

Late Eocene Chrysochloridae (Mammalia) from the Sperrgebiet, Namibia

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Abstract: The Bartonian Eocliff Limestone, Sperrgebiet, Namibia, has yielded early specimens of the exclusively African mammalian family Chrysochloridae. The material from Eocliff comprise the most complete and informative fossil specimens of the group ever found, with good representation of the skulls, mandibles, dentition and post-cranial skeleton. As such the assemblage sheds a great deal of light on the fossil record of this enigmatic family, indicating that it split from the other afrotherians a long time prior to the Bartonian. The fossils are surprisingly modern in many ways, leaving little doubt about their affinities to extant golden moles, but there is a suite of primitive features in the skeleton and dentition which reveals details of their ancestry. The dentition is extremely zalambdodont, but the lower molars have large talonids and the upper molars possess large protocones. The post-cranial skeleton shows many modifications indicating a sand-swimming lifestyle as in extant members of the family but there are several important differences in post-cranial anatomy. The family is not particularly closely related to potamogalids, the superficial dental resemblances in the two families being due, in the main, to convergent evolution – the underlying structures of the teeth are quite different, even though the molars can, in the two families, be described as zalambdodont. Material from the Fayum, Egypt, classified as *Eochrysochloris*, is probably not a chrysochlorid. A new genus and a new species are erected for the Namibian form.

Key Words: Chrysochloridae, Late Eocene, Namibia, Evolution, Zalambdodonty, Sand-swimming

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Introduction

Chrysochloridae are common in the Eocliff Limestone, Northern Sperrgebiet, Namibia (Fig. 1), and their skeletal remains are usually well-preserved, allowing detailed study of the cranium, dento-gnathic system and the post-cranial skeleton. The fossils often occur as associated elements, sometimes in small patches suggesting accumulation as regurgitation pellets. The undigested aspect of the bones and the nature of their depositional environment indicate that the pellets were probably regurgitated by owls roosting or nesting in trees that grew around a lime-charged spring which deposited tufa and onyx-like travertine in its vicinity.

The rich sample of post-cranial elements throws an enormous amount of light on the locomotor repertoire and body

proportions of the Eocliff chrysochlorids. The pre-Pliocene post-cranial fossil record of Tenrecoidea/Afrosoricida was previously almost non-existent. Seiffert (2010) illustrated a partial distal humerus attributed to *Dilambdogale* of Early Oligocene age from the Fayum, Egypt. The Early Pliocene deposits at Langebaanweg, South Africa, yielded an impressive assemblage of some post-cranial bones (Asher & Avery, 2010) which are essentially modern in aspect. The Eocliff chrysochlorid sample includes abundant specimens of bones that have seldom if ever previously been described or illustrated, such as the triplex bone, the IInd metacarpal-trapezium-trapezoid complex, the flexor bone and the clavicle.

Geological context



Figure 1. Palaeogene fossiliferous localities of Africa (starbursts) and the location of Eocliff (EC) and related sites in the Sperrgebiet, Namibia (BC – Black Crow, BE – Bull’s Eye, CT – Chalcedon Tafelberg, EK – Eisenkieselklippenbake, GB – Gamachab, SK – Steffenkop, SN – Silica North, SS – Silica South, WK – Werkopje, WR – White Ring).

The Eocliff Limestone crops out in the Northern Sperrgebiet, Namibia. The deposits are of Late Eocene age (Bartonian) (Pickford

et al., 2008b, 2008c, 2014; Mourer-Chauviré *et al.*, 2014).

Associated fauna

Aves

Scopelortyx klinghardtensis

Namapsitta praeruptorum

Primates 1 genus

Macroscelidea 3 or 4 genera

Chrysochloridae 1 genus

Potamogalidae 1 genus

Tenrecidae 2 genera

Rodentia

Silicamys cingulatus

Prepomonomys bogenfelsi

Namaphiomys sp.

Protophiomys cf *algeriensis*

Metaphiomys cf *schaubi*

Tufamys woodi

Phiomys aff *phiomyoides*

Phiomys aff *lavocati*

Hyracoidea Titanohyracidae

Material and methods

Fossil Chrysochloridae skeletal remains were extracted from limestone blocks collected from Eocliff, Northern Sperrgebiet, Namibia. Eocliff is a cylindrical hill capped by a layer of sedimentary carbonate about 15

metres thick and 150 metres in diameter containing approximately a million tons of fossiliferous, partly silicified limestone (Mourer-Chauviré *et al.*, 2014; Pickford *et al.*, 2014). The positions of limestone blocks extracted from the hill were recorded using a GPS set to WGS 84 and were numbered with

the site number followed by the year of extraction (eg EC 7'14 – Eocliff site 7 of 2014).

The limestone blocks collected in 2013 and 2014 were digested in weak (7%) formic acid buffered with calcium triphosphate,

Taphonomy

The concentrations of vertebrate fossils at Eocliff occur as discrete patches and layers where regurgitation pellets, probably of owls, accumulated beneath perches or nests in trees growing in the vicinity of a lime-charged spring (Fig. 2-4).

followed by consolidation in a dilute solution of glyptol in acetone. The treated limestone blocks yielded a crop of several thousand jaws, teeth and post-cranial elements.

A few pellets retain their form and contain one or two skeletons of small mammals, but many of the fossils occur in beds of disaggregated pellets which were concentrated into rich masses of skeletal elements. Transport was minimal as shown by the fresh, completely unabraded preservation of the fossils.

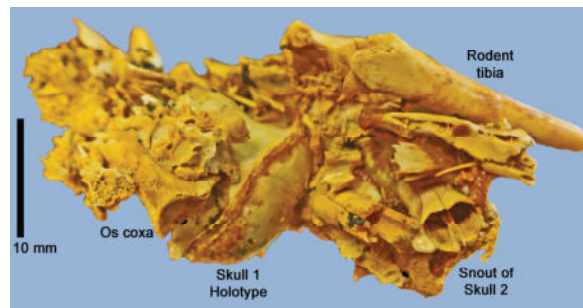


Figure 2. Taphonomy of Eocliff micromammals. Two skulls and bones of *Namachloris arenatans* (GSN Na 1 & Na 2) juxtaped with remains of other vertebrates (rodents, birds) at Eocliff, EC 7, Northern Sperrgebiet, Namibia. Note the form of the nasal bones in skull N° 2, in particular the narial flange (scale: 10 mm).

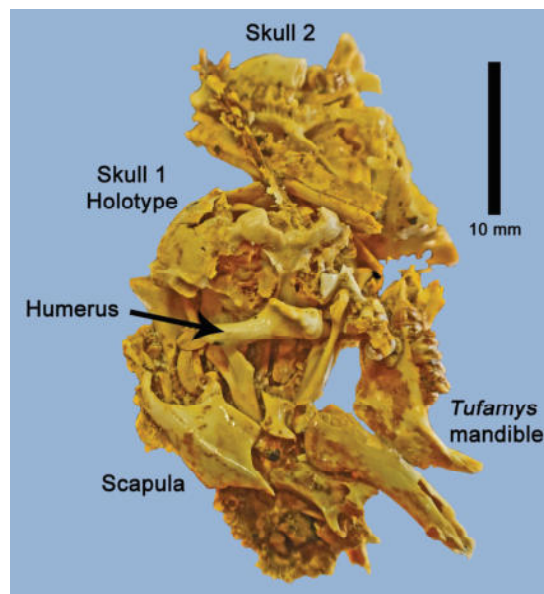


Figure 3. Taphonomy of Eocliff micromammals. Two skulls (GSN Na 1 & Na 2) and bones of *Namachloris arenatans* intermingled with remains of other vertebrates (rodents, birds) at Eocliff, EC 7, Northern Sperrgebiet, Namibia (scale: 10 mm).

