

New remains of *Struthio coppensi*, Early Miocene, Namibia

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Abstract :- Field surveys over the past decade in the Sperrgebiet, Namibia, have led to the recovery of additional fossil remains of the Early Miocene ostrich, *Struthio coppensi* Mourer-Chauviré *et al.* 1996, including three fossils from a locality, Grillental VI, from which the species had not previously been recorded. Among the new material, there are two pedal phalanges and a cervical vertebra, as well as additional leg bones (tibiotarsus, tarsometatarsus). Descriptions and illustrations are provided of the material, which conform in dimensions and morphology with what would be expected for *Struthio coppensi*, which had ca 65% the dimensions of the extant ostrich, *Struthio camelus*.

Key Words :- Ostrich, Early Miocene, Osteology, Body size, Africa

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Introduction

The earliest known fossil ostriches, *sensu stricto* (Family Struthionidae) in the world were collected at Elisabethfeld, Namibia, from red silt-clay deposits correlated to the Aquitanian-Burdigalian (Early Miocene, ca 20-21 Ma) (Mourer-Chauviré *et al.* 1996a, 1996b; Senut *et al.* 1998; Mourer-Chauviré, 2008). The next youngest fossil bones of this family of large flightless bird (described herein) have been collected from green silts-clays at Grillental VI (ca 20-19 Ma), that are slightly younger than the red sediments at Elisabethfeld. Even younger fossil ostrich material (un-named species) is known from Kenya (Kadianga West, ca 14 Ma, Fort Ternan, ca 13.7 Ma, Ngorora ca 12.5 Ma; Leonard *et al.* 2006) and North African sites (Rich, 1974; Widrig & Field, 2022). In Eurasia, the oldest known representative of the *Struthio* group is from Çandir, Turkey (late Middle Miocene) (Sauer, 1979).

As currently understood, it is probable that the crown group ostriches, Struthionidae, originated in Southern Africa and were confined to the subcontinent until the base of the Middle Miocene, after which the family dispersed northwards throughout Africa, reaching Eurasia

before the end of the Middle Miocene (Mayr & Zelenkov, 2021).

Stem group Struthioniformes occurred widely in Eurasia during the Palaeogene (Widrig & Field, 2022) and it is possible that one or other of these primitive Eurasian proto-ostrich lineages may have dispersed to Africa towards the end of the Eocene or Oligocene, where it gave rise to the 'true' ostriches. The apparent lack of fossil ostriches in African Palaeogene localities, could, however, be an artefact of the rather poor representation of sedimentary deposits of this period in the continent, with very little known from Sub-Saharan regions.

The palaeoenvironmental conditions at Elisabethfeld and Grillental 20 to 21 million years ago, based on the associated fauna (termites, pipid frogs, crocodiles, birds, rodents, macroscelidids, chrysochlorids, tenrecoids, erinaceids, creodonts, carnivores, lagomorphs, orycteropodids, hyracoids, proboscideans, suids, rhinocerotids, ruminants) are considered to have been somewhat more humid than they are today, probably savannah to open woodland, with at least 750 mm of rain per annum (Guérin, 2008; Mein & Pickford, 2008a-c; Morales &

Pickford, 2018; Morales *et al.* 1998, 2008a-b; Mourer-Chauviré, 2008; Mourer-Chauviré *et al.* 1996a-b, 2023; Pickford, 1997, 2006, 2008a-k, 2018; Pickford & Senut, 2008, 2018; Pickford *et al.* 2008a-b; Quiralte *et al.* 2008; Senut, 2000, 2008).

The fact that several of the small mammal taxa at Elisabethfeld and Grillental possessed hypsodont cheek teeth, indicates that grass was present, but possibly not in great enough quantities to support large mammals, most of which were brachyodont or bunodont.

The presence of the lovebird, *Agapornis* at Grillental VI (Mourer-Chauviré *et*

al. 2023) supports this inference, because the staple diet of eight out of the nine extant species of this bird, comprises grass seeds that need to be available all the year round.

The termite hives (*Hodotermes*) and the molluscan fauna found at Grillental VI indicate that during the Early Miocene the region was under a summer rainfall regime, but with a winter rainfall zone not far away, because the land snail, *Trigonephrus*, that is today confined to regions experiencing winter rainfall, occurs at the site, alongside large species of *Dorcasia*, typical inhabitants of summer rainfall zones.

Systematics

Order Struthioniformes Latham, 1790

Genus *Struthio* Linnaeus, 1758

Species *Struthio coppensi* Mourer-Chauviré *et al.* 1996

Holotype :- GSN EF 3'94, distal end left tibiotarsus.

