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# The “sixth sense” in Scolopacidae (Aves, Charadriiformes): an overview and a photographic collection

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**Abstract** - Scolopacidae are characterized by the presence of sensory pits innervated in the central-apical part of the bill, which allow species belonging to this family to locate prey hidden in mud or water with great precision. Although it is known that all Scolopacidae have these pits, the number has been described for only a few species. The authors examined 139 skulls belonging to 25 Palaearctic species (27% of known species) and present a photographic collection of the upper and lower mandibles, in which the sensory pits are clearly visible, their number varying according to species. The lowest number of pits has been recorded in *Phalaropus* spp., while the highest number has been recorded in *Scolopax rusticola*. Finally, for comparison, they present photos of the skulls of one species of Recurvirostridae and one of Burhinidae, which also have a modest number of apical pits in the bill.

**Key words**: waders, bird skulls, sensory tips, habitat, ecology.

**Riassunto** - Il “sesto senso” negli Scolopacidae (Aves, Charadriiformes): una panoramica e una collezione fotografica.

Gli Scolopacidae sono caratterizzati dalla presenza di fossette sensoriali innervate nella parte centro-apicale del becco che consentono alle specie appartenenti a questa famiglia di individuare con una grande precisione prede nascoste nel fango o nell’acqua. Benché sia noto che tutti gli Scolopacidae sono provvisti di queste fossette, di poche specie è stato descritto il numero. Gli autori hanno esaminato 139 crani appartenenti a 25 specie paleartiche (27% delle specie note) e di queste presentano un atlante fotografico delle mandibole superiori e inferiori, in cui sono evidenti le fossette sensoriali, il cui numero risulta variabile a seconda della specie. Il numero minore di fossette sensoriali è stato individuato nelle specie del genere *Phalaropus*, mentre il numero maggiore in *Scolopax rusticola*. A scopo comparativo, gli autori includono anche le fotografie dei crani di una specie di Recurvirostridae e di una di Burhinidae, che presentano anch’esse un modesto numero di fossette apicali nel becco.

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**Parole chiave**: limicoli, crani di uccelli, fossette sensoriali, habitat, ecologia.

## INTRODUCTION

Electroreception is the ability to detect electric fields, it arose in the earliest vertebrates over 500 million years ago in most cartilaginous fish (Collin, 2010). Electroreceptor organs were first identified in the 1950s by the British zoologist Hans W. Lissmann in the tail of a freshwater fish, and physiologically in the early 1960s from weakly electric fish by the American neuroscientist Theodore H. Bullock and collaborators, as well as by French scientists Thomas Szabo and Alfred Fessard (Hopkins, 2017). Sensory receptors of different kinds are found in many vertebrates: non-teleost fishes (ampullae of Lorenzini), such as Chondrichthyes, Polipteriformes, Acipenseriformes, Dipnoi and Coelacanthiformes (Newton *et al*., 2019), and two distinct lineages of teleosts (Actinopterygii Gymnotiformes, Perciformes, and Osteoglossiformes Notopteroidei) possess ampullary electroreceptors (Hopkins, 2017). Ampullae of Lorenzini are electroreceptors able to detect electric fields. They form a network of mucus-filled pores in the skin of cartilaginous fish and some of the bony fish. Furthermore, some Amphibia Caudata and Gymnophiona have electroreceptors (Crampton, 2019). Two types of electroreceptors are characteristic in teleost as well as non-teleost fishes and in some Amphibia: the ampullary (three types of ampullae) and the tuberous receptor organs (Andres & von Düring, 1988).

Probably the species most provided by electroreceptors are Mammalia Monotremata (Hopkins, 2017): the Echidna (Tachyglossidae) and the Platypus (Ornithorhynchidae) have thousands of mechanoreceptors and electroreceptors on their nose or bill skin to locate and hunt prey in murky rivers and streams, to burrow through land, and detect currents. Electroreception has also been found in some Cetacea (Wilkens & Hofmann, 2005; Hüttner *et al*., 2022) and a small group of invertebrates (bumblebees, spiders) (Hopkins, 2017).

Although much less studied, sensory activity in birds is present in at least three families, Apterygidae, Threskiornithidae (Cunningham *et al*., 2007, 2009, 2010a, 2010b, 2013; Martin *et al*., 2007), and Scolopacidae, the subject of the present paper. According to Piersma *et al*. (1998), in many shorebirds, a large number of Herbst corpuscles are found embedded in pits on the mandible that are believed to enable birds to sense prey under wet sand or soil. These small structures, named after the German embryologist Curt Alfred Herbst, are nerve-endings similar to the Pacinian corpuscles, but smaller and more elongated, with thinner and more closely placed capsules, and the axis-cylinder in the central clear space encircled by a continuous row of nuclei. They are found in the mucous membrane of the tongue, in pits on the bill, and in other parts of the bodies of birds.

The family Scolopacidae, containing 92 extant or recently extinct species divided into 16 genera (del Hojo, 2020), is the most representative of those in which these particular structures are present in the bill tip. In fact, sensory pits, in various forms, have been identified in many species of shorebirds, but the birds of the families Glareolidae, Charadriidae, Recurvirostridae, and Haematopodidae have only a few tiny pits on their bill bones, and they do not have the bill-tip organs with clusters of sensory pits like those found in the Scolopacidae (Gottschaldt, 1985; Lin, 2022). The Eurasian Oystercatcher *Haematopus ostralegus* has numerous Herbst corpuscles close to the tip within the bony core of the bill (Heppleston, 1970). Even though not specifically discussed by Burton (1974), he depicted the sensory pits on the skull of the Common Redshank *Tringa totanus*.

In accordance with Cunningham *et al.* (2013), Scolopacidae, Apterygidae, and Threskiornithidae have independently evolved long, narrow bills containing Herbst corpuscles, clusters of vibration-sensitive mechanoreceptors within pits in the bill tip. These 'bill-tip organs' allow birds to detect buried or submerged prey via substrate-borne vibrations and/or interstitial pressure gradients. Cunningham *et al.* (2013) found that the bill tip organ structure was broadly similar between the Scolopacidae and Apterygidae, with some variation in the number, shape, and orientation of sensory pits between the two groups. They share with waterfowls (Anseriformes) and parrots (Psittaciformes) hypertrophy or near-hypertrophy of the principal sensory trigeminal nucleus. Hypertrophy of the nucleus basorostralis, however, occurs only in waterfowl, kiwi, three scolopacid species, and a species of oystercatcher (Haematopodidae) (Cunningham *et al.*, 2013). Hypertrophy of the principal sensory trigeminal nucleus in Apterygidae, Scolopacidae, and other tactile specialists appears to have co-evolved alongside bill tip specializations, whereas hypertrophy of nucleus basorostralis may be influenced to a greater extent by other sensory inputs.

Following Nebel *et al.* (2005), Herbst corpuscles are mechanoreceptors located in 'sensory pits' under the keratin layer of the bill and are able to sense pressure gradients. Using high resolution microscopy, Nebel *et al.* (2005) measured number and size of sensory pits on the bill tip of Western Sandpiper *Calidris mauri*, Least Sandpiper *Calidris minutilla* and Dunlin *Calidris alpina* and discussed the implications of these findings to foraging adaptations and non-breeding site choice.

Gerritsen & Meiboom (1985) proposed the category of 'remote touch' in all *Calidris* species. The remote-touch sensory system, a unique specialized tactile 'sixth sense', allows birds to detect concealed prey at some distance from their probing bill-tips. The specialized bill-tip organ associated with remote-touch is made up of high numbers of mechano-receptors packed in dense clusters of foramina in the distal portions of the bone of the beak (du Toit, 2021; du Toit *et al.*, 2020, 2022, 2024); many Scolopacidae locate their prey by direct contact with the bill in combination with other sensory cues, but some possess a unique sensory modality known as 'remote touch', allowing them to detect buried prey at a distance from the bill through perception of high frequency acceleration components of mechanical vibrations in the sediment of water (du Toit *et al.*, 2020). The 'remote touch' foraging method can detect the pressure gradients caused by bill probing and the reflection of the prey in the sediment. These pits result from either the movement of the prey or changes in pressure gradients in the sediment caused by the birds' repeated probing action reflected from the surface of hard-shelled prey items (Piersma *et al.*, 1998). The method suggested by Piersma *et al.* (1998) for *Calidris canutus* was that with bill insertion, the birds use Herbst corpuscles at the bill tip organs to detect pressure gradients generated by bill probing and reflected by infaunal prey in wet substrates. The ability to use remote touch to locate buried prey in the absence of all other sensory cues has been demonstrated in multiple species using various behavioral assays (Zweers & Gerritsen, 1997; Piersma *et al.*, 1998; Gerritsen & Melboom, 1985; Nebel *et al.*, 2005; Cunningham *et al.*, 2013; de Fouw *et al.*, 2016). Piersma *et al.* (1998) found a positive effect on *Calidris canutus* foraging success when water was added to the sand they were probing in, while de Fouw *et al.* (2016), still using *Calidris canutus* as a study species, have shown that vegetation cover negatively affects the remote-touch capability of shorebirds, as the root systems of the plants obstruct the pressure fields of buried prey.

