Historical ostriches in the Libyan Desert, with ecological and taxonomic considerations

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Abstract - Many historical records extend the known range of the African ostrich Struthio camelus to include almost the entire state territory of Libya. This significant expansion augments the spatial potentialities to reintroduce captive-bred progeny of the endangered red-necked ostriches (S. c. camelus) from zoos and wildlife centres. The latest Libyan ostriches lingered in Cyrenaica and Fezzan into the late 19th century, and presumably near Kufra into the 1930s. Their extermination coincided with the occupation by colonial European administrations. These east Saharan biotopes are extraordinarily resource-poor and climatically challenging due to wide thermal amplitudes and extreme drought. Old photographs from Kufra and Wadi Howar leave undecided if the Libyan ostriches adhered to the subspecies S. c. camelus, which appears possible, or if additional, partly substantiated but yet unconfirmed claims should be heeded which demand up to three subspecies in North Africa. A review of taxonomic interpretations reveals a weak foundation by reliable data of a pan-Saharan subspecies S. c. camelus, and additional research is suggested to provide a sound taxonomic concept, not least for the management of various regional breeding lineages in zoos, which safeguard the survival of this endangered bird. As an auxiliary finding, African wild dogs (Lycaon pictus) are attested as inhabitants of the southern Libyan Desert until the 1930s, where they had preved upon the now equally extinct ostriches.

Key words: geographical variability, *Struthio camelus*, *Lycaon pictus*, Struthionidae, Sahara, subspecies, zoogeography.

Riassunto - Gli struzzi storicamente presenti nel deserto libico, con considerazioni ecologiche e tassonomiche.

Molti documenti storici estendono l'areale conosciuto dello struzzo africano *Struthio camelus* fino a comprendere quasi l'intero territorio nazionale della Libia. Questa significativa espansione aumenta le potenzialità spaziali di reintroduzione della progenie nata in cattività dello struzzo dal collo rosso (*S. c. camelus*), in via di estinzione, da parte di zoo e centri faunistici. Gli ultimi struzzi libici sono vissuti in Cirenaica e nel Fezzan fino alla fine del XIX secolo e presumibilmente nei pressi di Kufra fino agli anni '30 del Novecento. Il loro sterminio coincise con l'occupazione da parte delle amministrazioni coloniali europee. Questi biotopi del Sahara orientale sono straordinariamente poveri di risorse e climaticamente difficili a causa delle ampie escursioni termi-

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Received for publication: 3 April 2024 Accepted for publication: 7 October 2024 Online publication: 19 November 2024 che e dell'estrema aridità. Le vecchie fotografie di Kufra e Wadi Howar non consentono di stabilire se gli struzzi libici appartenessero alla sottospecie *S. c. camelus*, il che sembra possibile, o se si debba tener conto di ulteriori affermazioni, in parte fondate ma non ancora confermate, che sostengono la presenza di fino a tre sottospecie in Nord Africa. Una revisione delle interpretazioni tassonomiche non permette la certa attribuzione delle osservazioni a un'unica sottospecie pan-sahariana di *S. c. camelus*. Si suggeriscono ulteriori ricerche per la delineazione di una fondata tassonomia, non da ultimo per la gestione dei vari lignaggi regionali di riproduzione negli zoo, che salvaguardano la sopravvivenza di questo uccello in pericolo. Come ulteriore scoperta, si attesta la presenza di licaoni *Lycaon pictus* nel deserto libico meridionale fino agli anni '30 del Novecento, dove predavano gli struzzi, ora estinti.

Parole chiave: *Struthio camelus*, *Lycaon pictus*, Sahara, sottospecie, Struthionidae, variabilità geografica, zoogeografia.

INTRODUCTION

When studying problems of animal geography in the Sahara, the author encountered historical photographs of African ostriches Struthio camelus Linnaeus 1758 from the Kufra oases (Libya) in the archive of the Frobenius-Institute for Research in Cultural Anthropology (Frankfurt, Germany). The state territory of Libya is not a recognized range country for the ostrich, and ostriches near Kufra would expand the known species range to all of the wider Libyan Desert, which is the natural region spread over east Libya, west Egypt and northwest Sudan. This is the vastest expanse worldwide of hyperarid desert and arguably the least hospitable (former) ostrich biotope anywhere, by virtue of severe drought and exuberant thermal amplitudes. Aware of the limited insights into Saharan zoogeography, the author went for searching additional records from Libya and surrounds. This review provides evidence that ostriches were widespread in this country, and at least locally not uncommon. They persisted in Cyrenaica and Fezzan until the late 19th century, and presumably near Kufra into the 1930s, as a significant extension of the known range. Historical zoogeography can assist the various ongoing captive-breeding projects to conserve the endangered red-necked ostrich S. c. camelus Linnaeus 1758 conducted by zoological gardens and wildlife centers (Islam et al., 2008; Frerking, 2024; K. de Smet for Sahara Conservation Fund, in litt.), which intend to secure these stocks and to reintroduce their progeny into proven historical habitats. Zoogeography can assist such efforts by identifying pertinent reintroduction sites, and by either reinforcing or challenging taxonomic con-





cepts. As detailed in the subsequent Discussion section, the taxonomy of ostriches in North Africa has never been revised with nearly informative population and character samples. In the absence of holistic taxonomic groundwork, all ostriches from the vast subcontinent are often provisionally lumped into one subspecies, S. c. camelus, which in this delineation would inhabit some 12 million square kilometers. This is a priori a suspiciously large range for a taxon of flightless birds. It comprises the nondesertic steppes of the Maghreb, the Sahara, the Sahelian and Sudanian savannah belts of west and central Africa, and the drvlands near the Red Sea, to be replaced by the Somali ostrich S. molvbdophanes Reichenow 1883 from the arid ranges of the Horn of Africa approximately in central Djibouti. At the same time, the Sahara is in one of the regions worldwide whose megafauna has collapsed almost completely due to human impacts (Durant *et al.*.. 2014), and an intensified interest in Saharan ostriches appears timely to reverse this long-standing trend. Ostrich populations have dwindled throughout North and West Africa, and one important approach to guarantee their survival is captive lineages imported from Chad, Niger, probably Sudan, and the Danakil Desert for breeding and multiplication in zoological gardens and wildlife centers, for future reintroduction in suitable protected areas of their native range (Dittrich, 1978; Islam et al., 2008; Freking, 2024; K. de Smet, in litt.). In this context a pertinent scrutiny of regional taxonomy is needed to optimize the genetic management of these captive stocks.

Handbooks of African ornithology (e.g., Mackworth-Praed & Grant, 1952; Brown et al., 1982; Folch, 1992) or monographs on ratites (e.g., Davies, 2002) do not mention ostriches from Libya. Neither did inventories of the Libvan fauna refer to ostriches (Ghigi, 1913; Salvadori & Festa, 1921; Hartert, 1923; Tedesco Zammarano, 1930; Moltoni, 1934; Zavattari, 1934; Masseti, 2013). Only Desio (1941) and Toschi (1969) declared ostriches extinct since ages in the "Italian Sahara" without any details or supportive data. Neither is Libya rated as an original range state in the worldwide I.U.C.N. red list of threatened species (BirdLife International, 2018). The majority of published distribution maps of ostriches omit the Sahara from the species's range. The most precise cartography (Snow, 1978) mapped the localities taken from the specimen labels in the Natural History Museum at Tring (United Kingdom), but it restricts precise site records to the tropical savannahs, and merely adumbrates a vague "probable range" for the Sahara in the form of schematic hachures. The explanation for this vagueness was the complete absence of Saharan specimens or records in the worldwide largest bird collection at Tring (H. van Grouw, in litt.), on which this map had been based exclusively. Another map resulted from a workshop of conservationists aiming to raise awareness for the rescue of Saharan megafauna (Durant et al., 2014): this cavalier approach randomly defined the historical occurrence of ostriches to comprise all lands in North Africa surrounded by the 250 mm isohyet, blurring the facts that the North African ostriches have never be proven to occur everywhere within this arbitrary boundary, but that indeed they prolifically transcended this specified zone into the adjacent savannah belts. The case of the Arabian desert ostrich S. c. syriacus

Rothschild 1919 may serve as a warning to take such hypothetical maps too serious: similar to the comparable situation in the Sahara, a mere handful of Arabian and Syrian specimens ever collected had been arbitrarily extrapolated to indicate a vast, unbroken historical range throughout all Near Eastern deserts until a recent in-depth study of proven historical records provided the different result of a bipartite dispersion divided into two disjunct isolates separated by a gap of 800 km (Jennings, 1986). Analogous range gaps subdividing the extraordinarily widely spaced population(s) of North African ostriches are conceivable, with potential relevance for population evolution and the distinction of population management units for conservation.

Current efforts to rescue and to manage Saharan ostriches must depart from an unsatisfactory faunal knowledge, which also impedes a deeper evaluation of taxonomic hypotheses. Durant *et al.* (2014) justly deplored the neglect of conservation interest in support of the collapsing Saharan wildlife. With this background in mind the present account aims to reconstruct the historical distribution of ostriches in Libya and the eastern Sahara, and reviews what little has so far been worked out on the taxonomy of the Saharan populations. The paper is not a taxonomic revision but provides widely scattered materials towards this aim.

MATERIALS AND METHODS

The bibliographic findings of parallel studies by the author on Saharan and Sahelian wildlife (Schreiber, 2021; 2022a; 2022b) were complemented by screening the special literature collections for natural history, for African and for Colonial Studies at the Universitätsbibliothek J.C. Senckenberg (Frankfurt, Germany). Books digitalized on the internet, the literature stocks in the ethnological and the rock art image libraries of the Frobenius-Institute (Frankfurt University), and in the research libraries of several institutes for classical cultural studies at Heidelberg University added further sources.

RESULTS

Ostriches at Kufra

The ostrich photos (Fig. 1 a and b) from Kufra are credited to anonymous photographers of the German research expedition led by the ethnologist Leo Frobenius in the early 1930s ("11. Deutsche inner-afrikanische Forschungsexpedition in die Libysche Wüste und den Angloägyptischen Sudan 1933"; Frobenius, 1934). The archived captions refer to captive ostriches kept (in semi-liberty?) by a military officer, Commander Rolle. This refers to Maggiore (Major) Ottavio Rolle, head officer of the Italian colonial administration at Kufra (Cufra, Wahat al-Kufrah). Several authors referred in script to this commander (e.g., Monterin, 1935a; 1936b; Almasy, 1943; Brenner, 1995; Bierman, 2004; Menardi Noguera et al., 2005), but none of them mentioned ostriches at Kufra, not even the Hungarian adventurer Laszló Almásy, who was hosted by Rolle at Kufra in 1932 and provided many details about him and his household. One could therefore assume that Rolle had received his ostriches after Almasy's visit (perhaps in late 1932 or 1933?). Clearly, captive ostriches need not necessarily have originated locally at Kufra, but in principle could be imports from elsewhere. However, until the early 1930s, Kufra continued to be one of the most remote and least visited places of North Africa, and southeast Libya one of latest blank spots on the world map (Schiffers, 1950; Weis, 1990; Török, 2011). Kufra is located approximately 850 km inland from the Mediterranean coast, this distance including 150 km of wandering dunes with shifting sand hampering advancement, predominantly without water supplies (Newbold, 1924; Jany, 1963; Graziani, 1937; see Fig. 33c in Schiffers & Redmer, 1971). Despite a single pioneer mission to Kufra by the German explorer Gerhard Rohlfs in 1873, later caravans in 1896, 1888, and 1911 failed to arrive there. Hassanein Bey (1924) was the only second expeditionist to reach Kufra in 1923 (Newbold, 1924), and after a small Italian delegation had arrived in 1928 only to be kidnapped (Török, 2012), the Italian army conquered the oasis in order to complete the colony Libia Italiana in 1931 (Graziani, 1937), i.e., two years before the ostriches were found by German visitors. The Italian troops were the first



Fig. 1 – Historical photographs of ostriches in the Libyan Desert taken in the 1930s. a,b) Ostriches in the possession of Commander Rolle at Kufra (Libya), photographed by an anonymous participant of the expedition organized by Leo Frobenius (University of Frankfurt, Germany) into the Libyan Desert and the Anglo-Egyptian Sudan in 1933; c,d) some of many ostriches encountered by the British expedition led by the Major R. A. Bagnold to the southern Libyan Desert, observed in or near the Wadi Howar (in the original expedition report: Wadi Hawa) in northwest Sudan (Bagnold, 1933). Photos 1a-1d are previously unpublished, and reproduced here by courtesy of the Frobenius-Institute, University of Frankfurt (Fig. 1 a and b), and the Royal Geographical Society in London (Fig. 1 c and d). / Fotografie storiche di struzzi nel deserto libico scattate negli anni '30. a,b) struzzi in possesso del comandante Rolle a Kufra (Libia), fotografati da un anonimo partecipante alla spedizione organizzata da Leo Frobenius (Università di Francoforte, Germania) nel deserto libico e nel Sudan anglo-egiziano nel 1933; c,d) alcuni dei numerosi struzzi incontrati dalla spedizione britannica guidata dal nord-occidentale) o nei pressi di esso (Bagnold, 1933). Le foto 1a-1d sono inedite e qui riprodotte per gentile concessione del Frobenius-Institut, Università di Francoforte (Fig. 1 a e b) e della Royal Geographical Society di Londra (Fig. 1 c e d).

to travel by motorcars (Jany, 1963), and prior to this technical innovation any transport of ostriches or their embryonated eggs, on the back of camels for weeks, should have proven unrealistic. L. Almásy reached Kufra in 1932, as the first visitor to arrive by car from Egypt in an adventurous drive through pathless deserts (Almasy, 1943; Török, 2008). Graziani's report (1937) about the life and commerce at Kufra in the early 1930s witnesses only traditional caravan trade of basic goods needed for daily life, chiefly with oases in Tibesti and nearby Sudan. rather than with the Libyan north coast and the outside world. The airfield built by Italians before World War II (Jany, 1963) should have been of a later date, but Z. Török (pers. comm., 2022) was aware of very limited motor traffic in the early 1930s: Major Rolle himself possessed a car, and he drove by lorry from Kufra to Ain Duwa in the Jabal al Uweinat range (Bagnold, 1933). A crude map by Monterin (1935b) shows the coarse tracks from the north coast to Kufra, which crossed hardly navigable sand seas. Given this background, a long-distance transport of living ostriches to Kufra before or in 1933 is not plausible, and no real motivation can be discerned for such a technically demanding import to a remote oasis that just started to recover from one of the cruellest colonial battles ever in North Africa in the context of the Italian conquest.

There is no published confirmation for an ostrich farm in Libya before or during the early 1930s, although Rohlfs (1881) and Insabato (1914) had already speculated that Tripolitania could be ideal places for commercial ostrich breeding. The closest documented ostrich husbandries in the early 20th century were in Egypt, Tunisia and Algeria (cf. Rohlfs, 1881; Bonzom, 1898; Cooper *et al.*, 2008). The largest such institution operated at Matariyeh near Cairo (Egypt) from around 1880 until 1913 (Sclater, 1895; Mercier, 1898; Kammerer, 1904b; Decorse, 1904-1905; Raveret-Wattel, 1913; Manlius, 2001). The Giza Zoo near Cairo kept ostriches repeatedly in the early 20th century (Kammerer, 1904a; Flower, 1909a; 1909b), and possibly into the 1930s. However, the absence of traffic routes should have prevented their export to Kufra.