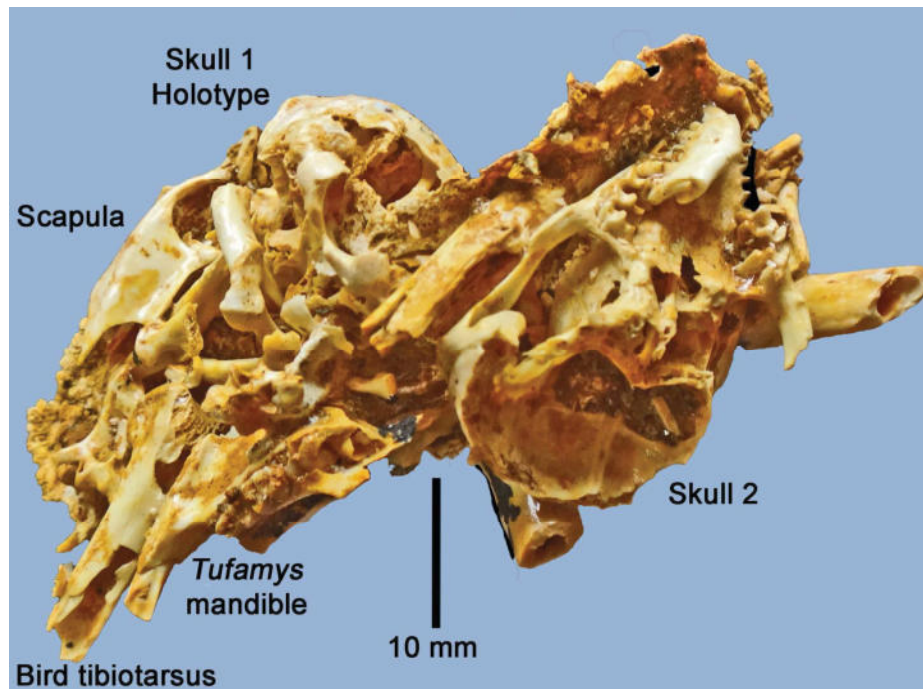


Figure 4. Taphonomy of Eocliff micromammals. Two skulls (GSN Na 1 & Na 2) and bones of *Namachloris arenatans* associated with bones of other vertebrates (rodents, birds) at Eocliff, EC 7, Northern Sperrgebiet, Namibia (scale: 10 mm).

Significant quantities of young adult mandibular specimens are present in the collection, in which the first or second lower molars are still in their crypts, but there are no infants or young juveniles as far as can be ascertained. This pattern of representation suggests that babies and young juveniles were protected from predation by owls, whereas

young adults and adults often fell prey to these predators. The relatively high number of young adults in the samples indicates that inexperienced individuals often fell prey to owls soon after leaving the protection of the nest or the parents.

Sample and measurements (See Tables 1 and 2)

Nomenclature

Dental nomenclature follows Asher & Sanchez-Villàgra (2005) and Seiffert *et al.*, (2007) (Fig. 5-7). Upper teeth are in capital letters followed by the meristic position followed by a forward slash which represents the occlusal surface (I1/, C1/, P2/, M3/, D4/ correspond to the upper central incisor, upper canine, the upper second premolar, the upper third molar and the upper fourth deciduous cheek tooth respectively). Lower teeth are in

lower case letters followed by a forward slash (the occlusal plane) followed by the meristic position (i/1, p/3, m/3, d/4 are the first lower incisor, third lower premolar, third lower molar and fourth lower deciduous cheek tooth respectively).

Cranial anatomical terms are from McPhee & Novacek (1993). Post-cranial skeletal nomenclature is based on Flower (1876) Sisson & Grossman (1953) and Barone (1999).

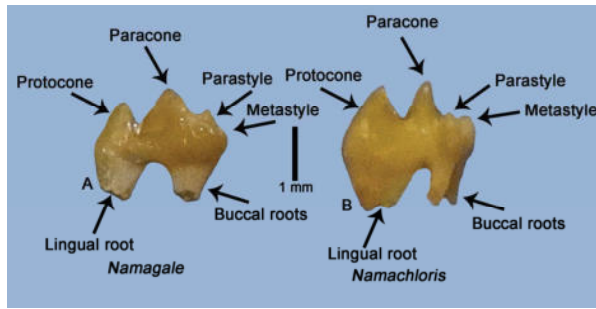


Figure 5. Upper molars of A) *Namagale* (GSN Ng 36, left M1/ from EC 9, distal view) and B) *Namachloris* (GSN Na 6.1, right M1/ from Eocliff EC 7, mesial view) to show the main differences in morphology. Note that the mesio-distally compressed lingual root of *Namachloris* is a compound of the protoconal and paraconal roots fused together throughout their height, save for the apices. The lingual root of *Namagale* is single, entirely protoconal and circular in outline (scale: 1 mm).

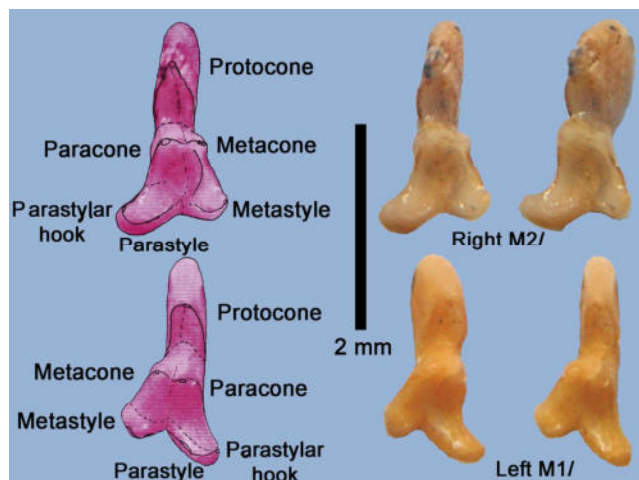


Figure 6. Nomenclature of the upper molars of *Namachloris arenatans*, interpretive drawings and stereo oclusal views of NA 50 from Eocliff, EC 6, left M1 and right M2/ (scale: 2 mm).

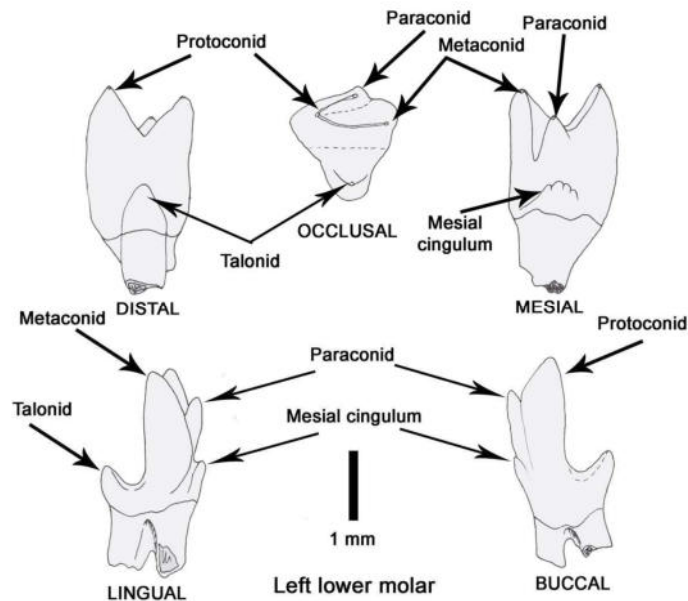


Figure 7. Nomenclature of left lower molar of *Namachloris arenatans* (scale: 1 mm).

Systematic Description

Superfamily Chrysochloridea Broom, 1915

Family Chrysochloridae Gray, 1825

Genus *Namachloris* nov.

