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ORIGINAL PAPER

Skeletal morphoanatomy of the Brown Skua *Stercorarius antarcticus lonnbergi* and the South Polar Skua *Stercorarius maccormicki*

Carolina Acosta Hospitaleche · Diego Montalti · Lucas José Marti

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Abstract The Brown Skua *Stercorarius antarcticus lonnbergi* and the South Polar Skua *Stercorarius maccormicki*, which breed sympatrically in the Southern Hemisphere, are difficult to identify in the field because of their similar coloration and external morphology. Although several morphological and biological aspects have been previously discussed, no data have been published about their skeletal anatomy. In this paper we make a comparative description of the cranial and appendicular skeleton of both skua species. As a result, and although the differences are small, it has been found that some characters of the skull and the thoracic and pelvic limbs, allow the distinction between *S. antarcticus lonnbergi* and *S. maccormicki*.

Keywords South Polar Skua *Stercorarius maccormicki* · Brown Skua *Stercorarius antarcticus* · Osteography · Antarctica

C. Acosta Hospitaleche · D. Montalti
CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina
e-mail: dmontalti@arnet.com.ar

C. Acosta Hospitaleche (&)
División Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina
e-mail: acostacaro@fcnym.unlp.edu.ar

D. Montalti · L. J. Marti
Departamento Biología, Aves, Instituto Antártico Argentino, Buenos Aires, Argentina
e-mail: lucasjosemarti@yahoo.com.ar

Introduction

Skuas and jaegers are costal and pelagic seabirds which nest on islands and tundra, colonially or solitary. Their distribution is cosmopolitan and they are represented by seven species of which only three breed in the Southern Hemisphere.

There are variations in their diet depending on the species, but most of them are scavengers or kleptoparasites, while others feed on fish or prey on eggs and chicks of other bird species (Furness 1996). They have been traditionally grouped in the family Stercorariidae (Order Charadriiformes), but more recent taxonomic proposals (Andersson 1999b; Sibley and Monroe 1990) have classified them as Laridae (Larinae, Stercorarinii) keeping their status as a clade.

Although two genera, *Stercorarius* Brisson 1760 (with three species known as jaegers) and *Catharacta* Brunnich 1764 (with four species known as skuas) have been classically recognized, nowadays it is considered that all the species could belong to *Stercorarius* (Cohen et al. 1997; Andersson 1973, 1999a). Skuas, firstly assigned to *Catharacta,* have been classified for a long time in different ways including a variable number of species and subspecies (according to Devillers 1977, 1978; Peter et al. 1990; Blechschmidt et al. 1993).

In the present work we follow Andersson (1999b) criteria, which based on molecular, behavioral and parasite specificity evidence, assigns all the southern species to *Stercorarius.* This genus includes three species: *Stercorarius antarcticus* (Lesson) 1831 (with the subspecies *S. a. lonnbergi* (Mathews) 1912, *S. a. antarcticus* (Lesson) 1831 and *S. a. hamiltoni* (Hagen, 1952), *Stercorarius maccormicki* Saunders, 1893 and *S. chilensis* Bonaparte 1857.

Stercorarius antarcticus nests colonially in the Antarctic Peninsula, sub-Antarctic islands and Atlantic islands of Patagonia, while *S. maccormicki* nests mainly in the Antarctic continent, extending its distribution limit towards the north of the Antarctic Peninsula up to the South Orkney Islands (Hemmings 1984; Ritz et al. 2006).

Both species breed sympatrically between the 61° and 65° SL, but they only hybridize in some particular areas in this zone (Fig. 1) (Parmelee et al. 1978; Trivelpiece and Volkman 1982; Reinhardt et al. 1997; Ritz et al. 2006). Despite the larger size and some other typical characteristics of the Brown Skua (Olsen and Larsson 1997), this area of hybridization had generated serious problems with their field identification and by consequence, its taxonomic assignment. In fact, Lowe and Kinnear (1930), Hamilton (1934), and Murphy (1936) have stressed the great individual variation that skuas present in their appearance, suggesting that there are no plumage characters that can be considered diagnostic of each species.

Many contributions have been made by different authors trying to emphasize the similarities and differences between these two species, including metric external characters (Murphy 1936; Montalti 2005 and references therein), coloration (Devillers 1978; Ainley et al. 1985; Marchant and Higgins 1993), body weight (Furness 1987; 1996), prey items (Pietz 1987; Reinhardt 1997), breeding biology (Pietz 1986; Peter et al. 1990), behavior (Pietz 1984), ectoparasite specificity (Furness et al. 1995), fungus specificity (Leotta et al. 2002), blood biochemical parameters (Montalti 2005) and molecular data (Blechschmidt et al. 1993; Cohen et al. 1997; Votier et al. 2004, 2007; Ritz et al. 2008). However, osteological characters have not been used so far.

The goal of this paper is to determine if there are skeletal differences between *Stercorarius antarcticus lonnbergi* and *S. maccormicki*, considering that every single tool would help and will be useful to be used with taxonomic purposes.

Materials and methods

Thirteen skeletons of *S. maccormicki* (seven males, six females) and 23 *S. antarcticus lonnbergii* (11 males and 12 females) were studied. Only adult and complete specimens of both sexes were selected for descriptions in order to minimize age or material preservation variability. The skulls and the appendicular bones (Table 1) were chosen for comparison being the most informative elements used in avian taxonomy.

These skeletons are housed in the Collection of the Instituto Antártico Argentino (IAA) at the Ciudad Autónoma de

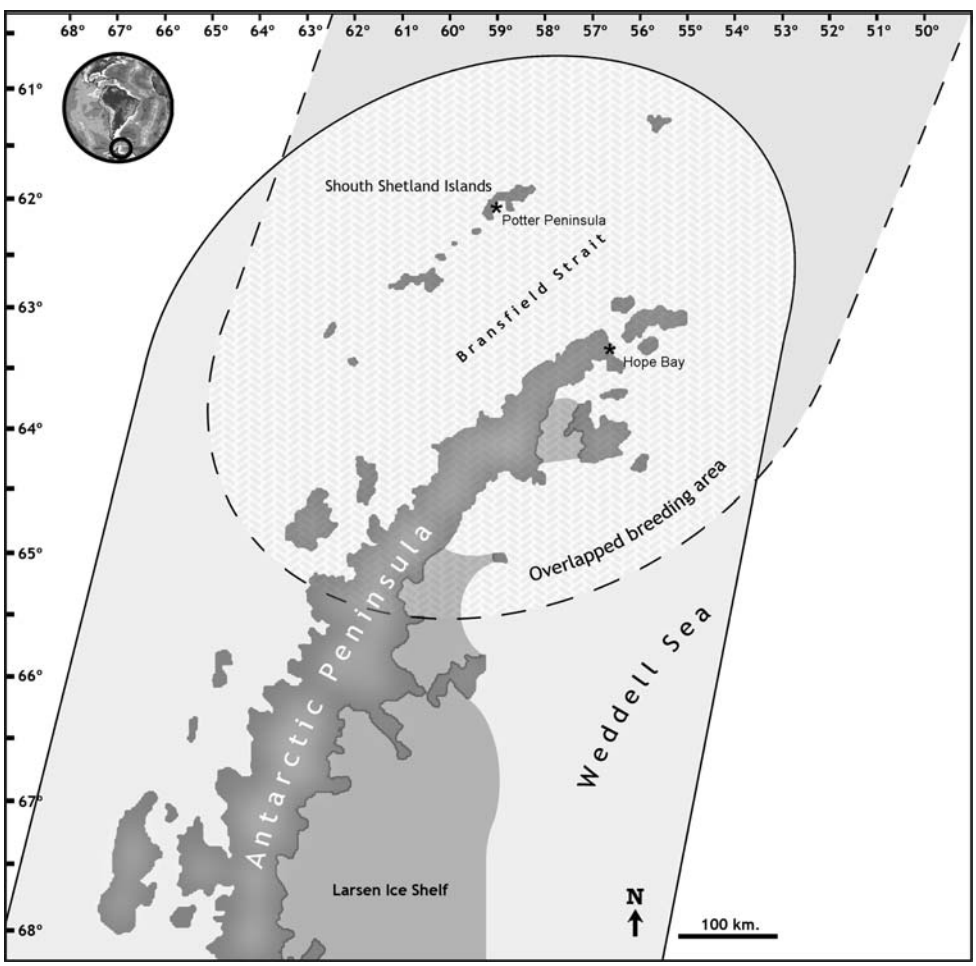


Fig. 1 Location map showing breeding area of Brown and South Polar Skuas in *dashes* and *full lines*, respectively. Localities of collection are also indicated