The significant historical trade in ostrich feathers, hides or leather in North Africa is not reviewed here, although Tripolitania alone had exported such goods for 2.500.000 francs in 1880 (Magaud d'Aubusson, 1889; Bonzom, 1898), and some Libyan oases, such as Ghat, were continent-wide trade centers (Bono, 1981). The bulk of this traditional trade might have implied trans-Sahara caravan transport from the Sahel to the African north coast. Indeed, Kufra was a rest station on the important caravan route from the Wadai Sultanate to Benghazi, and a side branch of this route connected Kufra with Tibesti (Fig. 8 in Schiffers, 1971). Still, the masses of ostrich feathers transported from the south to the Mediterranean ports might have been supplemented by some materials from Libya too. Lyon (1821), della Cella (1821), Hamilton (1896) and El Sayed Kita (2014) were aware of ostrich hunts for the feather trade within Libya. However, this trade receded as soon as commercial ostrich farms in South Africa started to satisfy the European market (Coró, 1961), and anyway trans-Saharan caravans could hardly have brought living ostriches to Kufra from on camel backs.

In conclusion, our two photographed ostriches plau-

sibly attest a persistent wild ostrich population in the ambit of the Kufra oases during the early 1930s, from which Rolle's bird had originated locally or regionally. Chudeau's (1909) observation that captured ostriches were raised in many villages of the more southerly Sahelian zone, such as in the Hausa lands and on the Niger River, grazing near the villages in semi-liberty, points to another possible interpretation for the photographed birds at Kufra; the Sahelian villagers used to pluck the ornamental feathers of their tamed ostriches annually for lucrative exports. Also in the former Sahara Español, Spanish military officers used to keep tame ostriches caught locally (Sanchez & Gil, 2024). Only after 1931, in the wake of European penetration into the innermost Libyan Desert, could this population be discovered by Europeans, since not only the Italians reached Kufra as late as in 1931, but also the British reconnaissance of the adjacent regions of the Libyan Desert in west Egypt and northwest Sudan intensified not earlier than in the same period (Bagnold, 1931; Bagnold & Harding King, 1931; Bagnold et al., 1933; 1939; Penderel, 1934). This late surge of exploration activities into some of the remotest districts of the Sahara was enabled by the late technical innovation of allterrain vehicles that mastered the desert beyond the more limited reach of camel caravans.

Published evidence of Libyan ostriches

Given the preceding, further records of ostriches in Libya were searched for in travel reports of explorers and in studies of archaeozoology. The findings from this research are reviewed hereafter, and the widespread historical range of ostriches in Libya (Fig. 2) and in adjacent portions of the Libyan desert emerges indeed.

The following account compiles information about ostriches in the entire "Libyan Desert", meaning the natural region in which Kufra is embedded. This geographical designation does not refer to all deserts within the state territory of the modern nation Libya but to the northeastern sector of the Sahara comprising the eastern half of Libya, Egypt west of the Nile ("Western Desert"), and northwest Sudan. Bates (1914) detailed the boundaries of this geographical region. This meaning of the modifier word "Libya" continues the classical antique connotation of "Libya" as a synonym of many parts of (north) Africa, rather than to the modern nation of this name. If only the dry lands within the state territory of contemporary Libya are referred to, we propose the designation "Sahara of Libya".

The evidence reviewed consists of: i) recent fossil remains of ostriches; ii) engravings or paintings of prehistoric rock art; and iii) historical sight records of living birds reported in books and journals.

Fossilized remnants

Numerous prehistoric or fossilized eggshell fragments are spread over sometimes expansive desert grounds in Libya and in adjacent countries. Broken ostrich eggs are the locally most abundant animal fossils in the Libyan Desert. Unfortunately, apparently none of these remains have been dated, and some or even most of them might date from periods in the Holocene (later Pleistocene?), when more humid climate regimes may have prevailed.



Fig. 2 - Sites in Libyan Desert with historical records of ostriches. Black squares: references in historical literature. 1: Richardson (1853), Kaleebah; Coró (1940), egg shell fragments at El Assa. 2: Richardson (1848), Sinawin oasis. 3: Lyon (1821), Waddan hills. 4: Synesius of Cyrene, Cyrenaica at the turn of 3rd to 4th century (current era). 5: Forbes (1921), Wadi el Farigh. 6: Menu von Minutoli (1824), Marmarica. 7: Pococke (1743), Browne (1799), Geoffroy Saint-Hilaire (1799), Langlès (1803), between Alexandria and Siwah. 8: Heuglin (1873), near Cairo. 9: Heuglin (1873), between Fayum, Wach el Chardjeh and El Dachleh. 10: Decorse (1904-1905), around Ghat. 11: Richardson (1853), between Murzuk and Tibesti. 12: Kufra oasis (1933), this study. 13: Rohlfs (1875), Dakhla osasis. 14: Al Hussaini (1959), latest record in the Libyan Desert of 1935, between Kharga and Dakhla. 15: Georg Schweinfurth (in Ascherson 1874), Qurqur oasis. 16: Gustav Nachtigal 1869–1874, near Afafi (in Malbrant 1954). 17: Nachtigal (1879), generalized record for Tibesti range. 18: Malbrant (1954), Djourab desert. 19: Malbrant (1954), Mourdi depression. 20: Malbrant (1954), Niethammer (1955), Ennedi. 21: Bagnold (1933), Szechenyi (1936), Almasy (1935), Wadi Howar and surrounds. White squares: fossil eggshell fragments found on the desert surface. 1: Moltoni (1931, 1932), el-Fogha. 2: Moltoni (1931), Marada. 3: Forbes (1921), Moltoni (1931), around Ajdabiya. 4: Ghigi (1932), Moltoni (1932), Sahabi. 5: Moltoni (1928), around Giarabub oasis. 6: Goodman and Meininger (1989), Matruh and from there to Quattara. 7: Walters (1982), Quattara depression. 8: Steindorff (1904), Wadi el-Natrun. 9: Moltoni (1932), Uau el-Chebir. 10: Moltoni (1932), Sarir Kalanshiyu. 11: Ghigi (1932), Wadi Zighen. 12: Gautier in Manlius (2001), Farafra. 13: Ascherson (1874, 1875), Rohlfs (1875), between Farafra and Dachel (Dakhla?), and to the southwest of Dachel. 14: Churcher (1992), Dakhla oasis. 15: Jany (1963), Salma Kabir. 16: Hassanein Bey (1925), location not precisely indicated. 17: Hassanein Bey (1925), Moltoni (1932), Archenu and surrounds of Jabal a-Uweinat. 18: van Neer and Uerpmann (1989), south of Gilf el-Kebir. 19: Gautier (pers. comm. to Churcher 1992), Gautier (1993), Bir Tarfawi. Districts stained in blue: Areas with prehistoric rock art showing ostriches, chiefly engravings in stone walls or occasionally paintings. 1: Messak Settafet and Messak Mellet, Fezzan: numerous authors, e.g. Le Quellec (1998). 2: Dor el Gussa and Jabal (Djebel) Ben Ghnema, Murzuq District (image database of the Frobenius-Institute, Frankfurt). 3: Jabal al-Uweinat, Kufra District: Rhotert (1935), Winkler (1939). 4: Wadi Sura (Sora) El Wadi El Gedid Governorate, Egypt: e.g., Kuper (2013). Basemap: Wikimedia Commons Africa relief location map. Copyright for reproduction granted under GNU Free Documentation License, Version 1.2 (https://commons.wikimedia.org/wiki/File:Africa_relief_location_map.jpg). / Siti nel deserto libico con testimonianze storiche di struzzi. Riquadri neri: riferimenti nella letteratura storica. 1: Richardson (1853), Kaleebah, Coró (1940), frammenti di guscio d'uovo a El Assa. 2: Richardson (1848), oasi di Sinawin. 3: Lyon (1821), colline di Waddan. 4: Sinesio di Cirene, Cirenaica a cavallo tra il III e il IV secolo (epoca attuale). 5: Forbes (1921), Wadi el Farigh. 6: Menu von Minutoli (1824), Marmarica. 7: Pococke (1743), Browne (1799), Geoffroy Saint-Hilaire (1799), Langlès (1803), tra Alessandria e Siwah. 8: Heuglin (1869), vicino al Cairo. 9: Heuglin (1869), tra Fayum, Wach el Chardjeh e El Dachleh. 10: Decorse (1904-1905), nei dintorni di Ghat. 11: Richardson (1853), tra Murzuk e Tibesti. 12: Oasi di Kufra (1933), questo studio. 13: Rohlfs (1875), oasi di Dakhla. 14: Al Hussaini (1959), ultimo record nel deserto libico del 1935, tra Kharga e Dakhla. 15: Georg Schweinfurth (in Ascherson 1874), oasi di Qurqur. 16: Gustav Nachtigal 1869-1874, vicino ad Afafi (in Malbrant 1954). 17: Nachtigal (1879), record generalizzato per l'areale di Tibesti. 18: Malbrant (1954), deserto di Djourab. 19: Malbrant (1954), depressione di Mourdi. 20: Malbrant (1954), Niethammer (1955), Ennedi. 21: Bagnold (1933), Szechenyi (1936), Almasy (1935), Wadi Howar e dintorni. Quadrati bianchi: frammenti di guscio d'uovo fossile trovati sulla superficie del deserto. 1: Moltoni (1931, 1932), el-Fogha. 2: Moltoni (1931), Marada. 3: Forbes (1921), Moltoni (1931), intorno ad Ajdabiya. 4: Ghigi (1932), Moltoni (1932), Sahabi. 5: Moltoni (1928), intorno all'oasi di Giarabub. 6: Goodman e Meininger (1989), Matruh e da lì a Quattara. 7: Walters (1982), depressione di Quattara. 8: Steindorff (1904), Wadi el-Natrun. 9: Moltoni (1932), Uau el-Chebir. 10: Moltoni (1932), Sarir Kalanshiyu. 11: Ghigi (1932), Wadi Zighen. 12: Gautier in Manlius (2001), Farafra. 13: Ascherson (1874, 1875), Rohlfs (1875), tra Farafra e Dachel (Dakhla?) e a sud-ovest di Dachel. 14: Churcher (1992), oasi di Dakhla. 15: Jany (1963), Salma Kabir. 16: Hassanein Bey (1925), località non indicata con precisione. 17: Hassanein Bey (1925), Moltoni (1932), Archenu e dintorni di Jabal a-Uweinat. 18: van Neer e Uerpmann (1989), a sud di Gilf el-Kebir. 19: Gautier (pers. comm. a Churcher 1992), Gautier (1993), Bir Tarfawi. Distretti colorati in blu: Aree con arte rupestre preistorica raffigurante struzzi, principalmente incisioni su muri di pietra o occasionalmente dipinti. 1: Messak Settafet e Messak Mellet, Fezzan: numerosi autori, ad esempio Le Quellec (1998). 2: Dor el Gussa e Jabal (Djebel) Ben Ghnema, distretto di Murzuq (database di immagini del Frobenius-Institut, Francoforte). 3: Jabal al-Uweinat, distretto di Kufra: Rhotert (1935), Winkler (1939). 4: Wadi Sura (Sora), governatorato di Wadi El Gedid, Egitto: ad esempio, Kuper (2013). Mappa di base: Wikimedia Commons Africa relief location map. Copyright per la riproduzione concesso secondo la GNU Free Documentation License, Version 1.2(https://commons.wikimedia.org/wiki/File:Africa relief location map.jpg).

In this context, a recurrent problem is the uncertainty of ancient eggshell fragments referring to an autochthonous, (pre)historical population or to anthropogenic leftovers from traded goods since ostrich eggs served as attractive merchandise (Anon., 1870). For example, eggshells from the Bronze Age (14th century BCE) settlement on Bates Island, an isle in the East Lagoon of Marsa Matruh (ancient Paraetonium) in coastal Cyrenaica (Conwell, 1987), might indicate early traffic in ostrich eggs within Libya, because this minute island provides insufficient habitat to sustain a population in situ. Artwork in a tomb at El Amarna (Egypt) depicts Libvans offering ostrich eggs as items of tribute to the Egyptian pharaoh Akhenaten (Conwell, 1987). The ostrich eggs built into a wall of the mosque at Jalu (Al Wahat District in northeast Libya, 230 km from the Mediterranean Sea) were explained as gifts brought by pilgrims from the distant trade center of Wadai (Forbes, 1921). Lyon (1821) rated ostrich skins and feathers as commercial articles exported from Fezzan to Bornu, Wadai, and Egypt. Eggs are also incorporated as decorative items in majestic buildings and mosques far outside the natural range of ostriches in Asia, from the Ottoman Empire east to India, and these might have been imported from the Near Eastern haunts of Arabian ostriches by travelling pilgrims after their hajj to Mecca (Anon., 1870; Finsch & Hartlaub, 1870). Equivalent imports by Islamic pilgrims or tradespeople from Arabia or from tropical African latitudes to the northern Sahara is apparently nowhere mentioned in documents but is well conceivable. Already in the Bronze and the Iron Ages, decorated ostrich eggs were widely traded luxury items, brought from Africa to Mediterranean Europe and Asia (Hodos, 2020; Hodos et al., 2020). Referring to Dakhla in northwest Egypt, Harding King (1925) supposed that eggshell fragments spread out in the local de-

sert could be traced to the travel provisions consumed by cameleers of historical caravans - this author considered the locality too arid to support a local ostrich population. Hartert (1913) suspected the same for eggshells concentrated in the vicinity of desert wells in Algeria, where humans might have camped regularly over millennia, and for perforated shell fragments, because these had been pierced to fit them on a thread for making necklaces. Forbes (1921) allocated a piece of ostrich eggshell picked up in the desert between the Mediterranean Sea and Kufra to the offal of a trading caravan. However, despite such exceptions, the sheer number of eggshell fragments and their wide distribution even in remote deserts argue for autochthonous former ostrich populations in the majority of regions where such ancient remains had been found in

plain nature, although these ostriches may have roamed there under more humid climatic conditions than those prevailing today. Nevertheless, some records of excavated eggshells may still refer to traded specimens, which were not only of dietary value throughout Africa, but also fabricated into containers used for liquid storage, and into disc beads for jewelry and amulets, which could be traded afar easily (Ezz El-Din, 2010). The following records may

refer to autochthonous populations. Shattered ostrich eggshells from a dry lake in the Salma Kabir ridge refer to a site only 100 km north of Kufra (Jany, 1963). The tour operator José Miguel Redondo (in *litt.*, 2023) found an assemblage of partly intact ostrich eggshells 200 km east of the Kufra oases in the Wadi Sura in southwest Egypt (https://www.elrincondesele.com/diario-de-la-expedicion-kamal-al-desierto-en-egipto-iv-wadisura/), during an expedition in 2014 (Fig. 3).

Further eggshells were found at Sahabi and Wadi Zighen, on the route from the Mediterranean Sea coast in the direction of Kufra (Ghigi, 1932), in the Serir Calansho (Sarir Kalanshiyu) in Kufra District, and near Jabal Archenu southeast of Kufra on the route towards the Jabal al Uweinat (Moltoni, 1932). Hassanein Bey (1925) found egg remains in the latter district (Wadi Maraheeg near Archenu), and south of Jabal al Uweinat towards Erdi (today possibly located in north Chad). Ardito Desio collected eggshells near Hatiet el Huedda and at the Giarabub oasis (Moltoni, 1928). Faret-Mazzala in Marada (at 145 km south of Al-Agheila, Al Wahat District), Maaten Risam (probably the well Ma'tan Risam near Ajdabiya in coastal Cyrenaica) and the nearby site Gare di Bir (Sahabi, coastal Cyrenaica), Uau el-Chebir (Waw al Kabir, Murzug District, Fezzan), and el-Fogha (Al Fuguha, Tripolitania) yielded further shells (Moltoni, 1931, 1932). A fairly intact ostrich egg with its acute pole perforated was interpreted by Moltoni (1931) as a human artefact, i. e. a container to store liquids, although picked up in mid-desert. Nevertheless, Moltoni (1931) concluded a fairly recent age for some of his ostrich eggshells from Libya, with ostriches to survive in east Libya until the period 1800-1850. Niethammer (1971) also believed, without providing evidence, that ostriches had inhabited Libya but disappeared from this country.

