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Metric variation in the postcranial skeleton of ostriches, *Struthio* (Aves: Palaeognathae), with new data on extinct subspecies

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Running title: Ostrich postcranial skeleton biometrics

Because of numerous fossil and subfossil finds of ostriches there is a great demand for a comprehensive osteometric data set for the living species and subspecies of the genus *Struthio*. We meet this demand by providing the set of over 100 measurements for a sample of 18 sexed skeletons including all living and recently extinguished species and subspecies of ostriches. We provide the first mensural data for two extinct subspecies, the hitherto questioned *S. c. spatzi* from northwestern Africa and the Arabian ostrich, *S. c. syriacus*. The unique skeletal proportions of *S. c. spatzi* with a relatively short wing, broad pelvis, short tarsometatarsus and big third toe confirm the validity of this taxon and suggest an increased stability at the expense of cursoriality, which may have contributed to its extermination by humans. Our biometric analysis of the entire sample suggests a subtle sexual dimorphism in the ostrich skeleton, with females having the limb bones more robust (especially wider and/or deeper at the ends) despite being on the average smaller than males. If confirmed by further research, this size-independent dimorphism may reflect the independent regulation of the longitudinal and transverse dimensions of bones as revealed by several independent studies of morphological integration (covariance among morphological traits) in the avian skeleton.

ADDITIONAL KEYWORDS: Highland ostrich – *Struthio camelus spatzi* – Arabian ostrich – *Struthio camelus syriacus* – anthropocene extinction – pelvic limb – pedal digit – Palaeognathae – sexual dimorphism – morphological integration

INTRODUCTION

Two living species of ostriches (*Struthio*), the genus comprising the largest living birds, are currently recognized (Folch *et al.*, 2020): the Common ostrich, *Struthio camelus* with three living and one extinct subspecies (*S. c. syriacus*), and the monotypic Blue-necked (Somali) ostrich, *S. molybdophanes*, recently elevated among many other subspecies to the species rank by del Hoyo & Collar (2014) following its divergence in both mitochondrial and microsatellite nuclear sequences (Miller *et al.*, 2011). Among the subspecies of *S. camelus*, the Southern ostrich *S. c. australis* is closest to the Massey ostrich *S. c. massaicus*, and the Red-necked ostrich, *S. c. camelus* to the extinct Arabian ostrich, *S. c. syriacus* (Robinson & Matthee, 1999; Miller *et al.*, 2011). Subspecies may slightly differ in body proportions with *S. c. australis* considered to be the heaviest (males up to 150 kg) but not tallest race (Brown *et al.*, 1982) but no exact data are available. Body mass in *S. c. massaicus* ranges 86-145 kg (Davies, 2002). At least in *S. c. camelus* females are shorter and lighter than males with, respectively, 175-190 vs. 210-275 cm of height (Cramp & Simmons, 1977) and 90-110 vs. 100-130 kg of body mass (Davies, 2002). The extreme values without subspecies identification are 64 kg for a female and 156.8 kg for a male (Davies, 2002). Juvenile reach the adult height at one year, but the adult body mass only at 18 months and sexual maturity at the age of 3-4 years (Cramp & Simmons, 1977; Folch, 1993; Davies, 2002: 269).

While the length measurements, primarily of the pelvic limb bones have been occasionally published (Lowe, 1931; Schaller *et al.* 2005), there is a great demand for a comprehensive osteometric data set based on all living ostriches as a reference for identification of numerous ostrich fossils which usually differ only in size and proportions. Only Burchak-Abramovich (1953) provided many measurements in addition to length for 6-12 (depending on the bone) specimens although without sex and (except for 2 specimens) subspecies data, and with some of them (including the only specimen identified as *S. molybdophanes*) being obviously immature. Since the osteometric reference for comparisons with fossil and, especially, subfossil ostriches should take into account both (sub)species and sex differences, we searched for the skeletal specimens of extant ostriches with both kinds of data. The task proved unexpectedly difficult as the majority of ostrich skeletons in the available collections (including some of the largest) do not have subspecies information, many specimens (including those in African museums) come from indeterminate hybrids which stem from over a century of ostrich farming (Petitte & Davis 1999), and very few have both kinds of data. Our sample may well approach the maximum number of sexed ostrich

skeletons with subspecies data that can be assembled, at least from the European collections (and possibly even worldwide) but remains too small to analyze possible differences between subspecies. However it provides the first and by far the best to date referential data set for comparisons with fossil specimens, and allows us to define the skeletal proportions in two extinct subspecies, the Arabian ostrich *S. c. syriacus* and the hitherto disputed *S. c. spatzi*.

Using our data set of nearly all possible measurements of the appendicular skeleton we found the first evidence for unexpected size-independent sexual dimorphism in the ostriches that affects primarily the transverse dimensions of limb bones. Studies of sexual dimorphism in the avian skeleton have been largely limited to the length of limb bones that correlate with size dimorphism as in the moas (Bunce *et al.*, 2003; Olson & Turvey, 2013), mihirungs, Dromornitidae (Handley, 2016) and a few neognaths including Steamer ducks, *Tachyeres* (Livezey & Humphrey, 1986), Common eiders, *Somateria molissima* (Ericson, 1987), Gray cranes, *Grus grus* (Stewart, 2007), owls (Winde, 1977), and diurnal raptors (Bährmann 1974, Solti, 1996). Preliminary data on size dimorphism of the skeleton in the anatids, phasianids, owls, and accipitrids have been gathered in the Munich school dissertations listed by Stewart (2007: 21). Aside from qualitative differences due to sexual selection such as the presence of tarsal spurs in the males of many Phasianidae (Davison, 1985; Sullivan & Hillgarth, 1993), size-independent dimorphism in the postcranial skeleton is so far known to occur only in the foot of some birds including galliforms and passerines in which pedal digit ratios II/III and II/IV of the females are lower compared to the males (Navarro *et al.*, 2007; Saino *et al.* 2007; Leoni *et al.* 2008), and in the legs of Burrowing owls (*Speotyto cunicularia*) in which the females have shorter tarsi even though they are larger than the males (Plumpton & Lutz, 1994).