Table 1 Osteological materials used in descriptions and morphometric analysis

Locality	*Stercorarius antarcticus lonnbergi*		*Stercorarius maccormicki*	
	Male	Female	Male	Female
Hope Bay	IAA 1296, IAA 1297, IAA 1392, IAA 1492, IAA 1527, IAA 1528, IAA 1534, IAA 1535, IAA 1647	IAA 1282, IAA 1285, IAA 1286, IAA 1289, IAA 1290, IAA 1291, IAA 1293, IAA 1389, IAA 1391, IAA 1394, IAA 1529, IAA 1536	IAA 1283, IAA 1284, IAA 1544, IAA 1648	IAA 1279, IAA 1288, IAA 1388, IAA 1525, IAA 1526
Potter Peninsula	IAA 1481, IAA 1482		IAA 1483, IAA 1484, IAA 1565	IAA 1115

Buenos Aires, Argentina and they were collected from the localities of Potter Peninsula, Isla 25 de Mayo (King George Island), South Shetland Islands (62°14′S, 58°40′W) and Hope Bay (63°23′S, 54°00′W), Antarctic Peninsula, Antarctica. According to these collection areas all the material assigned to *S. antarcticus* belongs to *S. a. lonnbergi,* the only Brown skua subspecies that hybridize with the South Polar Skua. Taxonomic determinations can be looked up in Montalti (2005).

All the materials used in the present contribution comply with the current laws of Argentina, the country in which they were performed. All the skeletons studied were collected from breeding colonies or individuals found already dead.

Skulls, humeri and tarsometatarsi were selected for geometric analysis. Ten points were chosen in the dorsal view of the skull (Fig. 2a), seven complementary points located in the palatal view (Fig. 2b), eight in the anterior face of the humerus (Fig. 2c) and eleven in the anterior face of the tarsometatarsus (Fig. 2d), including landmarks of type I, II, and III (Rabello Monteiro and Furtado dos Reis 1999).

Independent analyses were performed, comparing dorsal and palatal view of the skulls, the humeri and the tarsometatarsi in individuals of both taxa, testing the following: (1) interespecif differences, (2) sexual differences in *S. a. lonnbergi*, (3) sexual differences in *S. maccormicki*, and (4) geographic differences.

Variation in shape of the landmarks configurations was compared using procrustes superimposition (Rohlf and Slice 1990).

To show the results of each analysis, the computer graphics used here are the thin plate splines. A relative warp analysis, a modification of principal component analysis for shape coordinate data, was made using the software tpsRelw (Rohlf 2005). The relative warps were computed with the uniform component included and no weighing by bending energy (Bookstein 1996). A detailed explanation of this methodology can be consulted in Acosta Hospitaleche and Tambussi (2006).

Compared descriptions follow the terminology used by Baumel and Witmer (1993) and start with a description of the skull and mandible (Fig. 3a–c), followed by the chosen elements of the thoracic limb (humerus and carpometacarpus) (Fig. 3d–g) and finally, the ones of the pelvic limb (femur, tibiotarsus and carpometacarpus) (Fig. 4).

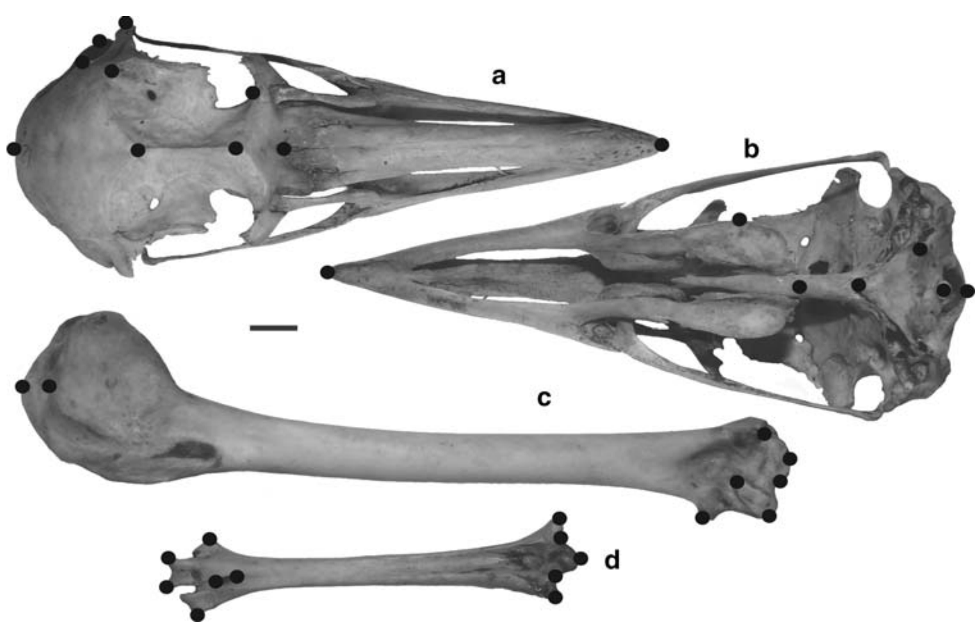


Fig. 2 Landmark selection: **a** skull in dorsal view, **b** skull in palatal view, **c** humerus in anterior view, **d** tarsometatarsus in anterior view. *Scale bar* 10 mm