Bates's (1914) record of eggs from "Hargah oasis, east Libva" needs interpretation, but this locality presumably refers to the Kharga Oasis (Arabic: al-Hāriğa) in western Egypt rather than to the east of the state of Libya. Bundy (1976) inferred from fossil eggs an extant ostrich population in the narrow belt of pre-desert running through northern Libva in parallel to the Mediterranean coast. However, no convincing sources supported this inference, and fossil eggs are much more widespread in Libya than claimed by Bundy (1976). Justifiably and not unexpectedly, therefore, Bundy's (1976) map was largely ignored by later reports about the avifauna of Libya.

The following additional sites yielded ostrich egg shells in the eastern Libyan Desert of Egypt: Wadi el Natrun (Steindorff, 1904); at every excavation site of west Egypt and northeast Sudan (van Neer & Uerpmann, 1989); all over the Libyan desert (Moreau, 1934); sand hills east of Matruh (Goodman & Meininger, 1989); areas of the Western Desert in Egypt (Caton-Thompson & Gardner, 1934; Peel & Bagnold, 1939; Wendorf et al., 1977; Gautier, 1980; 1984; Churcher, 1992); Quattara Depression (Walters, 1982); south of Bir Halda, 45 miles southeast of Marsa Matruh to Qattara (Goodman et al., 1986); Bir Tarfawi (Gautier pers. comm. to Churcher, 1992; Gautier, 1993); between Farafra and Dachel (Dakhla?), and southwest of Dachel in the Western Desert, 150 km east of the border to Libya (Ascherson, 1874; 1875; Rohlfs, 1875); Gilf Kebir and the southerly adjacent mud pans (van Neer & Uerpmann, 1989); Dakhla oasis (Churcher, 1992); Farafra oasis (Gautier in Manlius, 2001).

There is little doubt that prehistorically, perhaps during

pluvial periods in the Holocene, ostriches had ranged throughout what is today the Libyan Desert.

Prehistoric rock art

Virtually countless examples of prehistoric engravings (and less frequently paintings) of ostriches decorate the walls of rock shelters in various parts of the Sahara, including Libva. The centre of such rock art in Libva is situated in the Messak Mountains of the Fezzan Province. Le Ouellec (1998) counted 1130 ostrich images in this area, which made this bird the most abundant wildlife species depicted by prehistoric engravers (followed by giraffe), and the second-most common represented animal (after cattle). An impressive 11% of the numerous prehistoric engravings in this region, and 17 % of all engraved animals, represent the ostrich. Van Albada and van Albada (1994) confirmed the preeminence of ostriches in the rock art of the Messak from the earliest beginnings of such artwork until its end in the late camel period. Hunting and capture scenes propose that ostriches were persecuted by people, and two images could indicate taming or "domestication" of the birds. Some rock art reveals biological details (van Albada and van Albada 1994; Lutz and Lutz 1995), such as ostriches depicted sitting on nests or a scene with the mating display of a cock. The image database of the Frobenius-Institute for Research in Cultural Anthopology at Frankfurt (http://bildarchiv.frobenius-katalog.de) provides many engraved ostriches from this area, and also holds a few examples of ostrich art in Libya from outside the Fezzan, i.e., Dor el Gussa and the nearby Djebel (Jabal) el Ghnema in the Murzuq District, central Libya.

While the Libyan ostrich art is centered in (west) Fezzan, there are examples from the closer vicinity of Kufra too, e.g. in the valley Karkur Talh in the Jabal al Uweinat (Rhotert, 1935; some digital examples, even hunting scenes, are accessible in the previously mentioned image database). Elsewhere in Uweinat, such rock images revealed tamed specimens and a child playing with an ostrich (Winkler, 1939). These mountains extend across the border triangle of Libya, Egypt and Sudan, and the referred sites may refer to the Libyan territory. Further ostrich hunts with hounds and falcons were engraved in what is today the Gilf el-Kebir National Park in nearby Egypt (Rhotert, 1952).

The predominant concentration of ostrich rock art in the Messak, distant from all locations where fossil ostrich eggs have been found in central to eastern Libya, is remarkable, but can perhaps be understood by the different prerequisites for either kind of prehistoric evidence: Rock art needs stone walls which are bound to mountain ranges, while fossils accumulate best in plains and sedimentary basins. The ancient evidence for ostriches in both moun-



Fig. 3 – Ancient, undated eggshells found in the Wadi Sura (southwest Egypt) in 2014 by J. M. Redondo (*in litt.* 2023). Courtesy of J. M. Redondo. / Gusci d'uovo antichi e non datati trovati nel Wadi Sura (Egitto sud-occidentale) nel 2014 da J. M. Redondo (in litt. 2023). Per gentile concessione di J. M. Redondo.

tains and plains indicates that the species had abounded in both types of Libyan landscape.

A review of ostrich rock art in adjacent Egypt, Sudan and Chad falls outside the scope of this review. However, the famous paintings and engravings of the Cave of the Beasts in Wadi Sura must be emphasized because of the beauty of the rock images at this site (Kuper, 2013) and because this cave in the most south-western part of Egypt is in close proximity to the border with Libya.

Ancient literary sources of ostriches in the Libyan Desert

In this and the next following sections the literary records of Libyan ostriches are presented with sufficient detail so that readers can decide themselves if these statements are acceptable or not.

The taxonomic species name Struthio camelus and the designations in many European languages (*struzzo, struz*, strucc, Strauss, avestruz, autruche, ostrich) derive from the Greek strouthos (στρουθός) which means "sparrow" (Keller, 1913): This ambiguous name needed explicatory epithets such as "giant sparrow", "ground-dwelling sparrow" or indeed "Libyan sparrow (Λ i β υσσα)" - the latter name employed by Aristotle (Keller, 1913). This epithet might mark the earliest relation of ostriches to Libya. However, classical literature ascribed manifold lands to Libya, from (parts of) the territory of modern Libya to the entire North African or Africa land masses (Strenger, 1913). Even before, ostrich eggs and feathers had been used in ancient Egypt, sometimes imported from "Libva" (El Sayed Kita, 2014), Nubia, and the land of Punt on the African east coast (Laufer, 1926). During the first millennium BC the Garamantes civilization of Fezzan utilized ostrich eggs (Laufer, 1926) and engaged in the ostrich feather trade (Schiffers, 1950). Given the traffic conditions of that period, at least some of the traded ostrich products might have originated in Libya. The Macae, a Lixyna tribe living in the Wadi Ka'am (Cinyps River) in what is today coastal Tripolitania, used to wear ostrich skins as protective clothes in war battles (Herodotus, Histories, Book IV, 175; Laufer, 1926).

Four classical authors provided more concrete information (see also Keller, 1913; Toynbee, 1973): in the fifth century BCE Herodotus from Halicarnassus (Asia Minor) knew ostriches from "Libya of the nomads", which were the lands between Egypt and Tunisia (Histories of Herodotus, 4th book Melpomene, paragraph 192). The Roman poet Claudius Claudianus (ca. 370 - ca. 404 CE) commented on the behaviour of "great Libyan birds" (=ostriches) in his vituperative poem In Etropium II (verses 310-316): these ostriches escaped fast from persecutors by raising their wings curved like sails to catch the breeze over sun-heated, sandy grounds, but they froze still with their eyes closed when the persecutor had come close, assuming that the enemy could not spot them if only they could not discern him with closed eyelids (Platnauer 1922, p. 206). Synesius of Cyrene (c. 370- c. 413 CE), a bishop of Ptolemais in the Cyrenaica, mentioned ostrich hunting in Cyrenaica in his letter 133 to Pylaemenes at Byzantion (Petavio, 1859, p. 1521; Crawford, 1901, p. 346; Keller, 1913): These hunts were difficult, needing special strategies if capture was intended fort exporting the birds alive to destinies overseas. This bishop attempted in vain to send some ostriches alive by ship to Asia Minor. In his description "De dipsadibus", Lucian of Somasata (120-180/200 CE) referred to the use of ostriches by the Garamantes tribe living in what is today southwest Libya (Fowler & Fowler, 1905, p. 27): their eggs served as containers to replace ceramics in the sandy deserts where clay for pottery was absent, and cut in two halves they served as headdresses (Pauly, 1827, pp. 1518, 1521: Die Dipsaden 2, 6, 7). The ostriches parading the streets of Alexandria during the quadrennial grand procession celebrating the Egyptian ruler Ptolemy II. Philadelphus (in the third century BCE) may or may not have originated from the nearby Libyan Desert; these birds dragged chariots through the town (Toynbee, 1973). Some of the many ostriches displayed in animal shows of the Roman Empire (Toynbee, 1973) may have originated in Libya too, but Romans did not record any relevant zoological information.

Ostriches appear on mosaics decorating the houses in the North African provinces of the Roman Empire. Examples from within modern Libya are less common than from Tunisia or Algeria, but mausolea from the Roman settlement Ghirza (Gerisa) near the Limes Tripolitanus of the ancient province Tripolitania (in the modern Misrata District) contained reliefs of ostriches beside antelopes (Toynbee, 1973), and of ostrich hunts (Le Quellec, 2006), from the first centuries CE. However, the present author had to note that Roman mosaics are unreliable for zoological inference, such artwork being the product of an artisanal mass industry pleasing the taste of clients by displaying wildlife in a standardized, unobjective style shaped by fantasy. Not unlikely, therefore, imaginary mosaics were replicated all over the Roman Empire, both within and outside the geographical range of wild ostriches.

Alexandria was indicated as the main harbour exporting ostriches and their products to the Roman and the Byzantine Empires (Kinzelbach, 1993), and this trade route might have shaped the knowledge of Europeans of this "Libyan" species at least until the Renaissance period (e.g., Belon le Mans, 1555).

Literary records of Libyan ostriches in recent history

More recent records of ostriches in Libya were published so often that one wonders why Libya as a range country continues to be ignored till date.

Coró (1940) reported ostriches as common in the Fezzan and in the Al Jufrah district of central Libya until their extinction by overhunting in the late 18th century. The birds supplied venison and grease for the treatment of rheumatism. At the market of Tripoli, ostriches used to be sold alive as recently as in 1766 to tap the medical fat without slaughtering them.

Traversing Libya in 1818-1820, Lyon (1821) found wild ostriches in the mountains of Waddan (northeast Fezzan). Moreover, all graves in the cemetery of Sokna town were ornamented with ostrich eggs, as were the tombs and the mosque of Waddan and the graveyard of Mourzouk. Cherbonneau (1857) observed similarly decorated tombs at Ghadames. Forbes (1921) saw many ostrich eggs in a tomb wall at Jof, a town within the Kufra group of oases.

Della Cella (1821) described ostrich hunts in the hills near Labiar in Cyrenaica. Feathered hides used to be exported to the market of Benghazi. Ostrich feathers were also harvested near the Augiles oasis, i.e., the modern Awjila or Audschila (Augila) in the Al Wahat District of northeast Libya (Pacho, 1827). Richardson (1848) found a captive pet ostrich captured near Seenawan (= likely the Sinawin oasis, located 30 km east of the border of the Tunisian boundary on the old trade route from Tripoli to Ghadames). Dung of (wild) ostrich in the desert near the village Kaleebah southwest of Garyan (probably in modern Jabal al Gharbi District) indicated the species still closer to the Mediterranean coast (Richardson, 1853: p. 22). This site is not far from El Assa (Coró, 1940), where eggshells were seen at only 30 km from the seacoast (presumably the actual village El Assah, 10 km east of the Tunisian border). The German travel companion of James Richardson was Heinrich Barth, who was to become later the famous pioneer explorer of the central Sahara. According to Barth (1857) the village Kallebah (named by him in German language Kuleba) was on the Nafusah Plateau (Jabal Nafusah) within a few dozen kilometres from the Mediterranean Sea. Later, Barth's expedition found broken ostrich eggs (fossil or fresh?) near Murzuk (op. cit. p. 64), apparently in Fezzan. Local informants reported to Richardson (1853, p. 101) ostrich hunts with the help of dogs between Murzuk and Tibesti. El Hachaichi (1903) observed numerous ostriches in the desertic plains of El Kaf in northeast Fezzan in 1896 (Richardson, 1853, p. 141), which may or may not be identical with the record from El Kef between Sokna and Zighan (Richardson, 1853, p. 209).

Menu von Minutoli (1824) observed groups of 12-15 ostriches hunted by tribespeople during his travel from Alexandria to Darma in Cyrenaica in 1820. The record site likely refers northeastern Libya, or to immediately adjacent northwest Egypt. The expedition followed an inland route in parallel to the African north coast, westwards until halfway between the cities of Tobruk and Derna. Therefore, ostriches seem confirmed for the 19th century Cyrenaica, in what had been the antique landscape of Marmarica. Hunting ostriches in this region was lucrative, the hides selling for 40 Spanish thalers, and was performed from wooden ambush hides built near the drinking sites and pastures of the birds (loc. cit.). One of von Minutoli's expedition fellows mentioned ostriches from near the Siwah oasis in Egypt (Scholz, 1822).

In the mid-19th century ostriches had still roamed in the Wadi el Farigh, south of Ajdabiya in the Al Wahat District (between Cyrenaica and Kufra), where decades later Forbes (1921) still saw eggshells.

Hamilton (1856) met tame pet ostriches in Zalla (Zella) oasis in northeast Fezzan. Kept in houses under tidy conditions, they supplied clean high-quality feathers for export to distant markets, whereas wild ostriches yielded only dirty feathers selling cheaper. These pets confirm ostriches for central Libya in the first half of the 19th century.

Nachtigal (1871) rated ostriches among the birds of Ottoman Tripolitania, which he traversed to reach Cyrenaica in 1868. Subsequently, Nachtigal (1879) travelled from Tripoli via Fezzan to Tibesti and onwards in 1869, reporting ostriches from the "northern desert" (i.e., within Libya) in earlier times, which had retreated meanwhile to the Tibesti highlands. Occasional footprints and a few living birds in Tibesti (Nachtigal, 1879) could refer to the territory of either north Chad or south Libya. According to Malbrant (1954), Nachtigal had also seen ostriches near Afafi at the western terminus of the Tibesti range, perhaps 60-80 km south of the Libyan border. However, the present author was unable to verify this citation in his own copies of Nachtigal's monograph.

Around Ghat in Fezzan ostriches survived into the early 20th century (Decorse, 1904-1905). This record and the photographed birds from the Kufra oases in the early 1930s mark the latest confirmations for Libya.