Type locality and age :- Elisabethfeld, Sperrgebiet, Namibia, Early Miocene, ca 21-20 Ma.

Other localities :- Grillental VI, Sperrgebiet, Namibia, ca 20-19 Ma.

New material

Grillental :- GSN GT 54'16, tibiotarsus, distal part (Fig. 2); GSN GT 41'18, first phalanx pedal digit III (Fig. 9); GSN GT 8'13, second phalanx pedal digit III (Fig. 10).

Elisabethfeld :- GSN EF 7'23, cervical vertebra (Fig. 1); GSN EF 4'23, right tibiotarsus distal part (Fig. 3); GSN EF 1'14, left tibiotarsus distal end (Fig. 4, 5); GSN EF 1'16, right tarsometatarsus, distal part and shaft (Fig. 6); GSN EF 18'16, left tarsometatarsus (Fig. 7, 8).

Anatomical Descriptions

Cervical vertebra GSN EF 7'23

In comparison with neck vertebrae of the extant ostrich, *Struthio camelus*, this specimen can be considered to correspond to cervical vertebra 5 or 6. It is damaged and slightly crushed in the dorso-ventral direction. On the dorsal surface, the left transverse process is missing and the one on the right is incompletely preserved, but the *facies articularis*, which is oval in outline, is visible. On the ventral surface the two costal processes are broken but the ventral part of the *arcus vertebrae* shows a swelling at the level of the base of these processes. The two *foramina transversaria* are followed by lateral gutters which extend beyond the midpoint of the vertebral body. The *facies articularis cranialis*

is elongated laterally and flattened in the dorso-ventral direction. The 'wings' of the *facies articularis caudalis* are broken but the centre of this *facies* corresponds closely to the form observed in the extant ostrich.

The total length of this vertebra is close to that of the extant species, but the dorso-ventral height is appreciably less, probably because of the crushing that the specimen underwent during fossilisation. The main difference concerns the diameter of the vertebral foramen which, in the fossil, is considerably smaller than that of the extant ostrich.

Table 1. Measurements (in mm) of the cervical vertebrae of *Struthio coppensi* from Elisabethfeld and extant *Struthio camelus*.

Measurement	GSN EF 7'23	<i>S. camelus</i> VC 5	<i>S. camelus</i> VC 6
Total length of the <i>facies articularis cranialis</i> to the <i>facies articularis caudalis</i>	ca 51.1	50.4	55.4
Minimum breadth	16.0	17.5	16.0
Height at the same point	15.4	22.5	24.0
Dorso-ventral height of the <i>facies articularis caudalis</i>	ca 6.2	6.4	6.6
Breadth of the vertebral foramen	7.0	12.0	12.7
Dorso-ventral diameter of the vertebral foramen	6.0	11.5	11.7