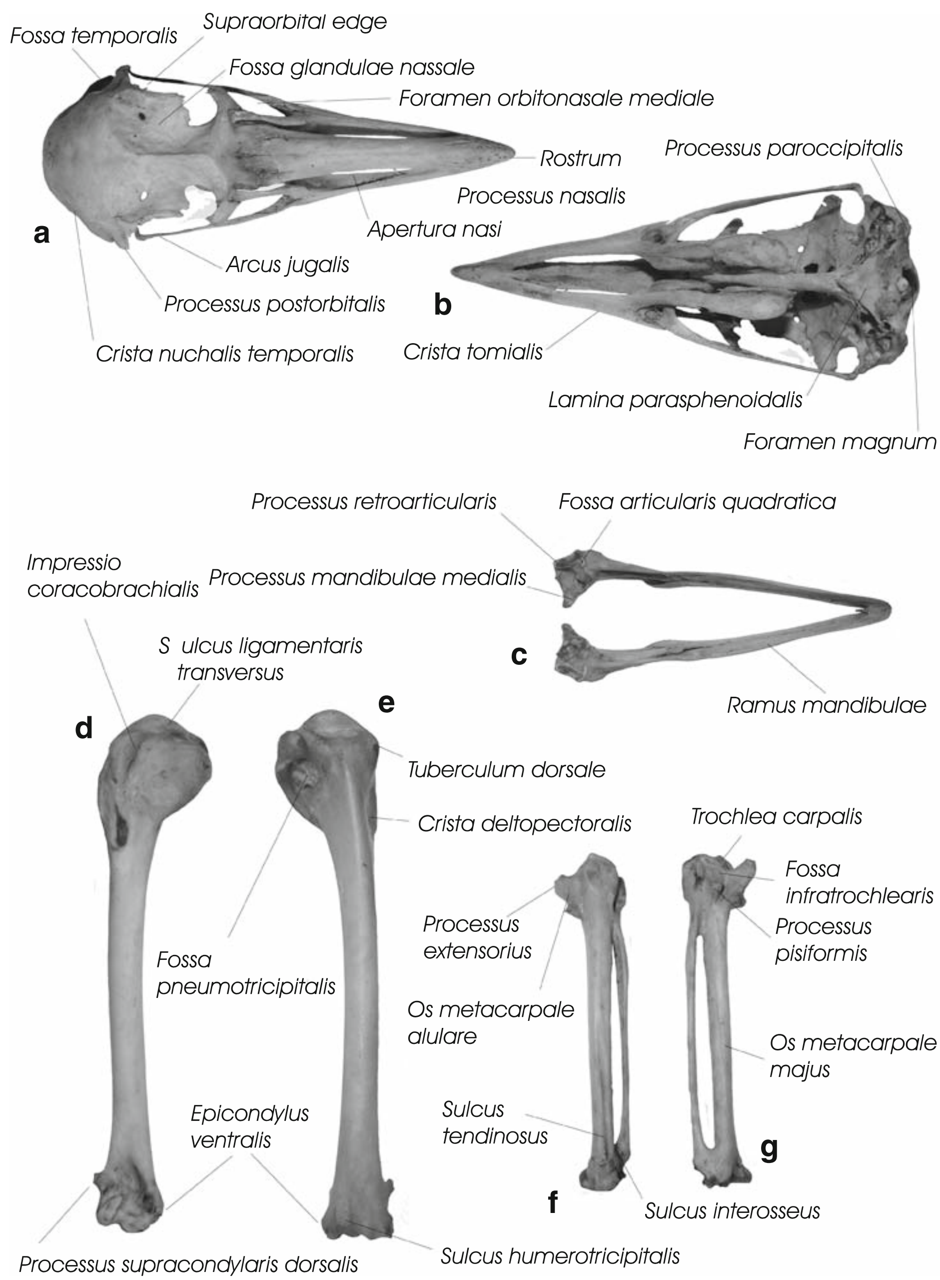


Fig. 3 Terminology employed in descriptions: **a** skull in dorsal view, **b** skull in palatal view, **c** mandible in dorsal view, **d** humerus in anterior view, **e** humerus in posterior view, **f** carpometacarpus in anterior view, **g** carpometacarpus in posterior view

Statistical analysis

Although more detailed comparisons of the skeletons between sexes and localities are still pending for future studies, a preliminary analysis could be done. None of the statistical analysis performed allowed differentiating males from females in *S. a. lonnbergi* (Figs. 5, 6) nor in *S. maccormicki* (Figs. 7, 8). It was not possible to identify either skeletal differences related to geographical variations in *S. maccormicki* (Fig. 9), the only species with a suitable sample for this kind of test.

Even though no morpho-geometric variations between the two compared species (Figs. 10, 11) were found, some qualitative differences were established when comparing the skeletons of *S. maccormicki* and *S. a. lonnbergi*.

Osteological descriptions

Skull (Fig. 12a–d)

In both species the *processus paroccipitalis* project ventrally being a little thinner in *S. antarcticus* than in *S. maccormicki*. The *foramen magnum* is framed by these *processus* and is divided into a ventral and dorsal part, the latter one being more caudally extended. The plane containing the *foramen*

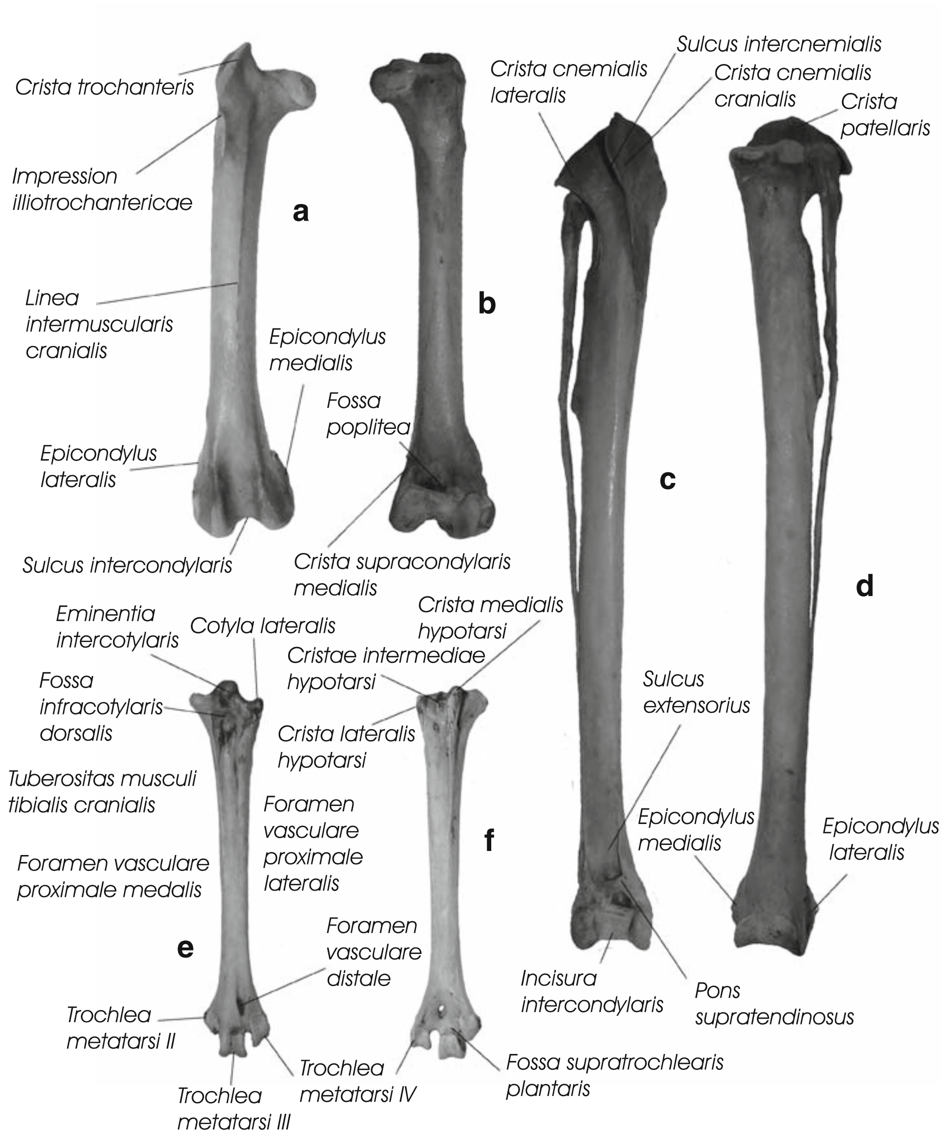


Fig. 4 Terminology employed in descriptions: **a** femur in anterior view, **b** femur in posterior view, **c** tibiotarsus in anterior view, **d** tibiotarsus in posterior view, **e** tarsometatarsus in anterior view, **f** tarsometatarsus in posterior view

magnum forms an angle with the *lamina parasphenoidalis* of 64° in *S. maccormicki*, while in *S. antarcticus* this angle is about 54°.

Having a triangular shape and situated at the same level and parallel to the *crista tomialis*, in both species the *lamina parasphenoidalis* has a pair of *processus* closer to each other in *S. maccormicki* than in *S. antarcticus.* The *arcus jugalis* is straight and extends along the *crista tomialis.*

The *crista nuchalis transversa* is more developed in *S. antarcticus* than in *S. maccormicki*. The *cristae nuchalis temporalis* project towards the *processus postorbitalis* delimiting a *fossa temporalis,* which is deeper in *S. maccormicki* than in *S. antarcticus*.

In both species, the left and right *fossae temporalis* do not reach the sagittal line on its dorsal end and do not develop a *crista nuchalis sagitalis*. Cranially, the *fossa temporalis* is separated from the *fossa glandulae nassale* by a thin septum developed over the *processus postorbitalis,* which are broader in *S. antarcticus* than in *S. maccormicki*.

The *fossae glandulae nassale* keep the same width along their length and are dorsally separated by an extremely slender frontal bone in the interorbital region. The supraorbital edge, which only limits the *fossa glandulae nasalis* on their caudal part, is similar in both species.

The *processus nasalis* of the premaxilar bones are narrow, leaving the wide *aperture nasi* uncovered in dorsal view. Each *apertura nasi* opens dorsally to the *foramen orbitonasale mediale*, which is fused to the orbit in *S. antarcticus* as well as in *S. maccormicki.*

The distal end of the *rostrum* is curved in both species. The palatines are broader in *S. antarcticus* while in *S. maccormicki* they have more curved edges. Pterigoids are thin and rod-like in both species.