Ostriches from the eastern Libvan Desert (= Western Desert) in adjacent Egypt were reported from the 1700s to the 1930s (reviews in Goodman et al., 1984, 1986; Goodman & Meiniger, 1989; Manlius, 2001). Pococke (1743) rated ostriches as common southwest of Alexandria, and hunted for flesh and fat for export to Alexandria. Sonnini (1807) reported hunts for fat and plumes in the Western Desert. Geoffroy Saint-Hilaire (1799, p. 46) deemed this bird common in the desert south-west of Alexandria. Browne (1799) and Langlès (1803) saw frequent ostrich tracks between Alexandria and Siwah. W. G. Browne had entered eastern Libya from Egypt, and his ostriches may, albeit not necessarily, refer to easternmost Libyan territory (Menu von Minutoli, 1824, p. XI). Heuglin (1873) reported ostriches from the lands between Fayum, Wach el Chardjeh and El Dachleh (= presumably El Dakhla), and that Prince Halim, a son of the de facto ruler of Egypt, Muhammad Ali Pasha, had observed destroyed ostrich nests near Cairo in 1854. In the Bejudah Steppe, where Hemprich and Ehrenberg had still hunted specimens, ostriches had become rare by 1860 (Hartmann, 1863). Heuglin (1873) and Finsch and Hartlaub (1870) (cf. Shelley, 1872) cited a record by Burckhardt (1822) from El Mogran between Cairo and Suez. Bedouins reported ostrich nests from the Western Desert before 1844 (Nicoll, 1919). Rohlfs (1875) heard of fresh ostrich tacks from the years shortly before 1873 near the village Oasr Dachl (Dakhla oasis), and Georg Schweinfurth (in Aschserson, 1874) of a fresh spoor at the Qurgur oasis, south of Chargeh (= presumably Kharga oasis). Bates's (1914) statement that ostriches had disappeared only recently from coastal eastern Libva seems to rest on older sources referring to west Egypt (already cited in the present review).

In the first decades of the 20th century various authors (not cited here) considered the ostrich extinct in the Western Desert, but one bird was captured at Abou-al-Oql (= Ezbet Zayat) between Kharga and Dakhla in 1935 (Al Hussaini, 1959). The even later ostriches claimed to persist near the two latter oases until 1959 (van Neer & Uerpmann, 1989) refer to an erroneous misquotation of Al Hussaini (1959). More recent records of ostrich from Egypt refer to the far southeast of this country, not to the Western Desert (Goodman & Meininger, 1989).

Ostriches were once common in many parts of semiarid and arid Sudan, e.g. in Darfur (Madden, 1934; Wilson, 1976), but the species retreated to the south during the 20th century, with the desert belt no longer occupied recently (Nikolaus, 1987).

Almasy (1937, p. 34) found the carcass of an ostrich freshly killed by African wild dogs *Lycaon pictus* (Temminck 1820) in the "southern part of the Libyan Desert"

during his travels 1931-1936, but he did not specify a locality. The hunting strategy of these canids could be reconstructed in detail from the footprints in the sand. Szechenyi (1936) recounted a very similar wild dog hunt from the first months of 1935 during an expedition from Egypt into the southern Libyan Desert in northwest Sudan, which had been led by his compatriot Almasy. The details of this second incidence match Almasy's (1937) report so closely to conclude the identity of both events, although the two authors - travelling in companion - avoided to refer to each other explicitly. Szechenyi (1936) did not specify the locality either, but from the context a site in or near the Wadi Howar in northwest Sudan can be inferred. Slightly previously in 1932, British travellers (Bagnold, 1933) found a brooding ostrich sitting on its nest and two further nests with clutches of 94 and 20 eggs in the same Wadi Howar. Elsewhere in the same wadi, deserted clutches of six to ten eggs were encountered repeatedly by this team, as well as an ostrich couple guarding more than fifty chicks. The paper by Bagnold (1933) was read at a meeting of the Royal Geographical Society at London by W.B.K. Shaw on 29th May 1933, accompanied by lantern slides not included in the publication (Bagnold, 1933). These images and further unpublished documents by this expedition are kept in the archive of the Royal Geographical Society at London, and excerpts from them are reproduced in Fig. 1 c and d and in Fig. 4b and d. Further archived photos not represented here depict the big clutch of many eggs mentioned in the paper, and groups of up to three dozen ostriches escaping fast, all likely from the Wadi Howar. One may conclude that ostriches cannot have been other than abundant in the Wadi Howar in the early 1930s. According to Oehm (2015), they no longer inhabit the Wadi Howar National Park now, although the species still graces a faunal list of this protected area in the recent letter of intent by the Sudanese government to have accepted this valley as a World Heritage site by the UNESCO (https://whc.unesco. org/en/tentativelists/1951/). Nevertheless, this latter faunal list might be erroneous, because the species was no longer confirmed regionally in several consulted works over decades (A. Schreiber, sources not given).

Longer than in northwest Sudan, ostriches were able to survive in adjacent French colonial territory (today: Chad), at least until the early 1950s. Recorded from Borku via Ennedi to Tibesti, the major concentration lingered on in the southern Ennedi Plateau, and some records referred to the Mourdi Depression of northeast Chad (250 km from the border to Libva) and further west to the Djourab Desert, to the south of the Tibesti range (Malbrant, 1954). Heavy rain during August 1950 elicited locally green pastures in north Chad, so that ostriches wandered to sites at 250 km southwest of Zouar (Malbrant, 1954), the latter settlement in Tibesti situated 270 km south of the Libyan border. Niethammer (1955) met groups of six to nine ostriches in Ennedi in 1954. Already in 1923, the expedition team led by Hassanein Bey (1925) attempted unsuccessfully to hunt a herd of 30-40 ostriches south of the Jabal al Uweinat in the Erdi landscape; only one immature bird could be bagged. Soon afterwards, another adult ostrich was noted in nearby Anglo-Sudanese territory (the area being now under Chadian administration, but not too far from the southern border with Libya).

DISCUSSION Ecological aspects

Except for the poorly known populations in northern Chad which were able to persist for longer in their remote haunts, protected by delayed European occupation due to border disputes between Italy and France, ostriches disappeared from the Libvan Desert during the early 1930s. This occurred in rapid succession from southeast Libva (Kufra), west Egypt (between Kharga and Dakhla), and northwest Sudan (Wadi Howar). The extinction process coincided with intensified penetration by Europeans in the context of the colonial conquests by Italy and the increased British reconnaissance of west Egypt and arid Sudan. Vast expanses of these deserts had previously remained hardly accessible sanctuaries for wildlife, only to be unclosed all of a sudden by the advent of motorized all-terrain vehicles. The colonial strifes implicated an influx of modern firearms likely enhancing poaching, and the occupation of the few natural drinking sites in this hyperarid region by administrative or military hubs might have cut off the lifeline of all water-dependent wildlife.

Expeditions with an interest in geographical exploration contributed the majority of ostrich records from the Libyan Desert rather than zoologists, wherefore deeper insights into behaviour or ecology are rare. The adaptations of ostriches for a life in the Libyan Desert remain virtually unexplored, although in terms of drought and wide thermal amplitudes this is one of the least hospitable deserts worldwide. The local population might have encountered greater abiotic challenges than any other ostriches in Africa.

The Libyan Desert represents the most arid heartland of the Sahara, and the vastest hyperarid region worldwide ("Extremwüste" sensu Schiffers, 1973), where drought provokes expanses of up to hundreds of miles without vegetation in places and a sparsely dispersed vegetation contracted in few depressions or wadis (Shaw, 1928; Blümel, 2013). At Kufra, a mean annual temperature of 30°C is accompanied by an average annual rainfall of 0.9 mm, with at times several years in suit without precipitation (Blümel, 2013). Food and water resources are not only sparse, but unpredictable. Ostriches are able to thrive with little water (Williams et al., 1993), aided by the uptake of moisture from succulent plants such as colocynths (Citrullus) (Bouet 1955). Versatile diets exploited opportunistically a wide range of fodder, but still chiefly herbivorous even in the full desert (Gosse, 1857; Bouet, 1955). Malbrant (1954) and Bouet (1955) described migratory behaviour ("seasonal migrants") in north Chad, in order to seek episodic and erratic plant growth after local rains. Most of the ostrich records reviewed here do not specify the biotopes, if open, unvegetated desert or the perimeter of oases, but at least some of them refer to the proximity of oases. Specifically, Kufra is a drawn-out assemblage of five groups of oases fed by brackish groundwater. There are locally swampy patches with reeds, rushes and tamarisks, and palm groves surrounded by grassy patches and acacia trees (see Fig. 4 in Jany, 1963 and Fig. 62 in Schamp, 1971; Rohlfs, 1880; Ascherson, 1881; Shaw, 1928; Jany 1969), sufficient also for a few dorcas gazelles (Rohlfs, 1880, 1881; Jany 1963). Even the plain Libyan Desert outside the oases comprises episodic "rain oases"

here and there, i. e. patches with therophytes and ephemeral herbs, which germinate amidst naked desert following a rare instance of precipitation before withering again soon (Weis, 1990).

The regional temperatures fluctuate more than elsewhere

in the Sahara, with 50°C as average summer daytime temperatures, and an absolute world record heat of 58°C (Marq de Villers & Hirtle, 2003). Winter temperatures average around 27°C during day-time, alternating with much colder nights and nocturnal frost down to -9°C (Marq de Villers &



Fig. 4 – Phenotypes of ostriches from North Africa. a) A male in nuptial dress at Souss Massa National Park (Morocco), of a lineage translocated to this protected area from Chad; b,d) male and cock group from Wadi Howar (Wadi Hawa), in the southern periphery of the Libyan Desert, Sudan, photographed by the Bagnold expedition in the early 1930s (Bagnold, 1933). Fig. 4b is a magnified extraction of Fig. 1d; c) the models of this tableau were a group of one male and two female ostriches imported to the gardens of the London Zoological Society from Morocco ("Barbary") in February 1859 (from Sclater, 1862); e) two ostriches at the Kufra oases, Libya, photographed in 1933. Magnified from Fig. 1a; f) male in nuptial display kept in the Hai-Bar Yotvata Nature Reserve in the Negev Desert (Israel), probably descending form a lineage imported from the Danakil Desert near the Red Sea (Dittrich 1978, N. Werner, in litt.). Photos 4a, 4f: Klaus Rudloff. Photos 4b, 4d: courtesy of Royal Geographical Society, London. 4e: Courtesy of Frobenius-Institute, Frankfurt. / Fenotipi di struzzi del Nord Africa. a) Un maschio in abito nuziale nel Parco Nazionale di Souss Massa (Marocco), di una stirpe traslocata in quest'area protetta dal Ciad; b,d) gruppo di maschi e galli di Wadi Howar (Wadi Hawa), nella periferia meridionale del Deserto Libico, in Sudan, fotografati dalla spedizione Bagnold all'inizio degli anni '30 (Bagnold, 1933). La Fig. 4b è un'estrazione ingrandita della Fig. 1d; c) i modelli di questo tableau erano un gruppo di un maschio e due femmine di struzzo importati nel 1933. Ingrandito rispetto alla Fig. 1a; f) maschio in esposizione nuziale conservato nella Riserva Naturale di Kufra, in Libia, fotografati nel 1933. Ingrandito rispetto alla Fig. 1a; f) maschio in esposizione nuziale conservato nella Riserva Naturale di Hai-Bar Yotvata nel deserto del Negev (Israele), probabilmente discored (Brabary") nel febbraio 1859 (da Sclater, 1862); e) due struzzi nelle oasi di Kufra, in Libia, fotografati nel 1933. Ingrandito rispe

Hirtle, 2003). Ostriches' slender, almost unfeathered necks and legs facilitate heat dissipation by modulated blood supply to the naked skin (Maloney, 2008), but they complicate the retention of body heat during frost. The mechanisms of frost tolerance of ratites are barely studied, but Schou et al. (2022) observed heritability of temperature resistance in captive farm ostriches without evaluating the physiological means. Ostriches are thermophilic in most parts of Africa, and although some populations in south and southwest Africa and in the savanna highlands of East Africa need to sustain regular frost too, the climatic volatility in the northeastern Sahara should be unsurpassed anywhere else. Intriguingly, the ostriches exposed to the less continental, more even-tempered climate in the west Sahara, where closer to the Atlantic Ocean frost is largely absent, possibly represented a smaller-bodied variant.

The historical abundance of ostriches in the Wadi Howar refers to a dry valley of 1100 km length (Nussbaum *et al.*, 2007) in the southern fringe zone of the Libyan Desert, even of the Sahara as such (Simons, 1973). Already within a gradient towards a Sahelian climate, portions of the Wadi Howar are vegetated by plant growth ranging from open fields of dispersed therophytes to thickets and some trees along the dry banks of this wadi. The lower valley holds a dry deciduous woodland (Nussbaum *et al.*, 2007). These are vestigial biota of once richer ecosystems during more humid pluvial periods, when the fossil river ("Yellow Nile") used to feed the lower Nile as its major affluent (Kröpelin, 2007).

An appealing ecological side aspect of historical desert ostriches is their predation by a now equally extirpated predator, i.e., the African wild dog Lycaon pictus. Almasy's (1937) and Szechenyi's (1936) hunting scene of these canids on Saharan ostriches is remarkable not only as one of the latest records of ostriches in this part of Africa, but as the probably northernmost record of African wild dog in northeast Africa. Their accounts seem compatible with the species identity of Lycaon pictus. Shaw (1936) also met a pack of 14 wild dogs in the Wadi Howar during the same years. The historical range of this longexterminated species in north Africa is just as poorly known as is the range of desert ostriches, and most of many consulted zoological treatises omit the Sahara from this canid's range altogether, except an isolated population in south Algeria. Only Skinner and Smithers (1990) indicated two additional, equally isolated, historical range patches in northeast Africa, one of which could coincide with the records from the Wadi Howar reviewed here, whereas the other is centered on the Tibesti region in Chad - no sources are indicated, however, for either range patch, and the present author found no confirmatory source for the Tibesti. Otherwise, wild dogs seem unrecorded in the Sahara, including the state of Libya (McNutt & Woodroffe, 2013). The only vague hint to their possible former presence in the Libyan Fezzan was a personal communication of the pioneer explorer Heinrich Barth, who recounted to the geographer Robert Hartmann to have heard Fezzanese natives talking of a beast which according to their description should have been African wild dogs (Hartmann, 1868). According to Joleaud (1936), already Herodotus mentioned painted wolves to roam in his "Libya of the nomads" (paragraph 192 of the

4th book, Melpomene, of his "Histories"). Herodotus enumerated "δίκτυεςn - dictyes" in his list of Libyan wildlife, a word whose translation is however open to debate. Joleaud (1936) equated it with *Lycaon pictus* on account of a slight linguistic affinity of "dictyes" with an old Greek term for wolves, and since another enigmatic animal name used by a clan of Predynastic Egyptians from the Nile delta, oupouat, would refer to painted wolves too. However, other translators (not cited here) did not dare to interpret the identity of Herodotus's "dictyes" or provided the imaginative translation "Netztiere" ("reticulated-animals"). This linguistic debate appears speculative, and one better concurs with Camps (1988) that Herodotus's "dictyes" are uncertain beasts. The historical range of painted wolves in the Sahara remains obscure.

Review of taxonomic interpretations

The substantial augmentation of the known original range of ostriches to include the state territory of Libva reported here raises the question of the taxonomic affiliation of this extinct regional stock. Recent compilatory treatises indicate one widespread subspecies, S. c. camelus, to range all over North Africa (e.g., Brown et al., 1982; Cramp, 1986; Folch, 1992), but the only two original papers dealing with characters of potential taxonomic value in ostriches from the northeastern Sahara, reporting on mtDNA and oology (Walters, 1982; Robinson & Matthee, 1999), implied potential introgression by the Arabian ostrich S. c. syriacus out of the Near East into the African northeast. Moreover, S. c. spatzi Stresemann 1926 was resurrected recently at least at the level of a distinct subspecies for yet insufficiently known parts of the Sahara (Elzanowski & Louchart, 2021). It is fair to conclude that the nomenclature for Saharan ostriches needs additional research. Therefore, the scattered and generally insufficient evidence concerning the classification of ostriches in the eastern Sahara is reviewed in detail here.

