Taxonomy, phylogenetic history and identification of sand plover complex.

Article *in* Dutch Birding · October 2023

Manuel Schweizer
Natural History Museum Bern

Liu Yang
Sun Yat-Sen University

Trends in systematics

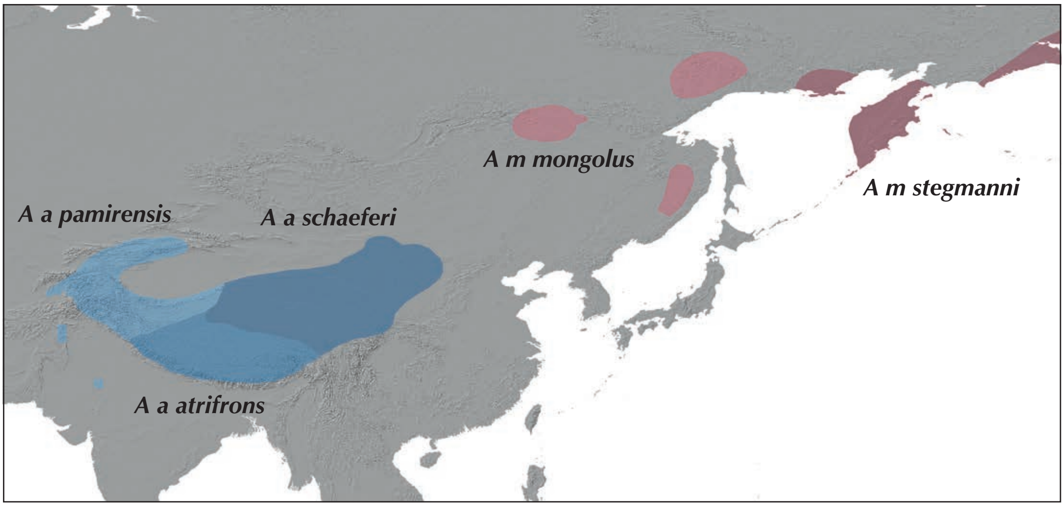
Taxonomy, phylogenetic history and identification of sand plover complex

Evolutionary diversification can unfold in many ways and sometimes leads to surprises. Famous examples include cases where non-sister species are phenotypically more similar to each other than to their respective sister species, a pattern for example prevalent in wheatears of the genus *Oenanthe* (Alaei Kakhki et al 2023). Morphological similarities are thus not always a good proxy to assess species relationships and can consequently fool taxonomists. This has been the case in the sand plover complex of the genus *Charadrius* as recently revealed by Wei et al (2022). It has traditionally been treated as comprising two species, Greater Sand Plover *C leschenaultii* and Lesser Sand Plover *C mongolus*. Within the latter, there are two groups differing in biometrics and plumage features that are not only separated when breeding but additionally only partly overlap in wintering grounds as shown, eg, in a comprehensive review by Hirschfeld et al (2000) (figure 1). The authors cautiously concluded that these two groups might possibly be separate incipient species. Based on a paper in Birding World by the late Martin Garner and co-authors proposing that the two groups within Lesser Sand can be separated in all plumages (Garner et al 2003), the editors of this journal were more bold and proposed that they be treated as two species. Although this proposal only gained little support, it was followed by the Commissie Systematiek Nederlandse Avifauna (CSNA) and consequently by Dutch Birding (Redactie Dutch Birding 2012). Following the proposal by Sangster et al (2016), Dutch Birding additionally placed the sand plovers in the genus *Anarhynchus* (Redactie Dutch Birding 2016). This proposal was based on the molecular phylogenetic evidence for paraphyly of *Charadrius* by Barth et al (2013) and Dos Remedios et al (2015) and was further supported by a recent analysis by Černý & Natale (2022).

Surprisingly, Wei et al (2022) demonstrated, based on genomic data, that the two groups of Lesser Sand Plover are not each other's closest relatives, thus providing the definitive piece of the puzzle supporting the split of the two. Apparently, morphological similarities seem to be a bad predictor of phylogenetic relationships in sand plovers.

This paper reviews the distribution, phylogenetic history and taxonomy of the sand plover complex and briefly discusses the identification of the two new 'Lesser Sand Plover' species, Siberian Sand Plover *A mongolus* and Tibetan Sand Plover *A atrifrons*.