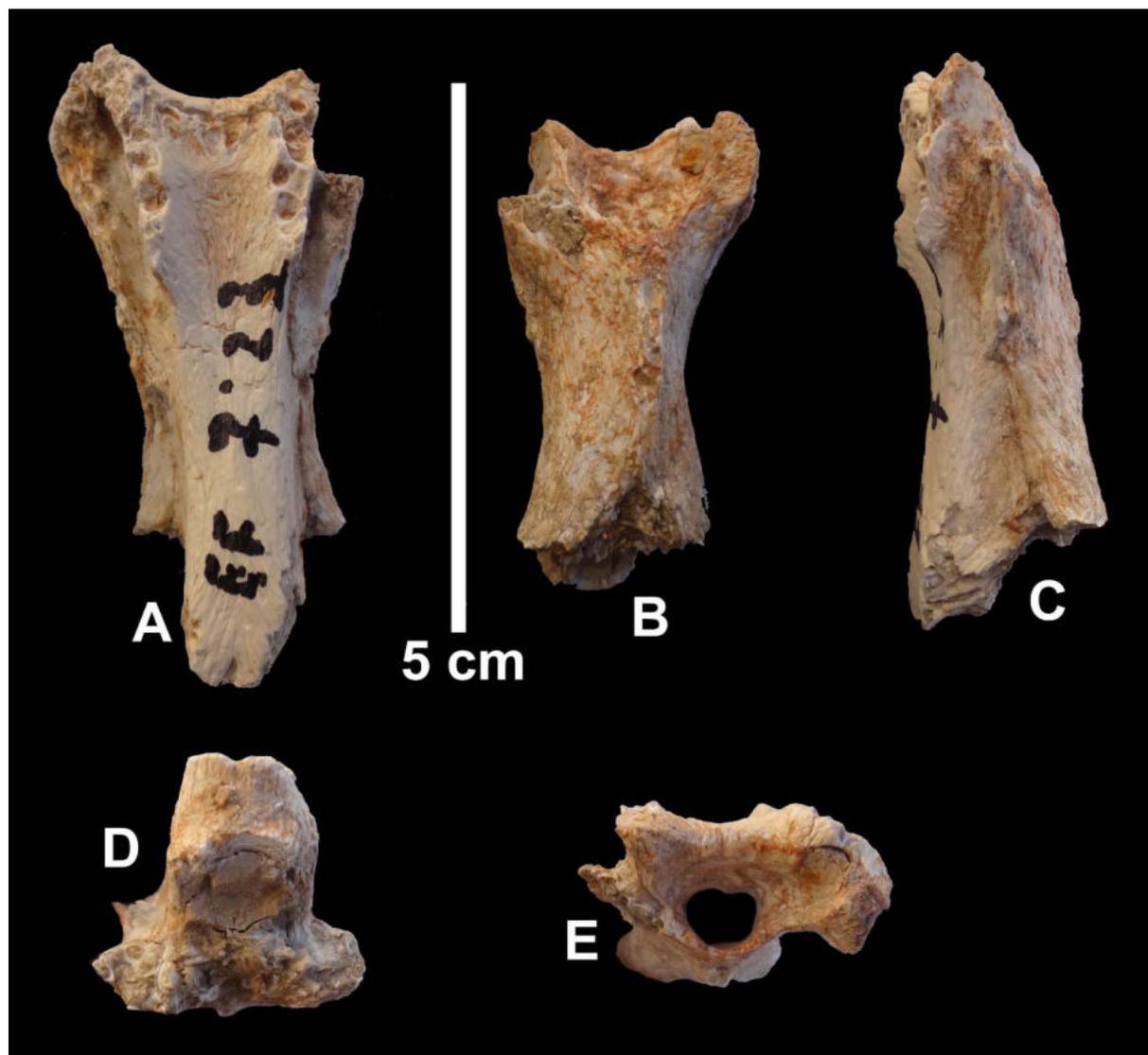


Figure 1. GSN EF 7'23 cervical vertebra 5 or 6. A) ventral view, B) dorsal view, C) right lateral view, D) caudal view, E) cranial view.

Right tibiotarsus, GSN GT 54'16

GSN GT 54'16 is a poorly preserved distal tibiotarsus. Part of the shaft is preserved along with much of the distal articulation, the width of which is

44 mm on the caudal side. What remains of the specimen closely resembles the holotype of *Struthio coppensi*.