Size-independent sexual dimorphism is better documented in the avian skulls, primarily in the size and shape of the jaws. The females of some birds of paradise (Paradisaeidae) have longer bills although they are smaller than the males (Frith, 1997). In the Green woodhoopoes, *Phoeniculus purpureus* slightly larger males have disproportionately larger bills and the difference is maintained by natural selection (Radford & du Plessis, 2004), which may also be true of some species of hummingbirds with slightly larger females having longer or more curved bills (Berns & Adams, 2010; Temeles *et al.*, 2010). Qualitative and thus prima facie size-independent are the extreme sexual dimorphism in the size and shape of the bill in the extinct huia, *Heteralocha acutirostris* (Lambert *et al.*, 2009) and the presence of cranial humps in the male but not female scoters *Melanitta* while sexual differences in size of the cranial protuberances in at least six species of other Anatidae and *Anseranas* are size-

dependent (Mayr, 2018). The male Great horned owls (*Bubo bubo*) have broader skulls (braincases) than the females which are otherwise larger (McGillivray, 1985).

ABBREVIATIONS

INSTITUTIONAL ABBREVIATIONS

IRSNB Institut Royal des Sciences Naturelles de Belgique, Brussels; ISEA Instytut Systematyki i Ewolucji Zwierząt, Kraków; NHMUK National History Museum, Tring; OUMNH Oxford University Museum of Natural History, Oxford; SAM Iziko South African Museum, Cape Town; SAPM Staatssammlung für Anthropologie und Paläoanatomie München; USNM National Museum of Natural History, Smithsonian Institution, Washington D.C.; ZMB Museum für Naturkunde, Berlin.

MATERIAL AND METHODS

Altogether we measured 18 sexed skeletons, ten males and seven females, from seven collections (Table S1). Subspecies/species identification was available for 13 specimens: one *S. c. australis*, three *S. c. camelus*, two *S. c. massaicus*, three *S. molybdophanes*, two *S. c. syriacus* and one *S. c. spatzi*. We took up to 128 measurements (Table 1, Fig. 1) from each skeleton, although for most skeletons this number was closer to 100 because of the lack of distal pedal phalanges and sometimes other elements. Measurements of paired elements were recorded separately and averaged. Each measurement was taken at least thrice using standard size calipers (for most measurements) and macrocalipers Sylvac ULIII for largest distances.

In order to promote standardization of osteological measurements, which should make them better usable for comparative research and easier repeatable by others as well as reduce the need of defining and illustrating them each time (except for special cases), we propose to categorize them in two types, as either defined-point or orthogonal measurements. A defined-point measurement is the distance connecting two predefined terminal points, which must be grasped between the opposite points of caliper jaws. An orthogonal measurement is the distance between two parallel planes of the planar grasping surfaces of calipers' jaws which grasp the most projecting points irrespective of their mutual position on the opposite planes, without the need of specifying any terminal points beforehand. A clear distinction between these two types is necessary for the precision and repeatability of osteological measurements. The most common orthogonal measurements are axial measurements of long bones, that is,

otherwise unspecified length, width, and depth, which all ultimately rely on the determination of the long axis. Unless specified otherwise, the term length means a distance between two parallel planes that are perpendicular to the long axis of a bone and cross its extreme points. Unless specified otherwise, the term width is consistently used for a mediolateral, and the term depth for a craniocaudal (as in stylopodia and zeugopodia), dorsoventral or dorsoplantar (as in autopodia) distance between planes that for both measurements are parallel to the long axis, but perpendicular to each other. Width and depth are here referred to jointly as transverse measurements. We also used other orthogonal measurements such as diameters which are distances between two parallel tangent planes. However, because bones have curvilinear and often irregular shapes, and their axes can only be approximated, some of the measurements are defined as minimum or maximum, commanding a search for the shortest or the longest distance within the limits of a geometric definition. This categorization is in terms of measuring practice as imposed by the special properties of bones.

Because of the low numbers of sexed specimens, the differences between males and females were tested using a non-parametric Mann-Whitney *U*-test, with the software PAST (Hammer *et al.*, 2001). In PAST3, we selected “Univariate: two sample tests: Mann-Whitney *U*-test”, and retained the *U*-value and the *p*-value with “exact permutation”. In the second step, sexual dimorphism was recognized when $p < 0.05$, but also a few cases with near-significant values of $0.05 < p < 0.1$ were considered. Because of a small sample size we provide the median and the minimum-maximum range as the most reliable result for each measurement. However, we also used the mean values for all wild-collected specimens in order to calculate coefficients of variation and compare them with literature data, and the mean values for all males and all females, which were used to calculate Storer’s indices (Storer, 1966) only for the measurements that proved sexually dimorphic in Mann-Whitney *U*-tests tests (significant or near-significant). It was not possible to test for differences between the two currently recognized living species of ostriches and among the subspecies of *S. camelus* because of the very low numbers of specimens with species/subspecies identification. However, we could define clear differences in proportions and/or size between all the living ostriches and specimens of the two extinct, species-level taxa.