FIGURE 1 Breeding distribution of Siberian Sand Plover *Anarhynchus mongolus* (purple) and Tibetan Sand Plover *A atrifrons* (blue) with approximate ranges of the different subspecies. Modified from BirdLife International & NatureServe (2014) with subspecies ranges adapted from Hirschfeld et al (2000) and Dickinson & Remsen (2013).



Distribution

Greater Sand Plover breeds from Asia Minor and the Levant over Central Asia to Mongolia, western China and southern Siberia, Russia, and winters along the coasts of the south-eastern Mediterranean, the Arabian Peninsula, South and South-East Asia and Australasia. It is divided into three subspecies (Hirschfeld et al 2000, Dickinson & Remsen 2013): ***1*** nominate *A l leschenaultii* in the eastern part of the range from Mongolia and north-western China to Central Asia, Transcaucasia and Transcaspia; ***2*** *A l scythicus* (formerly named *crassirostris*, see Carlos et al (2012)), breeding westwards from Central Asia to the eastern Caucasus; and ***3*** western *A l columbinus* of Asia Minor and the Levant, breeding from south-western Iran through Syria to Turkey.

The breeding range of Siberian Sand Plover, formerly called the *mongolus*-group of 'Lesser Sand Plover', is restricted to the Russian Far East and two subspecies are usually distinguished (Hirschfeld et al 2000, Dickinson & Remsen 2013, figure 1): ***1*** *A m stegmanni* from Chukotka south to Kamchatka and the Commander Islands and North Kuril Islands; and ***2*** nominate *A m mongolus* from the remaining western part of the breeding range.

Tibetan Sand Plover, formerly called the *atrifrons*-group of 'Lesser Sand Plover', chiefly breeds in high altitude regions of Central Asia, the Himalayas and the Tibetan plateau, and is divided into three subspecies: ***1*** *A a schaeferi* from the eastern part of the Qinghai-Tibetan plateau north to southern Mongolia; ***2*** nominate *A a atrifrons* breeding in the Himalayas and the southern Qinghai-Tibetan Plateau; and ***3*** *A a pamirensis* breeding from the western Kunlun Shan over the Karakoram and Pamir mountains to the western Tien Shan.

The non-breeding range of 'Lesser Sand Plover' extends from the Arabian Peninsula and East Africa over South and South-East Asia to Australia. While the region of Australia and Papua New Guinea is almost exclusively visited by Siberian Sand Plover and the area from the Indian Subcontinent westward by Tibetan Sand Plover, there is overlap between the two on their wintering grounds in South-East Asia, South-Eastern China and the Philippines (Hirschfeld et al 2000, Bakewell 2022).

Phylogenetic relationships and taxonomy

To infer the phylogenetic relationships of the sand plover complex, Wei et al (2022) first analysed two markers of the mitochondrial DNA (mtDNA) of 22 individuals of Siberian Sand Plover (14 individuals from the breeding range of *A m stegmanni* in Chukotka Autonomous Okrug, seven individuals from migratory routes in Sakhalin, Russia, and Northern China, and one migratory individual from Eastern China) and 21 individuals of Tibetan Sand Plover (19 individuals from the breeding range of *A a schaeferi* from Qinghai, China, one *A a pamirensis* from the Kuhistani Badakhshan Autonomous Region, Tajikistan, as well as one migratory individual from the coastal area of southern China). Additionally, 11 individuals of Greater Sand Plover were included (one from Tyva Republic, Russia, collected during the breeding season, and others comprising migratory individuals from China). The resulting mtDNA gene trees revealed a surprising result (figure 2): the two 'Lesser Sand Plovers' were found not to be each other's closest relatives. Instead, Tibetan Sand turned out to be the sister group of a clade of Siberian Sand and Greater Sand. However, gene trees from a single region of the genome such as mtDNA, may not necessarily reflect the actual evolutionary branching patterns and relationship of species, the so-called 'true' species tree (see, eg, Schweizer & Burri 2019). Therefore, Wei et al (2022) also analysed genome-wide variation for 11 individuals, comprising three Siberian Sand (*A m stegmanni*), five Tibetan Sand (one *A a pamirensis*, four *A a schaeferi*) and two Greater Sand. The results from mtDNA could be corroborated and the 'Lesser Sand Plover' as traditionally recognised was revealed not to be monophyletic (figure 2). Interestingly enough, although Siberian Sand and Tibetan Sand are close in size and shape, with Greater Sand generally being larger and bulkier (Hirschfeld et al 2000), the close relationship between Greater Sand and Siberian Sand was already indicated by a cladistic analysis of 1024 phenotypic characters (446 of the skeleton, 558 of the definitive integument, and 20 of natal patterns; Livezey 2010). In addition, Wei et al (2022) demonstrated differences in calls, with those of Siberian Sand being most distinct, while calls of Tibetan Sand and Greater Sand were more similar.