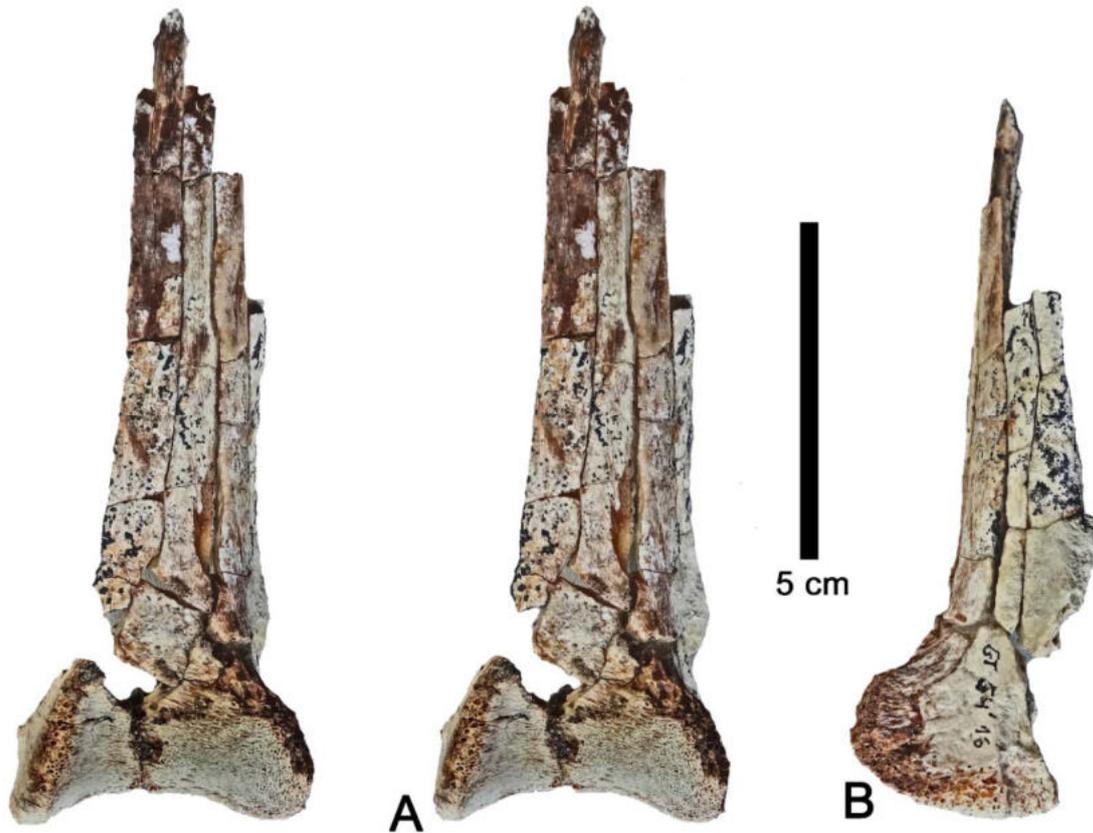


Figure 2. GSN GT 54'16, distal right tibiotarsus of *Struthio coppensi* from Grillental VI, Sperrgebiet, Namibia. A) stereo caudal view, B) medial view.

Right tibiotarsus GSN EF 4'23

The distal end of the right tibiotarsus is poorly preserved but shows the same characteristics as GSN EF 3'94, the holotype of the species *Struthio coppensi* Mourer-Chauviré *et al.* 1996 (Fig. 3). Its dimensions, where they can be measured, are slightly lower, but that is probably due to its poor state of preservation. The minimum diameter of the distal articulation is 26 mm which is the same as that of the holotype of *S. coppensi* (Mourer-Chauviré *et al.* 1996).

On the lateral side (Fig 3 B) and on the medial side (Fig. 3 D) all the cranial parts of the medial and lateral condyle are missing. On the medial side (Fig. 3 D) one can see the *fovea lig. collateralis*, which is circular in outline.

On the caudal side the shape of the *trochlea cartilaginis tibialis* is craniocaudally elongate while in *S. camelus* it is rectilinear and almost perpendicular to the axis of the shaft. The two condyles are similar and clearly less projecting than in *S. camelus*. In *S. camelus*, still on the caudal side, the medial condyle is rounded, while the lateral condyle is blade-like.

Table 2. Measurements (in mm) of GSN EF 4'23, distal right tibiotarsus from Elisabethfeld, Namibia.

Distal width cranial part	41.6
Distal width caudal part	34.7
Minimum trochlear diameter	26.0
Depth of medial condyle (as preserved)	34
Depth of lateral condyle (as preserved)	38