The distinction, originally as a full species, of S. c. camelus from North Africa seems to rest exclusively on the characters diagnosed by early authors (Nolte, 1895; Salvadori, 1895; Duerden, 1919; Reichenow, 1900; Duerden, 1919) who had at their disposal single ostriches from the north of the continent, and who typically did not indicate or even know their precise origins. Possibly not a single ostrich from the Sahara proper was regarded when extrapolating such data fragments to the subcontinent. The next required step of scientific advance would be comparisons of many characters in and among regional population samples. This remains undone in North Africa. from where insufficient materials had been collected for science: Even today not many more than a mere handful of Saharan specimens could be traced in natural history museums (A. Schreiber, unpubl.). Instead, an initial taxonomy based on lone birds has passed over directly into the multitude of recent field guides and encyclopaedias (among many others Brown et al., 1982; Cramp, 1986; Folch, 1992). Likely these recent compilations hand down the insights of the early pioneer authors unchanged, and thus concepts from the time before systematics became enriched by population thinking, lineage thinking and other evolutionary ideas. It seems that the ostriches from millions of square kilometres in North Africa have never been scrutinized by one trained systematist. This shortcoming leads to a hypothetical but not necessarily an erroneous classification, if ostrich populations are indeed genetically homogeneous over great distances, and if there was no range vicariance within North Africa during the relevant past. If otherwise, taxa are overlooked if not studied empirically with sufficient samples.

The stated characters of S. c. camelus refer to the outer phenotype (Duerden, 1919; Nolte, 1895; Salvadori, 1895; Reichenow, 1900; Duerden, 1919; Brown et al., 1982; Cramp, 1986; Folch, 1992; Davies, 2002): Males have the head and legs reddish, and in the nuptial dress the unfeathered three quarters of the neck shining brightly red. During the period of egg incubation or in the non-reproductive season the neck acquires a pale pink or brick colour. A collar of white down feathers separates the lower neck from the jet-black body plumage that may be tinged in reddish. The top plate of the head is a dirty brownish, bald patch, albeit less distinctly defined than in some other ostriches. The bill colour is incarnate, with a dirty yellowish tip. Hens and progressed juveniles are duller, with grey-brown plumage and light greyish-brown necks, legs and heads. Single specimens suggested an additional fourth claw, and the scutellation of legs and feet may prove subspecies-specific. Single genes of mtDNA assayed in one or several ostriches from one or two North African sample stations (Freitag & Robinson, 1993; Robinson & Matthee, 1999; Miller et al., 2011) cannot elucidate the genetic population structure within North Africa.

From an ancient, small ostrich egg from the Qattara Depression in Egypt (Tab. 1) (Aharoni, 1927; Schönwetter, 1927, 1960; Forbes-Watson, 1967; Walters, 1982), Walters (1982) inferred a population of diminutive ostriches in the Libyan Desert (also in Goodman & Meininger, 1989). Indeed, Walters's egg falls within the size range of eggs from the small-bodied Arabian ostrich *S. c. syriacus*, but a moderate overlap with the eggs of the nominal subspecies precludes a definite diagnosis. Eggs can be small not only due to genetic causation, but also due to deficient nutrition, pathology, stress of the laying hen, and further factors (Kummer, 1986). Nevertheless, the eggs of *S. c. syriacus* are statistically smaller than those of African ostriches (Tab. 1) (Aharoni, 1927; Schönwetter, 1927, 1960; Forbes-Watson, 1967; Walters, 1982).

In parallel, two Arabian ostriches from the type series in the British Museum and two birds from "Nubia" shared a common haplotype of a short mtDNA sequence, different from the genotype of individuals from elsewhere in Africa, wherefrom Robinson and Matthee (1996) concluded genetic introgression from Arabian into African stocks. Ostriches from Egypt or Libya are apparently not represented in natural history museums (A. Schreiber, pers. obs.), and the Arabian phenotype could, in principle, have extended into this corner of Africa unnoticed. The taxonomic identity and the body size of the single ostriches recorded historically in Sinai (Goodman & Meininger, 1989) are unknown. A cervical excavated near the Dakhla oasis in Egypt, and dated at 7,500 years BP, proved equal-sized with the vertebrae of (large-bodied) East African ostriches (Churcher, 1992). This equality could perhaps argue against a dwarfed population in the Libyan Desert, but the vertebral column of ostrich subspecies has never been compared, and cervicals may or may not vary geographically.

The claim for diminutive ostriches in northern Africa is not confined to the Libvan Desert. Sclater (1860) suspected that ostriches imported from Morocco to the London Zoo were smaller than South African birds (S. c. australis). Desert ostriches from Algeria proved smaller than stock from Senegal (Gosse, 1857). Small ostriches from the west Sahara and their small eggs let Stresemann (1926) describe S. c. spatzi, established on the basis of four immatures and eight eggs sent by Paul Spatz from the then Spanish Sahara to Berlin. When hand-raised by zookeepers at the Berlin Zoo, these juveniles failed to attain the body height of ostriches from Senegal and not even of those from Algeria (Stresemann, 1927). S. c. spatzi has not been reinvestigated for decades, and after a few passing citations (e.g., Schönwetter, 1927; Bouet, 1955; Schönwetter 1960; Heim de Balsac & Mayaud, 1962; Etchécopar & Hué, 1964) the subspecies name was dismissed without investigation. Only recently, Elzanowski and Louchart (2021) measured a skeleton of S. c. spatzi and resurrected this taxon at the level of "at least" a well-defined subspecies. Diagnostic were consistently shorter lengths of several functionally unrelated bones, suggesting a moderately diminutive body size, short wings, and a broad pelvis. The lengths of several bones of the single S. c. spatzi intercalated between those of ostriches from tropical Africa and from Arabia. One or two skeletons from The Gambia emerged as the largest African ostriches. These limited data proposed that the tallest and smaller-bodied ostriches coexisted in adjacent countries of north(west) Africa. The tarsometatarsus of S. c

Tab. 1 – Dimensions of ostrich eggs from various populations or subspecies. / Dimensioni delle uova di struzzo di diverse popolazioni o sottospecie.

Name	Samples	Egg lengths (mm)	Egg breadth (mm)	Average size (mm)	Authors
S.c. camelus	48	142-175	120-145	158.5×131.0	Schönwetter, 1927, 1960
S.c. spatzi	8	127-152	111-126	145.0×122.7	Schönwetter, 1927, 1960
S.c. syriacus	13	135-148.5	111.5-122	142.8×115.8	Schönwetter, 1927, 1960
	2	156-157	127-141	156.5×135	Forbes-Watson, 1967
	1	128	98		Aharoni, 1927
Egg from Quattara Depression, Egypt	1	138.6	119.4		Walters, 1982

spatzi was reduced disproportionately, being pronouncedly shorter but not narrower, and similarly short as in *S. c. syriacus*. The differentiated sizes of ostriches from Rio de Oro and The Gambia fit previous observations (Gosse, 1857; Stresemann, 1927) of taller ostriches in Senegal than further north.

Still, more specimens seem essential to demonstrate the osteology of West Saharan ostriches, not least because the single measured spatzi skeleton represented an individual raised in a zoo with artificial diets: Even many decades later, after developing modern feed, 5-30 % of the ostrich chicks raised currently in commercial farms develop skeletal pathologies due to unbalanced diets or when fed with food too rich in calories (Mushi et al., 1999; Hastings & Farrell, 1991; Nußstein, 2009). Specifically, the founder population of Saharan ostriches bred at Al Wabra Wildlife, Qatar, revealed limb bone disorders in the elevated frequency of one out of two hatched chicks (Wyss et al., 2014). Particularly common is the perosis disease, which often implies, among other deformities, a reduced tarsometatarsus. Exactly this bone was shortened disproportionately in the S. c. spatzi from the Berlin Zoo, and it adjoined enlarged rather than size-reduced phalanges of the third digit. Elzanowski and Louchart (2021) did not consider such disparate volumes of adjoining bones as pathological, but as a phylogenetic adaptation to locomotion on rocky substrates. However, Paul Spatz obtained his ostriches in the coastal sand dunes of Rio de Oro, and the idea of "mountain ostriches" (Elzanowski & Louchart, 2021) seems unsupported from the local geography (Hernández-Pacheco, 1949; Valverde, 1957). Prof. Elzanowski replied to the present author (in litt., 26 November 2021) that he considered pathology unlikely to explain the unusual pedal bones of his zoo-derived skeleton, trusting into the able performance of the animal keepers at Berlin Zoo feeding their ostriches properly. Still, more skeletons should be measured to interpret the osteology.

The originality of S. c. spatzi had already been concluded beforehand from the shape and arrangement of the respiratory pores of its eggshells, when compared to those of S. c. camelus and all tropical subspecies (Schönwetter, 1927, 1960). In this character complex Senegalese ostriches coincided with the series of S. c. spatzi, from Rio de Oro, different from all others in Africa (Schönwetter, 1960). Scanning electron microscopy recognized the egg shells of S. c. spatzi as distinctive too, with pore morphologies transitional between a plesiomorphic northern grouping S. c. camelus/S. c. svriacus and the derived ostrich subspecies in tropical Africa (Mikhailov & Zelenkov, 2020). The inferred evolutionary link between Palaearctic and Afrotropical ostriches would therefore be located somewhere within the (western) Sahara or the Sahel, likely within the range of populations often lumped into S. c. camelus.

In the present context it remains to hint at older literature claiming diminutive ostriches elsewhere in northern Africa; even though some of the following historical claims appear to modern biologists to be probable examples of fanciful cryptozoology: Temminck (1840) opened the debate about small ostriches when, based on an unpublished drawing by François Levaillant, of a "petit gralle bi-dactyle" whom he awarded the generic name Autruchon (= diminutive ostrich), without knowing its geographical origin. This enigmatic bird had two toes like ostriches have, but was only thrush-sized (sic). Macdonald (1945) justifiably questioned if Levaillant's image, most plausibly lacking a scale, had permitted Temminck's perception of such a dramatic body size reduction. However, also Sclater (1860, 1862a) purported a dwarf ostrich from the Anglo-Egyptian Sudan, more precisely from Kordofan according to Sclater and Mackworth-Praed (1920), based on hearsay from local officers and hunters who had caught such a bird alive. Heuglin (1859, p. 344) recorded a "little didactyle ostrich, not higher than *Otis arabs*, but in figure and colour much like S. camelus" from Jabal Dul, south of Fazogloa in Sudan, presumably referring to the historical region Fazogli on the border of Sudan and Ethiopia. The editor of the British journal "The Ibis" added to this phrase in this remark: [Autruchon, Temm.? - Ed.]. Heuglin (1873) had received news of a second species of ostrich from southernmost Senar (between the Hamedi Mountains and northern Sobat), this variety being only as tall as an Arabian bustard Ardeotis arabs (Linnaeus 1758), but having two toes, and several Sudanese informants had recounted information about this "l'autruchon Struthio bidactylus Temm.", regarded by them as an infant ostrich albeit belonging to a different species. The woodlands near the rivers Kir and Gazelle (=Bahr el Gazal?) were inhabited by another flightless bird, with nocturnal habits, rather dull in appearance and elusive (op. cit.). For modern observers these reports of extraordinarily dwarfed ostriches sound inauthentic, as already reasoned by Salvadori (1895) and Reichenow (1900). A connection of such predominantly Sudanese dwarfs to the enigmatic S. c. spatzi appears unplausible for geographical reasons alone, but Walters (1982) speculated about a relation of Temminck's creature with an African outlier population of S. c. syriacus. More recently, Hume and Walters (2012) felt unsure about the species identity of Temminck's bidactyle autruchon, which would differ in nothing except its minute size from North African or Syrian ostriches, but which had been considered a misidentified tinamou by other authors.

CONCLUSIONS

Ostrich taxonomy in North Africa has apparently never been revised thoroughly with informative population and character samples. Claims of up to three subspecies in the Sahara and Sahel are largely untested but cannot be refuted beforehand. Perhaps the recent study by Elzanowski and Louchart (2021) can stimulate deeper research. Saharan ostriches are threatened with extinction and are the subjects of various captive breeding projects in wildlife-keeping institutions. These have to decide which local populations can be merged into a common studbook flock without destroying patterns of evolutionary differentiation.

The present account is not a taxonomic revision, but Fig. 4 juxtaposes the historical ostriches from Kufra and the Wadi Howar to an adult male from Chad [after translocation of its lineage to Souss Massa National Park, Morocco, in the 1990s see Anon. (2015)], birds from Morocco [specimens received by the London Zoological Gardens in

February 1859 from Morocco, see Sclater (1862a)] and a male from a lineage imported from the Danakil Desert on the Red Sea. Morocco has rarely if ever been mentioned as an original range country of ostriches recently. Fig. 4c reminds of three Moroccan ostriches imported to England and donated to the London Zoo in 1859 (Sclater, 18562a, 1862b). A photograph of the ratite enclosures at the London Zoo taken in 1864 (Edwards, 1996) spotlighted a cassowary, but a male ostrich visible in the background could be the same Moroccan cock as in Fig. 4c. The author is unaware of other proof for or even pictorial documents of ostriches from Morocco, whereas ones from Algeria and Tunisia are widely referred to in the literature. Fig. 5 permits comparisons with two Arabian ostriches kept at the London Zoo in 1923, being rare documents of presumably the only representatives of this extinct taxon ever in a European institution (Cheesman, 1923; Anon., 1924; Jennings, 1986). Like in the case of the photographs in Fig. 4, those in Fig. 5 lack an internal scale to deduce the body height, but both birds appear gracile and diminutive. Further photos from probably the same individuals (in the Near East before their export to Europa) were published by Cheesman (1923), and another photo also by Major Cheesman (in Carruthers, 1935) possibly represents still the same individuals. More photographs of this exterminated taxon could not be found. Rothschild (1919) described the Arabian (formerly more often termed: Syrian) subspecies with a plumage resembling the Saharan ostrich, but distinctively smaller by one quarter, the bill shorter and narrower, and shortened tarsi and tails. Unfortunately, these characters are not clearly visible in the historical photos from Kufra or Wadi Howar. Despite the absence of an absolute scale in the photos, the adult human depicted next to the ostriches from Kufra attains about 70% of the birds' body height. Exact data for the body sizes of the various subspecies are scarce, but ostriches from Africa should reach a body height of 200-275 cm (Folch, 1992). No Arabian ostrich has been measured alive, but the dry skins of a cock and a hen from Syria revealed tarsus lengths of 75%, bill lengths of 90% (cock) or 78% (hen), and tail lengths of 61% (cock) or 81% (hen) of the homologous values of an adult female from Nigeria (Rothschild, 1919). An averaged body size reduction to roughly 75% relative to the Nigerian population would refer to the Arabian specimens a tallness of at most 200-210 cm. This size reduction is compatible with the bone measurements by Elzanowski and Louchart (2021) of two Syrian and single Gambian ostriches. Accepting this level of dwarfing, the human person photographed at Kufra would hardly attain 150 cm height if the ostriches besides were as small as S. c. syriacus, which is implausible for a human adult. Therefore, with reservations on account of the limited data, the ostriches from Kufra should be taller than S. c. syriacus. The current concept of S. c. spatzi implies size reduction relative to the nominate subspecies, but too little a difference to be apparent from the old photos.