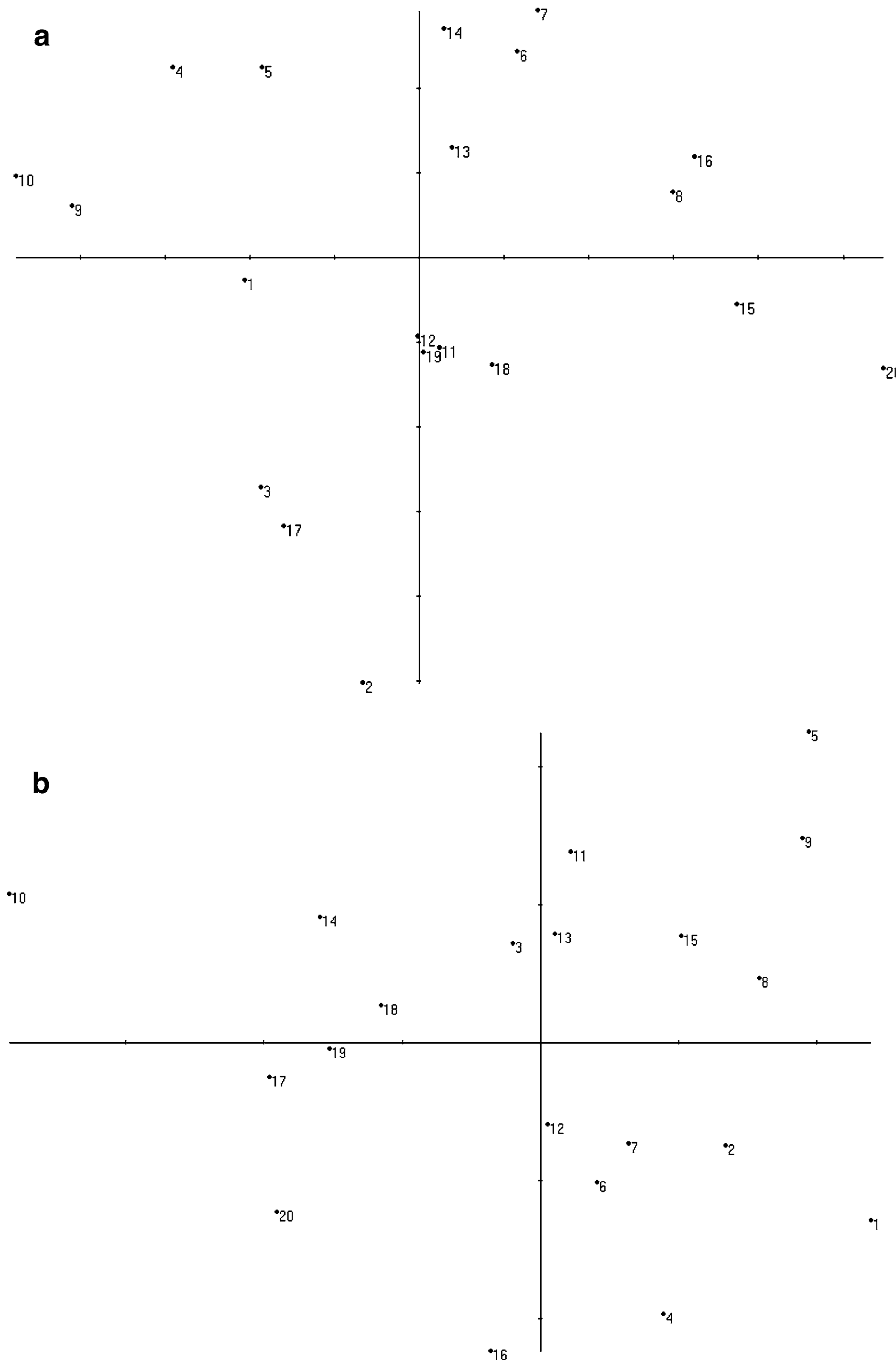


Fig. 5 Relative warps analysis of *S. antarcticus lonnbergi* (1–8: males, 9–20: females): **a** analysis of the skull in dorsal view, **b** analysis of the skull in palatal view

Mandible (Fig. 12f–h)

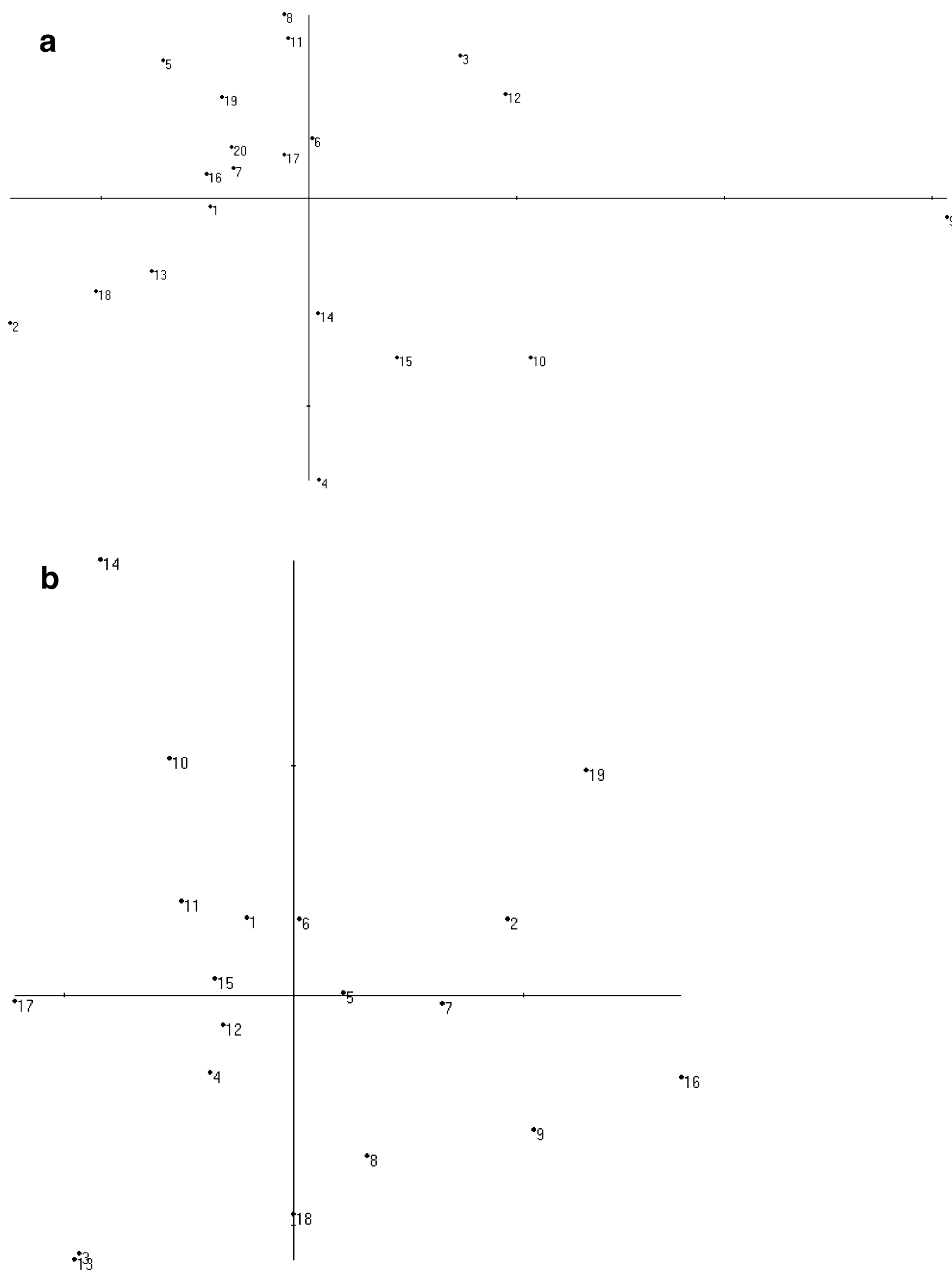
The *ramus mandibulae* is straight and the *fossa articularis quadratica* occupies a bigger area than the internal *processus articularis*. None of the two species have *processus retroarticularis*.

The *processus mandibulae medialis* is more robust in *S. antarcticus* than in *S. maccormicki.* In both species, only the *fenestra mandibularis cranialis* is open, while the *fenestra mandibularis caudalis* is completely obliterate.