Schneider *et al.* (2016) highlighted that environmental stimuli are detected by the peripheral nerve endings of pseudounipolar neurons housed in trigeminal or dorsal root ganglia. Trigeminal occupies a cavity at the base of the skull and innervates the head, while the dorsal root ganglia lie along the vertebral column and innervate body segments. Like their crocodilian ancestors, birds' rostrum is their primary tactile organ. Input from the bill, tongue, and face, conveyed via the trigeminal, facial, glossopharyngeal, and hypoglossal nerves, is first processed in the brain by the principal sensory nucleus of the trigeminal nerve (PrV) in the brainstem. Previous studies report that PrV is enlarged in some species that rely heavily on tactile input when feeding, but no extensive comparative studies have been performed. Herbst corpuscles are postulated to be common among *Calidris* sandpipers, but comparative data are lacking. Results indicate that three distinct groups of birds have a hypertrophied PrV: waterfowl (Anseriformes), beak-probing shorebirds (Charadriiformes), and parrots (Psittaciformes). Parrots likely require increased sensitivity in the tongue to manipulate food items. Thus, despite all sharing an enlarged PrV and feeding behaviors dependent on tactile input, each group has different requirements that have led to the independent evolution of a large PrV (Gutiérrez-Ibáñez *et al.*, 2009). However, the above-cited three groups have different sensory requirements from the orofacial region. For example, beak-probing shorebirds use pressure information from the tip of the beak to find buried prey in soft substrates, whereas waterfowl, especially filter-feeding ducks, use information from the beak, palate, and tongue when feeding.

The number of sensory pits in many species of Scolopacidae is still uncertain or unknown. The present paper aims to deepen our knowledge of this subject through the examination of 139 skulls belonging to 25 Palearctic species of this family and presents a lot of photographs of different genera and species belonging to Scolopacidae, showing these sensory pits.

## MATERIALS AND METHODS

We examined 139 skulls from various Scolopacidae species obtained from multiple collections: the Museum of Zoology 'P. Doderlein' University of Palermo, Italy (MZUP), the Museo Regionale di Storia Naturale of Terrasini (Palermo) (MSNP-T), the Museo Civico di Storia Naturale 'G. Doria' (Genoa, Italy) (MSNG), Marco Pavia's Ornithological Collection stored in the Dipartimento di Scienze della Terra of the Torino University (Turin, Italy) (MGPT-MPOC), the private collections of Renzo Ientile (RIPC, Siracusa, Italy), and that of the first author (BMPC, Palermo, Italy). All skulls were from adults; most of them were unsexed, thus it was impossible to ascertain sex differences in the pit numbers. The following species have been examined: Eurasian Woodcock *Scolopax rusticola,* Common Snipe *Gallinago gallinago*, Jack Snipe *Lymnocryptes minimus*, Dunlin *Calidris alpina*, Curlew Sandpiper *Calidris ferruginea*, Sanderling *Calidris alba*, Little Stint *Calidris minuta*, Temminck's Stint *Calidris temminckii*, Purple Sandpiper *Calidris maritima*, Red Knot *Calidris canutus*, Ruff *Calidris pugnax,* Common Sandpiper *Actitis hypoleucos*, Wood Sandpiper *Tringa glareola*, Green Sandpiper *Tringa ochropus*, Common Redshank *Tringa totanus*, Common Greenshank *Tringa nebularia*, Spotted Redshank *Tringa erythropus*, Bar-tailed Godwit *Limosa lapponica*, Black-tailed Godwit *Limosa limosa*, Eurasian Curlew *Numenius arquata*, Eurasian Whimbrel *Numenius phaeopus*, Ruddy Turnstone *Arenaria interpres*, Terek Sandpiper *Xenus cinereus*, Red Phalarope *Phalaropus fulicarius* and Red-necked Phalarope *Phalaropus lobatus*.

For each skull examined, if the rhamphotheca was intact, it was first immersed in water containing a small percentage of caustic soda to facilitate its careful removal. After cleaning, bill length measurements were taken with a caliper to the nearest 0.5 mm. The bills were then photographed at different magnifications to clearly display the sensory pits on both the upper and lower mandibles with a Nikon Coolpix 4500 digital camera, mounted on a Wild M3 Stereomicroscope, with an Olympus Stylus TG-5 Tough (cf. Mertens *et al*., 2017), and with a Leica M205C with a DMC2900 digital camera. Some bill measurements have been obtained after Prater *et al.* (1977).The percentage of bill length occupied by sensory pits has been obtained with the ratio of the measure of the bill length from its base to the apex and the portion of the bill occupied by sensory pits. Photographs were integrated using the freeware CombineZP (Hadley, 2008). Finally, the sensory pits were counted below a high-magnification Wild M3 Stereomicroscope. Numbers of samples of each species are reported in Tab. 1.

## RESULTS

Tab. 1 reports all the measurements and the percentage of bill length occupied by sensory pits. Figs. 1-11 show the sensory pits of 25 Palaearctic species (27% of known species). Sensory pits of many of them are depicted for the first time.

The percentage of the bill interested by sensory tips was variable in the different genera (between 14 and 24%), with a higher percentage in *Arenaria interpres* (40-50%) and *Xenus cinereus* (30-35%). A high percentage of bills covered by sensory pits has also been found in *Scolopax rusticola* (30-35%). Although the genera *Limosa* and *Numenius* have a rather long beak, even longer than that of the Woodcock *Scolopax rusticola*, the sensory pits are confined to the apical part of the bill, occupying no more than 15% of the surface area. The sensory tips of Woodcocks and Snipes are deeper than in other genera. All *Calidris* species show the presence of sensory pits confined to the apex of the mandibles; like in the genus *Calidris*, sensory pits of *Tringa* species are confined to the bill apex, but look more elongated than in other Scolopacidae. No significant correlation between bill length and the number of sensory pits was detected (r=0.19; P=ns), nor between bill length and the percentage covered by sensory pits (r=-0.1; P=ns), but a positive significant correlation between bill length and the number of sensory pits has been found in the genus *Tringa* (r=0.69; P=0.05). Sensory pits are also present in the inner part of the mandibles, mainly at the edges. The lowest number of sensory pits has been recorded in the species of the genus *Phalaropus*.

## DISCUSSION AND CONCLUSIONS

Overall, we report data on the sensory pits of 25 Palaearctic species of Scolopacidae, an apparently heterogeneous family of birds with sizes and shapes very different, long and short legs, long and short bills, straight, downcurved, or upcurved, but all sharing apical sensory pits on the bill. According to Lin (2022), among Scolopacidae, the genus *Calidris* generally has a high number of sensory pits (376-549 pits), *Tringa* has also a large number of pits (241-375 pits), and *Limosa lapponica* a lower number (201-250 pits), and species such as *Limosa lapponica*, *Xenus cinereus*, *Numenius minutus* have proportionally longer organs but fewer pits than those in *Calidris* (Lin, 2022). Additionally, Lin (2022) found a smaller number of pits in *Arenaria interpres* (149, we counted 130-140); sensory pits of this species are shallow, and their form looks quite different from other species. According to Whitfield (1990), data indicate that another plesiomorphic bony bill-tip organ may exist in *Arenaria interpres*, a Scolopacidae that uses non-tactile foraging strategies, which has a high number of distal bony pits associated with the remote touch bill tip organ but lacks the relatively long beak. According to Hayman *et al*. (1986), Turnstones live in rocky or stone coastlines, turning over stones or seaweed to find hidden prey. This species is actually often observed feeding on shoals of beached *Posidonia*, kelp fronds and other seaweed, and it is likely that its search for food is somewhere between tactile and visual.

The variation of sensory pits may stem from dietary differences, as pit numbers likely depend on the type of food consumed; for instance, *Limosa lapponica*, *Numenius phaeopus*, *Tringa brevipes*, and *Xenus cinereus* primarily probe for crabs or polychaetes (Bolze, 1968; Lin, 2022). However, generally Scolopacidae species chiefly feed on tactile than visual cues. In particular, Godwits (genus *Limosa*) feed in deep waters, Curlews (genus *Numenius*) use their long downcurved bills to remove worms from deep burrows in intertidal mud and also eat

Tab. 1 – Material examined and relative measurements of bills and sensory pits; in the fifth column the number of sensory pits detected by Lin (2022) is reported. Some measures after Prater *et al.* (1977), males and females together. / Materiale esaminato e relative misurazioni dei becchi e delle fossette sensoriali; nella quinta colonna è riportato il numero di fossette sensoriali rilevate da Lin (2022). Alcune misurazioni secondo Prater *et al.* (1977), maschi e femmine insieme.