Ostriches might have roamed in Libya wherever suitable biotopes prevailed. Most of the wider Libyan Desert populated by these ratites too, including some of the most hyperarid lands worldwide. The regionally inhospitable, continental climate with extreme heat and frost and extraordinarily little rain brings out the species's astonishing eco-



Fig. 5 – Two of the very few preserved photographs of the extinct Arabian or Syrian ostrich (S. c. syriacus). Specimens photographed by F. W. Bond at the London Zoo in 1923, representing probably the two birds imported in June 1923 from Jauf (today: Al-Jawf Province), northern Saudi-Arabia (Cheesman, 1923; Anon., 1924). If this dwarfed subspecies, hunted to extinction in the first half of the 20th century, had historically ranged into northeast Africa is unknown, although possibly some introgression into that continent is consistent with initial evidence (see text). Copyright: Courtesy of the Zoological Society of London. / Due delle pochissime fotografie conservate dell'estinto struzzo arabo o siriano (S. c. syriacus). Esemplari fotografati da F. W. Bond allo zoo di Londra nel 1923, che rappresentano probabilmente i due uccelli importati nel giugno 1923 da Jauf (oggi provincia di Al-Jawf), nel nord dell'Arabia Saudita (Cheesman, 1923; Anon., 1924). Non si sa se questa sottospecie nana, cacciata fino all'estinzione nella prima metà del XX secolo, si sia storicamente diffusa nell'Africa nord-orientale, anche se una possibile introgressione in quel continente è coerente con le prove iniziali (vedi testo). Copyright: Per gentile concessione della Zoological Society of London.

logical adaptability. By implication ostriches should be able to cope with every other desert in Africa as well from the viewpoint of abiotic ambience, since hardly anywhere the continent offers equally challenging conditions. In terms of aridity of the habitat the ostriches in the Libyan Desert emerge as ecological counterparts those in unvegetated districts of the Namib Desert (A. Schreiber, pers. obs. in the dry Kuiseb river basin, Namibia), where however equally scanty food resources combine with less extreme temperatures and predictably regular fog precipitation. Nevertheless, one cannot depart automatically from an originally continuous ostrich range throughout the Sahara. Rather, the historical distribution should be investigated with greater care, since a deeper study (Jennings, 1986) has refuted the equivalent time-honoured opinion of a formerly pan-Arabic distribution of S. c. syriacus, showing instead two widely isolated population patches, disjunct in north and south Arabia, and separated by a vast range gap. The southern isolate has probably never been seen by a taxonomist, just like most historical ostrich populations in North Africa. The suggestive but speculative impression of unbroken population cohesivity because of "boundless" desert needs not apply from the perspective of ostriches.

Several clues proposed to split north African ostriches into two (S. c. spatzi and S. c. camelus) or three (if S. c. syriacus extended into northeast Africa) taxa. However, prior to such splitting, a revision is clearly required, not least when it comes to serious projects for biodiversity conservation. At present, there are four lineages of ostriches imported from separate origins for captive conservation management, i.e. from Chad (studbook coordinated by several European zoos; Frerking, 2024), apparently Sudan (zoos in the Near East, Islam et al., 2008), from Niger (ex situ- project within Niger by Sahara Conservation Fund; K. de Smet, pers. comm.), and from the outlying Danakil Desert on the Red Sea (Dittrich, 1978; N. Werner, pers. comm.). Simple biometry of these captive birds could already improve taxonomic concepts, as would a revision of the very limited museum specimens. Clearly, a certain minor scatter of body size does not automatically justify splitting, depending of correlated characters that need to be identified. Even if accompanied by molecular markers the sometimes defect and poorly preserved museum remains might prove unsatisfactory for proper population taxonomy, and they are by any means entirely lacking from very wide portions of the Sahara. In this situation, an inspection of the eggshell pores would be a welcome complementary approach. Various investigators (Sclater, 1860; von Nathusius, 1885; Schenkling-Prévôt, 1895; Nolte, 1895; Oates et al., 1901; Duerden, 1919; Rothschild, 1919; Schönwetter, 1927, 1960; Sauer, 1972) emphasized the evolutionarily flexibility of egg shell pores as characters to differentiate ostrich subspecies, as well as "ootaxa" of fossil ostrich species (Mikhailov & Zelenkov, 2020). Eggshells could be studied also in the numerous prehistoric shell fragments scattered over many Saharan grounds. Such fields of fossils can promise more pleasing population samples to infer individual variation in any population than promise the single museum skins.

All northern desert ostriches from the Sahara and from Arabia have fewer and smaller shell pores ("eggs smooth, not pitted", Rothschild, 1919, p. 83; also Oates *et al.*, 1901;

Schönwetter, 1927, 1960; Mikhailov & Zelenkov, 2020) than are observed in other African populations, to the extent of being hardly visible without magnification. These downsized pores in desert habitats compare with the intermediate pores in the Atlantic fringe of west Sahara (Schönwetter, 1960), and the larger shell orifices in all tropical subspecies, a correlation which could well indicate different rates of evaporation to protect the embryo from dehydration or hyperthermia in various climate zones. Indeed, artificial incubation in a zoo revealed the relevance of an optimized air humidity and ambient temperature for successful hatching (Sanchez & Gil, 2024, see also experiences from ostrich farming Kistner, 2017). Therefore, the geographical differentiation of eggshell morphology may plausibly prove adaptive, albeit this correlation remains unstudied. Koyama and Tennyson (2016) recognized pore morphologies as responsive to environmental stress, but more specific studies are unavailable. The experimental demonstration of adaptiveness of shell pore patterns would emphasize the importance of regional ecotypes the conservation of regional lineages. Mikhailov and Zelenkov (2020) referred fossil egg shells from Libya to the "non-specialized" type known from S. c. camelus and S. c. syriacus.

Acknowledgments

The previously unpublished historical photos of ostriches from the Libyan Desert are reproduced under the licenses of the Frobenius-Institut für kulturanthropologische Forschung, Goethe-Universität Frankfurt am Main, Germany (Fig. 1a and b, and Fig. 4e), and the Royal Geographical Society in London, United Kingdom (Fig. 1 c and d, and Fig. 4b and d). The librarians of the Zoological Society of London, United Kingdom, painstakingly searched and permitted the reproduction of photographs from the London Zoo of the presumably only two Arabian ostriches ever kept in a European institution. Dipl.-Biol. Klaus Rudloff (formerly curator at Tierpark Berlin) provided photos for Figs 4 a and f. Mr. José Miguel Redondo (www.elrincondesele.com) permitted the inclusion as Fig. 3 of his photo of fossil ostrich egg shells from the Wadi Sura (Egypt). Prof. Dr. Zolt Török (Eötvös Loránd University Budapest, Hungary) and Mr. András Zboray (specialist operator for Sahara expeditions at the agency Fliegel Jezerniczky Expeditions Ltd., Newbury, United Kingdom) contributed insights into the biography of the explorer László Almásy. Kate Bogyim translated from books in the Hungarian language.

REFERENCES

- Aharoni J., 1927 Syrische Straußeier. Beiträge zur Fortpflanzungsbiologie der Vögel, 3: 186-188.
- Al Hussaini A.H., 1959 The avifauna of Al-Wadi Al-Gadid in the Libyan Desert. Bulletin Zoological. Society Egypt, 14: 1-14.
- Almásy L., 1937 Levegőben, homokon. Franklin-Társulat, Budapest (Hungary).
- Almasy L.E., 1943 Die Strasse der vierzig Tage. F. A. Brockhaus, Leipzig (Germany).
- Anon., 1870 Die Verbreitung des Strausses in Asien. Mittheilungen aus Justus Perthes' Geographischer Anstalt, 16: 380-382.
- Anon., 1924 Reports of the council and auditors of the Zoological Society of London, for the year 1923. Waterlow & Sons, London (UK).
- Anon., 2015 Erster Nachwuchs beim Nordafrikanischen Rothalsstrauß im Erlebnis-Zoo Hannover. Der Zoofreund, 178: 3-4.
- Ascherson P., 1874 Fragliches Vorkommen des Strausses in der Li-

byschen Wüste. Sitzungsberichte Gesellschaft naturforschende Freunde Berlin, 1874: 60-61.

Ascherson P., 1875 – Vorkommen des Strausses in der Libyschen Wüste. Sitzungsberichte Gesellschaft naturforschende Freunde Berlin, 1875: 70-71.

- Ascherson P., 1881 Die aus dem mittleren Nordafrika, dem Gebiete der Rohlf*schen Expedition nach Kufra bekannt gewordenen Pflanzen. In: Reise von Tripolis nach der Oase Kufra, ausgeführt in Auftrage der Afrikanischen Gesellschaft in Deutschland. Rohlfs G. (ed.). F. A. Brockhaus, Leipzig: 386-559.
- Bagnold R.A., 1931 Journeys in the Libyan Desert 1929 and 1930. *The Geographical Journal*, 78: 13-33.
- Bagnold R.A. & Harding King W.J., 1931 Journeys in the Libyan Desert 1929 and 1930. *The Geographical Journal*, 78: 523-535.
- Bagnold R.A., Myers O.H., Peel R.F. & Winkler H.A., 1939 An expedition to the Gilf Kebir and 'Uweinat, 1938. *The Geographical Journal*, 93: 281-312.
- Bagnold R.A., 1933 A further journey through the Libyan Desert. *The Geographical Journal*, 82: 103-126.
- Bagnold R.A., Sandford K.S., Shaw W.B.K., Moreau R.E., Riley N.D., Hutchinson T. & Craig V.F., 1933 – A further journey through the Libyan Desert (Continued). *The Geographical Journal*, 82: 211-235.
- Barth H., 1857 Reisen und Entdeckungen in Nord- und Central-Afrika in den Jahren 1849 bis 1885. Erster Band. J. Perthes, Gotha (Germany).
- Bates O., 1914 Eastern Libyans. An essay. Macmillan, London (UK).
- Belon le Mans P., 1555 Le cinquiesme livre sur la natvre des oyseavx. *Gilles Corrozet*, Paris (France).
- Bierman J., 2004 The secret life of Laszlo Almasy. *Penguin*, London (UK).
- BirdLife International. 2018 *Struthio camelus*. The IUCN Red List of Threatened Species 2018: e.T45020636A132189458. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T45020636A132189458. en>
- Blümel W.D., 2013 Wüsten. Entstehung, Kennzeichen, Lebensraum. *Ulmer UTB*, Stuttgart (Germany).
- Bono S., 1981 Il Commercio transahariano della Tripolitania dal 1900 al 1911. Africa: Rivista trimestrale di studi e documentazione dell'Istituto italiano per l'Africa e l'Oriente, 36: 1-31.
- Bonzom E., 1898 L'Algérie, contrée de production autruchière. *Bulletin Société de Géographie Alger*, 2: 57-63.
- Bouet G., 1955 Oiseaux de l'Afrique tropicale (première partie). *Librairie Larose*, Paris (France).
- Brenner W., 1995 Ein Wüstenforscher aus dem Burgenland. Zum 100. Geburtstag von Ladislaus Eduard von Almásy. Burgenländische Heimatblätter, 57, 1: 1-31.
- Brown L.H, Urban E.K. & Newman K., 1982 The birds of Africa. Volume 1. Academic Press, London (UK).
- Browne W.G., 1799 Travels in Africa, Egypt, and Syria: from the year 1792 to 1798. *T. Cadell Junior and W. Strand*, London (UK).
- Bundy G., 1976 The birds of Libya. British Ornithologists 'Union, London (UK).
- Burckhardt J.L., 1822 Travels in Syria and the Holy Land. *Murray*, London (UK).
- Camps G., 1988 La faune de l'Afrique du Nord et du Sahara d'après Hérodote. *Espacio, Tiempo y Forma*, 2: 209-221.
- Carruthers D. 1935 Arabian adventure. To the Great Nafud in quest of the oryx. *H.F. & G. Witherby*, London (UK).
- Caton-Thompson G. & Gardner E.W., 1934 The desert Fayum. *The Royal Anthropological Institute of Great Britain and Northern Ireland*, London (UK).
- Cheesman R.E., 1923 The Arabian ostrich. The Ibis, 1923: 359.
- Cherbonneau A., 1857 Relation du voyage de M. le Capitain De Bonnemain à R'dames (1856-1857). In: Nouvelles annales des voyages de la géographie, de l'histoire et de l'archéologie. Malte Brun V.A. (ed.). A. Bertrand, Paris (France).
- Chudeau R., 1909 Sahara Soudanais. In: Mission au Sahara, Tome II. Gautier E.F. & Chudeau R. (eds). *Librairie Armand Colin*, Paris (France).
- Churcher C.S., 1992 Ostrich bones from the neolithic of Dakleh oasis, western desert of Egypt. *Palaeoecology of Africa and Surrounding Islands*, 23: 67-71.

- Conwell D., 1987 On ostrich eggs and Libyans. Penn Museum Expedition Magazine, 29: 25-34.
- Cooper R.G., Mahrose K.M.A., El-Shafei M.I.F.M. & Marai I.F.M., 2008 – Ostrich (*Struthio camelus*) production in Egypt. *Tropical Animal Health and Production*, 40: 349-355.
- Coró F., 1940 La fauna grossa esistente in Libia. Alla caccia di antilopi e gazzelle, di Iepri e ottarde. *"Libia", Rivista mensile illustrata*, 4, 2: 9-14.
- Coró F., 1961 Oggi non è più che il ricardo di un grande passato: il commercio carovaniero fra la Libia e i paesi dell'Africa centrale. *Africa: Rivista trimestrale di studi e documentazione dell'Istituto italiano per l'Africa e l'Oriente*, 16: 87-90.
- Cramp, S. (ed.), 1986 Handbook of the birds of Europe, the Middle East and North Africa: the birds of the western Palearctic. 1, ostrich to ducks. *Oxford University Press*, Oxford (UK).
- Crawford W. S., 1901 Synesius: the Hellene. Rivingtons, London (UK).
- Davies S., 2002 Ratites and tinamous: Tinamidae, Rheidae, Dromaiidae, Casuariidae, Apterygidae, Struthionidae. Oxford University Press, Oxford (UK).
- Decorse J., 1904-1905 Elevage de l'autruche en Tunisie. *Bulletin de la Société nationale d'Acclimatation de France*, 51-52: 337-350.
- della Cella P., 1821 Reise von Tripolis an die Gränzen von Aegypten im Jahre 1817. *Landes-Industrie-Comptoir*, Weimar (Germany).
- Desio A., 1941 Die italienische Sahara. Zeitschrift Gesellschaft Erdkunde Berlin, 9/10: 369-378.
- Dittrich S., 1978 In Noahs Garten. Der Zoofreund, 30: 16-119.
- Duerden J.E., 1919 Crossing the North African and the South African ostrich. *Journal of Genetics*, 8: 155-198.
- Durant S.M., Wacher T, Bashir S., Woodroffe R., De Ornellas P., Ransom C., Newby J., Aaigar T., Abdelgadir M., El Alqamy H., Baillie J.E.M, Beddiaf M., Belbachir F., Amel B., Berbash A., Bemadjim N.E., Beudels-Jamar R.C., Boitani L., Breitenmoser C., Cano M., Chardonnet P., Ben Collen B., Cornforth W.A., Cuzin F., Gerngross P., Haddane B., Hadjeloum M., Jacobson A.P., Abdelkader J., Lamarque F., Mallon D.P., Minkowski K., Monfort S., Ndoassal B., Niagate B., Purchase G., Samaila S., Samna A.K., Sillero C., Soultan A., Stanley R.M. & Pettorelli N., 2014 Fiddling in biodiversity hotspots while deserts burn? Collapse of the Sahara's megafauna. *Diversity and Distribution*, 20: 114-142.
- Edwards J., 1996 London Zoo from old photographs 1852-1914. Edward Charles, London (UK).
- El Hachaichi M.I.O., 1903 Voyage au pays des Senoussia à travers la Tripolitaine et les pays Touareg. *Challamel*, Paris (France).
- El Sayed Kita S., 2014 Ostrich egg and its symbolic meaning in the ancient Egyptian monastery churches. Mağallar Al-Itihād Al-'ām Lil Atārīyin Al-'arab (JGUAA), 15: 23-41.
- Elzanowski A. & Louchart A., 2021 Metric variation in the postcranial skeleton of ostriches, *Struthio* (Aves: Palaeognathae), with new data on extinct subspecies. *Zoological Journal of the Linnean Society*, 20: 1-18.
- Etchécopar R.D. & Hué F., 1964 Les oiseaux du nord de l'Afrique. Éditions N. Bobée & Cie, Paris (France).
- Ezz el-Din D.M., 2010 Ostrich eggs in predynastic Egypt. Journal of General Union of Arab Archaeologists, 11, 1: 40-56.
- Finsch O. & Hartlaub G., 1870 Die Vögel Ost-Afrikas. Baron Carl Claus von der Decken's Reisen in Ost-Africa in den Jahren 1859-1865. Band 4. C. F. Winter 'sche Verlagshandlung, Leipzig and Heidelberg (Germany).
- Flower S. S., 1909a Zoological Gardens Giza, near Cairo. Report for the year 1908 (tenth annual report). *Government of Egypt Printing Department*, Cairo (Egypt).
- Flower S. S., 1909b Zoological Gardens Giza, near Cairo. List of animals. Special report 4. Government of Egypt Printing Department, Cairo (Egypt).
- Folch A., 1992 Family Struthionidae. In: Handbook of the birds of the world. Volume 1: ostrich to ducks. Del Hoyo (ed.). *Lynx Ediciones*, Barcelona: 76-83.
- Forbes R., 1921 The secret of the desert: Kufara. *Goerge H. Doran*, New York (USA).
- Forbes-Watson A.D., 1967 Eggs of the Arabian ostrich. East African Wildlife Journal, 5: 167.