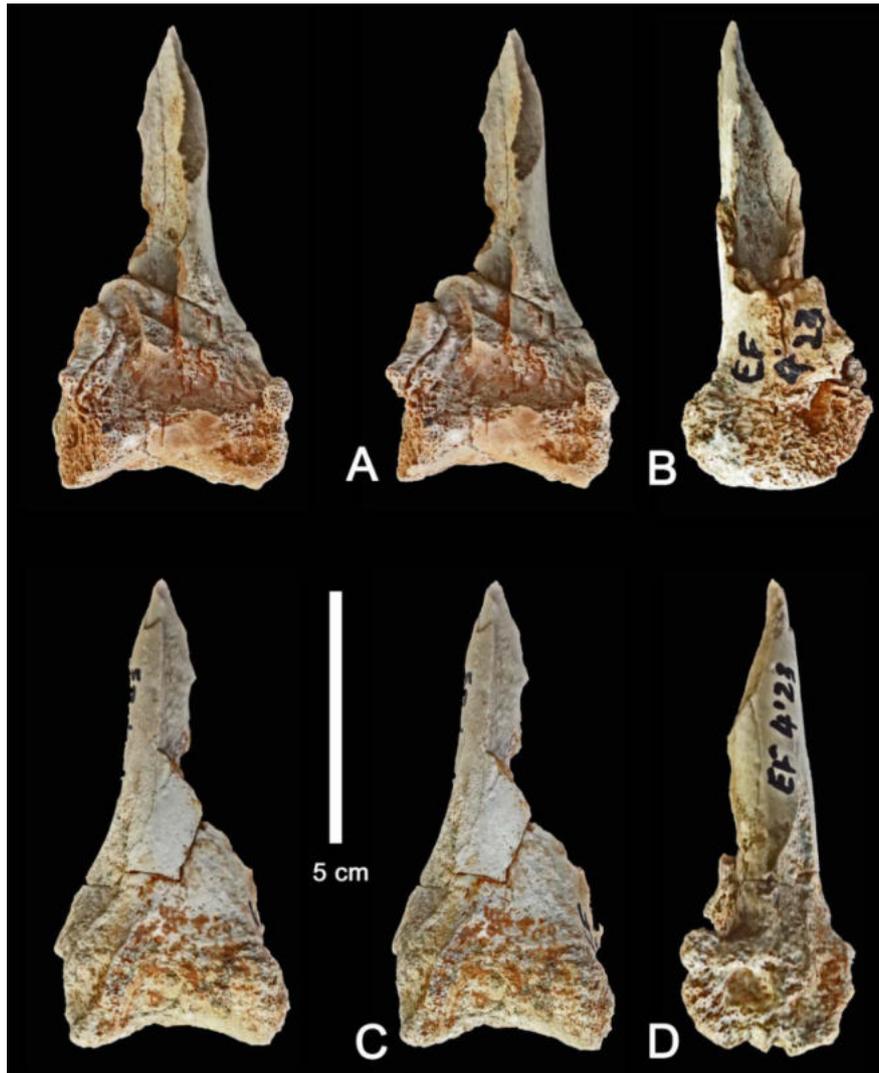


Figure 3. GSN EF 4'23, distal end of the right tibiotarsus. A) stereo cranial view, B) lateral view, C) stereo caudal view, D) medial view.

Left tibiotarsus GSN EF 1'14

GSN EF 1'14 preserves much of the shaft and the distal end of a left tibiotarsus (Fig. 4, 5). Its morphology is similar to that of the holotype of *Struthio coppensi* Mourer-Chauviré *et al.* 1996, but it is larger. Unlike the holotype, the shaft has not been crushed but there are several cracks in the bone, but with little or no displacement of the fragments.

The distal part is not as flattened as in the holotype, GSN EF 3'94. It is probable that the holotype has been squashed somewhat during fossilisation. On the cranial side the two condyles are linked by a wide open indentation. In the supracondylar fossa a flattened tubercle

which is the supra articular tubercle (TSA) can be seen (Fig. 5).

As in *S. camelus*, on the cranial side, the medial condyle projects strongly cranially and the lateral condyle is more developed in the proximal direction. On the medial side the *depressio epicondylaris medialis* has the shape of a semilunate fossa, and above the *epicondylus medialis* there is a distinct attachment scar for the *ligamentum collaterale longum*. Both of these characters are present in the recent genus, *Struthio*, and in the extinct genus, *Palaeotis* (Mayr & Zelenkov, 2021). On the caudal side, as on the specimen EF 4'23, the two condyles do not project strongly caudally.