Humerus (Fig. 13a–d)

The *fossa pneumotricipitalis* is sub-rounded and is surrounded by a *tuberculum ventrale* that is better developed in *S. antarcticus*. The *crus dorsale fossae* and the *crus*

Fig. 6 Relative warps analysis of *S. antarcticus lonnbergi* (1–8: males, 9–20: females): **a** analysis of the humerus in anterior view, **b** analysis of the tarsometatarsus in anterior view



ventrale fossae are more pronounced in *S. antarcticus* than in *S. maccormicki.*

The *tuberculum dorsale* is elongated and blunt, but less conspicuous in both species. The *crista deltopectoralis* is widely expanded and its sharpened distal end projects cranially in both species.

The *processus supracondylaris dorsalis* project cranially with a slight inclination towards the proximal end, with no differences between species. The *epicondylus ventralis* is rounded and slightly marked in *S. antarcticus* and *S. maccormicki*.

The *sulcus humerotricipitalis* is wide and connected to the *fossa olecrani*. The *impressio coracobrachialis* is shallow and proximally connected to the *sulcus ligamentaris transversus* which is narrow but deep in both taxa. The *fossa m. brachialis* is larger in *S. antarcticus* but more rounded in *S. maccormicki.*

Carpometacarpus (Fig. 13e–h)

It is larger in *S. antarcticus* than in *S. maccormicki.* The proximal end of the *trochlea carpalis* is sharper in *S. antarcticus* than in *S. maccormicki,* while the notch that joins it to the *processus extensorius* (which is also larger) is broader. The *fovea carpalis caudalis* does not show significant differences between both species, but the *os metacarpale*

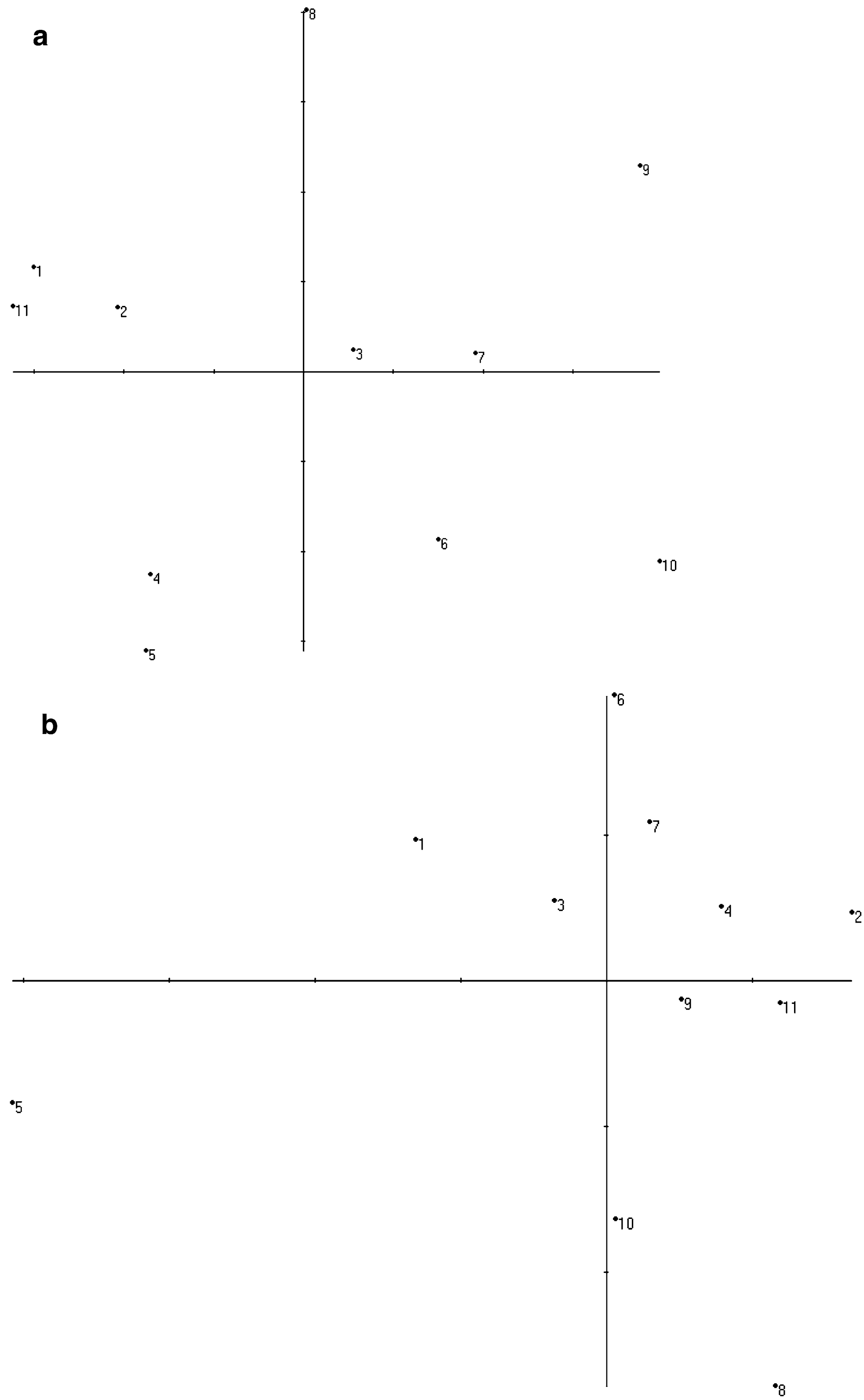


Fig. 7 Relative warps analysis of *S. maccormicki* (1–6: males, 7–11: females): **a** analysis of the skull in dorsal view, **b** analysis of the skull in palatal view

alulare displays a more closed hook shape in *S. antarcticus* than in *S. maccormicki*.

The triangular *sulcus interosseous* is broader in *S. antarcticus*, and in both species it is connected with the *sulcus tendinosus* that reaches the half of the *os metacarpale majus*.

The *fossa infratrochlearis* is rounded in *S. maccormicki*, and more elongated in proximal–distal sense in

