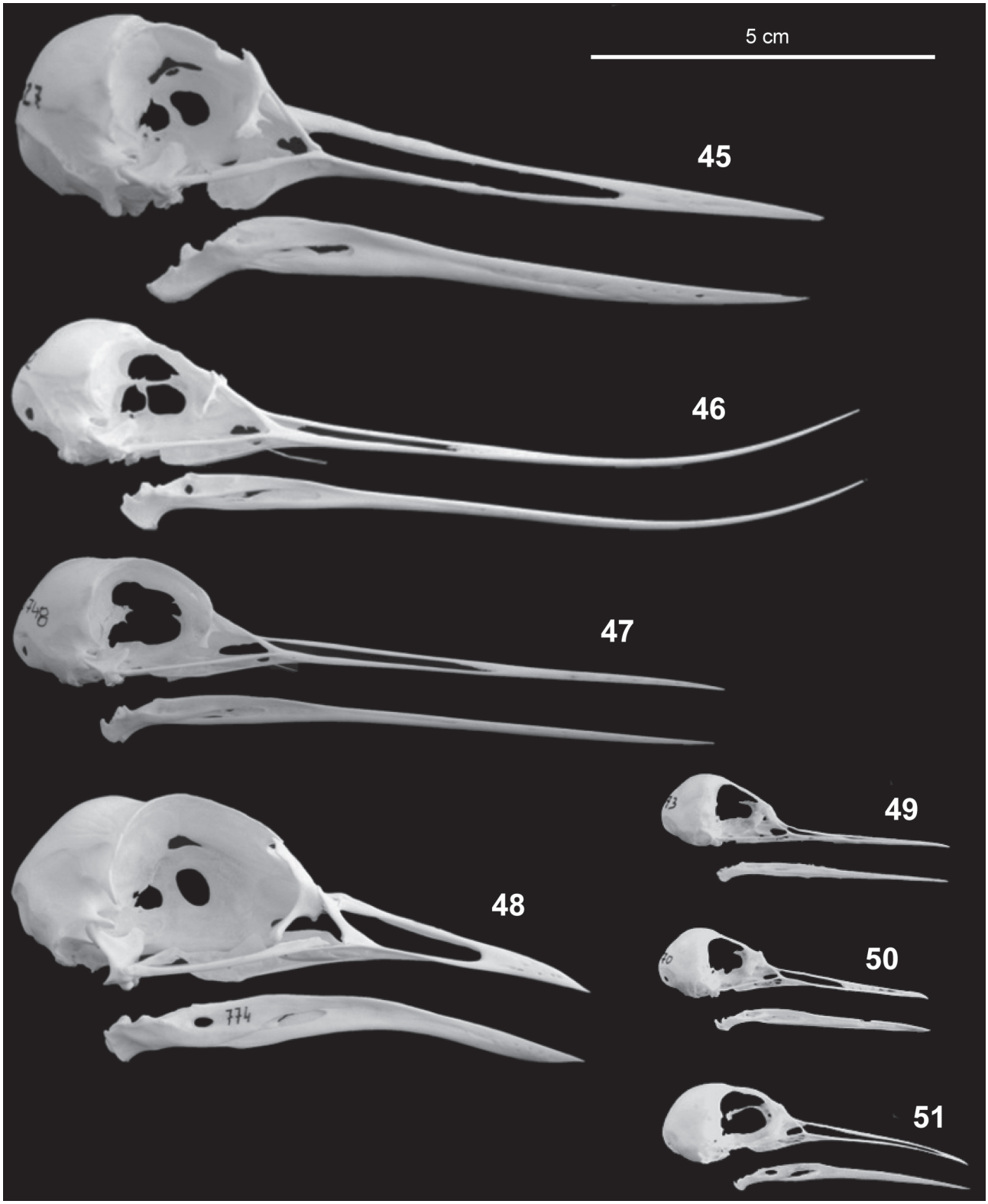

Figs. 45–51. Skulls of Haematopodidae, Recurvirostridae, Burhinidae, *Phalaropus* and *Actitis*, lateral view. **45**. *Haematopus ostralegus*. **46**. *Recurvirostra avosetta*. **47**. *Himantopus himantopus*. **48**. *Burhinus oedicnemus*. **49**. *Phalaropus lobatus*. **50**. *P. fulicarius*. **51**. *Actitis hypoleucos*.

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Manuscript received: 7.V.2015, accepted: 11.XI.2015.

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