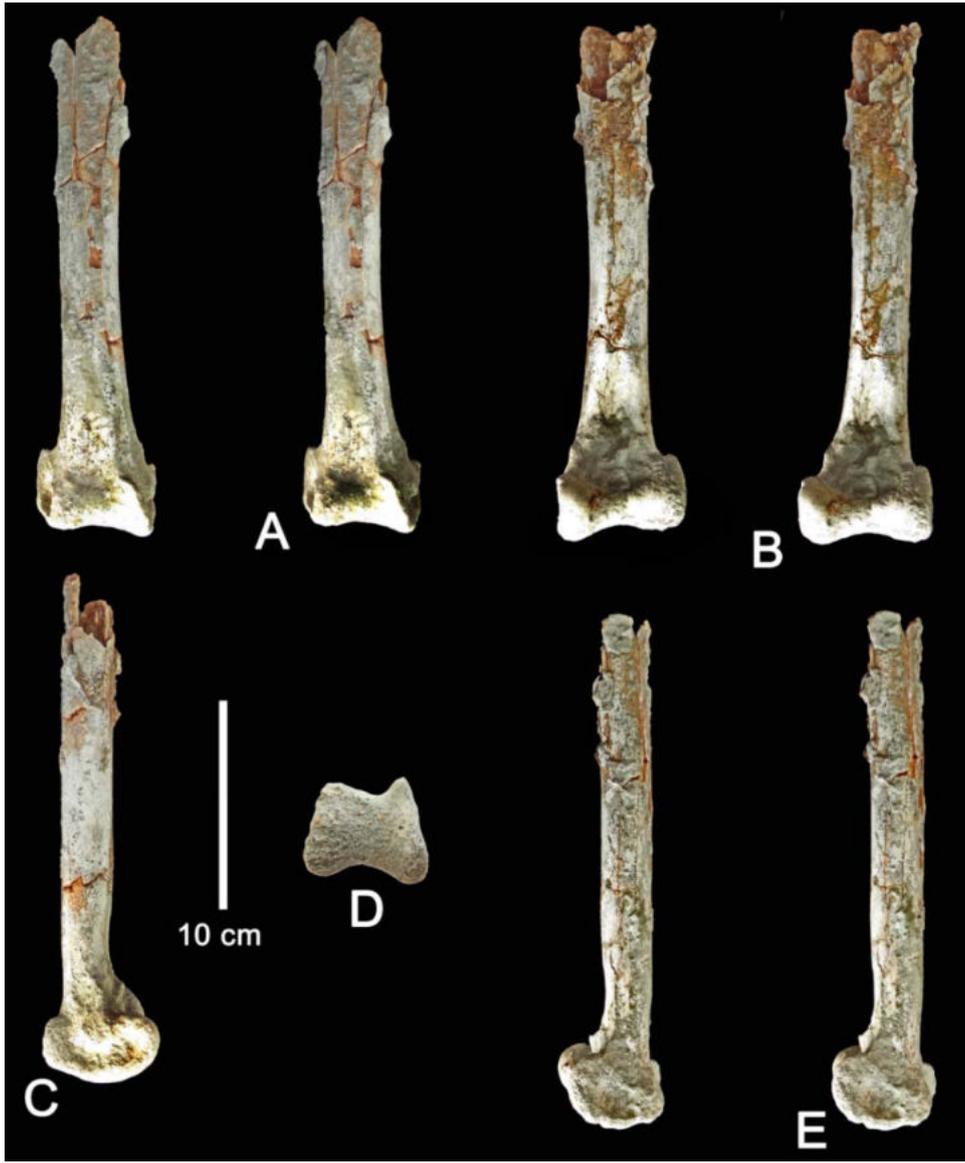


Figure 4. GSN EF 1'14, left tibiotarsus of *Struthio coppensi* from Elisabethfeld, Namibia. A) stereo caudal view, B) stereo cranial view, C) medial view, D) distal view, E) stereo lateral view.

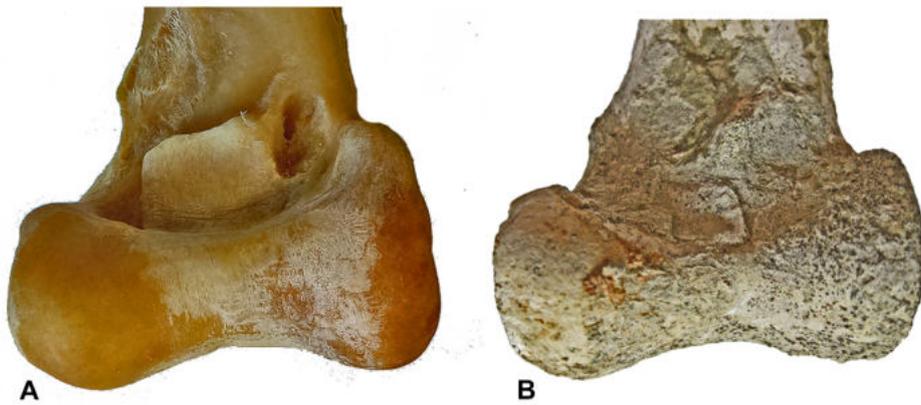


Figure 5. Comparison of the supra articular tubercle (TSA) of the distal left tibiotarsus in A) *Struthio camelus* (specimen Sh1 in the Musée des Confluences, Lyon) and B) *Struthio coppensi* (GSN EF 1'14). The images are produced at the same size to facilitate comparisons.

Right tarsometatarsus GSN EF 1'16

The right tarsometatarsus, GSN EF 1'16, is crushed cranio-caudally, and the distal articulations are damaged (Fig. 6). However, the overall length of the specimen is impressive, much of the diaphysis being preserved. The shaft is curved, being slightly outbowed, but this appearance could be enhanced by the crushing that the bone has undergone. The trochleae for the pedal phalanges are damaged and slightly distorted, but their dimensions indicate that they were somewhat larger than in the holotype of the species.

On the dorsal side the *foramen vasculare distale* is situated at the end of a short groove and at some distance from the *incisura intertrochlearis lateralis* while in *S. camelus* the foramen opens just above the *incisura* and the groove is absent. The vestigial *trochlea metatarsi II* was present on the tarsometatarsus GSN EF 1'94 paratype of the species (Mourer-Chauviré, 2008, fig. 1, B3) but is not visible on this specimen.