| Species (sample size) | Bill length (mm) ♂ and ♀ (min-max) | Percentage of bill length occupied by sensory pits (min-max) | Number of sensory pits (min-max) | Number of pits according to Lin (2022) | Figures |
|---|---|---|---|---|---|
| Scolopacidae | | | | | |
| *Scolopax rusticola* (n=35) | 63.2-82.8 | 30-35 | 620.8±7.0 (610-630) | Not available | 1a-1e |
| *Scolopax rusticola* 'brevirostris' (n=2) | 45.9 | 50 | 610-620 | Not available | 1f-1h |
| *Gallinago gallinago* (n=22) | 56.4-70.2 | 25-27 | 454.9±3.4 (450-460) | Not available | 2a-2d |
| *Lymnocryptes minimus* (n=2) | 39.0-42.0 | 25 | 440-450 | Not available | 2e-2g |
| *Calidris alpina* (n=7) | 23.2-29.1 | 19-21 | 250-280 | Not available | 3a-3c |
| *Calidris ferruginea* (n=5) | 32.7-41.6 | 19-20 | 260-270 | 500 | 3d-3f |
| *Calidris alba* (n=2) | 21.0-27.0 | 20 | 180-200 | Not available | 3g-3i |
| *Calidris minuta* (n=5) | 18.2-19.3 | 18-20 | 240-250 | Not available | 4a-4d |
| *Calidris temminckii* (n=2) | 16.0-18.0 | 18-20 | 240-260 | Not available | 4e-4g |
| *Calidris maritima* (n=1) | 26.0-33.0 | 18 | 230 | Not available | 4h-4i |
| *Calidris canutus* (n=2) | 29.0-37.0 | 22-24 | 250-270 | 420-440 | 5a-5c |
| *Calidris pugnax* (n=8) | 28.0-38.0 | 18-20 | 260-290 | Not available | 5d-5h |
| *Calidris tenuirostris* | - | - | - | 376 | |
| *Calidris acuminata* | - | - | - | 549 | |
| *Calidris ruficollis* | - | - | - | 410 | |
| *Actitis hypoleucos* (n=5) | 22.0-25.0 | 14-15 | 180-190 | Not available | 6a-6e |
| *Tringa ochropus* (n=4) | 31.0-37.0 | 15-16 | 220-240 | Not available | 6f-6l |
| *Tringa nebularia* (n=2) | 54.0-56.0 | 18-20 | 230-280 | 380 | 7a-7c |
| *Tringa erythropus* (n=2) | 54.0-62.0 | 18-20 | 220-240 | Not available | 7d-7f |
| *Tringa totanus* (n=3) | 43.0-46.2 | 18-20 | 220-230 | Not available | 7g-7i |
| *Tringa glareola* (n=3) | 28.5-32.2 | 14-15 | 220-240 | 320 | - |
| *Tringa brevipes* | - | - | - | 241-244 | - |
| *Tringa stagnatilis* | - | - | - | 320 | - |
| *Limosa lapponica* (n=3) | 70.0-98.0 | 15 | 200-240 | 201-250 | 8a-8b |
| *Limosa limosa* (n=3) | 74.0-100.0 | 15 | 210-230 | Not available | 8c-8e |
| *Numenius arquata* (n=6) | 95.0-180.0 | 14-16 | 220-240 | Not available | 9a-9e |
| *Numenius phaeopus* (n=3) | 74.0-98.0 | 15 | 220-240 | 200 | 9f-9h |
| *Arenaria interpres* (n=3) | 20.0-23.0 | 40-50 | 130-140 | 149 | 10a-10c |
| *Xenus cinereus* (n=2) | 42.0-52.0 | 30-35 | 140-160 | 220 | 10d-10f |
| *Phalaropus fulicarius* (n=2) | 20.0-24.0 | 14 | 90-100 | Not available | 11a-11d |
| *Phalaropus lobatus* (n=2) | 19.0-22.0 | 15 | 80-90 | Not available | 11e-11h |
| Recurvirostridae | | | | | |
| *Himantopus himantopus* (n=2) | 55.0-70.0 | 15 | 25-30 | Not available | 12a |
| Burhinidae | | | | | |
| *Burhinus oedicnemus* (n=1) | 34.0-42.0 | 50 | 25 | Not available | 12b-12d |

crabs and small mollusks (Hayman *et al*., 1986). Interestingly, the long-billed Scolopacidae belonging to the genera *Limosa* and *Numenius* have a small number of sensory pits (but much deeper) occupying only the tip of the bill. The species belonging to these genera have fairly long legs and are generally able to catch prey where the water is higher than 15 cm. These characteristics make them different from the species belonging to other genera, all of which have fairly shorter legs and bills. It is possible that the limited number of sensory pits is somehow connected with the fact that they forage in the mud where the water is higher; the few sensory pits are therefore concentrated in the apical part of the bill, unlike other Scolopacidae.

Recent phylogenetic analysis by Li *et al*. (2024) shows that *Xenus* and *Actitis* form a sister group, *Phalaropus* is more closely related to *Tringa*, and *Limnodromus*, *Gallinago*, and *Scolopax* constitute a monophyletic group. Nevertheless, we found no similarity in the shape and distribution of sensory pits between *Phalaropus* and *Tringa* or between *Actitis* and *Xenus*, suggesting that these structures are more influenced by feeding habits and habitat than by taxonomic relationships. The Common Sandpiper *Actitis hypoleucos* is known to forage mainly by sight (less on tactile) on the ground, on the rocks by the sea or the rivers, or in shallow water, picking up small prey, such as insects and crustaceans. Compared to the species of the genus *Tringa*, it shows less deep sensory pits that explain its behavior.

Among the Scolopacidae examined, *Scolopax rusticola* exhibited the highest count of sensory pits (610-630), as previously noted by Cunningham *et al*. (2013) and Aradis *et al*. (2019). Cunningham *et al*. (2013) reported around 380 pits in Woodcock’s bill, with notable size variability. Woodcocks feed in soft ground by probing deeply with the long bill, which is particularly distinctive: its upper mandible curves toward the lower, forming a pronounced notch into which the lower mandible fits (Fig. 1b). Burton (1974) also observed this notch, suggesting it might prevent prey from slipping out. Moreover, the bill tip of the Woodcock resembles that of Kiwi (*Apteryx* spp.) (Cunningham *et al*., 2013), indicating a potential case of convergent evolution driven by terrestrial feeding habits. Photographs (Fig. 1f-h) are provided of a rare ‘brevirostris’ form of the Woodcock in which 610-620 pits cover nearly half the bill’s surface, underscoring the importance of these structures in prey detection by this species. Although terrestrial animals generally exhibit limited electroreception due to air’s high resistance (Hopkins, 2017), *Scolopax rusticola,* the most terrestrial of Scolopacidae species inhabiting woodlands and adjacent grasslands, stands out within the family for its high pit density. Cunningham *et al*. (2013) propose that similarities between the bill tip organs of Apterygidae and Scolopacidae, along with associated somatosensory brain regions, result from comparable ecological pressures, with interspecific differences reflecting niche specialization. However, the variability in the dimensions of the mechano-receptors within these pits (Nebel *et al*., 2005) warrants further investigation.

*Gallinago gallinago* and *Lymnocryptes minimus* exhibit high sensory pit counts (450-460 and 440-450, respectively); they and Dowitchers (genus *Limnodromus*) inhabit grassy marshland with muddy edges. Species of the genus *Tringa* feed actively in freshwater margins, pecking visible prey. A positive correlation exists between their bill length and the number of sensory pits. Sandpipers (genus *Calidris*) and allies occur in estuaries and foreshore, pecking or probing in a frenzy way small prey (Hayman *et al*., 1986), using remote touch to detect vibrations generated by motile prey buried in sand.

Finally, Phalaropes (genus *Phalaropus*) show different sensory organs, probably due to their different habitat; in fact, they swim, spinning around and picking small prey off the water surface, and likely for this reason, they have a small number of sensory pits (80-100). However, du Toit *et al*. (2024) have demonstrated that the “sixth sense” works better in wet conditions; so, water or humidity are the essential conditions for the sensory pits to function.

Interestingly, according to Burton (1974), the ratio tongue/bill length in Scolopacidae is generally high (about 0.7), but lower and lower in *Tringa ochropus* (0.62), *T. nebularia* (0.52), *Bartramia longicauda* (0.49), *Limosa lapponica* (0.48), *Numenius phaeopus* (0.33), and *N. arquata* (0.24). This should suggest that different kinds of information arrive from the tongues of these birds, but this information is still far from being well explored.

As reported in the Introduction, other Charadriiformes (families Glareolidae, Charadriidae, Recurvirostridae, and Haematopodidae) have a few tiny pits on their bills, without organs of sensory pits, present in the Scolopacidae. Fig. 12a shows the bill tip of one species belonging to the Recurvirostridae, the Black-winged Stilt *Himantopus himantopus*, where it is possible to detect small pits, and Figs. 12b-d the bill tips of the Eurasian Stone Curlew *Burhinus oedicnemus*, belonging to the family Burhinidae (foramina previously reported only by du Toit *et al*., 2020), also showing some big pits on the upper, lower, and inner side of the lower mandibles. The presence of pits on the bill of these birds belonging to families different from Scolopacidae could be interpreted as a remnant of a formerly present character that has probably been lost through non-use. Species like Stone Curlew, Collared Pratincole *Glareola pratincola*, or Oystercatcher, mainly hunt out of the water on sight, and consequently, this may be the reason why sensory pits no longer have any purpose. The loss of sensory pits in other species, such as those belonging to the family Charadriidae, is more difficult to interpret.