- Fowler H.W. & Fowler F.G., 1905 The works of Lucian of Samosata, complete with exceptions specified in the preface. *Clarendon Press*, Oxford (UK).
- Freitag S. & Robinson T.J. 1993 Phylogeographic patterns in mitochondrial-DNA of the ostrich (*Struthio-camelus*). Auk, 110: 614-622.
- Frerking M., 2024 Nordafrikanische Strauße Artenschutz in Marokko. Der Zoofreund, 211: 10-11.
- Frobenius L., 1934 Die Ergebnisse der 11. Deutschen (inner-afrikanischen) Forschungsexpedition in die Libysche Wüste und den Angloägyptischen Sudan 1933. *Mitteilungen Forschungsinstitut für Kulturmorphologie*, Frankfurt, (Germany).
- Gautier A., 1980 Contributions to the archaeozoology of Egypt. In: Prehistory of the Eastern Sahara. Wendorf F. & Schild R. (eds). Academic Press, New York: 317-344.
- Gautier A., 1984 Quaternary mammals and archaeozoology of Egypt and the Sudan: a survey. Origin and early development of food-producing cultures in North Eastern Africa. In: Origin and early development of food-producing cultures in North Eastern Africa. Krzyzaniak L., Kobusiewicz M. (eds.). *Polish Academy of Sciences*, Poznan: 43 - 56.
- Gautier A., 1993 The Middle Paleolithic archaeofaunas from Bir Tarfawi (Western Desert, Egypt). In: Egypt during the last interglacial.. Wendorf F., Schild R. & Close A.E. (eds.). *Plenum Press*, New-York: 121-143.
- Geoffroy Saint-Hilaire E., 1799 Observation sur l'aile de l'autruche. Décade Egyptienne, 1: 46-51.
- Ghigi A., 1913 Materiali per lo studio della fauna libica. Memorie della Reale Accademia delle Scienze dell'Istituto di Bologna, Classe di Scienze Fisiche, 6 (10): 253-296.
- Ghigi A., 1932 Spedizione scientifica all'oasis di Cufra (Marzo-Luglio 1931). Uccelli. Annali del Museo civico di storia naturale Giacomo Doria, 55: 268-292.
- Goodman S.M., Houliban P.F. & Helmy I., 1984 Recent records of the ostrich Struthio camelus in Egypt. Bulletin British Ornithologists' Club, 104: 39-44.
- Goodman S.M. & Meininger P.L., 1989 The birds of Egypt. Oxford University Press, Oxford (UK).
- Goodman S.M., Meininger P.L. & Mullik W.C., 1986 The birds of the Egyptian western desert. *Miscellaneous Publications, Museum of Zo*ology, University of Michigan, Ann Arbor (USA).
- Gosse L.A. 1857 Des avantages que présenterait en Algérie la domestication de l'autruche d'Afrique Struthio camelus (Linné). L. Martinet, Paris (France).
- Graziani R., 1937 Pace romana in Libia. Mondadori, Milano (Italia).
- Hamilton J., 1856 Wanderings in North Africa. Murray, London (UK).
- Harding King W. J., 1925 Mysteries of the Libyan Desert. *Seely, Service* & *Co.*, London (UK).
- Hartert E., 1913 Expedition to the central Western Sahara. IV. Birds. Novitates Zoologicae, 20: 37-76.
- Hartert E., 1923 On the birds of Cyrenaica. *Novitates Zoologicae*, 30: 1-32.
- Hartmann R., 1863 Reise des Freiherrn Adalbert von Barnim durch Nord-Ost-Afrika in den Jahren 1859 und 1860. G. *Reimer*, Berlin (Germany).
- Hartmann R., 1868 Geographische Verbreitung der im nordöstlichen Afrika wild lebenden Säugethiere. Zeitschrift Gesellschaft Erdkunde, 3: 28-69.
- Hassanein Bey A.M., 1924 Through Kufra to Darfur. *The Geographical Journal*, 64: 273-291.
- Hassanein Bey A.M., 1925 The lost oases. *Thornton Butterworth*, London (UK).
- Hastings M.Y. & Farrell D.J. 1991 A history of ostrich farming—its potential in Australian agriculture. In: Recent advances in animal nutrition in Australia. University of North England, *Armidale*: 292-297.
- Heim de Balsac H. & Mayaeud N, 1962 Les oiseaux du nord-ouest de l'Afrique. *Paul Lechevalier*, Paris (France).
- Hernández-Pacheco & Estevan E., 1949 El Sahara español: estudio geologico, geografico y botanico. Instituto de Estudios Africanos (Consejo Superior de Investigaciones Científicas), Madrid (Spain).
- Heuglin T., 1859 List of birds observed and collected during a voyage in the Red Sea. *The Ibis*, 1: 337-352.

- Heuglin T., 1873 Ornithologie Nordost-Afrika's, der Nilquellen- und Küsten-Gebiete des Roten Meeres und des nördlichen Somal-Landes. Zweiter Band. Erste Abtheilung. *Theodor Fischer*, Cassel (Germany).
- Hodos T., 2020 Eggstraordinary artefacts: decorated ostrich eggs in the ancient Mediterranean world. *Humanities & Social Sciences Communications*, 7: 45.
- Hodos T., Cartwright C.C., Montgomery J., Nowell G., Crowder K., Fletcher A.C. & Gönster Y., 2020 – The origins of decorated ostrich eggs in the ancient Mediterranean and Middle East. *Antiquity*, 94: 381-400.
- Hume J.P. & Walters M., 2012 Extinct birds. *T. & A.D. Poyser*, London (UK).
- Insabato E., 1914 –La vita italiana all'estero. Importanza e utilità dell'allevamento degli struzzi nelle colonie italiane e specialmente in Tripolitania. *Rivista Internazionale di Scienze Sociali e Discipline Ausiliarie*, 64: 506-508.
- Islam M.Z., Ismail K. & Boug A. 2008 Re-introduction of the rednecked ostrich, *Struthio camelus camelus*, in Mahazat as-Sayd Protected Area in central Saudi Arabia. *Zoology in the Middle East*, 44: 31-40.
- Jany E., 1963 Salma Kabir Kufra Djabal al-Uwenat Ein Reisebericht aus der östlichen Sahara. *Die Erde*, 94: 334-362.
- Jany E., 1969 Pflanzen aus der libyschen Sahara. *Willdenowia*, 5: 295-341.
- Jennings M. C., 1986 The distribution of the extinct Arabian ostrich Struthio camelus syriacus Rothschild, 1919. Fauna of Saudi Arabia, 8: 447-461.
- Joleaud L., 1936 Les mammifères de la Libye et du Sahara central au temps de l'antiquité classique. Révue Africaine, 79 (368-369): 285-312.
- Kammerer P., 1904a Zoologische Schaustellungen in Ägypten und im Sudan. I. Der Zoologische Garten in Gizeh (bei Kairo). Der Zoologische Garten, 45: 233-241.
- Kammerer P., 1904b Zoologische Schaustellungen in Ägypten und im Sudan (Schluss). Der Zoologische Garten, 45: 265-276.
- Keller O., 1913 Die antike Tierwelt. Wilhelm Engelmann, Leipzig (Germany).
- Kinzelbach R., 2003 The natural history of the ostrich (*Struthio camelus* Linnaeus, 1758) in North Africa, with special reference to Tunisia. *Kaupia*, 12: 57-70.
- Kistner C., 2017 Strauße: Zucht, Haltung und Vermarktung. Ulmer, Stuttgart (Germany).
- Koyama T. & Tennyson A.J.D., 2016 Respiratory pores on ostrich Struthio camelus (Aves: Struthionidae) eggshells. Advances in Experimental Medicine and Biology, 923:51-55.
- Kröpelin S., 2007 The Wadi Howar. In: Atlas of cultural and environmental change in arid Africa. Bubenzer O. Bolten A. & Darius F. (eds). *Heinrich-Barth-Institut*, Köln: 38-39.
- Kummer J., 1986 Uber Spar- und Zwergeier. Beiträge Vogelkunde, 32:17-26.
- Kuper R., 2013 Wadi Sura, the cave of beast: a rock art site in the Gilf Kebir (SW-Egypt). *Heinrich Barth-Institut*, Köln (Germany).
- Langlès L., 1803 Mémoire sur les oasis, composé principalement d'après les auteurs arabes. Voyage de F. Hornemann dans l'Afrique septentrionale. *Imprimérie Dentu*, Paris (France).
- Laufer B., 1926 Ostrich egg-shell cups of Mesopotamia and the ostrich in ancient and modern times. *Field Museum of Natural History Anthropology Leaflet*, 23: 1-51.
- Le Quellec J.L., 1998 Art rupestre et préhistoire du Sahara. Le Messak lybien. *Payot & Rivages*, Paris (France).
- Le Quellec J.L., 2006 Ghirza, la vallée aux mausolées. *Le Saharien*, 179: 49-59.
- Lutz R. & Lutz G., 1995 Das Geheimnis der Wüste. Die Felskunst des Messak Sattafet und Messak Mellet – Libyen. Golf-Verlag, Innsbruck (Austria).
- Lyon G. F., 1821 A narrative of travels in Northern Africa, in the years 1818, 19, and 20: accompanied by geographical notices of Soudan. *John Murray*, London.
- Macdonald J.D., 1945 Problematical Sudan birds. Sudan Notes and Records, 26: 301-304.
- Mackworth-Praed C.W. & Grant H.B., 1952 Birds of Eastern and north eastern Africa. Volume 1. *Longmans, Green and Co.*, London (UK).

- Madden J.F., 1935 Notes on the birds in southern Darfur. Sudan Notes and Records, 18: 83-101.
- Magaud d'Aubusson L., 1889 L'industrie de l'autruche. Revue Sciences Naturelles Appliquées, 36: 726-734.
- Malbrant R., 1954 Contribution à l'étude des oiseaux du Borkou-Ennedi-Tibesti. L'Oiseau et la Revue Française d'Ornithologie, 24: 1-47.
- Maloney S.K., 2008 Thermoregulation in ratites: a review. Australian Journal of Experimental Agriculture 48, 10: 1293-1301.
- Manlius N., 2001 The ostrich in Egypt: past and present. Journal of Biogeography, 28: 945-953.
- Marq de Villers, Hirtle S., 2003 Sahara: The life of the great desert. *Walke*, New York (USA).
- Masseti M., 2013 Libyan birds. The remains of the Italian ornithological collection in the Al Hamra Museums of Tripoli, Libya. *Rivista italiana di Ornitologia*, 81: 111-121.
- McNutt J. W., Woodroffe R. 2013 Lycaon pictus African wild dog (painted dog, Hunting dog) In: Mammals of Africa. Volume V: carnivores, pangolins, equids and rhinoceroses. Kingdon J. & Hoffmann M. (eds). Bloomsbury Publishing, London: 51-59.
- Menardi Noguera A., Carmignoto P., Laberio Minozzi S., Romanzi F., Schirato G., Soffiantin, M. & Tormena T., 2005 – New rock art sites in the southwestern sector of Jebel Uweinat (Libya). Sahara, 16: 107-120.
- Menu von Minutoli H., 1824 Reise zum Tempel des Jupiter Ammon, in der Libyschen Wüste, und nach Ober-Aegypten in den Jahren 1820 und 1821. *A. Ruecker*, Berlin (Germany).
- Mercier A., 1898 Une visite à la ferme d'autruches de Matarieh, près du Caire (Egypte). *La Terre et la Vie*, 45: 250-253.
- Mikhailov K.E. & Zelenkov N., 2020 The late Cenozoic history of the ostriches (Aves: Struthionidae), as revealed by fossil eggshell and bone remain. *Earth-Science Reviews*, 208: 103270.
- Miller J.M., Hallager S., Monfort S.L., Newby J., Bishop K., Tidmus S.A., Black P., Houston B., Matthee C.A. & Fleischer R. C. 2011 – Phylogeographic analysis of nuclear and mtDNA supports subspecies designations in the ostrich (*Struthio camelus*). *Conservation Genetics*, 12:423-431.
- Moltoni E., 1928 Risultati zoologici della Missione inviata dalla R. Societa Geographica Italiana per l'esplorazione dell'oasi di Giarabub (1926-1927). Annali del Museo civico di Storia naturale Giacomo Doria, 52: 387-401.
- Moltoni E., 1931 Uccelli raccolti della "Missione Desio" in Sirtica nel 1930. *Rivista Italiana di Ornitologia*, 1: 129-134.
- Moltoni E., 1932 Elenco degli uccelli riportati della "Missione Desio nel Deserto Libico". Atti Reale Accademia Nazionale dei Lincei, 319, Serie Sesta: 398-402.
- Moltoni E., 1934 Uccelli riportati del Prof. Giuseppe Scortecci dal Fezzan. Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale, Milano, 73, 4: 343-382.
- Monterin U., 1935a L'esplorazione del Tibesti settentrionale e delle zone confinarie del sud libico. *Bollettino del Società Italiana per il Progresso della Scienza*, 1935: 113-130.
- Monterin U., 1935b Relazione delle ricerche compiute dalla Missione della Reale Società Geografica Italiana nel Sahara Libico e nel Tibesti. *Bollettino della Società Geografica italiana*, 12: 115-162.
- Moreau K.E., 1934 A contribution to the ornithology of the Libyan Desert. *The Ibis*, 3: 595-632.
- Mushi E.Z., Binta M.G., Chabo R.G., Isa J.F. & Phuti M.S., 1999 Limb deformities of farmed ostrich (*Struthio camelus*) chicks in Botswana. *Tropical Animal Health and Production*, 31: 397-404.
- Nachtigal G., 1871 Von Tripolis nach Alexandrien. Beschreibung der im Auftrage Sr. Majestät des Königs von Preussen in den Jahren 1868 und 1869 ausgeführten Reise. ">https://www.loc.gov/resource/gdcmassbookdig.vontripolisnacha00rohl/?sp=4&st=gallery>
- Nachtigal G., 1879 Saharâ und Sûdân. Ergebnisse sechsjähriger Reisen in Afrika. Erster Theil. Weidmannsche Buchhandlung und Wiegandt, Hempel und Parey, Berlin (Germany).
- Newbold D., 1924 Two journeys to Kufra oasis. Sudan Notes and Records, 7: 103-107.
- Nicoll M. J., 1919 Handlist of the birds of Egypt. *Government Press*, Cairo (Egypt).