Table 3. Measurements (in mm) of GSN EF 1'16, distal right tarsometatarsus from Elisabethfeld, Namibia.

Preserved length	300
Width of trochlea III	ca 29
Width of trochlea IV	18.7



Figure 6. GSN EF 1'16, distal right tarsometatarsus of *Struthio coppensi* from Elisabethfeld, Namibia. A) stereo caudal view, B) stereo cranial view.

Left tarsometatarsus GSN EF 18'16

GSN EF 18'16 is a left tarsometatarsus lacking the proximal extremity and parts of the distal end. In addition it is broken and slightly crushed but parts of the distal end are reasonably well preserved (Fig. 7, 8). The trochlea of digit IV is well preserved and diverges at an angle of ca 30° from the axis of the condyle of digit III. Its extremity curves

medially and caudally. Parts of the groove of the trochlea of digit III are missing, but the medial and lateral margins are reasonably well preserved, allowing the overall morphology to be observed. The width of the trochlea III is 26.5 mm which is slightly greater than in the holotype of *Struthio coppensi*.

Table 4. Measurements (in mm) of GSN EF 18'16, distal left tarsometatarsus from Elisabethfeld, Namibia.

Depth of trochlea III	ca 25
Width of trochlea III	26.5
Depth of trochlea IV	ca 18.2
Width of trochlea IV	11.0



Figure 7. GSN EF 18'16, left tarsometatarsus of *Struthio coppensi*, at the moment of discovery. Aeolian deflation of the red silts exposes the fossils, but the boisterous winds also break them into fragments. This fossil was not visible in 2015, and its condition when found explains why surveys in the Sperrgebiet are necessary every year. Had it not been collected in 2016, within a few months it would have been an unrecognisable assemblage of small bone flakes.



Figure 8. Stereo images of GSN EF 18'16, distal left tarsometatarsus of *Struthio coppensi* from Elisabethfeld, Namibia, after reconstruction. A) cranial view, B) caudal view, C) medial view, D) lateral view.

On this tarsometatarsus the *trochlea met. IV* diverges strongly laterally, as in the paratype tarsometatarsus GSN EF 1'94, while on the specimen GSN EF 1'16, the two trochleae are compressed together, probably due to crushing during fossilisation. On other

tarsometatarsi from Elisabethfeld, the *trochlea metatarsi II* is very close to the trochlea III in GSN EF 172'01 and widely diverging from it in GSN EF 35'96 (Mourer-Chauviré, 2008, fig. 3, B and C).

Pedal first phalanx digit III GSN GT 41'18

GSN GT 41'18, the first pedal phalanx, digit III, from Grillental VI, is damaged, but its length and the morphology of one side can be reasonably well estimated (Fig. 9). With a

length of 60 mm, it is 142% of the length of the second phalanx, digit III (see below). The fossa for the distal ligamentar insertion is deep and occupies about half the height of the distal end.

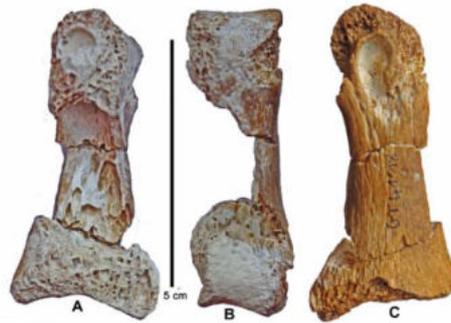


Figure 9. GSN GT 41'18, pedal first phalanx digit III. A) side view, B) plantar view, C) side view.

Pedal second phalanx digit III GSN GT 8'13

GSN GT 8'13 is a pedal second phalanx of digit III (Fig. 10). This phalanx differs strongly from that of *S. camelus* where the *corpus phalangis* is constricted both dorsoplantarly and mediolaterally. A similar, juvenile, phalanx has already been found in Elisabethfeld, (GSN EF 240'01, Mourer-Chauviré, 2008, fig. 3 E).

Its length is 42.2 mm. In extant *S. camelus* the mean length of this phalanx is 60

mm in females and 57.6 mm in males (Elzanowski & Louchart, 2021). The ratio between the length of the Grillental specimen and those of extant ostriches is thus ca 70 %, which corresponds closely with what was found at Elisabethfeld, where *S. coppensi* was shown to be about 65% of the dimensions of *S. camelus*.

Table 5. Measurements (in mm) of GT 8'13, pedal second phalanx, digit III, from Grillental VI, Namibia.