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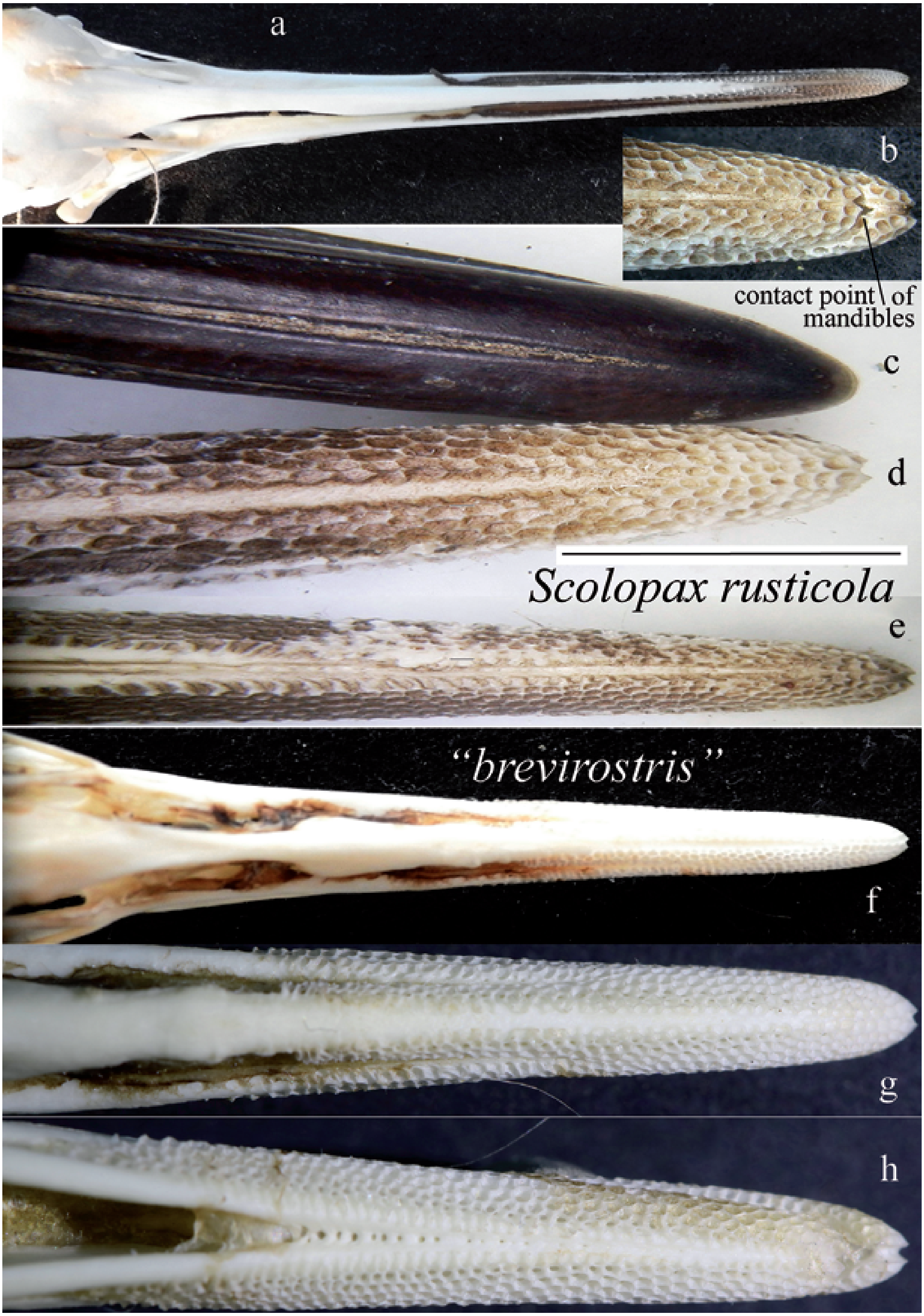

Fig. 1 – Woodcock *Scolopax rusticola*: a) dorsal view of the skull; b) particular of the tip in ventral view; c) upper mandible with rhamphoteca; d) upper mandible without rhamphoteca; e) lower mandible without rhamphoteca; f) upper mandible of 'brevirostris' specimen; g) the same at higher magnification; h) lower mandible of 'brevirostris' specimen (all stored in BMPC). Scale bar: 20 mm. / Beccaccia *Scolopax rusticola*: a) visione dorsale del cranio; b) particolare della punta in visione ventrale; c) mandibola superiore con ranfoteca; d) mandibola superiore senza ranfoteca; e) mandibola inferiore senza ranfoteca; f) mandibola superiore di esemplare "brevirostris"; g) lo stesso a ingrandimento maggiore; h) mandibola inferiore di esemplare "brevirostris" (tutti conservati presso la BMPC).

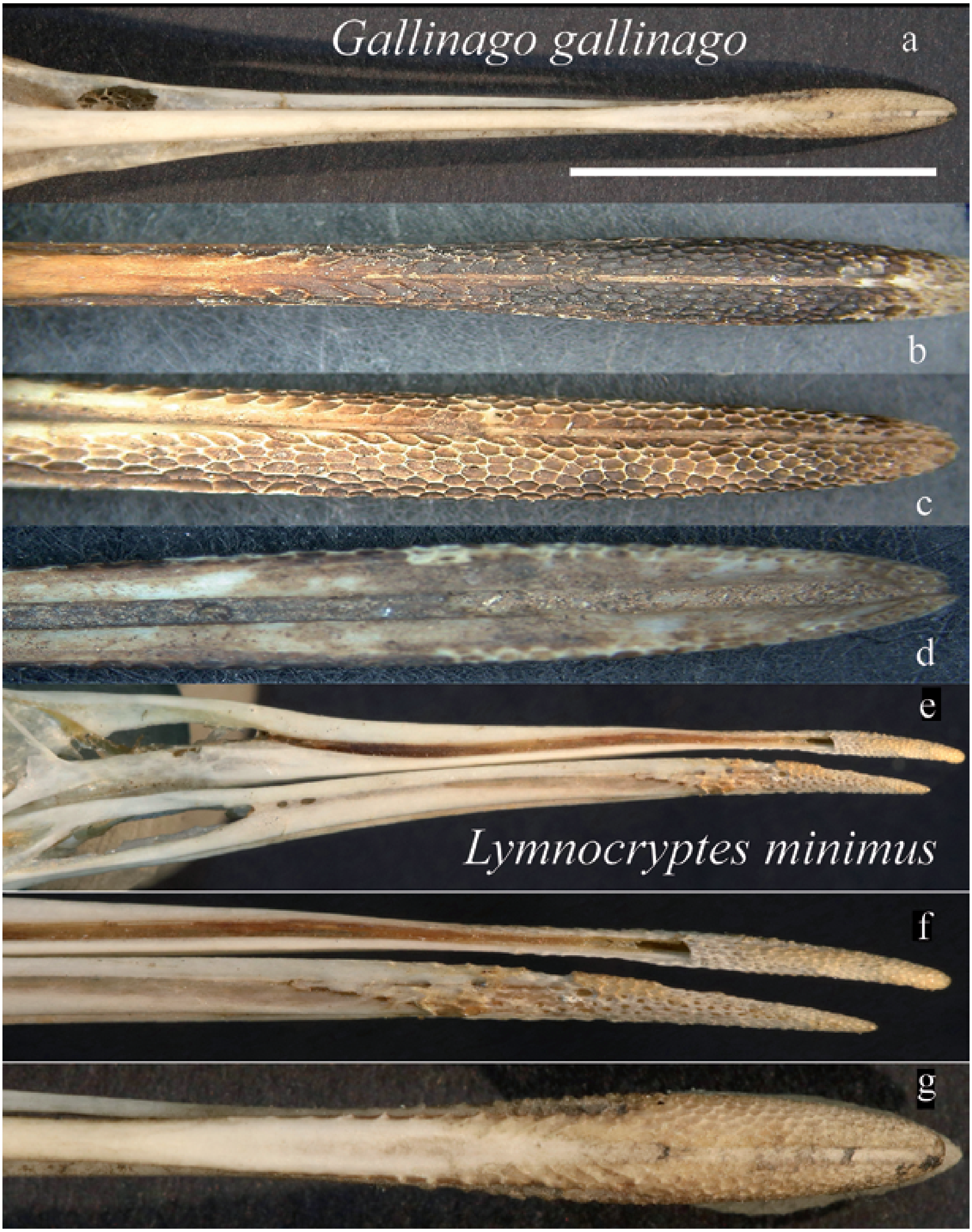

Fig. 2 – Snipe *Gallinago gallinago* (a-d) and Jacksnipe *Lymnocryptes minimus* (e-g): a) dorsal view of the skull of *G. gallinago*; b) upper mandible tip; c) lower mandible tip; d) inner side of lower mandible (stored in MZUP); e) lateral view of the skull of *L. minimus*; f) lateral view of mandible tips; g) lower mandible tip (stored in MZUP). Scale bar: 20 mm. / Beccaccino *Gallinago gallinago* (a-d) e Frullino *Lymnocryptes minimus* (e-g): a) visione dorsale del cranio di *G. gallinago*; b) punta della mandibola superiore; c) punta della mandibola inferiore; d) lato interno della mandibola inferiore (conservato presso MZUP); e) visione laterale del cranio di *L. minimus*; f) visione laterale delle punte delle mandibole; g) punta della mandibola inferiore (conservata presso MZUP).