Etymology.- The genus name combines “*Nama*” in its sense of “*Wasteland*” or “*Desert*” with the suffix “*chloris*” Latin transliteration of the name of the Greek Goddess of Flowers, one meaning of which is greenish-yellow (from which the Latin word *floris* (flower) originated). The suffix “*chloris*” has often been employed when naming Golden Moles on account of the greenish tinge of the fur.

Type species.- *Namachloris arenatans* nov.

Diagnosis.- Chrysochlorid with lower dental formula : incisors – 3, canine – 1, premolars – 3, molars – 3, upper dental formula : incisors – 3, canine - 1, premolars - 3, molars - 3. The protocone dominates the upper molars, being larger than the buccal complex comprising the paracone, parastyle and metastyle; M3/ not greatly reduced in bucco-lingual dimensions relative to other molars; root under the protocone of upper molars often shows a bifid apex, and has a faint distal groove; talonids of lower molars large, paraconid rudimentary and close to the metaconid; palatine torus present; narial flange present lateral to the anterior nares; nasals fused distally with frontals, but not fused laterally with maxilla or premaxilla; nasals with no “*encoche*” proximally; angular process of mandible extends well-beneath the level of the base of the ramus and points obliquely backwards and leans lingually; 1st rib solid and short with concave, paddle-shaped distal expansion which articulates with the manubrium; scapular blade almost parallel-sided and relatively narrow, acromion forming an elongated apophysis which overhangs and extends well beyond the glenoid cavity of the scapula and eventually splits into two tines (acromion and metacromion), the shorter one of which has a cartilaginous joint terminally for the clavicle; clavicle rod-like proximally, blade-like distally where it articulates with the manubrium; humerus with extremely broad distal epiphysis, hemi-spherical caput, small entepicondylar foramen, no fenestra in the

olecranon fossa; ulna with elongated, curved and flattened olecranon process, enlarged sigmoid notch with extensive flanges laterally and medially, distal end with elongated peg-like styloid process; radius with groove on its caudal aspect, a depression on the ulnar side where strongly developed interosseous ligaments bound the radius to the distal flange of the ulna and no distal volar bone bridge; flexor bone with swollen middle part sporting two facets for contact with the radius and ulna, its distal end having articular facets for the triplex bone; metacarpal II and two carpal bones (trapezoid, trapezium) fused together forming a complex “*ttm*” bone; metacarpal III, 1st and 2nd phalanges of digit 3 fused together forming a “*triplex*” bone; ungual phalanx of digit 3 greatly enlarged with bifid extremity, other ungual phalanges smaller with bifid extremities; synsacrum comprised of four or more vertebrae; os coxae with narrow obturator foramen, sometimes partly filled in with bone leaving two fenestrae; femur flattened cranio-caudally with large third trochanter about half way down the shaft where there is a bend in the diaphysis; tibia and fibula fused proximally and distally, with large inter-osseous space; distal fibula with small but sharp lateral flange, distal aspect with hemispherical depression comprising the articulation for the ball-like facet of the calcaneum; talus with short neck and small head; calcaneum with ball-like facet which articulates with the distal fibula, tuber calcis not elongated, body of calcaneum massive with two distinct facets for talus, medially flaring sustentaculum, short navicular and cuboid part.

Differential Diagnosis.- *Namachloris* differs from *Eochrysochloris tribosphenus* Seiffert *et al.*, 2007, from the Fayum, Egypt, by the presence, in the lower molars, of a vestigial paraconid close to the metaconid, and less well developed talonid compared to the large paraconid and talonid in *Eochrysochloris*. The differences are great enough to render doubtful the appurtenance of the Egyptian genus to the Chrysochloridae and to approach it to the Potamogalidae and Tenrecidae.

Namachloris differs from extant chryso-chlorids by the large protocone in its upper molars and P4/, by the presence of metacones in the M1/ and M2/, a relatively

large M3/ and by the absence of a bony bridge on the volar aspect of the distal radius.

Species *Namachloris arenatans* nov.

Etymology.- “*arenatans*” is a contracted form of the Latin for “*sand-swimmer*” : from “*arena*” (sand, desert) and “*natans*” (swimmer) in allusion to the sand-swimming adaptations of the post-cranial skeleton of the genus.

Material

Table 1. Specimen list of material from Eocliff, Northern Sperrgebiet, Namibia attributed to *Namachloris arenatans* gen. et sp. nov., (specimen N° 1 is the holotype) (EC – Eocliff; Lt – left, Rt – right).

Institute	Catalogue	Site	Material
GSN Na	1	EC 7	Skull with both mandibles, fragments of scapula, humerus, ulna fragment, os coxa, 3rd phalanx, metapodial
GSN Na	2	EC 7	Skull with rt mandible
GSN Na	3	EC 7	Lt maxilla, fragment maxilla with molar
GSN Na	4	EC 7	18 mandible fragments
GSN Na	5	EC 7	3 rt mandibles, 2 lt mandibles, all with teeth
GSN Na	6	EC 7	30 upper molars, 38 lower molars, 10 canines and incisors
GSN Na	7	EC 10	2 x malleus
GSN Na	8	EC 10	Lower molar fragment
GSN Na	9	EC 7	2 x manubria
GSN Na	10	EC 7	Partial skeleton; maxilla with P3/, manubrium, scapula fragment, 2 radii, os coxa, sacrum with os coxa attached, complete tibia, proximal and distal tibia, metapodials, phalanges, 2 small 3rd phalanges
GSN Na	11	EC 7	12 x humeri
GSN Na	12	EC 7	Ulna
GSN Na	13	EC 7	Humerus and bone mash
GSN Na	14	EC 7	14 x 1st ribs
GSN Na	15	EC 7	21 x ulnae
GSN Na	16	EC 7	19 x radius
GSN Na	17	EC 7	10 x flexor bones
GSN Na	18	EC 7	17 x triplex bones digit III
GSN Na	19	EC 7	20 x 3rd phalanges digit III
GSN Na	20	EC 7	2 x 2nd phalanges
GSN Na	21	EC 7	3 x 3rd phalanges digit I
GSN Na	22	EC 7	Associated bones; 2 x calcanea, 3 x tali, 3 x 3rd phalanges digit III, 2 x triplex bones, 2 x metapodials, 3 small 3rd phalanges, 1 odd bone
GSN Na	23	EC 7	5 x humeri and fragments
GSN Na	24	EC 10	Humerus, flexor bone, distal femur, 2 x patella, calcaneum, 2 nd phalanx, 3 rd phalanx manual digit III.
GSN Na	25	EC 7	5 x femora
GSN Na	26	EC 7	24 x calcanea
GSN Na	27	EC 7	15 x tali
GSN Na	28	EC 7	Associated post-cranial bones; ulna, 2 x flexor bones, 3rd phalanx digit III, small 3rd phalanges, patella, distal femur, 4 x calcanea, 3 x tali, metapodials, phalanges
GSN Na	29	EC 7	6 x small 3rd phalanges
GSN Na	30	EC 9	Lt maxilla, rt maxilla
GSN Na	31	EC 9	2 x lt mandibles, 2 x lower molars
GSN Na	32	EC 9	4 x upper molars
GSN Na	33	EC 9	20 teeth
GSN Na	34	EC 9	Rt mandible with molar in crypt, 8 teeth, 4 x 3rd phalanges digit I, 4 x 2nd phalanges, 1 metapodial
GSN Na	35	EC 7	3 x lower premolars, lower molar
GSN Na	36	EC 9	Scapula

Holotype.- GSN Na 1, skull with mandibles attached and associated post-cranial elements from Eocliff site 7, Sperrgebiet, Namibia (Table 1).

Diagnosis.- Species slightly larger than extant *Eremitalpa granti*, p/4-m/3 - 4.6 mm, P4/-M3/ - 4.9 mm.