These results clearly indicate that the traditional taxonomic arrangement of the sand plover complex comprises a paraphyletic grouping, ie, Siberian Sand Plover and Tibetan Sand Plover are treated as conspecifics despite not being closest relatives. One potential solution could be to treat the complex as a single species. However, this would not appropriately take into account the morphological, vocal and genetic variation found within the complex. Wei et al (2022) showed that Tibetan Sand split from the others around two million years ago, a level of divergence time usually docu-

412 Tibetan Sand Plover / Tibetaanse Plevier *Anarhynchus atrifrons*, male summer plumage, Ma'agan Michael, Israel, 1 August 2013 *(Yoav Perlman)*

413 Siberian Sand Plover / Mongoolse Plevier *Anarhynchus mongolus*, male summer plumage, Heuksando Island, South Korea, 6 May 2009 *(Aurélien Audevard)*

414 Tibetan Sand Plover / Tibetaanse Plevier *Anarhynchus atrifrons*, adult winter plumage, Miri, Sarawak, Malaysia, 17 November 2021 *(Dave Bakewell)*

415 Siberian Sand Plover / Mongoolse Plevier *Anarhynchus mongolus*, adult winter plumage, Miri, Sarawak, Malaysia, 14 November 2021 *(Dave Bakewell)*

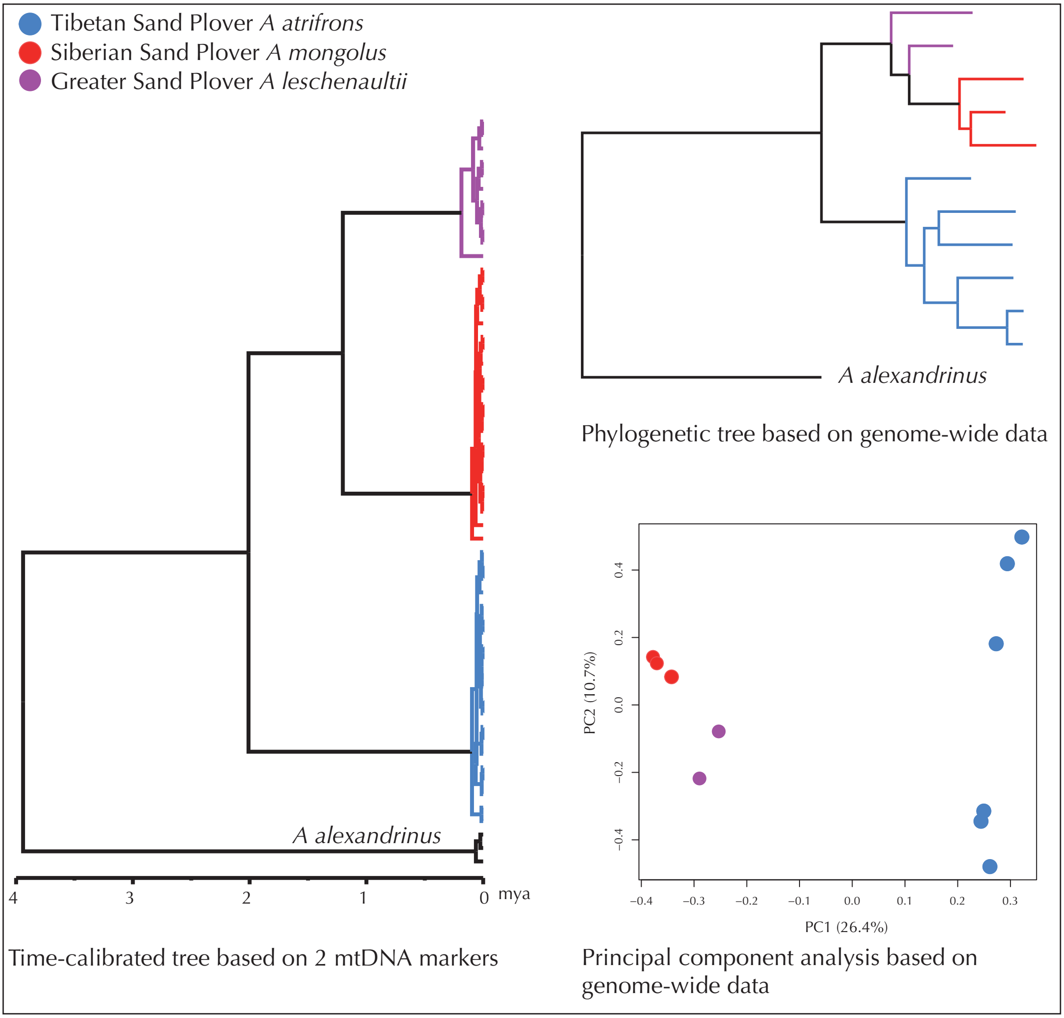


FIGURE 2 Left: time-calibrated Bayesian phylogenetic hypothesis of sand plovers based on two mtDNA markers with Kentish Plover *Anarhynchus alexandrinus* as outgroup. Timescale in millions of years ago (mya). Top right: maximum likelihood phylogenetic hypothesis based on 765 092 variable positions (SNPs) distributed throughout genome, again with Kentish as outgroup. Bottom right: principal component analysis of genome-wide variation among sand plovers indicating close similarity of Greater Sand Plover *A leschenaultii* and Siberian Sand Plover *A mongolus* in relation to Tibetan Sand Plover *A atrifrons* in congruence with results of phylogenetic reconstructions. Modified from Wei et al (2022).

mented for species level taxa (Price 2008). Additionally, Wei et al (2022) inferred a very distinct demographic history of Tibetan Sand over at least the last million years. Moreover, no interbreeding is documented between Greater Sand Plover and Tibetan Sand, although their breeding ranges come into close proximity in Central Asia. However, they differ in their preferred habitat, with Greater Sand breeding in lowland desert, semi-deserts or steppes, while Tibetan Sand breeds above the treeline at high altitudes (Cramp & Simmons 1983). Also, arctic Siberian Sand breeds above or beyond the treeline (Cramp & Simmons 1983).

Another potential solution would be to treat Tibetan Sand Plover as a species on its own but lump allopatric Greater Sand Plover and Siberian Sand Plover. However, given their distinctiveness