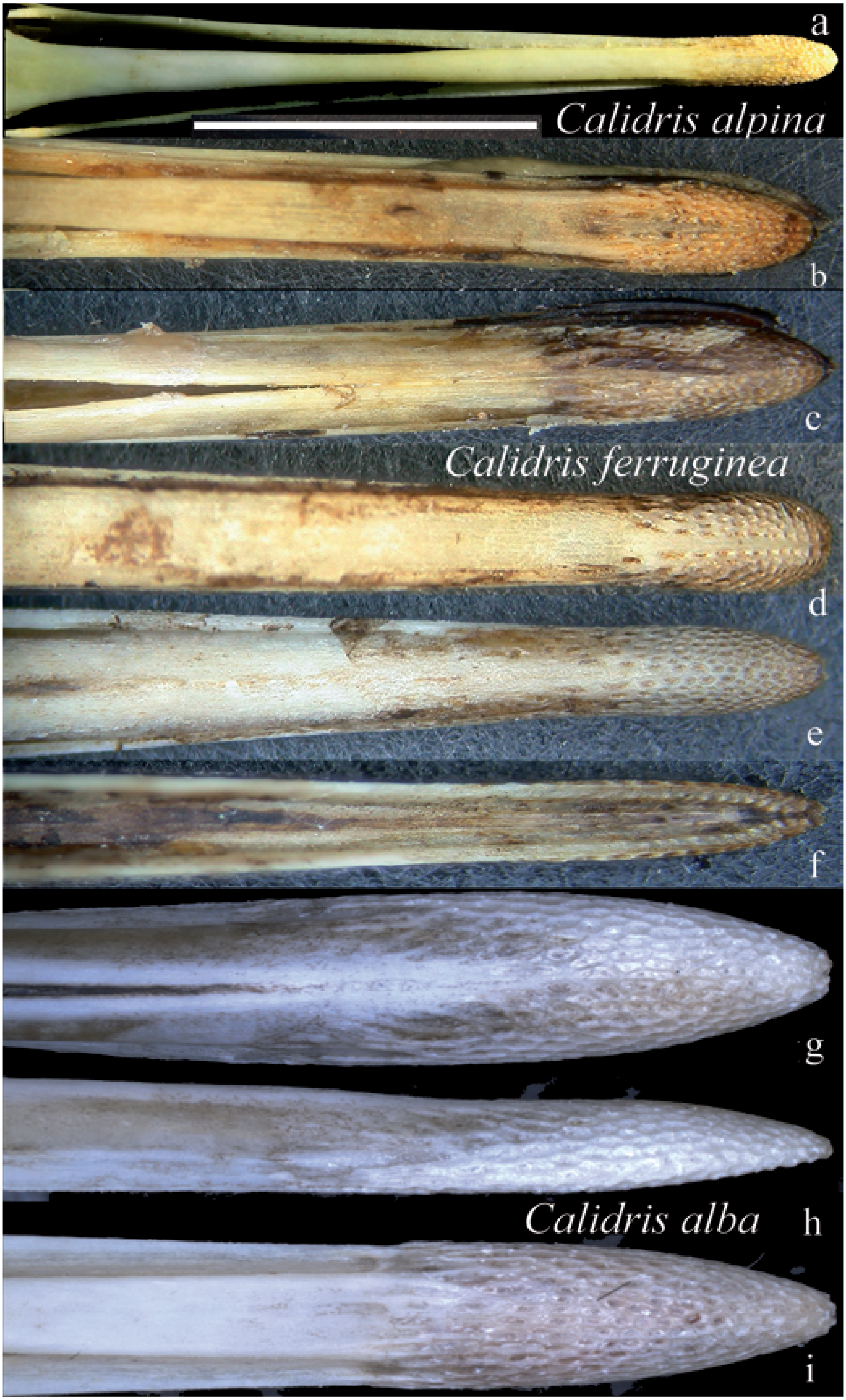

Fig. 3 – Species of the genus *Calidris*; a-c: *C. alpina* a) dorsal view of the skull; b) upper mandible tip; c) lower mandible tip (stored in MZUP); d-f: *C. ferruginea* d) upper mandible tip; e) lower mandible tip; f) inner side of lower mandible (stored in MZUP); g-i: *C. alba* g) upper mandible tip; h) lateral view of upper mandible; i) lower mandible tip (stored in MGPT-MPOC). Scale bar: 10 mm. / Specie del genere *Calidris*; a-c: *C. alpina* a) visione dorsale del cranio; b) punta della mandibola superiore; c) punta della mandibola inferiore (conservata presso MZUP); d-f: *C. ferruginea* d) punta della mandibola superiore; e) punta della mandibola inferiore; f) lato interno della mandibola inferiore (conservato presso MZUP); g-i: *C. alba* g) punta della mandibola superiore; h) visione laterale della mandibola superiore; i) punta della mandibola inferiore (conservato presso MGPT-MPOC).

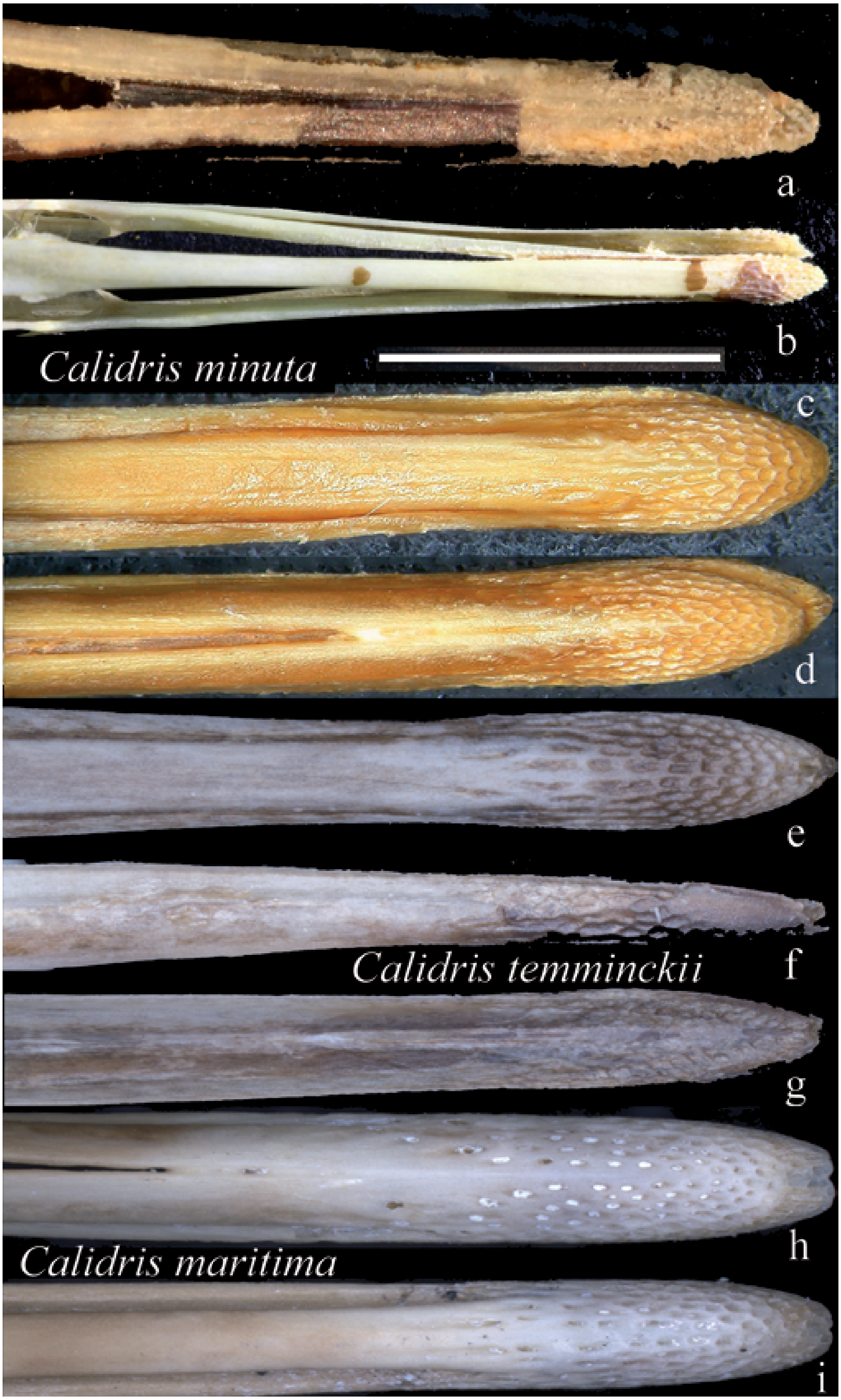

Fig. 4 – Other species of the genus *Calidris*; a-d: *C. minuta* a) view of upper mandible; b) lower mandible; c) upper mandible tip; d) lower mandible tip (a-b: stored in MZUP; c-d: stored in BMPC); e-g: *C. temminckii* e) upper mandible tip; f) lateral view of lower mandible; g) lower mandible tip (stored in MGPT-MPOC); h-i: *C. maritima* h) upper mandible tip; i) lower mandible tip (stored in MGPT-MPOC). Scale bar: 10 mm. / Altre specie del genere *Calidris*; a-d: *C. minuta* a) visione dorsale della mandibola superiore; b) mandibola inferiore; c) punta della mandibola superiore; d) punta della mandibola inferiore (a-b: conservate presso MZUP; c-d: conservate presso BMPC); e-g: *C. temminckii* e) punta della mandibola superiore; f) visione laterale della mandibola inferiore; g) punta della mandibola inferiore (conservata in MGPT-MPOC); h-i: *C. maritima* h) punta della mandibola superiore; i) punta della mandibola inferiore (conservata in MGPT-MPOC).