GSN Na	37	EC 9	8 x humeri, 4 x humeral heads, and fragments
GSN Na	38	EC 9	13 ulnae
GSN Na	39	EC 9	3 x radius
GSN Na	40	EC 9	19 triplex bones
GSN Na	41	EC 9	11 x 3rd phalanges digit III, 3 x small 3rd phalanges
GSN Na	42	EC 9	5 x 1st ribs
GSN Na	43	EC 9	2nd phalanx
GSN Na	44	EC 9	11 x metapodials
GSN Na	45	EC 9	3 x os coxae
GSN Na	46	EC 9	Femur distal epiphysis
GSN Na	47	EC 9	Tibia proximal epiphysis
GSN Na	48	EC 9	15 x calcaneum
GSN Na	49	EC 9	3 x talus
GSN Na	50	EC 6	Maxilla and mandible fragments, 2 lower molars
GSN Na	51	EC 6	Rt mandible, molar in crypt
GSN Na	52	EC 6	Associated calcaneum, 3 x talus, 3rd phalanx digit III, phalanx
GSN Na	53	EC 6	2 x humeri, 3 x humeral heads, ulna, 1 x small 3rd phalanx, 1 x phalanx, 1 tooth
GSN Na	54	EC 6	Associated bones; basicranium, radius, femur
GSN Na	55	EC 6	2 x manubria, 1 x humerus fragment, 2 x ulna, 3 x radius, 7 x triplex bones, 4 x 3rd phalanges digit III
GSN Na	56	EC 6	4 x scapula fragments, 2 x os coxae, 1 x calcaneum, 1 x metapodial, 1x phalanx
GSN Na	57	EC 6	Distal femur, 8 x calcaneum, 6 x metapodials, 14 x 2nd phalanges, 3 bones
GSN Na	58	EC 6	5 teeth
GSN Na	59	EC 7	2 x third phalanges, carpal
GSN Na	60	EC 10	Associated bones; manubrium, 1st rib, 2 x humeral heads, 2 x ulna, 1 x radius, tibia
GSN Na	61	EC 7	3 x small terminal phalanges
GSN Na	62	EC 10	Lt mandible, lower molar
GSN Na	63	EC 1	Rt mandible with molar in crypt, Lt mandible, 2 lower molars, flexor bone
GSN Na	64	EC 1	Lt maxilla, clavicle, manubrium, humerus fragment, 2 x metapodials, 3rd phalanx digit III, os coxa
GSN Na	65	EC 10	Bone fragment
GSN Na	66	EC 4	Associated bones; manubrium, 2 x humerus, ulna, radius, tibia, calcaneum, 2 x talus, 3 triplex bones, metapodial, 3 rd phalanx digit III
GSN Na	67	EC 8	Lt maxilla fragments, Lt mandible, talus, 18 teeth
GSN Na	68	EC 8	Lt P4/
GSN Na	70	EC 8	Associated bones; 2 x 1st ribs, humerus head and distal end, ulna, 3 x radius, 3 triplex bones, 2 x 3rd phalanges digit III, femur shaft, 2 x calcaneum, metapodial
GSN Na	71	EC 8	2 x clavicles, 2 x scapula, humerus head
GSN Na	72	EC 8	3rd phalanx digit I
GSN Na	73	EC 8	Complete tibia
GSN Na	74	EC 7	Patella
GSN Na	75	EC 9	Two upper molars
GSN Na	76	EC 7	Two lower molars
GSN Na	78	EC 7	Rt maxilla and various teeth
GSN Na	79	EC 7	Os coxa, femur, 2 x tibia and second phalanx
GSN Na	80	EC 7	Two lower molars
GSN Na	81	EC 7	Two Lt mandibles, rt mandible, lower molar
GSN Na	82	EC 7	Scapula, distal humerus
GSN Na	83	EC 10	Two upper molars, lower molar, calcaneum, 3 rd phalanx
GSN Na	84	EC 9	Lt & Rt juvenile mandibles, 5 isolated lower teeth
GSN Na	86	EC 6	Distal femora, calcaneum, flexor bone
GSN Na	87	EC 6	Edentulous Lt mandible
GSN Na	88	EC 6	Three lower molars
GSN Na	89	EC 8	Associated post-cranial bones (phalanges, metatarsals)
GSN Na	90	EC 8	Edentulous rt mandible
GSN Na	91	EC 10	Two lower teeth, femur, calcaneum, talus
GSN Na	92	EC 10	3 rd phalanx
GSN Na	93	EC 10	Lower molar, humerus, ulna, ttm bone, two 3 rd phalanges

GSN Na	94	EC 7	Ulna fragment, 4 x carpals
GSN Na	95	EC 7	Edentulous rt mandible, upper molar, small 3 rd phalanx, carpal, 3 x tali
GSN Na	96	EC 10	M2/ buccal half
GSN Na	97	EC 9	Scapula fragment
GSN Na	98	EC 10	Clavicle, manubrium, basi-occipital, 2 x humeri
GSN Na	99	EC 8	7 x metatarsals
GSN Na	100	EC 8	Diaphysis of femur (juvenile)
GSN Na	101	EC 9	Juvenile mandible, two mandible fragments, ear ossicle
GSN Na	102	EC 9	2 x upper molars, humerus head, radius shaft, talus
GSN Na	103	EC 9	Two juvenile mandibles, metatarsal
GSN Na	105	EC 7	Incisor, 1 st rib, proximal humerus, radius, metacarpal, 2 nd phalanx, 3 rd phalanx, talus
GSN Na	106	EC 7	2 x Upper molars, humerus head, 2 nd phalanx
GSN Na	107	EC 7	Associated post-cranial bones
GSN Na	108	EC 7	Premolars and incisors
GSN Na	109	EC 7	Upper molar and post-cranial bones
GSN Na	110	EC 7	P4/, 2 x upper molars, lower molars, incisors
GSN Na	111	EC 7	Associated post-cranial bones
GSN Na	112	EC 7	Maxillae, mandibles and isolated teeth
GSN Na	113	EC 7	Isolated upper molar
GSN Na	114	EC 7	Associated post-cranial bones
GSN Na	115	EC 9	Humerus, distal femur, phalanx
GSN Na	116	EC 10	Ulna, proximal femur, phalanx
GSN Na	117	EC 7	Humerus, femur
GSN Na	118	EC 10	Manubrium, radius, femur, two tibio-fibula shafts
GSN Na	119	EC 10	Mandible fragment, P3/, 3 x upper molars, maxilla fragment with M3/, triplex bone, metacarpal, 2 nd phalanx,

Description

Skull and mandible

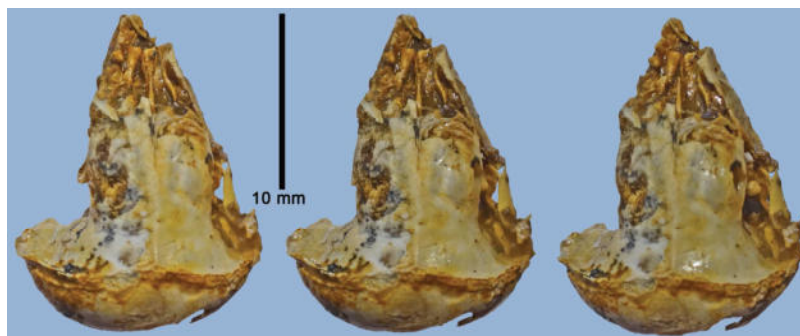


Figure 8. GSN Na 1, holotype skull of *Namachloris arenatans* from Eocliff, EC 7, in dorsal stereo triplet view (scale: 10 mm).

In dorsal view the skull of *Namachloris arenatans* is sharp anteriorly (damaged in the holotype but well preserved in the 2nd skull) and broad posteriorly, broadest at the occipito-squamosal crest (Fig. 8, 9). There is a low sagittal ridge. The occipital is

bulbous behind, with a beaded crest where it meets the frontal+parietal and the squamosal. The zygomatic arch is slender but complete and has a tall contact with the squamosal and occipital.