RESULTS

EXTINCT OSTRICHES

The measurements of appendicular skeleton in a sample comprising specimens from all extant and recently extinct species-level taxa of ostriches are provided in Tables S2-S16. Except for

a few measurements of pelvis and femoral length taken by Lowe (1931) we provide the first skeletal measurements for the extinct Arabian ostrich *S. c. syriacus* which derive from two male specimens at the Natural History Museum, Tring, England (Table S1), probably the only at least nearly complete skeletal specimens of this subspecies available in the collections worldwide (Trombone, 2013). Unfortunately one of them (NHMUK 1923.6.10.1) is incompletely ossified and the other (NHMUK 1924.4.8.1) partly damaged.

The length measurements of the wing bones are in *S. c. syriacus* by 8-16.5%, and those of the femur, tibiotarsus and tarsometatarsus by 10-15% lower than the means for the males of living ostriches. The differences in size of pedal phalanges are higher, in the range of 15-18%, meaning that *S. c. syriacus* had relatively shorter and otherwise smaller toes. The only length measurement that is even lower (by 22-27%) in *S. c. syriacus* is that of postacetabular pelvis, probably due to incomplete ossification of its caudal end (Table S4). Lower by 20% and more are also numerous transverse measurements including those of the scapulocoracoid, sternum and humerus (Table S2), two depth values for tibiotarsus (Table S6), fibula (Table S7), corpus width of the tarsometatarsus (Table S8), and three depths and width values for each phalanx 1 and 2 of pedal digit III (Tables S9-S10).

We also provide the first skeletal measurements for the hitherto questionable and largely dismissed taxon *Struthio camelus spatzi* (Tables S2-S10). A single available specimen revealed a striking distinctness of its skeletal proportions. Most of its length dimensions place it between the living ostriches, beyond or at the minimum end of their ranges, and much smaller Arabian ostriches. The wing bones of *S. c. spatzi* are consistently shorter (especially the carpometacarpus, less so phalanx 1 of the middle digit) but the distal width of the humerus is markedly higher than for the living ostriches. Most pelvic dimensions are below or barely approach the means for extant ostriches except for the greater (107-108%) width of the postacetabular pelvis starting from the level of the acetabula. Most femoral dimensions are slightly below (91-97%) the means for the living ostriches except for the corpus diameter which is distinctly smaller (86%, as in one specimen of *S. c. syriacus*), and the distal width which is distinctly higher (109%) than in the living ostriches. The tibiotarsus is intermediate in length and all other dimensions between *S. c. syriacus* and the living ostriches (Table S6). In contrast, the tarsometatarsus has the same length as in *S. c. syriacus* whereas its proximal and distal depths approach (96-99%) the means for the living ostriches (Table S8). Pedal digit III phalanges approach or exceed the means for the living ostriches in length and, consistent with the tarsometatarsus, both proximal and distal depths (Tables S9 and S10).

Struthio c. spatzi was definitely smaller than any of the living ostriches. Stresemann (1927) referred to the three adult individuals (two males and one female) raised in Berlin Zoo as looking diminutive in comparison to a big male of *S. c. camelus*. In body mass *S. c. spatzi* may have matched the Arabian ostrich judging from the identical least diameter of the femoral corpus (Table S5) or may have been larger judging from the width and depth of the tarsometatarsal shaft both of which are greater than in *S. c. syriacus* (Table S8). Diameters of the femur and tarsometatarsus are considered to be equally reliable ($R^2 = 0.93$) for body mass estimates in birds (Field *et al.*, 2013) although the cross section shape was shown to be less variable for the femoral compared to the tarsometatarsal corpus (Campbell & Marcus, 1992), which may lend more weight to the femoral corpus least diameter as an indicator of body mass in birds.

The unique proportions, especially the combination of short legs with big feet, differentiate *S. c. spatzi* which is much more distinct from all other subspecies of *S. camelus* than the newly erected species *S. molybdophanes* that may possibly differ from *S. camelus* at the most by a longer scapulocoracoid (Fig. 2). We therefore confirm a separate taxonomic status of *S. c. spatzi* at least as a subspecies, and propose the vernacular name ‘Highland ostrich’.

Struthio camelus spatzi Stresemann, 1926

Struthio camelus spatzi Stresemann, 1926: 139.

Holotype: egg, Museum für Naturkunde, Berlin, ZMB B. 1180a (not examined)

Referred specimen: male skeleton ZMB 36879 Stresemann, 1927: 135.

Remark: the skeleton ZMB 36879 comes from one of three birds, referred to by Stresemann (1927) as “cotypes”, kept at that time in Berlin Zoo.

Expanded diagnosis: Smaller than the living subspecies (with most dimensions 88-100%) except for the synsacrum (Table S3), postacetabular pelvis (Table S4), distal ends of the humerus (Table S2), femur except for a smaller corpus diameter (Table S5), and pedal phalanges III/1 and III/2 (Fig. 2; Tables S9-S10). Tarsometatarsus length below 440 mm (as in *S. c. syriacus*). The tibiotarsus / tarsometatarsus length ratio above 1.15 compared to 1.11-1.14 in extant ostriches. Phalanges III/1 and III/2 as in extant ostriches with the respective total lengths of ca. 90 mm (in the lower range of *S. c. camelus*) and 60 mm (as in *S. c. camelus*). The tarsometatarsus / phalanx III/2 length ratio 7.1 compared to 7.6-9.0 (8.0-9.0 for males) in extant ostriches. The pattern of egg pores of the intermediate type as described by Schönwetter (1927), Sauer (1968, 1972) and Mikhailov & Zelenkov (2020).

SKELETAL VARIATION AND SEXUAL DIMORPHISM

While the coefficients of variation of most measurements in the living ostriches do not exceed 6% (Tables S2-S13), some of them are distinctly higher as a result of variable ossification (intrinsic variation) or, in addition, to some indeterminacy due to the absence of exact measurement points when taking minimum width or depth measurements across continuous surfaces. A high intrinsic variability affects single details such as the sternal interspinal width (CV=7.4), pelvic angular width (CV=10.1), the cranial (CV=8.5) and caudal (CV=12.1) interforaminal distances of the tarsometatarsus, and the proximal width between the cotylar margins of phalanx III/1 (CV=7.1).