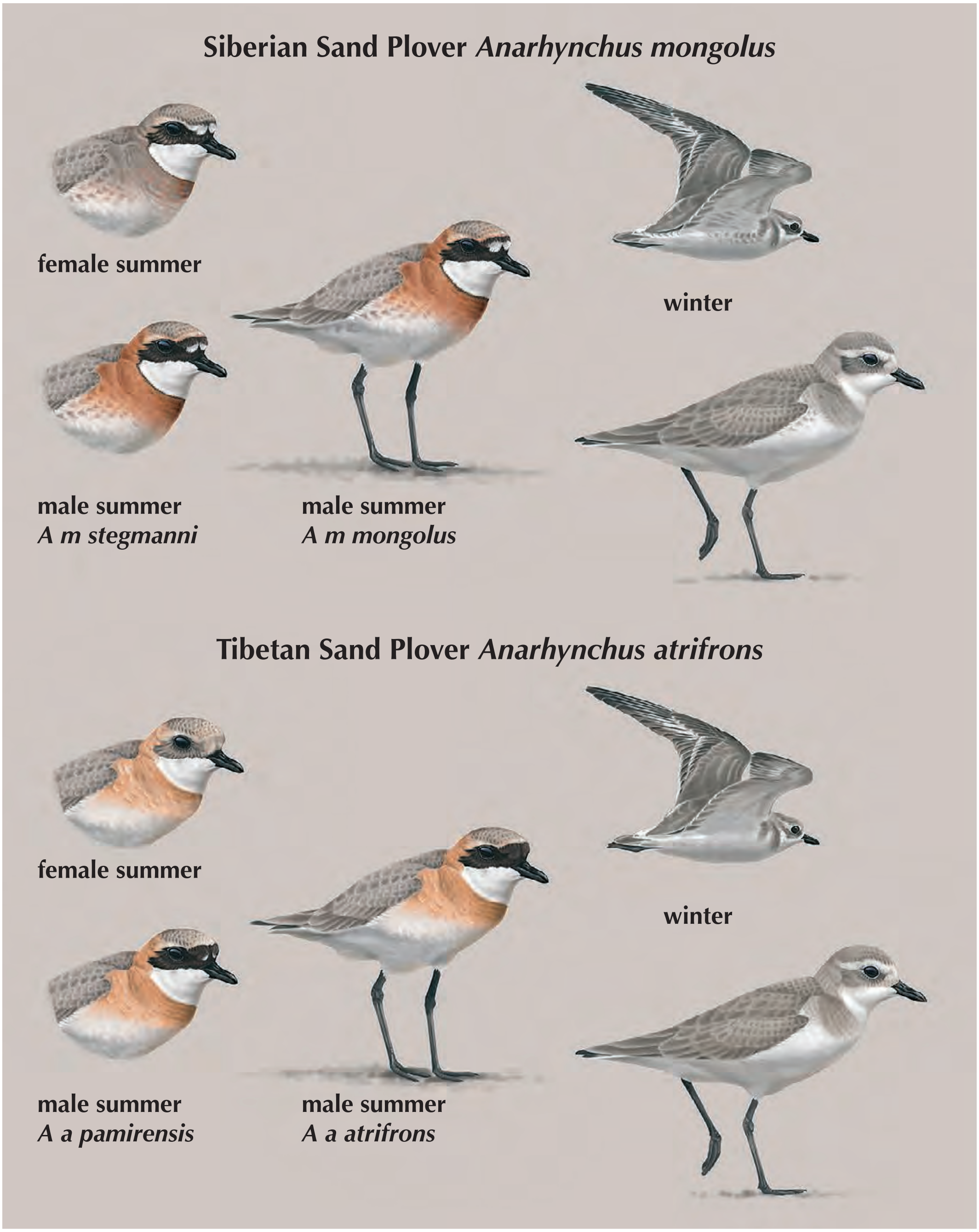


FIGURE 3 Differences between Siberian Sand Plover *Anarhynchus mongolus* and Tibetan Sand Plover *A atrifrons* *(Manuel Schweizer)*

TABLE 1 Structural differences between Siberian Sand Plover *Anarhynchus mongolus* and Tibetan Sand Plover *A atrifrons* (adapted from Bakewell 2022)

Feature	Siberian Sand Plover	Tibetan Sand Plover
Size	Averages slightly larger, though not always apparent in field	Slightly smaller
Shape	May appear fat bodied and deep chested	Often looks better proportioned and slimmer bodied
Bill	Normally shorter (all subspecies)	Normally longer, especially eastern subspecies *schaeferi* and *atrifrons*
	Thick, has pronounced culmenary bulge near tip and is blunt tipped	Slimmer, with less prominent culmenary bulge and more pointed tip
		Juveniles of both species may have shorter bills than adults
Legs	Slightly shorter tarsus	Slightly longer tarsus
In flight	Longer winged, apparent when birds are seen in flight	
	Toes do not (or barely) project beyond tail-tip in flight	Obvious toe projection beyond tail in flight (toe projection may be least in *pamirensis*)

in plumage, morphometrics and vocalisations, ecology and their genetic divergence with a split dated around one million years ago (Wei et al 2022), such a treatment would conflict with an integrative approach towards species delimitation (Schweizer et al 2023). As a consequence, we think that a split into three species best reflects the evolutionary diversity in the sand plover complex: ***1*** Tibetan Sand Plover *A atrifrons* Wagler, 1829, with subspecies *A a pamirensis* (Richmond, 