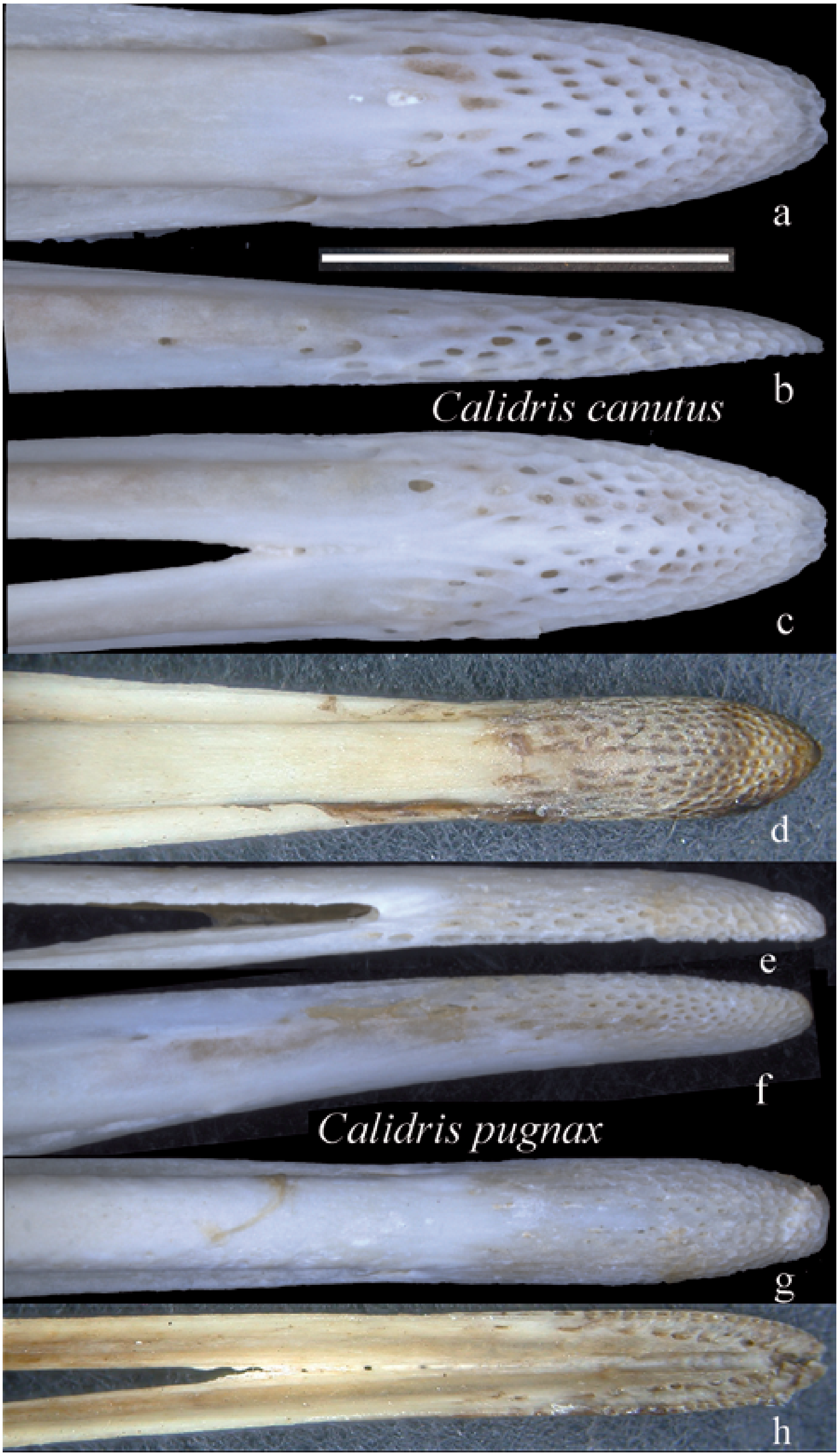

Fig. 5 – Other species of the genus *Calidris*; a-c: *C. canutus* a) upper mandible tip; b) lateral view of upper mandible; c) lower mandible tip (stored in MGPT-MPOC); d-h: *C. pugnax* d) upper mandible tip (specimen 1) (stored in RIPC); e) lateral view of upper mandible (specimen 2); f) lateral view of lower mandible (specimen 2); g) lower mandible tip (specimen 2) (e-g: stored in MGPT-MPOC); h) inner side of lower mandible (specimen 1) (stored in RIPC). Scale bar: 10 mm. / Altre specie del genere *Calidris*; a-c: *C. canutus* a) punta della mandibola superiore; b) vista laterale della mandibola superiore; c) punta della mandibola inferiore (conservata presso MGPT-MPOC); d-h: *C. pugnax* d) punta della mandibola superiore (esemplare 1) (conservata presso RIPC); e) vista laterale della mandibola superiore (esemplare 2); f) vista laterale della mandibola inferiore (esemplare 2); g) punta della mandibola inferiore (esemplare 2) (e-g: conservato presso MGPT-MPOC); h) lato interno della mandibola inferiore (esemplare 1) (conservato presso RIPC).

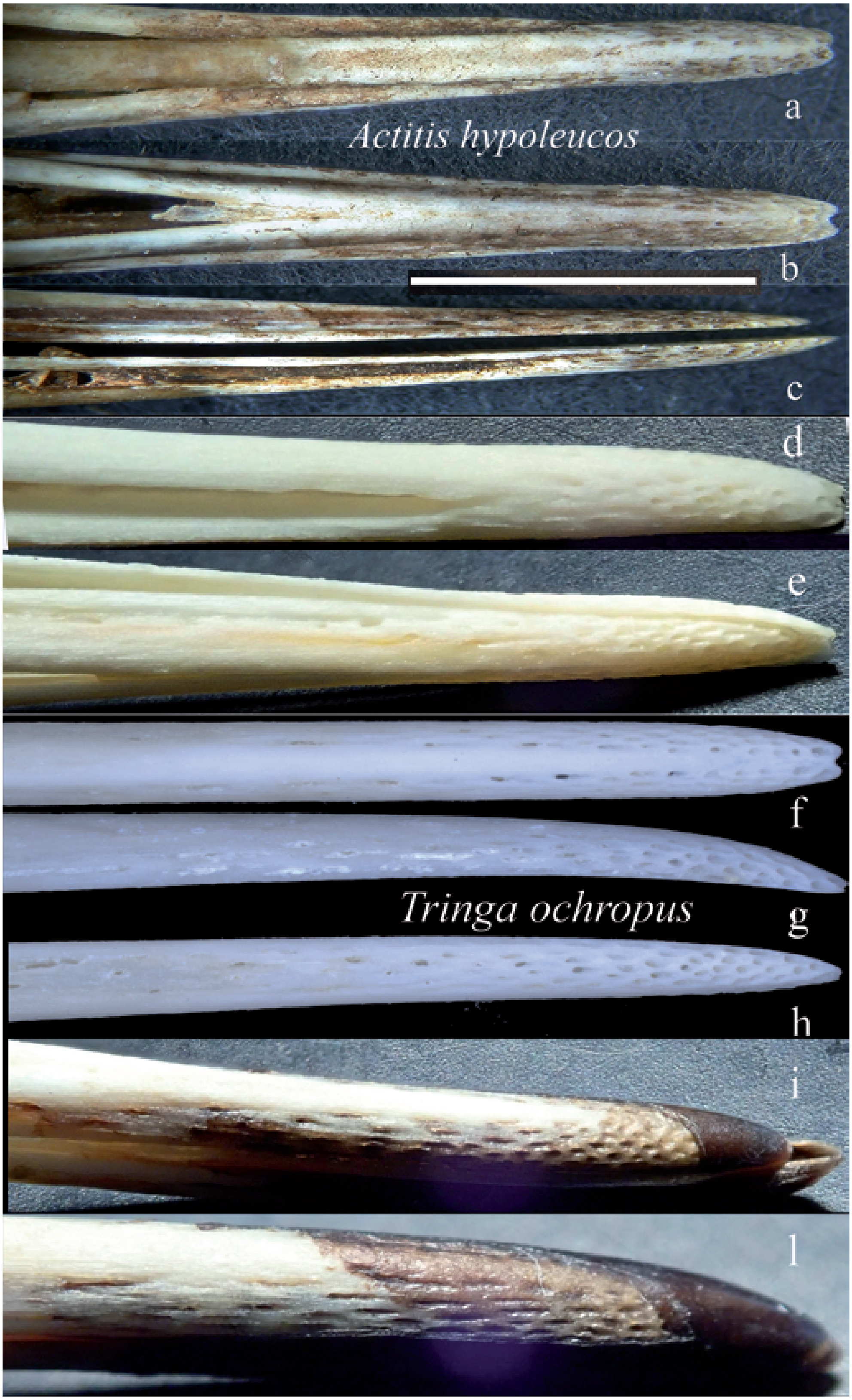

Fig. 6 – *Actitis hypoleucos* (a-e) and *T. ochropus* (f-l); a) upper mandible tip (specimen 1); b) lower mandible tip; c) lateral view of mandibles (stored in RIPC); d) upper mandible tip (specimen 2); e) lower mandible tip in lateral view (specimen 2) (stored in MSNG); f-h: f) upper mandible tip; g) lateral view of upper mandible; h) lower mandible tip (stored in MGPT-MPOC); i) upper mandible tip (specimen 2); l) lower mandible tip (RIPC). Scale bar: 10 mm. / *Actitis hypoleucos* (a-e) e *T. ochropus* (f-l); a) punta della mandibola superiore (esemplare 1); b) punta della mandibola inferiore; c) visione laterale delle mandibole (conservate presso RIPC); d) punta della mandibola superiore (esemplare 2); e) punta della mandibola inferiore in vista laterale (esemplare 2) (conservato presso MSNG); f-h: f) punta della mandibola superiore; g) vista laterale della mandibola superiore; h) punta della mandibola inferiore (conservata presso MGPT-MPOC); i) punta della mandibola superiore (esemplare 2); l) punta della mandibola inferiore (RIPC).