The indeterminacy and variability of measurement position may have contributed to the variation of the sternal postcostal width (CV=9.6), pelvic postacetabular width (CV=8.9), fibular corpus width (CV=8.8), tarsometatarsal corpus depth (CV=8.4), and many transverse measurements of phalanx III/2: corpus with (CV=9.1), apical width (CV=7.0), trochlear depth (CV=7.1), and foveal width (CV=7.1), the latter also being highly variable in phalanx III/3 (CV=9.5). The most variable and thus the least usable turned out to be the interischadic width (ischadic span) of the pelvis (CV=19.9), suggesting a strong intrinsic component of this variability in addition to the indeterminacy of the measurement point.

With a notable exception for the length of tibiotarsus (Table S6) and, especially, tarsometatarsus (Table S8), most measurement values (71 out of 95 medians), including the transverse measurements of tibiotarsus and tarsometatarsus, tend to be higher in females. However, only in 14 measurements the differences proved to be statistically significant or near-significant (Table 2). In ten of them the ostrich females have consistently wider and/or deeper ends of limb bones, which suggests that the female skeleton (at least the appendicular skeleton) is more robust even if the males are taller due to longer tarsometatarsi and tibiotarsi. Only three bones, scapulocoracoid, humerus, and pedal phalanx III/3 are significantly longer compared to males.

DISCUSSION

EXTINCT OSTRICHES

The Arabian ostrich *S. c. syriacus* has long been known as the smallest subspecies with the tarsometatarsus (measured as tarsus) of 390-465 mm (average 420 mm) compared to 450-530 mm (average 490 mm) reported for *S. c. camelus* (Vaurie, 1965). Our measurements of the tarsometatarsus (Table S8), 426 mm for the fully ossified male *S. c. syriacus* as compared to

the mean of 487.3 mm for the living subspecies (492.5 for males only), are in perfect agreement with these data. In skeletal proportions *S. c. syriacus* does not seem to differ substantially from the larger subspecies (Figs. 2-3) except for the relative shortness of the postacetabular pelvis with 73-78% of the median length for the living subspecies compared to 84-96% for other pelvic measurements (Table S4), and the relatively small size of pedal digit III, especially its phalanx 1 (Fig. 2, Table S9).

The subspecies *Struthio camelus spatzi* was erected by Stresemann (1926) for small ostriches from the southern part of Western Sahara (historically known as the Rio de Oro area, between 26° N and 21° 20' S). The diagnosis was initially based on the size of eight eggs (from various clutches) and the shape of eggshell pores as later described in more detail by Schönwetter (1927). Four young ostriches also were brought from the same area and placed in the Berlin Zoo. Three of them (two males and female) grew up by June 1927, were in good health, and yet looked dainty compared to a male *S. c. camelus* from Senegal (Stresemann, 1927). Unfortunately there is no record of their skeletal measurements that Stresemann (1927) intended to take.

Sauer (1968) has shown that the eggs assigned to *S. c. spatzi* by Schönwetter (1927) vary in shape and size but the eggshells differ from *S. c. camelus* in the pore pattern which reminds of a small mountain population of *S. c. australis* of south-western Africa. Sauer (1972: 42-43) envisioned the eggshell pore pattern of *S. c. spatzi* as intermediate between two wide spread patterns of ostrich eggs, and thought that it “must have evolved in a group of isolated birds aside from the mainstream of ostrich evolution”. This notwithstanding, the distinctiveness of *S. c. spatzi* has come to be denied. According to Brown *et al.* (1982: 33) both *spatzi* and *syriacus* merged through hybridization with *camelus* but this seems to be a pure speculation without any supporting evidence. Bertram (1985) asserted that “the so called Dwarf ostrich *S. c. spatzi* from Mauretania was mistakenly classified on inadequate information”. Folch (1992) referred to the subspecies *spatzi* as of “doubtful validity” and recently (Folch *et al.*, 2020) deemed differences in the eggshell to be attributable to individual variation. However, a recent detailed study by Mikhailov & Zelenkov (2020) confirmed the distinctiveness and intermediate status of the eggshell pore pattern in *S. c. spatzi* between non-specialized and specialized struthioid types, essentially as put forward by Sauer (1972).

The referred skeleton ZMB36879 of *S. c. spatzi* differs from all other ostriches in having a short tarsometatarsus, of nearly identical length as in otherwise smaller *S. c. syriacus* (Fig. 1, Table 8), i.e., 86-88% of extant ostriches mean, and a big pedal digit III, as big or apparently slightly bigger than in the living ostriches, 93-105% of the means for the living

ostriches (Fig. 1, Tables 9-10). The large size of the third toe correlates with the striking enlargement of the femur at the distal end (Table S5), which provides origins for the toe flexors (Gangle *et al.*, 2004; Smith *et al.*, 2006). While some of their tendons attach in the popliteal fossa, which may or may not influence the femoral distal width, the thick tendon of origin of the powerful musculus flexor perforatus digiti III (which itself provides the place for the origin m. flexor perforatus digiti IV) attaches to the lateral condyle of the femur and thus may influence its size.