Total length	42.2
Proximal breadth	37.8
Proximal height	21.3
Distal breadth	22.0
Distal height	13.0
Mid-shaft breadth	20.2
Mid-shaft height	13.0

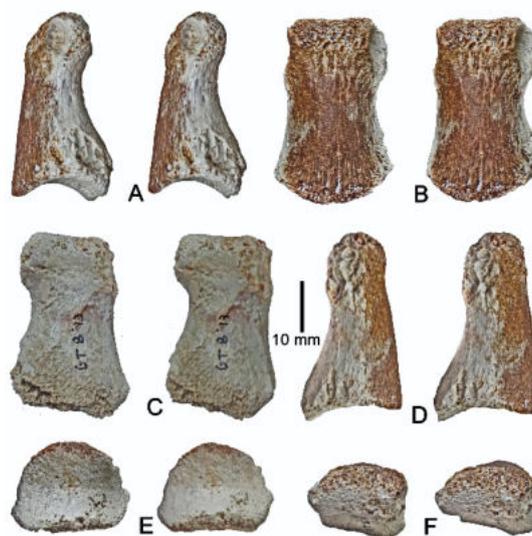


Figure 10. Stereo images of GSN GT 8'13, pedal second phalanx, digit III of *Struthio coppensi* from Grillental VI, Namibia. A) side view, B) dorsal view, C) ventral view, D) side view, E) proximal view, F) distal view.

Discussion and Conclusions

The fossil remains of *Struthio. coppensi* differ from those attributed to *Struthio* sp. from the middle Miocene of Kenya (Leonard *et al.* 2006). On a left tibiotarsus from Kadianga West, the medial condyle is not preserved on the cranial side but on the caudal side it is blade-like, as in *S. camelus*. On the cranial side the lateral condyle is very projecting, rounded, and the proximal border of the *incisura intercotylaris* is rectilinear, while it is incurved in *S. coppensi*. In contrast, in the distal tarsometatarsus from Fort Ternan, the *trochlea met. III* is wide and the *trochlea met. IV* is thin and much shorter than the *trochlea met. III*. In these characters, the Fort Ternan form seems to be more advanced than *S. camelus* in the process of reduction of the pedal digits.

The discovery of additional postcranial elements of struthioniform birds at Elisabethfeld and Grillental, Sperrgebiet, Namibia, confirms the presence of a primitive ostrich in the Early Miocene of Southern Africa, that was about 2/3 the dimensions of the extant ostrich *Struthio camelus*. The new collections include a cervical vertebra and two pedal phalanges, elements that were not represented in the original material described by Mourer-Chauviré *et al.* (1996) and subsequently by Mourer-Chauviré (2008) and not surprisingly, they also recall their counterparts in the extant species, apart from their smaller dimensions. There are however, some morphological differences between the two species, but these are not considered to be of sufficient weight to warrant separation of the species at the genus level.

The fossil struthious eggshells from the same localities in the Sperrgebiet, however, are rather different from those of extant ostriches, being more akin to those of aepyornithoids (Senut *et al.* 1998; Senut, 2000). The eggshells were formally named by Pickford (2014) as

Tsondabornis minor, with a known distribution at Elisabethfeld, Fiskus, Grillental and Langental, all sites in the Sperrgebiet.

There is debate about the continent in which the family Struthionidae originated. Mikhailov & Zelenkov (2020) wrote that “*The first appearance of ostriches in the fossil record in the early Miocene of Namibia supports the South African origin of at least the crown representatives of the group*”. In contrast, Widrig & Field (2022) wrote: “*With the reassignment of Eogruidae, there is now a clear record of stem Struthionidae in Eurasia well before the first crown struthionids appear in the Miocene of Africa. It now appears likely that this iconic clade of extant African birds first arose outside the continent....With Palaeotids interpreted as stem struthionids the case for an Eurasian origin of Struthioniformes is strengthened even further*”. The latter hypothesis was supported by Mayr (2022) who wrote “*Recognition of the European Palaeotididae, the North American Geranoididae, and the Asian Eogruidae as stem group representatives of the Struthioniformes supports a Northern Hemisphere origin of ostriches and a dispersal into Africa toward the late Paleogene or earliest Neogene.*”

Whatever the outcome of the debate, it seems that the earliest known ‘true’ ostriches are from the Early Miocene of Namibia. To some extent, the debate is more about ranks in classification of the ostrich-like birds (family, superfamily, etc.) and their ancestors, which may well have had an origin in the Northern Hemisphere, with the final transition to ‘true’ ostriches (family Struthionidae *sensu stricto*) taking place in southern Africa, as was postulated by Mourer-Chauviré *et al.* (1996), followed by dispersal into the northern continents during the Middle Miocene.

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