1896), nominate *A a atrifrons*, and *A a schaeferi* Meyer de Schauensee, 1937; ***2*** Greater Sand Plover *A leschenaultii* Lesson, 1826, with subspecies *A l columbinus* Wagler, 1929, *A l scythicus* 'Carlos, Roselaar & Voisin', 2012, and nominate *A l leschenaultii*; and ***3*** Siberian Sand Plover *A mongolus* Pallas, 1776, with subspecies *A m mongolus* and *A m stegmanni* Portenko, 1939.

Evolutionary history of sand plovers

Past evolutionary processes such as range dynamics and associated demographic changes or events of gene exchange with other species leave their signature in individual genomes and can be reconstructed and modelled with sophisticated methods based on whole-genome data (Green et al 2010, Durand et al 2011, Li & Durbin 2011). This was also done by Wei et al (2022) for the sand plovers and again revealed an unexpected result: ancestors of Tibetan Sand Plover and Greater Sand Plover seem to have hybridised and exchanged genes in the past. This might have happened upon secondary contact as a result of climate-driven range expansions. As indicated by reconstructions of demographic histories, the ancestor of Greater Sand might have extended its range during dry glacial periods in the late Pleistocene potentially leading to range contact followed by interbreeding with the ancestor of Tibetan Sand. More and more studies have shown that intermittent gene flow between distinct evolutionary lineages seems to be more common than previously thought and an integral part of the diversification history in many taxa (eg Ottenburghs et al 2017, Marques et al 2019, Alaei Kakhki et al 2023).