In terms of the leg intramembral proportions femur / tibiotarsus / tarsometatarsus and tibiotarsus / tarsometatarsus / digit III phalanx 1, *S. c. spatzi* is separated from all other ostriches (including *S. c. syriacus*) by the same distance as from *Dromaius novaehollandiae*, and in terms of tarsometatarsus/digit III phalanx 1/ digit III phalanx 2 proportions *S. c. spatzi* stands midway between the living flightless palaeognaths (including the ostriches) and the moas, being equidistant to *Dinornis* and other ostriches (Fig. 3). These differences in skeletal proportions make the separate subspecies status of *S. c. spatzi* much better supported than the currently accepted species status of *S. molybdophanes*, which not supported by the intramembral proportions in the leg. There is no slightest reason to believe that the recorded differences, such as the relatively short tarsometatarsus and long toes, represent an anomaly resulting from rearing conditions inasmuch as leg deformities in farmed ostriches have been given special attention (Mushi *et al.*, 1999) and no such differences are known from numerous ostrich skeletons in museum collections, most of which come from captive birds.

The shank and tarsus lengths determine jointly the maximum stride length in birds (Alexander, 1977; Jones *et al.*, 2000). With the longest tibiotarsus and tarsometatarsus of all birds the living ostriches are the fastest avian runners with the stride length up to 5 m (Schaller *et al.*, 2011). However, in *S. c. spatzi* both the tibiotarsus and especially the tarsometatarsus are shorter by, respectively, 8 and 12% compared to the living ostriches (Tables S6 and S8) whereas the bones supporting the trunk, including the scapulocoracoid, sternum and especially pelvis, are much closer or, as in the case of synsacrum, match or exceed in size the living ostriches (Tables S2-S4). This indicates the Highland ostriches must have been slower than the living ostriches, and this may have contributed to their demise. In northwestern Africa the ostriches were “hunted on horseback, having first been tracked until within sight and then chased until cornered” (Davies, 2002: 57).

Long legs or, more precisely, a greater “hip height”, impose less stability (Hildebrandt 1985; Zeffler *et al.*, 2003), which can be compensated by a larger foot span (Hildebrandt, 1985). Recent studies confirm that the mechanics of running across rough terrain is similar in

all terrestrial birds independent of size (Birn-Jeffrey *et al.*, 2014) and involves the adjustments of limb angle (Daley & Biewener, 2006) thus conveying significance to differences in the length of toes. According to Stresemann's (1926, 1927) informers, *S. c. spatzi* inhabited a vast area that covered a part of Atlas Mts. in Morocco and the hamadas or rocky deserts (regs) with a pronounced relief and steep escarpments (Fairbridge, 1968) as in a part of today's Western Sahara. These landscapes are very different from those inhabited by most living ostriches, and certainly impose special requirements on locomotion, especially regarding maneuverability and balancing. We therefore propose that these ostriches were less cursorial and better adapted for the rough terrain of rocky highlands, hence we propose the vernacular name "Highland ostrich". Consistent with this interpretation is the similarity of the eggshell pore patterns in *S. c. spatzi* and an isolated mountainous population of *S. c. australis* (Sauer, 1968).

The unique foot proportions in *S. c. spatzi* must have had significant biomechanical consequences as they affect the action of the ankle (metatarso-phalangeal) joint, which in ostriches as the only birds, is elevated above the ground. Pedal digit III supports the majority of the load (Schaller *et al.*, 2011) and its (plantar) flexion provides the main propulsion force (Hutchinson, 2004; Smith *et al.*, 2006). The metatarso-phalangeal III/1 joint acts as a shock absorber and elastic energy storage (Rubenson *et al.*, 2011; Schaller *et al.*, 2011) and its action differs between walking and running on a solid substrate (Zhang *et al.*, 2017) but not on sand (Zhang *et al.*, 2018), which supports our hypothesis that the unique foot proportions in *S. spatzi* evolved as an adaptation to the rugged landscapes of northwestern Africa.

In the foot proportions, especially in the relative lengths of pedal digit III and tarsometatarsus, *S. c. spatzi* (Fig. 2) seems to be paralleled among moas by *Megalapteryx didinus*, a relatively small (ca. 21 kg) species that inhabited "high country" of the South Island (Worthy & Scofield, 2012) up to at least 1800 m a.s.l. (Atkinson & Greenwood, 1989) and seems to have had the locomotory power limited compared to other moas (Kooyman, 1991). Thus *S. c. spatzi* and *M. didinus* seem to provide another example of adaptive counterparts that evolved independently in similar, geographically separated habitats. All other moas have pedal digit III smaller than in *M. didinus*, whose foot also shows similarities to that of *Apteryx* (Farlow *et al.*, 2013). This raises a possibility that the enlargement of pedal digit III, especially its phalanx 2, and the relative shortening of tarsometatarsus evolved in *S. c. spatzi* and *M. didinus* in response to the same demand of maintaining greater stability in the rugged habitat.

SKELETAL VARIATION AND SEXUAL DIMORPHISM

Intraspecies metric variation in the skeleton of Neognathae remains usually in the range of 2-6% (Schneider & Dunn, 1924; Larson, 1930; Engels, 1936; Simpson, 1946; Bährmann, 1970; Bährmann, 1974; Lidauer, 1982; Solti 2002) with coefficients of variations (cv) higher for the transverse measurements of the ends and shafts compared to the lengths of bones (Goodge, 1951; Ericson, 1987). The recorded variation in two closely related species of living ostriches (Tables S2-S13) is higher than intraspecific variation in the neognath species as one could expect from the taxonomic diversification of the set including three subspecies of *S. camelus* and *S. molybdophanes*. However, it is unexpectedly lower than in two species of other living flightless palaeognaths, the emu *Dromaius novaehollandiae* (Long, 1965) and, except for the distal widths of femur and tarsometatarsus, the kiwi *Apteryx australis* (Cracraft, 1976b). It also is much lower than for the “expanded species” of the moas as defined by (Cracraft, 1976b). Aside from the problems of distinguishing species and sexing individuals of moas, now largely resolved through aDNA analyses (Bunce *et al.*, 2003, 2009), the lower intraspecific variation recorded in our study may represent an artifact of using a set of better-defined measurements.