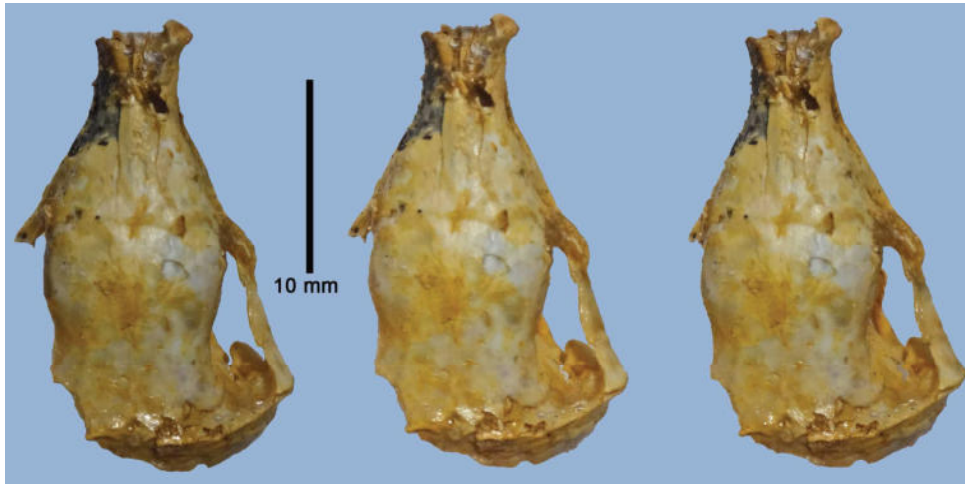


Figure 9. GSN Na 2, second skull of *Namachloris arenatans* from Eocliff, EC 7, in dorsal stereo triplet view (scale: 10 mm).

The nasals are unfused to the premaxilla and maxilla, but are fused to the frontals. The nasals do not have an encoche proximally (damaged during preparation, but Fig. 2, obtained prior to complete extraction of

the fossil shows the original form). The premaxilla sports a prominent flange on the supero-lateral margin of the narial opening. The orbit is small with only a minor swelling in the skull roof defining its posterior limit.

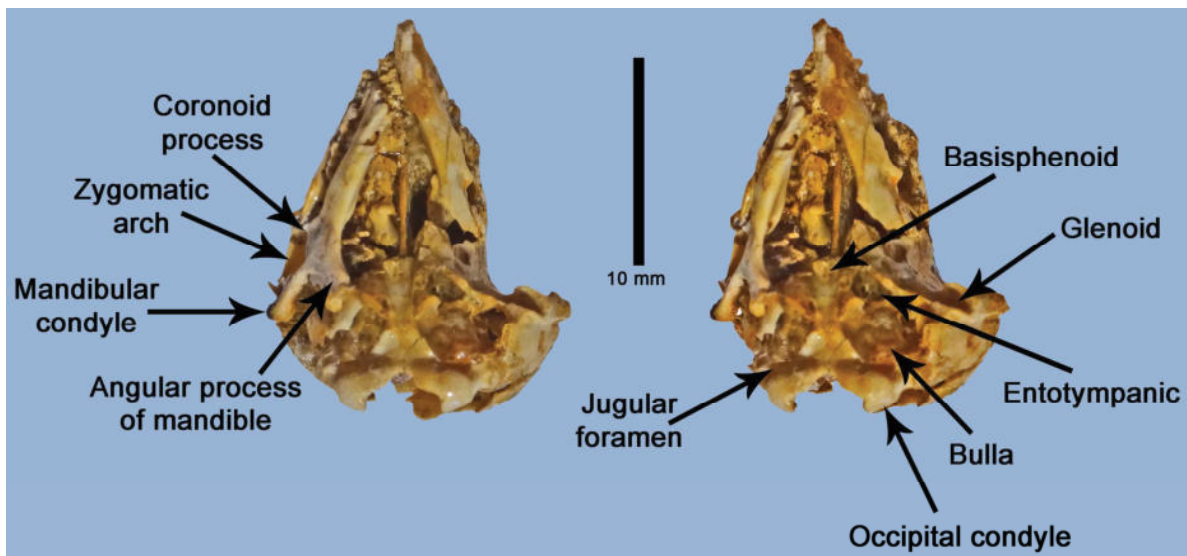


Figure 10. GSN Na 1, holotype skull of *Namachloris arenatans* from Eocliff, EC 7, in ventral stereo view (scale: 10 mm).

In ventral view, the sharply pointed contour of the skull is clearly evident, the two mandibles meeting in a point anteriorly (Fig. 10). The occipital condyles are strongly developed and quite wide apart, and the basi-cranium broad and strongly built. The glenoid cavity is stopped below and above by strongly curved ridges. The bullae are damaged but the space where they occurred reveals that they

were large and extended from the glenoid to the basicranial plate of the occipital. In front of the bulla is the entotympanic. The palate is damaged in the holotype, revealing a strong central rib separating the nasal cavity into two halves. This ridge extends forwards as far as the anterior narial opening.

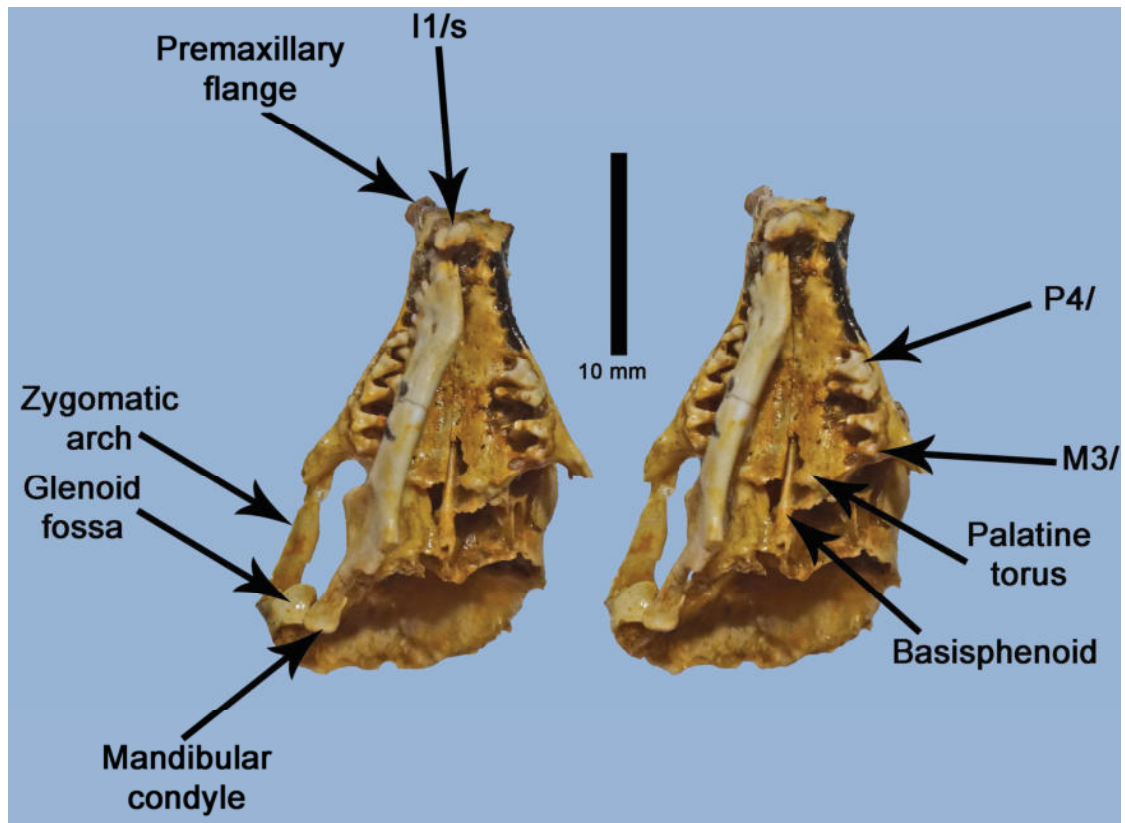


Figure 11. GSN Na 2, second skull of *Namachloris arenatans* from Eocliff, EC 7, in ventral stereo view before removal of the mandible (scale: 10 mm).