The question remains how the morphological similarity between Siberian Sand Plover and Tibetan Sand Plover can be explained despite not being each others closest relatives. Such phenotypic similarities that do not reflect species' history of descent can evolve through three processes (as summarised, eg, in Alaei Kakhki et al 2023): ***1*** through independent novel mutations in the same or in different genes; ***2*** retention of traits that were already present in the common ancestor of the species involved through incomplete lineage sorting (see Schweizer & Burri 2019); and ***3*** through the exchange of genetic material between non-sister species. Given that Wei et al (2022) found no signs for historical gene flow between ancestors of Siberian Sand and Tibetan Sand, this third option seems unlikely. Hence, the similarities of the two might be considered a result of the first process (ie, the result of independent adaptions). However, the most parsimonious explanation would involve the second process, ie,

TABLE 2 Differences between Siberian Sand Plover *Anarhynchus mongolus* and Tibetan Sand Plover *A atrifrons* in adult winter plumage (adapted from Bakewell 2022)

Feature	Siberian Sand Plover	Tibetan Sand Plover
Head	Ear-coverts often slightly darker than crown and nape	Ear-coverts concolorous with crown
	Large, triangular, white patch on forehead always well defined along upper edge, often bordered by blackish feathering	White on forehead usually blends gradually into brown of forecrown
Upperparts	Usually darker and colder brown	Usually paler and warmer brown
Underparts	Breast-band usually complete or almost so	Breast-band usually incomplete
	Dusky feathers along flank on most, but not all birds; diagnostic when present	White, unmarked flank
In flight	Upper wing-bar averages thinner and less extensive. Usually, only four inner primaries show white base	Upper secondary wing-bar sometimes broader and white on primaries sometimes more extensive than Siberian Sand
	Brown on central rump broad, with little white on rump-side	Brown on central rump narrow, with much white on rump-side
	Dusky flank present on most birds (diagnostic when present)	White flank (but beware birds in moult, which can show darker areas where feathers have dropped)
	Axillaries and mid-underwing-coverts may show dusky markings	Axillaries and mid-underwing-coverts white

retention of ancestral variation with morphological and ecological differentiation in Greater Sand Plover. Interestingly, vocal differentiation revealed a different pattern, with Greater Sand and Tibetan Sand being most similar, demonstrating that tempo and direction of evolution can diverge among different phenotypic traits.

Identification

The separation of Greater Sand Plover from 'Lesser Sand Plover' has been extensively covered by Hirschfeld et al (2000) (see also Shirihai et al 1996). Here, we focus on the separation of Siberian Sand Plover and Tibetan Sand Plover by providing an updated compilation of the main identification features presented by Bakewell (2022). Siberian Sand and Tibetan Sand differ both in structure and plumage, however, as pointed out in the latter paper, separation between Siberian Sand and Tibetan Sand usually require excellent views under optimal field conditions and should always rely on multiple features. Identification features are presented in tabular form focusing on differences in structure (table 1) and between individuals in winter (table 2), summer (table 3) and juvenile plumage (table 4).

Concluding remarks

A three-way split of the sand plover complex is the only reasonable taxonomic treatment. Given that most individuals of Siberian Sand Plover and Tibetan Sand Plover can be separated in the field, all documented records of vagrant 'Lesser Sand Plovers' should be re-evaluated. Both have already been recorded in the Western Palearctic. A shortcoming of the study by Wei et al (2022) is that the genetic sampling of Greater Sand Plover was far from comprehensive. Unfortunately, no individuals of the subspecies *A l scythicus* or *A l columbinus* were included. Especially the latter, westernmost subspecies of Greater Sand could be of interest: although its plumage basically matches the other two subspecies, it differs in timing of the post-breeding moult and approaches Siberian Sand and Tibetan Sand in size and shape (Cramp & Simmons 1983, Hirschfeld et al 2000). Given the surprising finding that Siberian Sand and Tibetan Sand were not closely related, we do not want to exclude the possibility that the complex has more surprises in store, before the phylogeographic structure of Greater Sand is comprehensively documented.