The scarcity of specimens with reliable subspecies identification (rather than farmed hybrids) does not permit a meaningful biometric comparison of the living species and subspecies. The subspecies of *S. camelus* and *S. molybdophanes* cluster together in the limb length and proportions except that all three *S. c. camelus* specimens have relatively shortest scapulocoracoids, as does *S. c. syriacus* (Fig. 1), the closest relative of *S. c. camelus* (Miller *et al.*, 2011). However, the sample does provide a reliable information on the range of variation among the living ostriches which is essential for comparisons with the fossils and identification of numerous subfossil and archaeozoological finds. In addition, while the sample of sexed specimens is small, it contains specimens of very heterogenous origins including wild, zoo, and a few farmed specimens, which rules out any bias due to hunting, husbandry or farming practices. We therefore believe that the use of non-parametric statistics warrants a meaningful test for differences between sexes.

The evidence of subtle sexual dimorphism we discovered in the ostrich skeleton is rather unexpected because male ostriches are known to be slightly larger and heavier than females (e.g., Folch *et al.*, 2020) and yet the latter turn out to have most of their limb bones bulkier and a few of them slightly longer than in males. The dimorphism in ostrich skeletons turns out to be size-independent and thus calls for a different explanation, which is likely to be found in the genetically determined covariance of morphological traits known as

morphological integration (Klingenberg, 2014). Eleven out of fourteen statistically significant (or nearly so) differences between sexes involve width and/or depth (Table 2), which makes our results consistent with the independence of longitudinal and transverse postcranial dimensions as established independently in the moas (Cracraft, 1976a), anatids (Livezey & Humphrey, 1986), pigeons (Nemeschkal, 1999), and passerines (Power, 1971; Nemeschkal, 1999). The increased thickness of female limb bones may have evolved to enhance the storage of calcium in the skeleton for egg production or to compensate for the faster gains of body mass in female chicks (Mushi *et al.*, 1998). However, in the absence of comparable detailed osteological studies, it is unclear whether the same morphogenetic mechanism of global limb bone thickening is involved in sexual dimorphism in other birds.

The remaining three significant sexual differences are in the length of bones in two anatomically and thus morphogenetically widely isolated bones, the scapulocoracoid and humerus, and in pedal digit III phalanx 3 (Table 2). The covariation of scapulocoracoid and humerus seems accountable in terms of the known proximodistal patterning of vertebrate limbs including avian wings (Towers & Tickle, 2009), but other than that no published data on size-independent dimorphism of these bones are available.

Most of the pelvic limb bones do not show any distinct dimorphism in length, in agreement with Schaller *et al.* (2005) although the tarsometatarsus tends to be slightly longer in the males (Table S8). The dimorphic length of pedal digit III phalanx 3 may have gone unnoticed by Schaller *et al.* (2005) because measurements of the entire digit III, that is of the assembled phalanges (including the variable ungual), necessarily lack the precision of measuring single bones.

CONCLUSIONS

With all due caution commanded by a limited sample of selected skeletons, our analysis of a comprehensive set of 95 statistically usable measurements suggests subtle, size-independent sexual dimorphism in the skeleton of ostriches. Despite being overall smaller, the females tend to have the limb bones thicker (i.e., wider and/or deeper) than males. Such dimorphism is accountable in terms of the morphological integration (or covariance among characters) in the avian skeleton where an independent regulation of the longitudinal and transverse dimensions of bones has been demonstrated. This subtle dimorphism may need to be taken into account when identifying numerous Neogene ostriches across Eurasia and Africa.

We validate the extinct subspecies *S. c. spatzi* from northwestern Africa as distinguished by unique skeletal proportions with relatively short wing bones, broad pelvis,

short tarsometatarsi and big feet, suggesting an adaptation for increased stability of locomotion in the rugged landscapes that are specific for this part of Africa. We also confirm the subspecies status of the Arabian ostrich, *S. c. syriacus* which, in contrast to *S. c. spatzi*, is consistently smaller than the living ostriches by ca. 10%-25% in all skeletal dimensions.

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Supporting Information may be found in the online version of this article at the publisher's web-site.

Table S1. Skeletal specimens of ostriches.

Table S2. Shoulder girdle and wing skeleton measurements (in mm) with statistics.

Table S3. Synsacrum measurements (in mm) with statistics.

Table S4. Pelvis measurements (in mm) with statistics.

Table S5. Femur measurements (in mm) with statistics.

Table S6. Tibiotarsus measurements (in mm) with statistics.

Table S7. Fibula measurements (in mm) with statistics.

Table S8. Tarsometatarsus measurements (in mm) with statistics.

Table S9. Pedal digit III phalanx 1 measurements (in mm) with statistics.

Table S10. Pedal digit III phalanx 2 measurements (in mm) with statistics.

Table S11. Pedal digit III phalanx 3 measurements (in mm) with statistics.

Table S12. Pedal digit IV phalanx 1 measurements (in mm) with statistics.

Table S13. Pedal digit IV phalanx 2 measurements (in mm) with statistics.

Table S14. Pedal digit IV phalanx 3 measurements (in mm) with statistics.

Table S15. Pedal digit IV phalanx 4 measurements (in mm).

Table S16. Digit III phalanx 4 (ungual) measurements (in mm).

Table S17. Lengths of segments used for the Simpson's diagram in Figure 1.

Table S18. LOG values of segment lengths in all taxa minus the respective LOG value for the living *S. camelus* subspecies, as used for Figure 1.