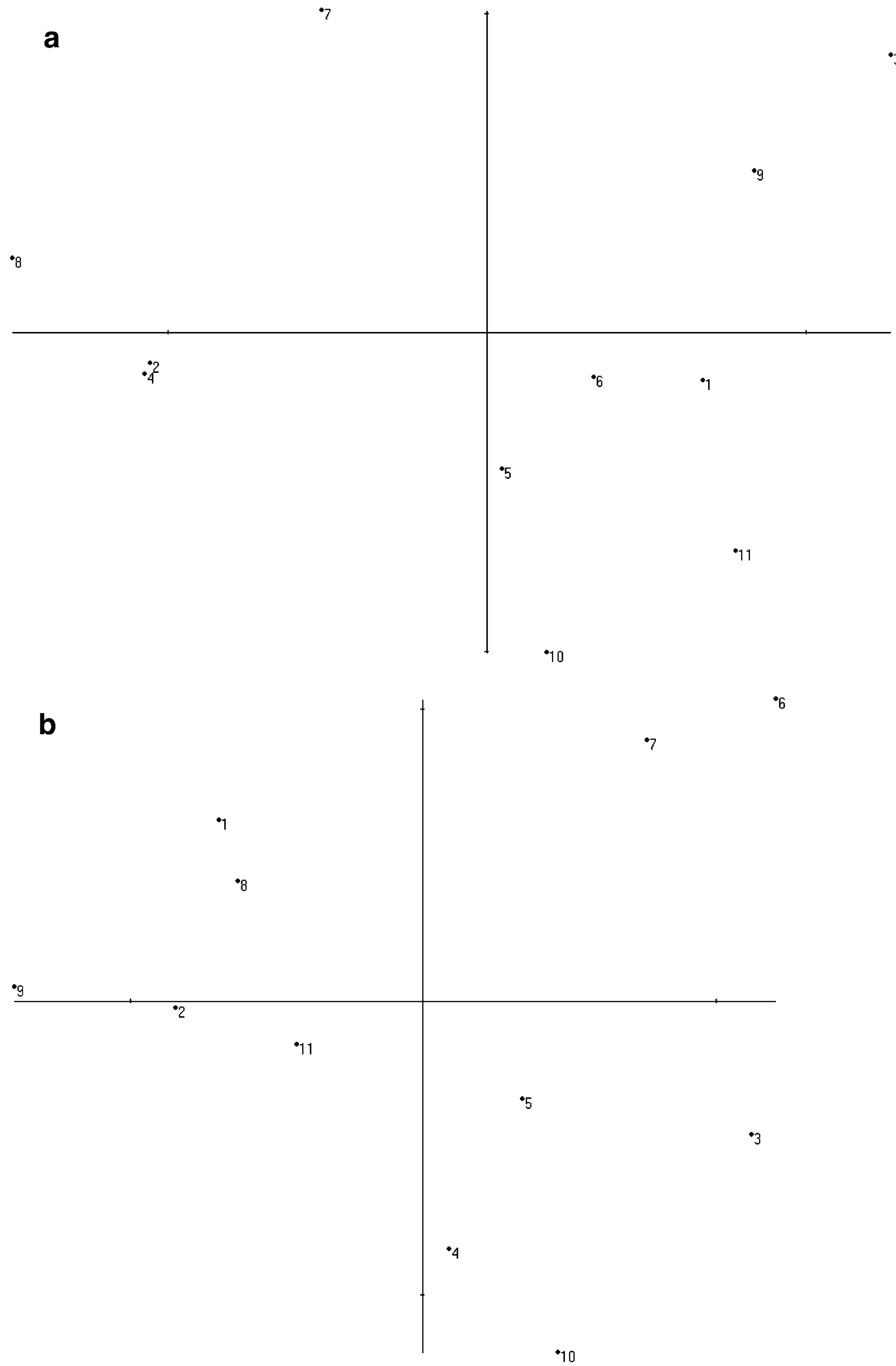


Fig. 8 Relative warps analysis of *S. maccormicki* (1–6: males, 7–11: females): **a** analysis of the humerus in anterior view, **b** analysis of the tarsometatarsus in anterior view

S. antarcticus. The *processus pisiformis* is sharper in the latter species.

Femur (Fig. 14a–d)

The *crista trochanteris* is more marked and proximally projected in *S. antarcticus*. Following the line of the *crista trochanteris* are the *impression iliotrochantericae*, which are well developed. The *linea intermuscularis cranialis* disappears before reaching the distal end in both species. The *sulcus intercondylaris* is symmetrical with respect to the distal condyles in *S. antarcticus* while in *S. maccormicki* it is deeper and displaced toward the inner side.

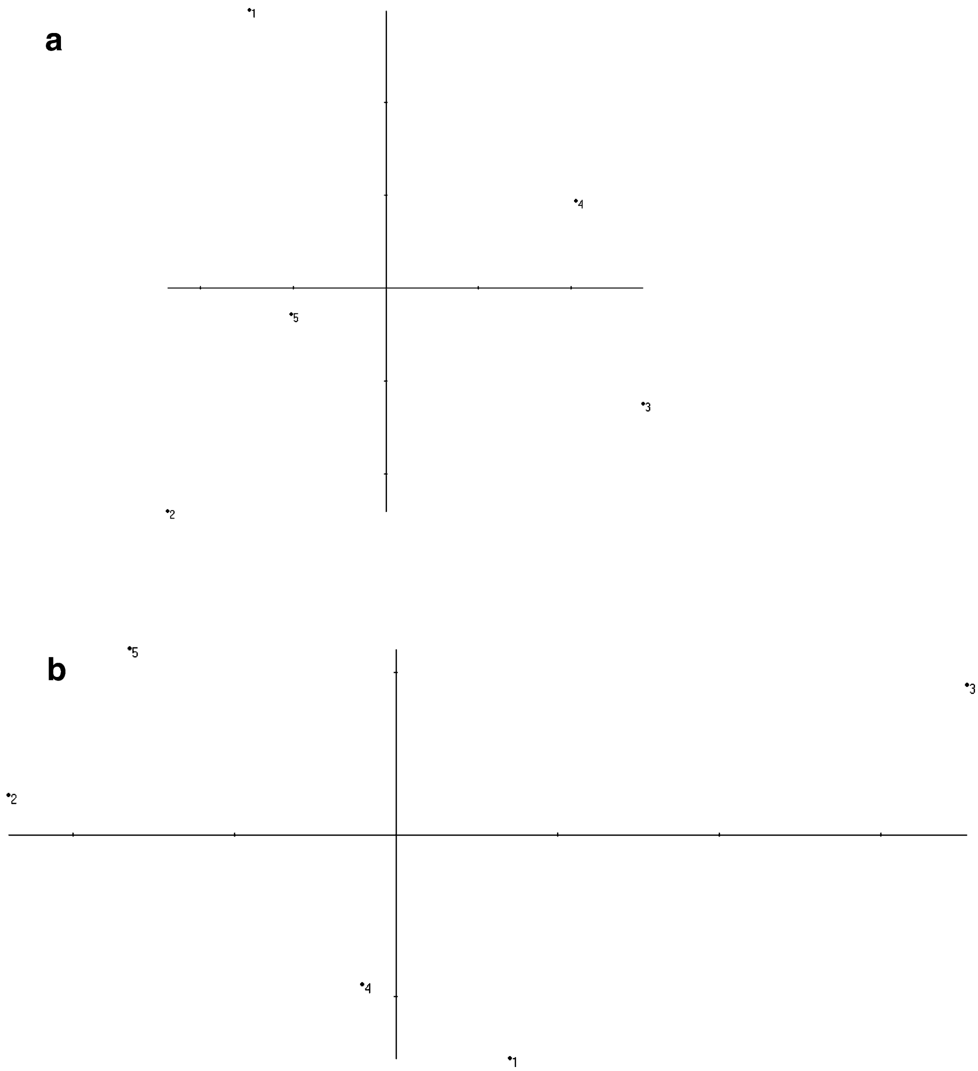


Fig. 9 Relative warps analysis of *S. maccormicki* (1–3: from Hope Bay, 4–5: from Potter Peninsula): **a** analysis of the skull in dorsal view, **b** analysis of the skull in palatal view

The *epicondylus medialis* and *lateralis* are weakly developed in both species. The *trochanter femoris* is smaller in *S. antarcticus* and continues with the *facies articularis antitrochanterica* in both species. The *fossa trochanteris* is minimally developed in these taxa.

The *fossa poplitea* has an irregular shape and is medially limited by a weak *crista supracondylaris medialis* which is higher in *S. maccormicki* than in *S. antarcticus*.

Tibiotarsus (Fig. 14g–j)

The *sulcus intercnemialis* shows a little distal extension, and its depth diminishes gradually and distally in both species. The *crista cnemialis cranialis* is elevated and its edge is more rounded in *S. antarcticus*. The *crista cnemialis lateralis* develops a sharpened border and projects cranially in both taxa.

The *sulcus extensorius* is broad and its lateral and medial limits are represented by poorly defined crests. The *pons supratendinosus* is slightly broader in *S. antarcticus*, and runs obliquely to the axis of the diaphysis in both taxa.

The *incisura intercondylaris* is oval and shallow, showing no differences between the species.

The *crista patellaris* and the *facies articularis lateralis* present a proximal extension in *S. antarcticus* and in *S. maccormicki*, minor to the one of the fibula. In both species the *epicondylus medialis* is little conspicuous but more developed than the *epicondylus lateralis.*

Tarsometatarsus (Fig. 14e, f, k, l)

The *eminentia intercotylaris* is more rounded and robust in *S. antarcticus* and it is aligned with the *trochlea metatarsi III* in both species. The *cotyla medialis* is displaced medially towards the *trochlea metatarsi II*, while the *cotyla lateralis is* aligned with the *trochlea metatarsi IV*. The *fossa infracotylaris dorsalis* is very deep and shows no differences between taxa. The *tuberositas musculi tibialis cranialis*