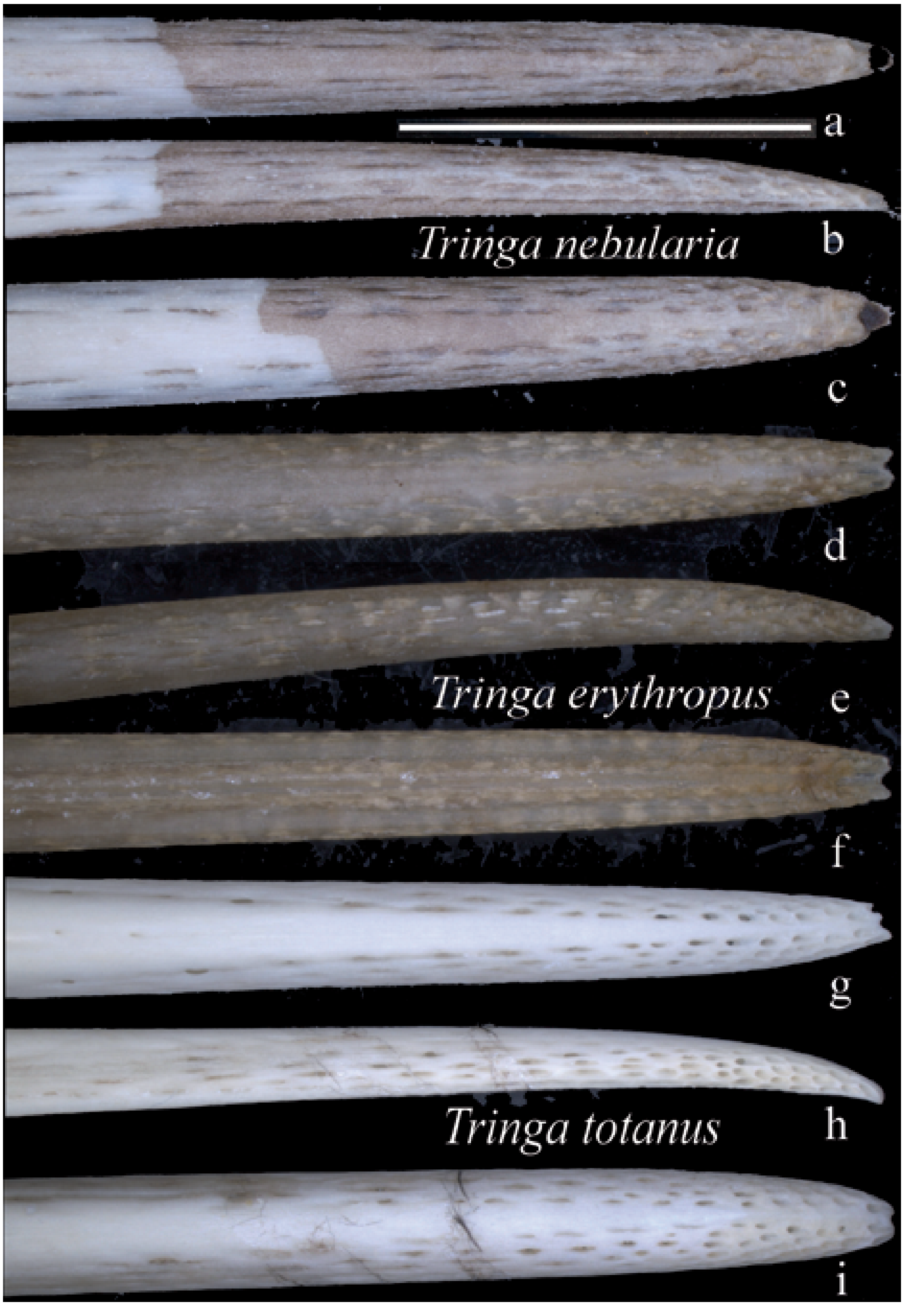

Fig. 7 – Species of the genus *Tringa*; a-c: *T. nebularia* a) upper mandible tip; b) lateral view of upper mandible; c) lower mandible tip; d-f: *T. erythropus* d) upper mandible tip; e) lateral view of upper mandible; f) lower mandible tip; g-i: *T. totanus* g) upper mandible tip; h) lateral view of upper mandible; i) lower mandible tip (all stored in MGPT-MPOC). Scale bar: 10 mm. / Specie del genere *Tringa*; a-c: *T. nebularia* a) punta della mandibola superiore; b) visione laterale della mandibola superiore; c) punta della mandibola inferiore; d-f: *T. erythropus* d) punta della mandibola superiore; e) visione laterale della mandibola superiore; f) punta della mandibola inferiore; g-i: *T. totanus* g) punta della mandibola superiore; h) visione laterale della mandibola superiore; i) punta della mandibola inferiore (tutte conservate presso MGPT-MPOC).

Fig. 8 – Two species of *Limosa*; a-b: *L. lapponica* a) upper mandible tip; b) lower mandible tip; c-e: *L. limosa* c) upper mandible tip; d) lateral view of upper mandible; e) lower mandible tip (all stored in MGPT-MPOC). Scale bar: 20 mm. / Due specie di *Limosa*; a-b: *L. lapponica* a) punta della mandibola superiore; b) punta della mandibola inferiore; c-e: *L. limosa* c) punta della mandibola superiore; d) vista laterale della mandibola superiore; e) punta della mandibola inferiore (tutte conservate presso il MGPT-MPOC).

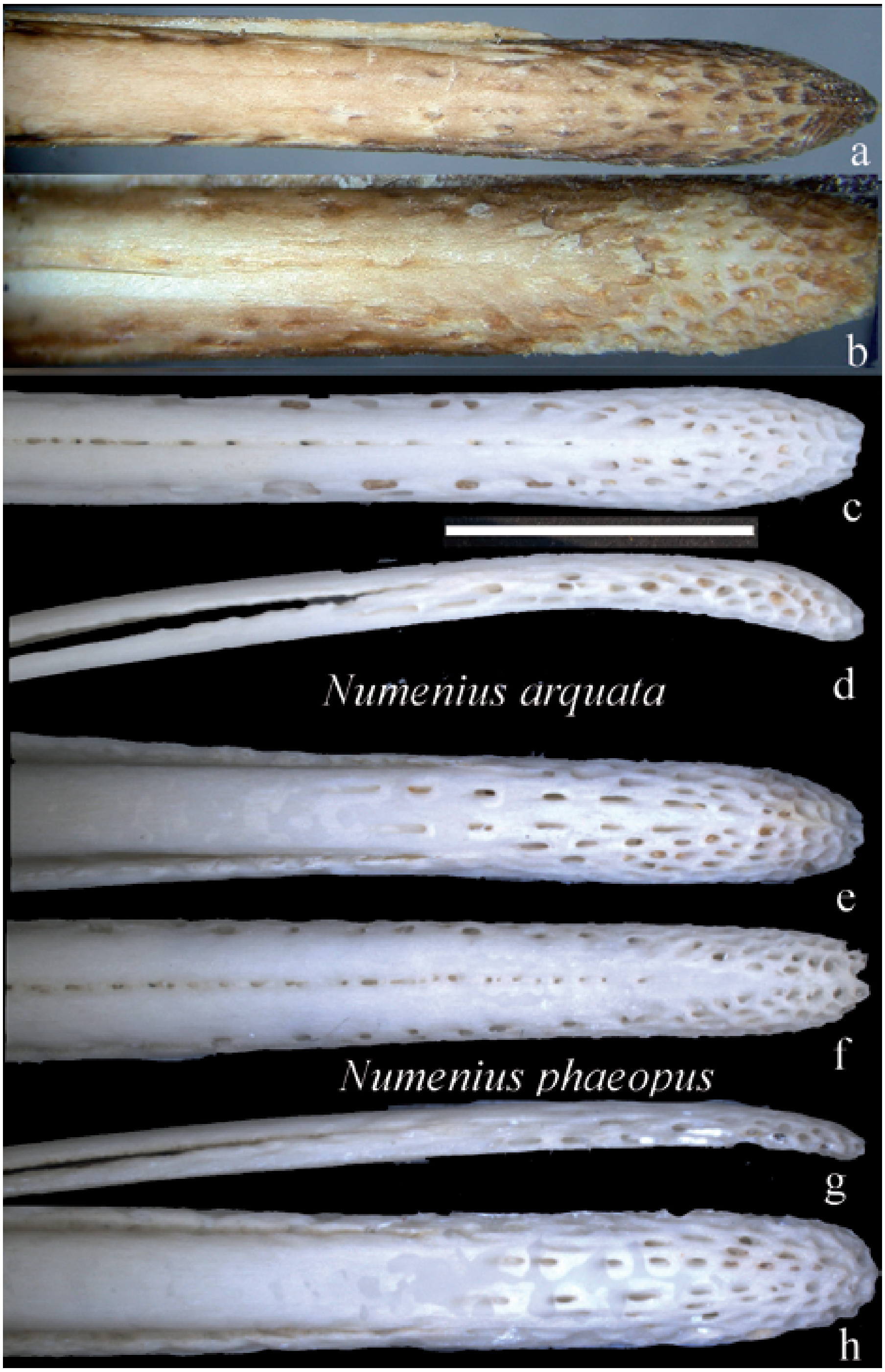

Fig. 9 – Two species of *Numenius*; a-e: *N. arquata* a) upper mandible tip (specimen 1); b) lower mandible tip (specimen 1) (stored in RIPC); c) upper mandible tip (specimen 2); d) lateral view of upper mandible; e) lower mandible tip (specimen 2); f-h: *N. phaeopus* f) upper mandible tip; g) lateral view of upper mandible; h) lower mandible tip (stored in MGPT-MPOC). Scale bar: 20 mm. / Due specie di *Numenius*; a-e: *N. arquata* a) punta della mandibola superiore (esemplare 1); b) punta della mandibola inferiore (esemplare 1) (conservato presso RIPC); c) punta della mandibola superiore (esemplare 2); d) vista laterale della mandibola superiore; e) punta della mandibola inferiore (esemplare 2); f-h: *N. phaeopus* f) punta della mandibola superiore; g) vista laterale della mandibola superiore; h) punta della mandibola inferiore (conservato presso il MGPT-MPOC).