Table S19. Ternary ratios (in %) of femur (F) / tibiotarsus (TT) / tarsometatarsus (TM) in the living flightless palaeognaths and moas as used for ternary diagram in Figure 2A.

Table S20. Ternary ratios (in %) of tibiotarsus (TT) / tarsometatarsus (TM) / pedal phalanx III/1 in the living flightless palaeognaths and moas as used for ternary diagram in Figure 2B.

Table S21. Ternary ratios (in %) of tarsometatarsus (TM) : pedal phalanx III/1 : pedal phalanx III/2 in the living flightless palaeognaths and moas as used for ternary diagram in Figure 2C.

Table 1. Measurements of the appendicular skeleton and synsacrum in the ostriches (*Struthio*), in the order of their left to right sequence in the tables S2-S16.

Bone	Abbreviation and definition	Type
Scapulocoracoid (Fig. 1A)	L_T total length, perpendicular to the sternal margin	orthogonal
	W_{St} sternal width, between the tips of medial and lateral angles of the sternal margin	defined point
Sternum (Fig. 1B)	W_{Is} interspinal width between the lateral margins of the spinae sternocoracoideae	defined point
	W_{Pc} postcostal width, minimum, between dorsal edges, at the narrowest point behind ribs	defined point
Humerus	L_v ventral length between ventral tubercle and ventral condyle	defined point
	W_d distal width between the epicondyles (oblique)	defined point
Ulna, radius, carpometacarpus, manual digit II phalanx 1	L_T total length, parallel to the long axis	orthogonal
Synsacrum (Fig. 1C)	L_M midline length, ventrally between the (concave) cranial facet of vertebra 1 corpus and caudal margin of the last synsacral vertebra ^d	defined point
	L_C midline corpus length, ventrally	defined point
	W_C corpus width, minimum	orthogonal
	D_T total depth (including spinal process)	orthogonal
	W_{par} the span of parapophyses	defined point
	W_{prz} the span of praezygapophyses	defined point
Pelvis (Fig. 1C)	L_L lateral length, minimum, between the anterior embayment of the ala praeacetabularis and the tip of spina dorsolateralis ilii	defined point
	L_{PA} preangular length ^a , minimum, between the cranial embayment of the ala praeacetabularis and the angulus ilii	defined point
	L_{PO} postangular length ^a , maximum, between the angulus ilii and the tip of spina dorsolateralis ilii	defined point
	W_{PrA} preacetabular width, minimum	orthogonal
	W_{Ant} antitrochanteric width between the outermost points of antitrochanters ^b , maximum	defined point
	W_{Ang} angular width between the anguli ilii	defined point
	W_{PoA} postacetabular width (close to the caudal end), minimum	orthogonal

	W_{int} interischadic width between medial margins of ischia, minimum	orthogonal
	D_{PrA} preacetabular depth (of ala praeacetabularis), minimum	orthogonal
	Δ_{TA} transacetabular distance, minimum, between the iliopubic margin (concave) and the tip of antitrochanter	defined point
	Ø_{Ac} acetabular diameter, between the cranial wall and the caudal rim of the acetabulum ^c	defined point
Femur (Fig. 1D)	L_T total length, perpendicular to the straight between the most proximal points of the capitulum and trochanter	orthogonal
	L_M medial length, maximum between the caput and the most distal point of the medial condyle	defined point
	L_L lateral length between the trochanter and the lateral condyle, maximum	defined point,
	Ø_H head diameter, cranio-caudal, in a transverse plane of the bone	orthogonal
	Ø_C corpus least (minimum) diameter, in a transverse plane of the bone	orthogonal,
	W_D distal width, maximum, between the medial condyle and fibular semicondyle	defined point
	W_P proximal width, maximum, between the head and the outermost margin of trochanter	defined point
	Ø_{CM} medial condyle diameter (oblique to the long axis of femur)	orthogonal
Tibiotarsus (Fig. 1E)	L_{IA} interarticular length	orthogonal
	W_C corpus minimum width (distally)	orthogonal
	D_C corpus depth, minimum (just above the impressio ligamenti collateralis medialis longi), perpendicular to the flat cranial surface	orthogonal
	W_P , proximal width, perpendicular to the bone's long axis	orthogonal
	D_P proximal depth (including cranial cnemial crest) perpendicular to the bone's long axis	orthogonal
	W_D , distal width as measured cranially, perpendicular to the plane of the lateral condyle's margin	orthogonal
	D_{MD} medial distal depth, perpendicular to the bone's long axis	orthogonal
	D_{LD} lateral distal depth, perpendicular to the bone's long axis	orthogonal
Fibula (Fig. 1F)	D_C corpus depth, maximum, across the iliofibular tubercle, perpendicular to the distal tibial facet	orthogonal
	D_H head depth, maximum, perpendicular to the head's caudal margin (oblique to the long axis of the bone) across the tibial tuberosity	orthogonal
	W_C corpus width, minimum, in the narrowest part between the head and distal tibial facet, perpendicular to the bone's long axis	orthogonal