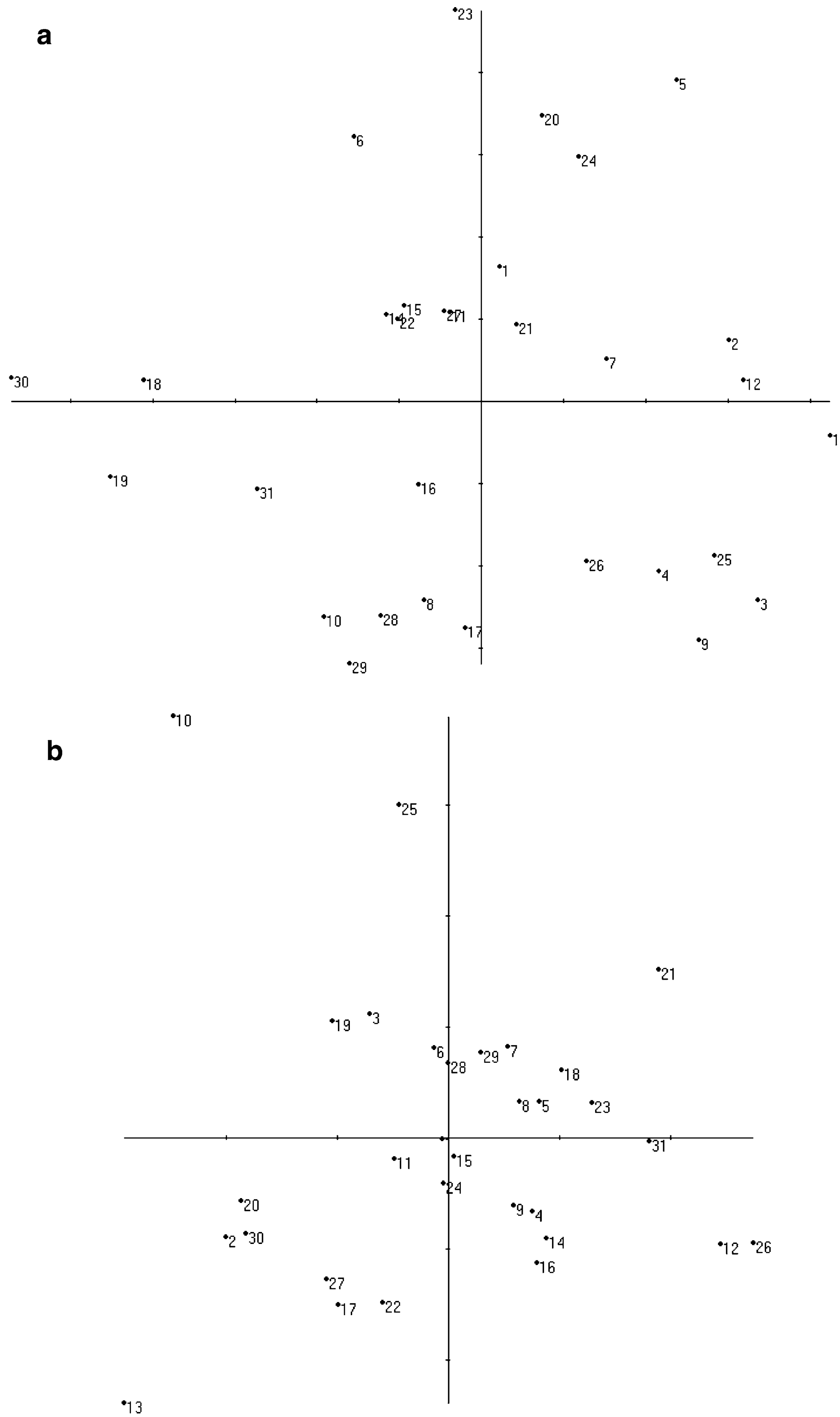


Fig. 10 Relative warps analysis of *S. maccorimcki* (1–11) and *S. antarcticus lonnbergi* (12–20): **a** analysis of the skull in dorsal view, **b** analysis of the skull in palatal view

forms a single protuberance, larger and more elongated in *S. antarcticus* than in *S. maccormicki*. In both cases, the *tuberositas musculi tibialis cranialis* separates the *fossa infracotylaris dorsalis* from the *sulcus extensorius*.

The *foramina vascularia* of the tarsometatarsus do not show any differences between species. The *foramen vasculare proximale lateralis* is very small and opens caudally as well as cranially while the *foramen vasculare proximale*

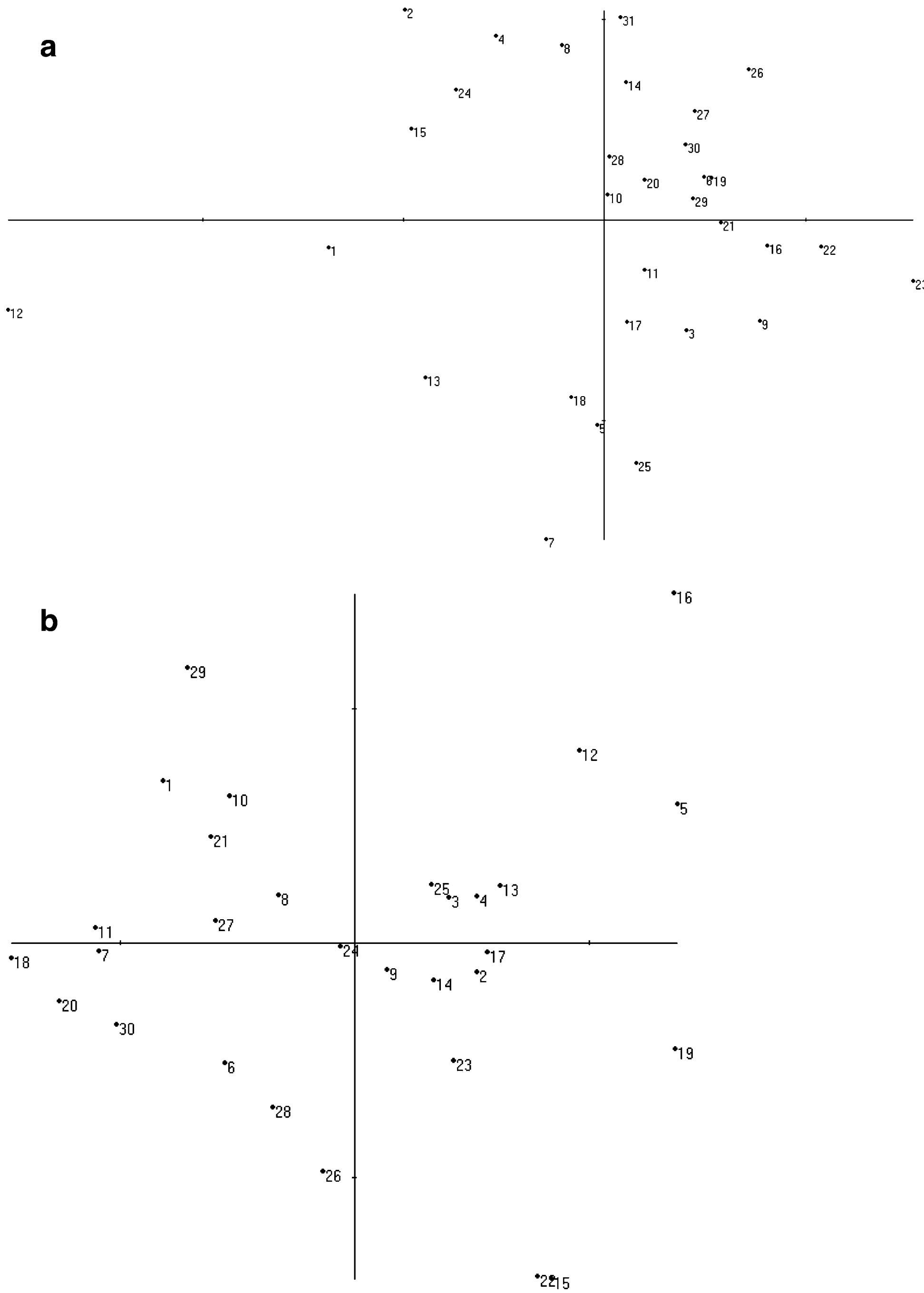


Fig. 11 Relative warps analysis of *S. maccormicki* (1–11) and *S. antarcticus lonnbergi* (12–20): **a** analysis of the humerus in anterior view, **b** analysis of the tarsometatarsus in anterior view

medialis is absent. In the inner part of the deep *fossa supratrochlearis plantaris* opens the *foramen vasculare distale*, which is sub-rounded and bigger than the *foramina vascularia proximalia.* The last foramina form a channel that runs from the *facies cranialis* to the *caudalis* in both species.