- Niethammer G. 1955 ---Zur Vogelwelt des Ennedi-Gebirges (französisch Äquatorial-Afrika). Bonner Zoologische Beiträge, 6: 29-80.
- Niethammer G., 1971 Die Fauna der Sahara. In: Die Sahara und ihre Randgebiete. Band I. Physiogeographie. Schiffers H. (ed.). Weltforum Verlag, München: 499-587.
- Nikolaus G. 1987 Distribution atlas of Sudan's birds, with notes on habitat and status. Zoologische Monographien. Zoologisches Forschungsinstitut und Museum, Bonn (Germany).
- Nolte C.W.J., 1895 Strauße und Straußenzucht in Südafrika. Journal für Ornithologie, 43: 44-79.
- Nussbaum S., Kröpelin S. & Darius F., 2007 The flora and vegetation of Wadi Howar. In: Atlas of cultural and environmental change in arid Africa. Bubenzer O. Bolten A. & Darius F. (eds). Heinrich-Barth-Institut, Köln: 40-41.
- Nußstein C.E., 2009 Untersuchung der Haltungsbedingungen von Nandus (*Rhea americana*), Emus (*Dromaius novaehollandiae*) und Straußen (*Struthio camelus*) in Süddeutschland. PhD Thesis, Ludwig-Maximilians-Universität München (Germany).
- Oates E., Ogilvie-Grant W.R. & Reid P.S.G., 1901 Catalogue of the collection of birds' eggs in the British Museum. Volume 1. British Museum (Natural History), London (UK).
- Oehm S., 2015 Nationalparks im Sudan. Sozioökonomische Entwicklung und Naturschutz im Schutzgebietsmanagement. Dinder und Wadi Howar Nationalpark. Südwestdeutscher Verlag für Hochschulschriften, London, (UK).
- Pacho M.J.R., 1827 Relation d'un voyage dans la Marmarique, la Cyrénaïque, et les oasis d'Audjelah et Maradèh. *Firmin and Didot*, Paris (France).
- Pauly A., 1827 Lucian's Werke. Erstes Bändchen. J. B. Metzler, Stuttgart (Germany).
- Peel R.F. & Bagnold R.A., 1939 An expedition to the Gilf Kebir and 'Uweinat, 1938. Archaeology. *Geographical Journal*, 93: 291-295.
- Penderel H.W.G.J., 1934 The Gilf Kebir. *The Geographical Journal*, 83: 449-456.
- Petavio D., 1859 Synesius: Synesii Ptolemaidis in Libyca Pentapoli episcopi opera quae extant omnia. Tomus unicus. J. P.Migne Editorum, Paris (France).
- Platnauer M., 1922 Claudian. Volume I. W. *Heinemann*, London (UK).
- Pococke R., 1743 A description of the East, and some other countries. Volume the first: Observations on Egypt. *W. Bowyer*, London (UK).
- Raveret-Wattel C., 1913 Une visite au parc à autruches de Matariyeh (Egypte). Bulletin de la Société nationale d'acclimatation de France, 60: 584-587.
- Reichenow A., 1900 Die Vögel Afrikas. Erster Band. J. Neumann, Neudamm.
- Rhotert H., 1935 Libysche Felsbilder: Ergebnisse der 11. und 12. Deutschen Inner-Afrikanischen Forschungs-Expedition (DIAFE) 1933/1934/1935. Wittich, Darmstadt (Germany).
- Rhotert H., 1952 Libysche Felsbilder. L. C. Wittich, Darmstadt (Germany).
- Richardson J., 1848 Travels in the great desert of Sahara, in the years of 1845 and 1846. Volume 1. *Richard Bentley*, London (UK).
- Richardson J., 1853 Narrative of a mission to Central Africa: performed in the years 1850-51 under the orders and at the expense of Her Majesty's government. Volume 1. *Chapman and Hall*, London (UK).
- Robinson T.J. & Matthee C.A., 1999 Molecular genetic relationships of the extinct ostrich, *Struthio camelus syriacus*: consequences for ostrich introductions into Saudi Arabia. *Animal Conservation*, 2: 165-171.
- Rohlfs G., 1875 Drei Monate in der Libyschen Wüste. *Theodor Fischer*, Cassel (Germany).
- Rohlfs G., 1880 Reise nach Kufra und Beschreibung der Oase. Mittheilungen der afrikanischen Gesellschaft in Deutschland, 2: 17-39.
- Rohlfs G., 1881 Kufra: Reise von Tripolis nach der Oase Kufra, ausgeführt in Auftrage der Afrikanischen Gesellschaft in Deutschland. F. A. Brockhaus, Leipzig (Germany).
- Rothschild L.W., 1919 Description of a new subspecies of ostrich from Syria. *Bulletin British Ornithologists' Club*, 39: 81-83.
- Salvadori T, 1895 Catalogue of the Chenomorphae, Crypturi and Ratitae in the collection of the British Museum. *Longmans & Co.*, London (UK).
- Salvadori T. & Festa E., 1921 Missione zoologica del Dr. E. Festa in

Cirenaica. Bollettino dei Musei di Zoologia ed Anatomia comparata della R. Università di Torino, 24: 1-28.

- Sanchez I. & Gil J., 2024 Les avestruzes del Zoo de Jerez y la labor pionera de Valverde. *Quercus*, 457: 28-32.
- Sauer E.G.F., 1972 Ratife egg shells and phylogenetic questions. Bonner Zoologische Beiträge, 23, 1: 3-48.
- Schamp H., 1971 Der Kufra-Oasen-Archipel in der libyschen Sandwüste. In: Die Sahara und ihre Randgebiete. Band III. Regionalgeographie. Schiffers H. (ed.). Weltforum Verlag, München: 189-194.
- Schenkling-Prévôt, 1895 Strausse, Straussenzucht und Straussenfedern. Der Zoologische Garten, 36: 193-203.
- Schiffers H., 1950 Die Sahara und die Syrtenländer. Franckh, Stuttgart (Germany).
- Schiffers H., 1971 Die Nomaden. In: Die Sahara und ihre Randgebiete. Band III. Regionalgeographie. Schiffers H. (ed.). Weltforum Verlag, München: 22-65.
- Schiffers H. & Redmer H., 1971 Die Se
 ßhaften. A. Die Grundz
 üge. In: Die Sahara und ihre Randgebiete. Band III. Regionalgeographie. Schiffers H. (ed.). Weltforum Verlag, M
 ünchen: 66-107.
- Schiffers H., 1973 Der Südosten und Osten des libyschen Raums. In: Die Sahara und ihre Randgebiete. Band III. Regionalgeographie. Schiffers H. (ed.). Weltforum Verlag, München: 370-432.
- Scholz J.M.A., 1822 Reise in die Gegend zwischen Alexandrien und Parätonium, die libysche Wüste, Siqa, Egypten, Palästina und Syrien in den Jahren 1820 und 1821. Friedrich Fleischer, Leipzig (Germany).
- Schönwetter M., 1927 Die Eier von *Struthio camelus spatzi* Stresemann. Ornithologische Monatsberichte, 35: 13-17.
- Schönwetter M., 1960 Handbuch der Oologie. Lieferung 1. Akademie-Verlag, Berlin (Germany).
- Schreiber A., 2021 Cameroon as a historical range country of the dama gazelle (Mammalia, Bovidae). Annali del Museo Civico di storia naturale "G. Doria", 114: 329-347.
- Schreiber A. & Striedter K.H., 2022a The dama gazelle Nanger dama (Pallas, 1766) in Saharan rock art. Anthropozoologica, 57, 8: 185-209.
- Schreiber A., 2022b Evolution of horn shape and sex dimorphism in subspecies of the dama gazelle (Bovidae: Nanger dama (Pallas 1766)). Hystrix, Italian Journal Mammalogy, 33: 173-186.
- Schou M.F., Engelbrecht A., Brand Z., Svensson E.I., Schalk C. & Cornwallis C.K., 2022 – Evolutionary trade-offs between heat and cold tolerance limit responses to fluctuating climates. *Science Advances*, 8, 21: 1-9.
- Sclater P.L., 1860 On the rheas in the Society's menagerie, with remarks on the known species of struthious birds. *Proceedings of the London Zoological Society*, 28: 207-211.
- Sclater P.L., 1862a On the struthious birds in the Society's menagerie. Transactions London Zoological Society, 4: 353-383.
- Sclater P.L., 1862b List of vertebrated animals living in the gardens of the Zoological Society of London. *Messr. Longman, Green, Logmanns, and Roberts*, London (UK).
- Sclater P.L., 1895 [Untitled note on Egyptian menageries]. *Proceedings* of the Zoological Society of London, 26: 400-401.
- Sclater W.L. & Mackworth-Praed C., 1920 A list of the birds of the Anglo-Egyptian Sudan, based on the collections of Mr. A. L. Butler, Mr. A. Chapman and Capt. H. Lynes, R. N., and Mr. Cuthbert Christie, R. A. M. C. (T. F.). Part IV (concluded). Pelecanidae – Struthionidae. *The Ibis*, 11: 781-854.
- Shaw W.B.K., 1928 Exploration of the south Libyan Desert. Appendix V. Botanical. Sudan Notes and Records, 11: 157-161.
- Shaw W.B.K., 1936 An expedition in the Southern Libyan Desert. The Geographical Journal, 87: 193-217.
- Shelley G.E., 1872 A handbook to the birds of Egypt. *Jan van Voorst*, London (UK).
- Simons P., 1973 Der Osten der Sahara. B. Die Nilwüste. In: Die Sahara und ihre Randgebiete. Band III. Regionalgeographie. Schiffers H. (ed.). Weltforum Verlag, München: 433-535.
- Skinner J.D. & Smithers R.H., 1990 The mammals of the southern African subregion. University of Pretoria, Pretoria (South Africa).
- Snow D.W., 1978 An atlas of speciation in African non-passerine birds. Trustees of the British Museum (Natural History), London (UK).
- Sonnini C.S.N., 1807 Travels in Upper and Lower Egypt: undertaken

by order of the old government of France. J. Stockdale, London (UK).

- Steindorff G., 1904 Durch die Libysche Wüste zur Amons-Oase. Velhagen und Klassing, Leipzig (Germany).
- Strenger F., 1913 Strabos Erdkunde von Libyen. *Weidmann Buchhandlung*, Berlin (Germany).
- Stresemann E., 1926 Die Vogelausbeute des Herrn Paul Spatz in Rio de Oro. Ornithologische Monatsberichte, 34, 5: 131-139.
- Stresemann E., 1927 Ueber die einstige Verbreitung on Struthio camelus in Algerien. Ornithologische Monatsberichte, 35, 5: 135-136.
- Szechenyi S., 1936 Hengergő homok. Author's edition, Budapest (Hungary).
- Tedesco Zammarano V., 1930 Fauna e caccia. *Ministero delle colonie*, Roma (Italia).
- Temminck J. C., 1840 Manuel d'ornithologie, ou tableau systématique des oiseaux qui se trouvent en Europe : précédé d'une analyse du système générale d'ornithologie. Quatrième partie. *H. Cousin*, Paris (France).
- Török Z.G., 2008 The 'English' patient, fools, foxes and rats: exploration, mapping and war in the Libyan Desert. In: Symposium on "Shifting Boundaries: Cartography in the 19th and 20th centuries". *International Cartographic Association, Commission on the History* of Cartography, Portsmouth: 1-18.
- Török Z.G., 2011 Crossing borders: cartographic and military operations in the Libyan Desert before WWII. In: Proceedings of the XXV International Cartographic Conference: Enlightened view on Cartography and GIS. Ruas A (ed.). *International Cartographic Association*, Paris: 187-205.
- Török Z.G., 2012 From expedition cartography to topographic mapping: Italian military maps of the southern Libyan Desert from the 1930s. Schriftenreihe Institut für Geodäsie, 87: 259-273.
- Toschi A., 1969 Introduzione alla ornitologia de la Libia. *Tipografia Compositori*, Bologna (Italia).
- Toynbee J.M.C., 1973 Animals in Roman life and arts. *Thames and Hudson*, London (UK).
- Valverde J.A., 1957 Aves del Sahara español : (estudio ecologico del desierto). Instituto de Estudios Africanos (Consejo Superior de Investigaciones Científicas), Madrid (Spain).
- van Albada A. & van Albada A.M., 1994 De nombreux centres culturels. Art rupestre du Sahara. Les pasteurs-chasseurs du Messak libyen. Les Dossiers d'Archéologie, 197: 22-45.
- van Neer W. & Uerpmann H.-P. 1989 Palaeoecological significance of the Holocene faunal remains of the B.O.S.-missions. In: Forschungen zur Umweltgeschichte der Ostsahara. Kuper R. (ed.). *Heinrich-Barth-Institute*, Köln: 309-341.
- von Nathusius W., 1885 Ueber die charakteristischen Unterscheidungszeichen von Straussen-Eiern. *Journal für Ornithologie*, 33: 165-178.
- Walters M., 1982 A small ostrich egg from Egypt. Sandgrouse, 4: 116-117.
- Weis H., 1990 Die Feldforschungen von Graf Ladislaus Eduard Almasy (1929-1942) in der östlichen Sahara. Mitteilungen Österreichische Geographische Gesellschaft, 132: 249-356.
- Wendorf F., Schild R., Said R., Haynes C.V., Kobusiewicz M., Gautier A., El Hadidi N., Wieckowska H. & Close A.E., 1977 – Late Pleistocene and recent climatic changes in the Egyptian Sahara. *The Geographical Journal*, 143: 211-234.
- Williams J.B., Siegfried W.R., Milton S.J., Adams N.J., Dean W.R.J.D., du Plessis M.A. & Jackson S., 1993 – Field metabolism, water requirements, and foraging behavior of wild ostriches in the Namib. *Ecology*, 74: 390-404.
- Wilson R.T., 1976 The ostrich Struthio camelus in Darfur, Republic of Sudan. Bulletin British Ornithologists' Club, 96: 123-125.
- Winkler H., 1939 Rock pictures in Uweinat. The Geographical Journal, 93: 307-310.
- Wyss F., Hebel C., Deb A., Tugade D., Arif A., Dorrestein G.M. & Hammer S., 2014 – Manganese deficiency-associated deformities in red-necked ostriches (*Struthio camelus camelus*). In: Proceedings of the international conference on diseases of zoo and wild animals, May 12th – 15th, 2010, Madrid: 301-397.
- Zavattari E., 1934 Prodromo della fauna della Libia. *Tipografiaza già Cooperativa*, Pavia (Italia).