Tarsometatarsus (Fig. 1G)	L_T total length	orthogonal
	W_C corpus width, minimum as determined by at least three trials at different locations	orthogonal
	D_C corpus depth, minimum (distally)	orthogonal
	W_P proximal width	orthogonal
	D_{MP} medial proximal depth	orthogonal
	D_{LP} lateral proximal depth (includes the protuberances for the lateral collateral ligament and fibularis brevis muscle)	orthogonal
	Δ_{IFA} dorsal interforaminal distance, maximum between the outer margins of dorsal (proximal vascular) foramina	defined point
	Δ_{IFP} plantar interforaminal distance between the inner margins of plantar (proximal vascular) foramina, minimum	defined point
	W_{TD} trochlea III distal width, taken conformably (perpendicular to the parallel planes of both trochlear labra)	orthogonal
	\emptyset_{TL} trochlea III lateral labrum diameter	orthogonal
Pedal digit III phalanx 1 (Fig. 1H)	L_T total length perpendicular to and extending from the straight connecting the trochlear apices to the ventral basis (with flexor tubercles)	orthogonal
	L_D dorsal length between the apex of the dorsal cotylar labrum and the distal midpoint of the trochlea	defined point
	L_M medial length, between the medial margin of the cotyla and the apex of the medial trochlear labrum	defined point
	L_L lateral length, between lateral margin of the cotyla (at the mid-depth) and the apex of the lateral trochlear labrum	defined point
	W_C corpus width, minimum	orthogonal
	D_C corpus depth, minimum, perpendicular to the ventral surface just distal to the ligament scars	orthogonal
	W_P proximal width (between the cotylar margins, exclusive of the lateral insertional protuberances)	orthogonal
	D_P proximal depth (including the dorsal and ventral insertional protuberances), perpendicular to the straight between the tips of flexor tubercles	orthogonal
	W_T trochlear width, ventrally	orthogonal
	D_T trochlear mid-depth (at the midline)	orthogonal
D_{MT} medial trochlear depth, across the medial labrum	orthogonal	
Pedal digit III phalanx 2 (fig. 1I)	L_T total length, between (and perpendicular to) the straight connecting the trochlear apices and the ventral cotylar labrum	orthogonal
	L_D dorsal length between the apex of the dorsal cotylar labrum and the distal midpoint of the trochlea	defined point
	L_M medial length between medial margin of the cotyla and apex of medial trochlear labrum	defined point

	L_L lateral length, between lateral margin of the cotyla and apex of lateral trochlear labrum	defined point
	W_C corpus width, minimum	orthogonal
	D_C corpus depth, minimum	orthogonal
	W_P proximal width (between the cotylar margins, exclusive of the lateral insertional protuberances)	orthogonal
	D_P proximal depth perpendicular to the ventral labrum	orthogonal
	W_A apical width, between the trochlear apices (as seen in dorsal view)	defined point
	W_F foveal width, minimum between the inner margins of the foveae ligg. collaterales ^e	defined point
	W_T trochlear width, ventral, perpendicular to the medial labrum	orthogonal
	D_T trochlear mid-depth, in the midline	orthogonal
Pedal digit III phalanx 3 (as in Fig. 11)	L_T total length, between (and perpendicular to) the straight connecting the trochlear apices and the ventral cotylar labrum	orthogonal
	L_D dorsal length between the apex of the dorsal cotylar labrum and the midpoint of the trochlea	defined point
	L_M medial length between medial margin of the cotyla and apex of medial trochlear labrum	defined point
	L_L lateral length between lateral margin of the cotyla and apex of lateral trochlear labrum	defined point
	W_P proximal width (between the cotylar margins, exclusive of the lateral insertional protuberances)	orthogonal
	D_P proximal depth perpendicular to the ventral labrum	orthogonal
	W_T trochlear width, maximum, ventrally between the proximal ends of the trochlear labra	defined point
	W_A apical width between the trochlear apices (in dorsal view)	defined point
	W_F foveal width, minimum, between the inner margins of the foveae ligg. collaterales	defined point
	D_T trochlear mid-depth, in the midline	orthogonal
Pedal digit IV phalanges 1,2,3,4	As for pedal digit III	-----

^a Those two measurements approximately correspond to pre- and postacetabular lengths which were not taken because the acetabulum does not offer a precise and convenient measurement point.

^b Lowe's (1931) "span from outer ridge of one-antitrochanter to the other"

^c Close to Lowe's (1931) "diameter at right angles" to the "antitrochanteric diameter", the latter being imprecise because of the irregularities of the antitrochanteric rim of the acetabulum.

^d This measurement should be accompanied by the count of synsacral vertebrae, which is variable.

^e This measurement value may vary between the mid-length and the distal end of the fovea.

Table 2. Evidence of sexual dimorphism in the ostrich (*Struthio*) limb skeleton including significant (asterisked) and near-significant differences as calculated from data in Tables S2-S13. For the definitions of measurements see Table 1 and Fig. 1.

Measurement	Mann-Whitney U / p	Storer's index median-based	Storer's index	Difference between medians*
Scapulocoracoid total length	8 / 0.073	5.97	5.27	5.8%
Humerus ventral length	8 / 0.073	2.61	3.52	2.6%
Humerus distal width	5 / 0,019	3.67	5.17	3,6%
Femur proximal width	6 / 0.017	9.15	8.0	8.75%
Femur distal width	7.5 / 0.028	8.59	6.93	8.2%
Tibiotarsus medial distal depth	4 / 0.014	10.03	6.53	9.55%
Tarsometatarsus corpus depth	4 / 0.006	14.36	10.33	13.4%
Tarsometatarsus plantar interforaminal distance	7 / 0.026	18.09	16,07	16.6%
Tarsometatarsus trochlea III lateral labrum diameter	6.5 / 0.082	4.24	6.08	4.1%
Pedal digit III phalanx 1 trochlear mid-depth	8 / 0.068	6.58	5.45	5.6%
Pedal digit III phalanx 2 proximal depth	4.5 / 0.065	7.17	4.71	4.7%
Pedal digit III phalanx 3 lateral length	0 / 0.057	13.78	12.91	12.9%
Pedal digit IV phalanx 1 lateral trochlear depth	1 / 0.071	8.3	6.94	8.0%
Pedal digit IV phalanx 1 trochlear mid-depth	0.071 / 0.036	14.19	12.87	13.25%

* In percent of the female median.