Acknowledgements

The authors would like to thank Birding ASIA's editor Alex J Berryman for giving permission for the use of tables originally published in Bakewell (2022). MS thanks Stephan Lauper and Paul Walser Schwyzer for their support while studying sand plovers in Oman in February 2023 and earlier in China, Kazakhstan, Kyrgyzstan, South Korea, Thailand and Uzbekistan.

TABLE 3 Differences between Siberian Sand Plover *Anarhynchus mongolus* and Tibetan Sand Plover *A atrifrons* in adult summer plumage (adapted from Bakewell 2022)

Feature	Siberian Sand Plover	Tibetan Sand Plover
Head	Ear-coverts, lore and bar across forecrown black (male)	Ear-coverts, lore and forehead black (male), with no, or faint whitish smudge or spot on each side
	May have some orange on forecrown and nape	May have extensive orange on crown and nape
	Large triangular white forehead blaze, some with thin black central line (*mongolus*) or twin 'headlights' separated by thick central line (*stegmanni*)	Birds moulting to winter plumage in late summer can show more extensive white forehead spots
	Black areas largely replaced by dark brown in females	Black areas largely replaced by brown in females
Upperparts	Usually darker and colder grey-brown	Usually paler and warmer brown
	No or few feathers faintly tinged orange	Some feathers may be strongly tinged orange
Underparts	Breast-band very broad (male) or broad (female), dark brick-red to orange, often with dark edge to upper border	Breast-band very broad (male) or broad (female), bright orange to peach, normally lacks dark edge to upper border
	Dusky brown feathers along mid-rear flank on most birds, diagnostic when present	Orange extends on to foreflank, typically ending in point, never brown on mid-rear flank
In flight	Upper wing-bar averages thinner and less extensive than on Tibetan Sand	Upper secondary wing-bar sometimes broader and white on primaries, sometimes more extensive than on Siberian Sand
	Brown on central rump broad, with little white on rump side	Brown on central rump narrow, with much white on rump side
	Axillaries and mid-underwing coverts may show dusky markings	Axillaries and mid-underwing coverts white
	Broad terminal tail-band much darker than rump and back	Terminal tail-band concolorous with or only slightly darker than rump and back

References

Alaei Kakhki, N, Schweizer, M, Lutgen, D, Bowie, R C K, Shirihai, H, Suh, A, Schielzeth, H & Burri, R 2023. A phylogenomic assessment of processes underpinning convergent evolution in open-habitat chats. Mol Biol Evol 40: msac278.

Bakewell, D N 2022. Identification of Siberian *Charadrius [mongolus] mongolus* and Tibetan *C. [m.] atrifrons* Sand Plovers. Birding ASIA 38: 23-35.

Barth, J M I, Matschiner, M & Robertson, B C 2013. Phylogenetic position and subspecies divergence of the endangered New Zealand Dotterel (*Charadrius obscurus*). PLoS One 8 (10): e78068.

BirdLife International & NatureServe 2014. Bird species distribution maps of the world. Cambridge.

Carlos, C J, Roselaar, C S & Voisin, J-F 2012. A replacement name for *Charadrius leschenaultii crassirostris* (Severtzov, 1873), a subspecies of Greater Sand Plover. Bull Br Ornithol Club 132: 63-65.

Černý, D & Natale, R 2022. Comprehensive taxon sampling and vetted fossils help clarify the time tree of shorebirds (Aves, Charadriiformes). Mol Phylogenet Evol 177: 107620.

Cramp, S & Simmons, K E L (editors) 1983. The birds of the Western Palearctic 3. Oxford.

Dickinson, E C & Remsen Jr, J V (editors) 2013. The Howard and Moore complete checklist of the birds of the world. Fourth edition, volume 1: non-passerines. Eastbourne.

Dos Remedios, N, Lee, P L M, Burke, T, Székely, T & Küpper, C 2015. North or south? Phylogenetic and biogeographic origins of a globally distributed avian clade. Mol Phylogenet Evol 89: 151-159.

Durand, E Y, Patterson, N, Reich, D & Slatkin, M 2011. Testing for ancient admixture between closely related populations. Mol Biol Evol 28: 2239-2252.

Garner, M, Lewington, I & Slack, R 2003. Mongolian and Lesser Sand Plovers: an identification overview. Birding World 16: 377-385.