The *trochlea metatarsi III* has stronger trochlear edges and it is placed more cranially than the other trochleas in *S. maccormicki.*

The *hypotarsus* occupies a small area over the *facies caudalis* in both species. The *crista medialis hypotarsi* is the biggest and it is broader in *S. antarcticus* than in *S. maccormicki*. Both *cristae intermediae hypotarsi* are similar and much smaller than the *crista medialis hypotarsi*, while the *crista lateralis hypotarsi* is not developed by either species. The *sulcus extensorius* is deeper in *S. antarcticus*.

Discussion and conclusions

Plentiful data about the biology of these species were provided by previous authors. External measurements show

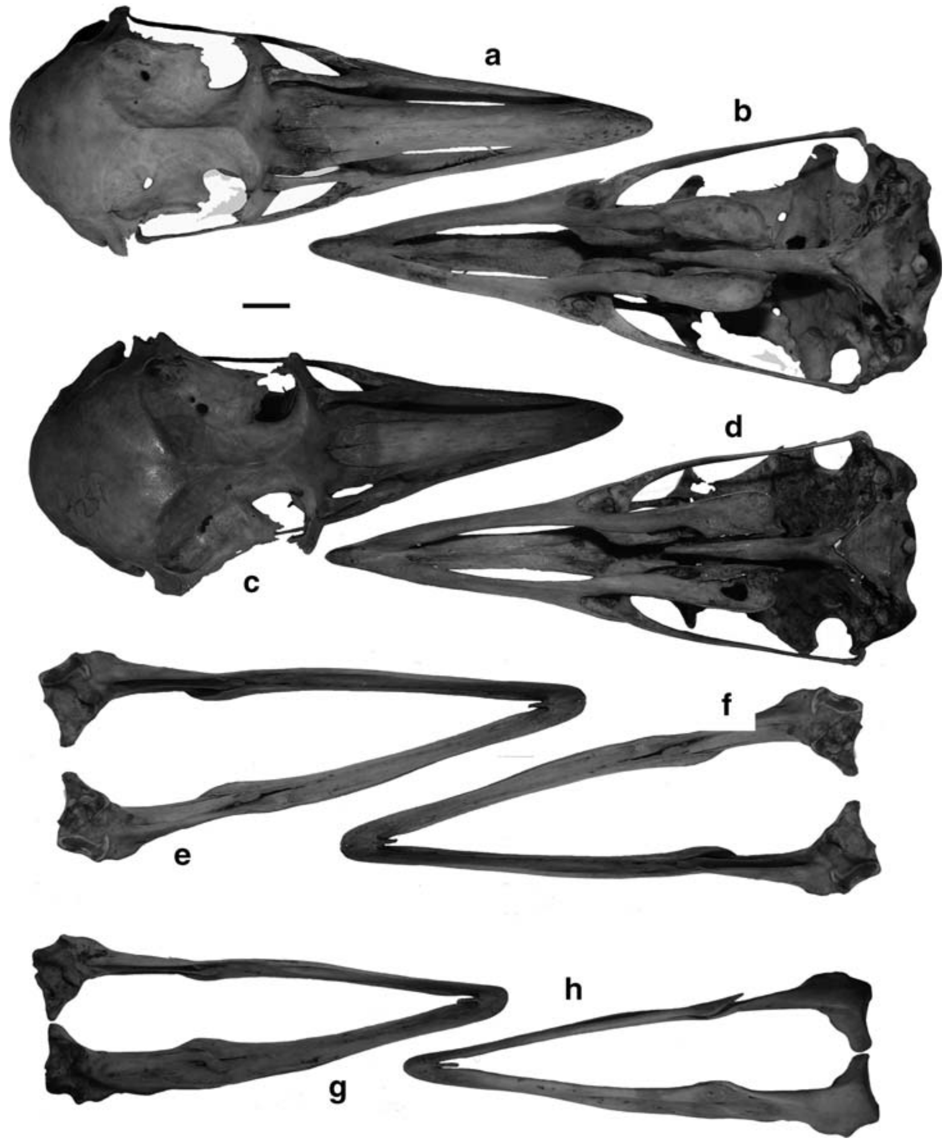


Fig. 12 Skull and mandible. *S. antarcticus lonnbergi*: a- skull in dorsal view, b- skull in ventral view, **e** mandible in dorsal view, **f** mandible in ventral view, *S. maccormicki*: **c** skull in dorsal view, **d** skull in ventral view, **g** mandible in dorsal view, **h** mandible in ventral view. *Scale bar* 10 mm

that the South Polar Skua is smaller than the Brown Skua (Devillers 1978), *S. a. lonnbergi* is the largest and heaviest of all the southern skuas (Devillers 1977; Reinhardt et al. 1997), whereas *S. maccormicki* is intermediate in size (Furness 1987; Reinhardt et al. 1997). However, they have not been consistent in the species identification, since the results are highly variable. For this reason, combinations of these data have been usually made to differentiate *S. antarcticus lonnbergi* from *S. maccormicki*. The external morphologic differences reported between the Brown Skua and the South Polar Skua are little, and comparative studies between these two species are unusual (Devillers 1978; Peter et al. 1990; Olsen and Larsson 1997). It has led not to even discuss about the use of the skeletal characters of the South Hemisphere Skuas with taxonomic purposes (e.g., Furness 1987; de Korte et al. 1994; Cohen et al. 1997; Montalti 2005).

Although skeletal morphoanatomical differences between *S. a. lonnbergi* and *S. maccormicki* are small, they still constitute a legitimate taxonomical tool. The advantages in its implementation are obvious, especially for those remains with no biological data or any other complementary information.

In relation to the statistical analyses, none of the groups identified allowed the recognition of taxonomic, sexual or geographical differences.

The present results show that *S. antarcticus* differentiates from *S. maccormicki* in a number of osteological characters. In the skull and mandible the *processus paroccipitalis* are thinner, the angle between the plane containing the *foramen magnum* and the *lamina parasphenoidalis* is minor, the *processus* of the *lamina parasphenoidalis* are more separated between each other, the *crista nuchalis transversa* is stronger, the *fossa*

Fig. 13 Pectoral limb. *S. antarcticus lonnbergi*: **a** humerus in anterior view, **c** humerus in posterior view, **e** carpometacarpus in dorsal view, **g** carpometacarpus in ventral view, *S. maccormicki* **b** humerus in anterior view, **d** humerus in posterior view, **f** carpometacarpus in anterior view, **h** carpometacarpus in posterior view. *Scale bar* 10 mm

temporalis is shallower, the *processus postorbitalis* are broader, the palatines are broader and less arched and the *processus mandibulae medialis* are more robust. In the humerus: the *tuberculum ventrale* is bigger, the *crus dorsale fossae* and the *crus ventrale fossae* are more developed and the *fossa m. brachialis* is bigger and longer. In the carpometacarpus the proximal end of the *trochlea carpalis* is sharper, the notch that joins the *trochlea carpalis* (which is longer) to the *processus extensorius* is broader, the *os metacarpale alulare* presents a more closed hook shape, the *sulcus interosseous* is broader, the *fossa infratrochlearis* is longer *proximo–distally* and the end of the *processus pisiformis* is sharper. In the femur the *crista trochanteris* is more marked and proximally

Fig. 14 Pelvic limb. *S. antarcticus lonnbergi*: **a** femur in anterior view, **c** femur in posterior view, **e** tarsometatarsus in anterior view, **g** tibiotarsus in anterior view, **i** tibiotarsus in posterior view, **k** tarsometatarsus in posterior view, *S. maccormicki* **b** femur in anterior view, **d** femur in posterior view, **f** tarsometatarsus in anterior view, **h** tibiotarsus in anterior view, **j** tibiotarsus in posterior view, **l** tarsometatarsus in posterior view. *Scale bar* 10 mm

elongated, the *sulcus intercondilaris* is shallower and more symmetric to the distal condyles, the *trochanter femoris* is smaller and the *crista supracondylaris medialis* is less elevated. In the tibiotarsus the *crista cnemialis cranialis* has a more rounded edge and the *pons supratendinosus* is broader. In the tarsometatarsus the *eminentia intercotylaris* is more robust and rounded, the *tuberositas musculi tibialis cranialis* is larger, the *trochlea metatarsi III* develops slender trochlear edges, the *crista medialis hypotarsi* is broader and the *sulcus extensorius* is deeper.

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