The right glenoid fossa and zygomatic arch are well preserved in the second skull of *Namachloris arenatans* (Fig. 11, 12). The palatines are thin, but show a ventral swelling which resembles a palatine torus. A break in the palatine reveals the central ridge of the basi-sphenoid above. The palate is broadest at

the M2/. The narial flange of the premaxilla is prominent, flaring antero-laterally from the end of the nasal opening. The palate is adorned with pin-prick depressions. The incisive foramen is far forwards, just behind the pair of large upper central incisors (Fig. 13).



Figure 12. GSN Na 1, holotype skull of *Namachloris arenatans* from Eocliff, EC 7, in right lateral stereo view. Arrow depicts the angular process of the mandible which underlies the bullae (scale: 5 mm).

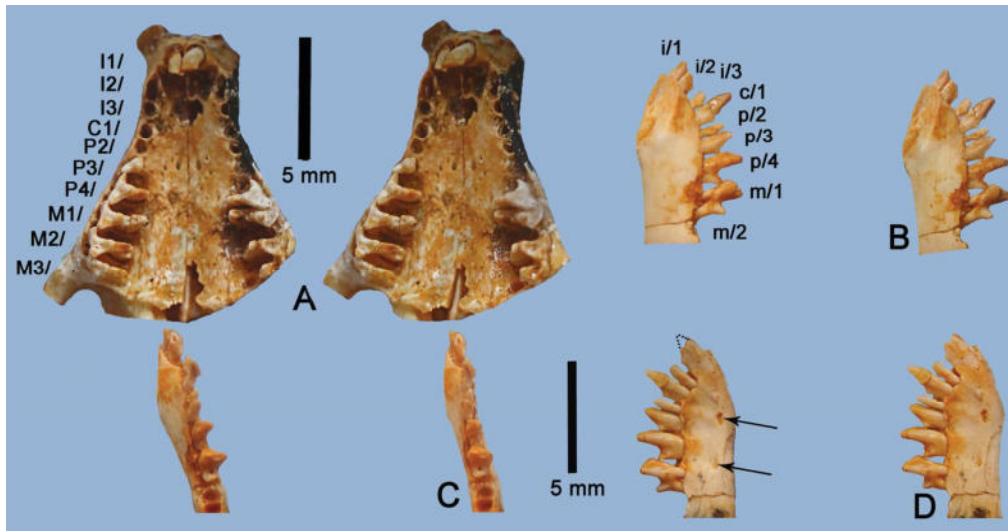


Figure 13. Upper and lower dentitions of skull N° 2 of *Namachloris arenatans*, A) stereo palatal view, B) stereo lingual view of mandible, C) stereo occlusal view, D) stereo buccal view. Arrows in 'D' show the mental foramina. The missing apex of the crown of i/2 is dotted in (scale: 5 mm).

The infra-orbital foramen is located beneath the leading edge of the orbit, which translates into a very short infra-orbital canal (Fig. 12). The zygomatic arch is slender and shallow anteriorly but becomes taller as it approaches its articulation with the occipito-squamosal crest where it contributes to the

making this the broadest part of the skull. There is no post-orbital process, but a low swelling in the brain case shows where the orbit ends behind. From this it is deduced that the orbit was very small, being barely longer than the length of the molar row.

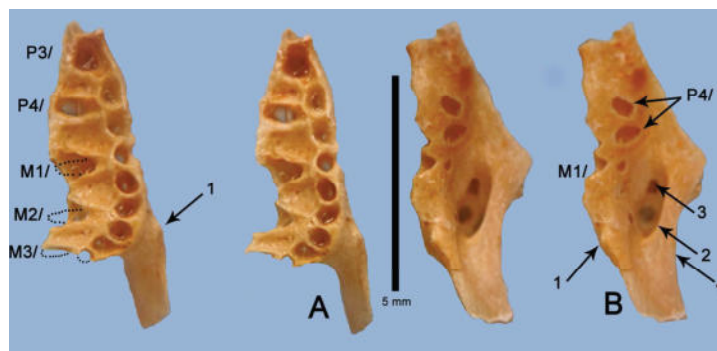


Figure 14. GSN Na 67, edentulous left maxilla of *Namachloris arenatans* from Eocliff EC 8, to show the layout of the roots of the cheek teeth and the structure of the infra-orbital foramen and surrounding parts. A) stereo occlusal view, B) stereo lateral view. 1 – facial tubercle at anterior base of zygomatic arch, 2 – infraorbital foramen, 3) foramen passing from the infra-orbital foramen into the nasal cavity, 4 – zygomatic arch defining the antero-inferior part of the orbit (scale: 5 mm).

An edentulous maxilla, GSN Na 67, is interesting for displaying the layout of the roots of the cheek teeth and the form of the infra-orbital foramen which is damaged in the holotype (Fig. 14). P4/-M3/ possess three roots, one each under the protocone, the parastyle and metacone. The protoconal root is smaller in the P4/ than it is in the molars. In the M3/ the metaconal root is located in the centre

line of the crown, slightly distal to the line joining the protoconal and parastylar roots. In the other molars the metastylar and parastylar roots are located on the buccal margin of the maxilla. There are depressions in the palate between the protocones of the P4/-M1/-M2/ and M3/, as a result of which the alveolar margins of the protoconal roots are raised.

The infra-orbital foramen is well-preserved in this specimen. It is an elongated oval shape and lies above the M1/-M2/. In its depths there is another foramen which passes from its antero-superior corner forwards into the nasal cavity (as in extant *Calcochloris leucorhinus*). The zygomatic arch is slender and at its anterior root there is a small facial tubercle.

Ear ossicles

Extant chrysochlorids have hyper-developed ear ossicles (malleus and incus)

(Mason, 2003a, 2003b, 2007; Narins & Willi, 2012). The only ear ossicles from Eocliff that fit with chrysochlorid morphology comprise a few specimens of incus about 1 mm tall with a swollen short arm, and a narrower long arm (Fig. 15). The incudo-malleolar joint is flat with an ovoid outline. Unlike rodent ear ossicles from Eocliff in which the malleus and incus are fused together in most individuals found, none of the incus specimens attributed to *Namachloris* has the malleus attached to it. Extant chrysochlorids have unfused malleus and incus.

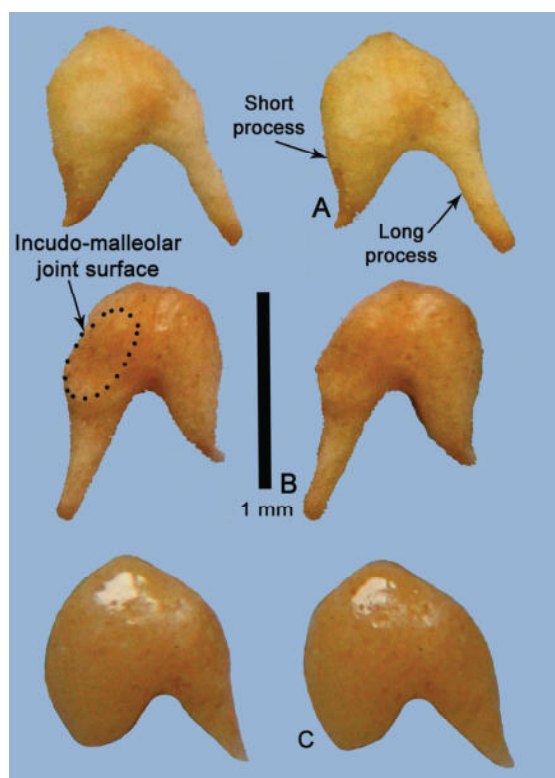


Figure 15. Stereo views of incus attributed to *Namachloris arenatans*, A-B) GSN Na 9 from Eocliff, EC 10; C) GSN Na 101, from Eocliff, EC 9 (scale: 1 mm).