Green, R E, Krause, J, Briggs, A W, Maricic, T, Stenzel, U, Kircher, M, Patterson, N, Li, H, Zhai, W W, … Paabo, S 2010. A draft sequence of the Neandertal genome. Science 328: 710-722.

Hirschfeld, E, Roselaar, C S & Shirihai, H 2000. Identification, taxonomy and distribution of Greater and Lesser Sand Plovers. Br Birds 93: 162-189.

Li, H & Durbin, R 2011. Inference of human population history from individual whole-genome sequences. Nature 475: 493-496.

Livezey, B C 2010. Phylogenetics of modern shorebirds

TABLE 4 Differences between Siberian Sand Plover *Anarhynchus mongolus* and Tibetan Sand Plover *A atrifrons* in juvenile and first-winter plumage (adapted from Bakewell 2022)

Feature	Siberian Sand Plover	Tibetan Sand Plover
Head	Other than bill shape and length, no consistent differences from Tibetan Sand when in juvenile plumage	Bill may appear short on some juveniles, inviting confusion with Siberian Sand
	In juvenile plumage, there may be little white on forehead, and what there is may grade into grey-brown of crown; in first-winter plumage, white forehead demarcated from brown crown but not as clearly as on adults in winter plumage	Forehead variably pale to white, usually blending gradually into brown crown, similar in juvenile and first-winter plumage
Upperparts	In juvenile plumage, grey-brown with thin whitish fringes; especially thin on mantle and scapulars, wearing off quickly	Brown with thin or broad buff fringes
	After post-juvenile moult, covert fringing is mostly worn away	After post-juvenile moult, aged by fringes remaining on coverts
Underparts	In juvenile plumage, breast-band often complete, lateral breast-patch broad, often bordered below by extensive brown mottling on foreflank	Breast-band usually incomplete, lateral breast-patch broad
	Lacking or limited peach wash in central breast	Often extensive peach-orange wash across breast
	Dusky flank markings diagnostic when present but often absent	Flank white
	After post-juvenile moult, breast-patches and flank similar to adult	After post-juvenile moult, resembles adult
In flight	Differences as adult winter	Differences as adult winter

(Charadriiformes) based on phenotypic evidence: analysis and discussion. Zool J Linn Soc 160: 567-618.

Marques, D A, Meier, J I & Seehausen, O 2019. A combinatorial view on speciation and adaptive radiation. Trends Ecol Evol 34: 531-544.

Ottenburghs, J, Kraus, R H S, van Hooft, P, van Wieren, S E, Ydenberg, R C & Prins, H H T 2017. Avian introgression in the genomic era. Avian Res 8: 30.

Price, T 2008. Speciation in birds. Greenwood Village.

Redactie Dutch Birding 2012, 2016. Naamgeving van taxa in Dutch Birding. Dutch Birding 34: 46-48; 38: 97-101.

Sangster, G, Collinson, J M, Crochet, P-A, Kirwan, G M, Knox, A G, Parkin, D T & Votier, S C 2016. Taxonomic recommendations for Western Palearctic birds: 11th report. Ibis 158: 206-212.

Schweizer, M & Burri, R 2019. Trends in systematics: New insights in taxonomy of wheatears. Dutch Birding 41: 115-120.

Schweizer, M, Marques, D A, Olsson, U & Crochet, P-A 2023. The Howard & Moore complete checklist of birds of the world: framework for species delimitation. Avian Syst 1 (9): 35-41.

Shirihai, H, Christie, D A & Harris, A 1996. The Macmillan birder's guide to European and Middle Eastern birds, including North Africa. London.

Wei, C, Schweizer, M, Tomkovich, P S, Arkhipov, V Y, Romanov, M, Martinez, J, Lin, X, Halimubieke, N, Que, P, Mu, T, Huang, Q, Zhang, Z, Székely, T & Liu, Y 2022. Genome-wide data reveal paraphyly in the sand plover complex (*Charadrius mongolus/leschenaultii*). Ornithology 139: ukab085.

Manuel Schweizer, Naturhistorisches Museum, Bern, Switzerland / Institute of Ecology and Evolution, University of Bern, Bern, Switzerland (manuel.schweizer@nmbe.ch)
David N Bakewell, Miri, Sarawak, Malaysia (ecopermai@gmail.com)
Yang Liu, State Key Laboratory of Biocontrol, College of Ecology School of Life Science, Sun Yat-sen University, Guangzhou, China (liuy353@mail.sysu.edu.cn)