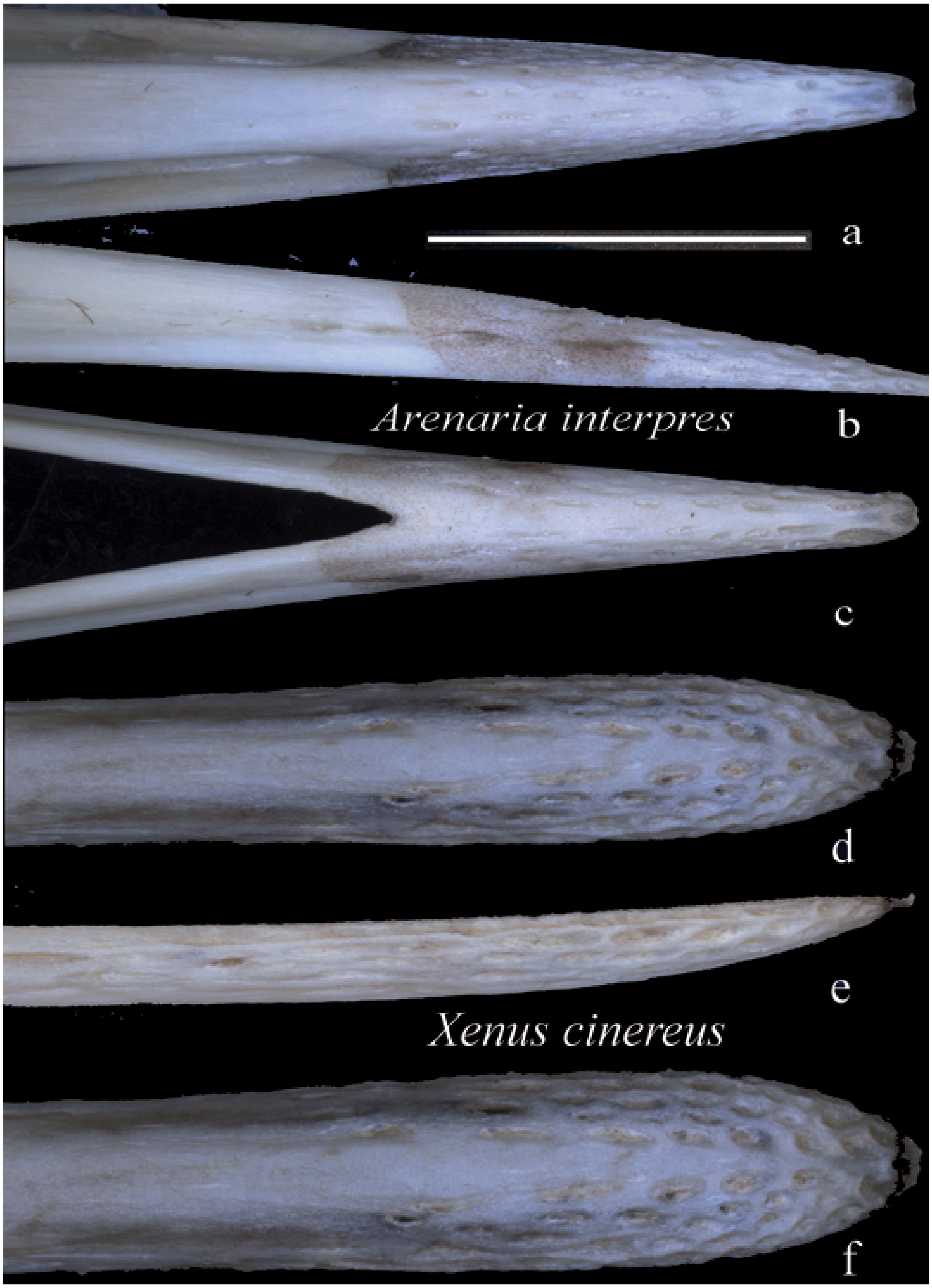

Fig. 10 – *Arenaria interpres* and *Xenus cinereus*; a-c: *A. interpres* a) upper mandible; b) lateral view of upper mandible; c) lower mandible; d-f: *X. cinereus* d) upper mandible; e) lateral view of upper mandible; f) lower mandible (all stored in MGPT-MPOC). Scale bar: 5 mm. / *Arenaria interpres* e *Xenus cinereus*; a-c: *A. interpres* a) mandibola superiore; b) visione laterale della mandibola superiore; c) mandibola inferiore; d-f: *X. cinereus* d) mandibola superiore; e) visione laterale della mandibola superiore; f) mandibola inferiore (tutti conservati presso il MGPT-MPOC).

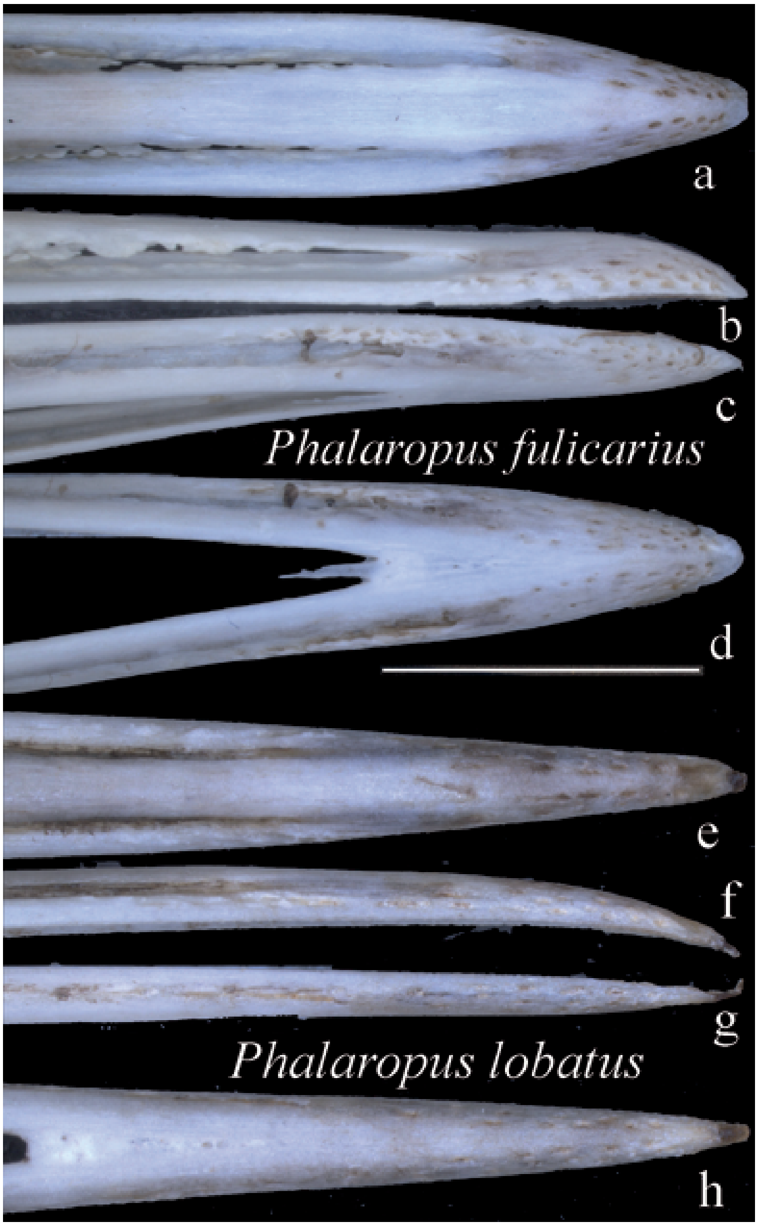

Fig. 11 – Species of the genus *Phalaropus*; a-d: *P. fulicarius* a) upper mandible tip; b) lateral view of upper mandible; c) lateral view of lower mandible; d) lower mandible tip; e-h: *P. lobatus* e) upper mandible tip; f) lateral view of upper mandible; g) lateral view of lower mandible; h) lower mandible tip (all stored in MGPT-MPOC). Scale bar: 5 mm. / Specie del genere *Phalaropus*; a-d: *P. fulicarius* a) punta della mandibola superiore; b) visione laterale della mandibola superiore; c) visione laterale della mandibola inferiore; d) punta della mandibola inferiore; e-h: *P. lobatus* e) punta della mandibola superiore; f) visione laterale della mandibola superiore; g) visione laterale della mandibola inferiore; h) punta della mandibola inferiore (tutti conservati presso il MGPT-MPOC).

Fig. 12 – a) *Himantopus himantopus* (Fam. Recurvirostridae), upper mandible tip showing some foramina; b-d) *Burhinus oedicnemus* (Fam. Burhinidae): b) upper mandible with some big foramina; c) lower mandible with big foramina; d) inner side of lower mandible with some foramina (all stored in MSNG). Scale bar: 20 mm. / a) *Himantopus himantopus* (Fam. Recurvirostridae), punta della mandibola superiore che mostra alcuni resti di fossette sensoriali; b-d) *Burhinus oedicnemus* (Fam. Burhinidae): b) mandibola superiore con alcune grandi fossette sensoriali; c) mandibola inferiore con grandi fossette sensoriali; d) lato interno della mandibola inferiore con alcune fossette sensoriali (tutte conservate presso il MSNG).

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