Mandible

In the lateral view of the holotype, the form of the mandible is clearly visible (Fig. 16-19). The coronoid process is steep anteriorly, but distally it slopes only a short way ventrally before turning distally towards the elongated condylar process which is higher than the occlusal surface of the cheek teeth.

The angle of the mandible is elongated and descends obliquely ventro-distally with a tall, rectilinear termination which is well beneath the level of the base of the horizontal ramus. The rise in the mandible beneath the m/3 is subtle. There is a long retro-molar space. Mental foramina occur beneath the p/2-p/3 and p/4-m/1.

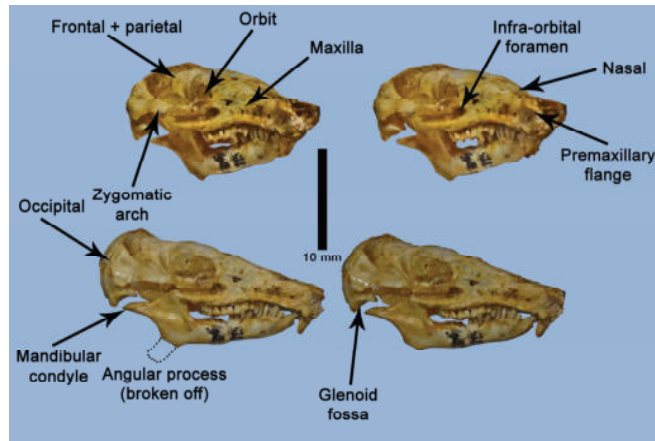


Figure 16. GSN Na 2, second skull of *Namachloris arenatans* from Eocliff, EC 7, in oblique right lateral stereo view and right lateral stereo view (scale: 10 mm).

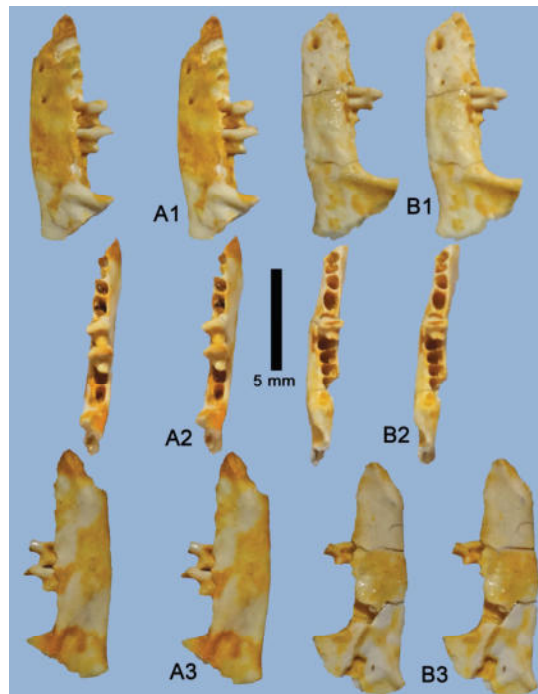


Figure 17. Mandibles of *Namachloris arenatans*, A) GSN Na 5.1, left mandible with m/1-m/2, B) GSN Na 5.2, left mandible with m/1; 1- stereo buccal views, 2 – stereo occlusal views, 3 – stereo lingual views (scale: 5 mm).



Figure 18. GSN Na 101, stereo image of left juvenile mandible of *Namachloris arenatans* from Eocliff, EC 9. 1 – symphysis of mandible, 2 – base of the angular process of the mandible (scale: 5 mm).

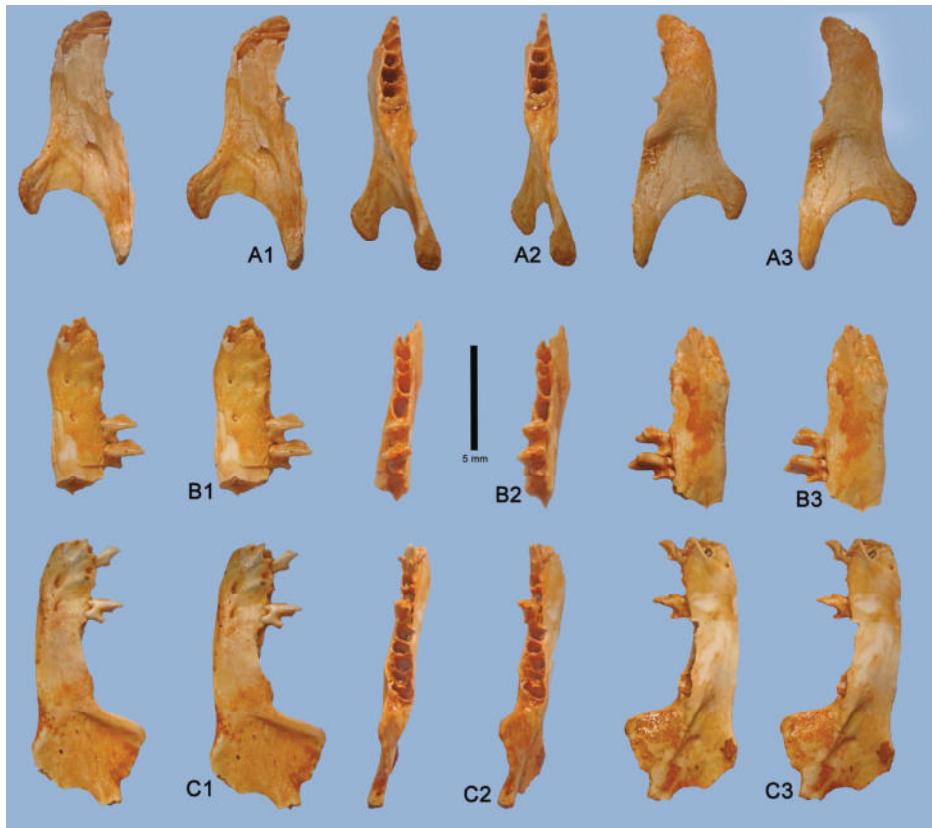


Figure 19. Mandibles of *Namachloris arenatans*. A) GSN Na 34 right mandible with unerupted m/1, from Eocliff, EC 9, A1 – stereo lingual view, A2 – stereo occlusal view, A3 – stereo buccal view; B) GSN Na 81 left mandible with m/1-m/2 from Eocliff, EC 7, B1 – stereo buccal view, B2 – stereo occlusal view, B3 – stereo lingual view, C) GSN Na 5, left mandible with p/2 and p/4 from Eocliff, EC 7, C1 – stereo buccal view, C2 – stereo occlusal view, C3 – stereo lingual view (scale: 5 mm).

Discussion

The skull and mandible of *Namachloris arenatans* nov. gen. nov. sp., resemble those of recent chrysochlorids in many ways, yet they show several features which distinguish them from extant taxa (Fig. 20). The skull is broad behind with a globose occipital, snout narrow anteriorly, with a narial flange in the premaxilla indicating that a nose pad was present in this extinct species. The infra-orbital canal is short and opens close to the orbital margin. The zygomatic arch is complete, yet slender and straight, terminating distally in a tall articulation with the temporo-occipital crest. There is a subtle inter-frontal ridge, and the nasals are fused with the frontals, but not with the maxilla or premaxilla. The anterior ends of the nasals do not have an encoche. The bullae are large with a well formed entotympanic in front, the ear ossicles are enlarged with a swollen short arm in the incus. There is a palatine torus and the palate has numerous tiny pits in its surface. The

occipital condyles are strongly developed and relatively far apart.

The angular process of the mandible projects obliquely downwards and backwards and curves linguallly. It probably had contact with the hyoid complex (Bronner *et al.*, 1990; Bronner, 1991) as in recent *Chrysochloris* and *Eremitalpa*, in which the angular process overlies the bulla, probably being a component of the seismic sensing system, employing the mandibles to transmit signals directly to the surface of the bulla. The mandibular condyle is rounded and posed at the end of a long apophysis somewhat above the level of the occlusal surface of the cheek teeth. It articulates with a well-defined glenoid fossa in the skull. There is a long retro-molar space and the coronoid process is steep and tall in front, but the rear margin does not descend much before sloping backwards towards the condylar apophysis. Mental foramina occur beneath the p/2-p/3 and below the contact between and p/4 and m/1.

Dentition



Figure 20. Right lateral view of the second skull of *Namachloris arenatans* (GSN Na 2) to show the teeth and the form of the coronoid process and condylar apophysis (scale: 5 mm).



Figure 21. A-D) GSN Na 6.12-6.15, stereo lateral views of incisiform teeth of *Namachloris arenatans* from Eocliff, EC 7 (scale: 4 mm).

Incisiform teeth

Upper central incisors of *Namachloris arenatans* are stout and tall pillar-like teeth (Fig. 20) which point downwards and slightly backwards, much as in extant golden moles. They are in contact inter-proximally, but are

separated by a short diastema from the succeeding tooth. Other incisiform teeth of the species have a tall, sharp pointed main cusp and a low, sharp hook-shaped distal cusp (Fig. 21).

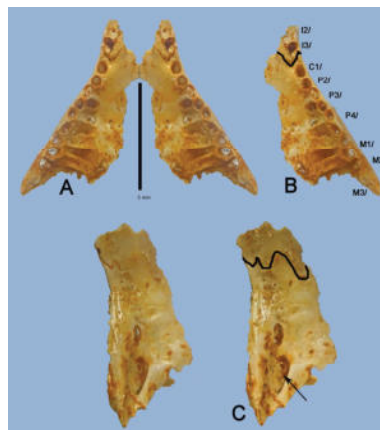


Figure 22. GSN Na 3 from Eocliff, EC 7, left maxilla and premaxilla of *Namachloris arenatans* showing the premaxillo-maxillary suture (black line) which helps resolve the upper dental formula. Arrow depicts the infra-orbital foramen. A) mirror image placed along part of the intermaxillary suture B) stereo palatal view with, C) stereo lateral view (scale: 5 mm).

There are four alveoli between the P3/ and the upper central incisor, one each for the I2/, I3/, the canine and the P2/ (Fig. 22). There is a short diastema between the upper central incisor and the second incisor.

The P3/ of *Namachloris* is a single cusped tooth with a compressed triangular occlusal outline posed on a single root in GSN Na 2, but with two roots in GSN Na 67 and three roots in GSN Na 3. There are shallow mesial and distal depressions in the buccal side of the crown of the P3/.

The P4/ of *Namachloris* has an irregular triangular occlusal outline with a prominent parastylar hook (Fig. 23). The protocone is lower than the paracone. The metastyle and parastyles are located at the ends of sharp crests that run from the apex of the paracone, the parastyle bending anteriorly to form a parastyle hook, the metastyle more or less in line with the protocone and paracone, thereby forming a blade-like structure. The metastyle fits snugly into the M1/ where the parastyle hook of the latter tooth curves anteriorly from the parastyle. The P4/ is as big

as the molars, but is bucco-lingually slightly narrower than them.

The upper molars of *Namachloris arenatans* are extremely zalambodont, but unusual for teeth of this type, and remarkably different from extant golden moles, the protocone dominates the crown, being bucco-lingually broader and taller than the complex comprising the paracone + metacone + parastyle + metastyle (Fig. 23-25). The metacone is reduced in stature and is close to the paracone. In occlusal view the protocone is short mesio-distally but broad bucco-lingually. The crown as a whole becomes mesio-distally longer on the buccal side where the parastyle hook and metastyle hook project outwards and mesially and distally respectively. In M1/ and M2/ the root beneath the protocone is large and bifid at its apex and often has a posterior groove indicating an underlying two-rooted morphology. What appears to have happened, which may be unique among mammals, is that in the upper molars, the paraconal root has shifted its orientation so that it fuses with the protoconal root.

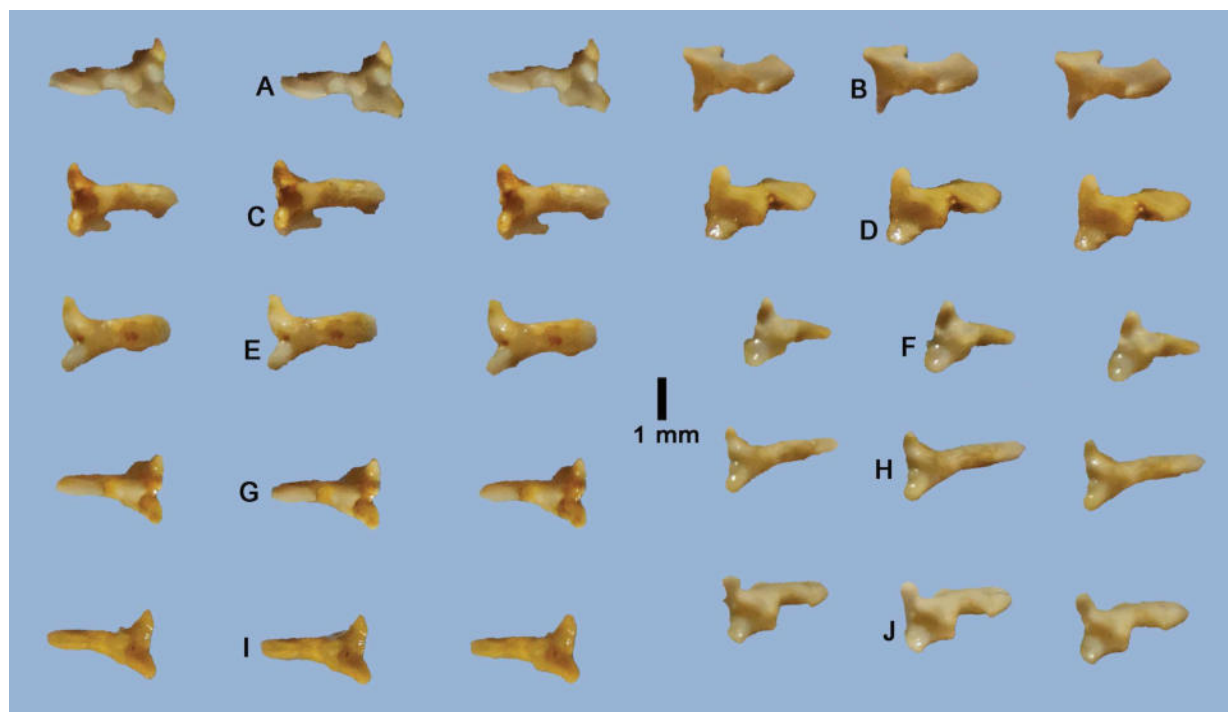


Figure 23. GSN Na 6.2-6.11, occlusal stereo triplet views of P4/ (F) and upper molars of *Namachloris arenatans* from Eocliiff EC 7 (A-E, G-J) mesial to top of image (scale: 1 mm).

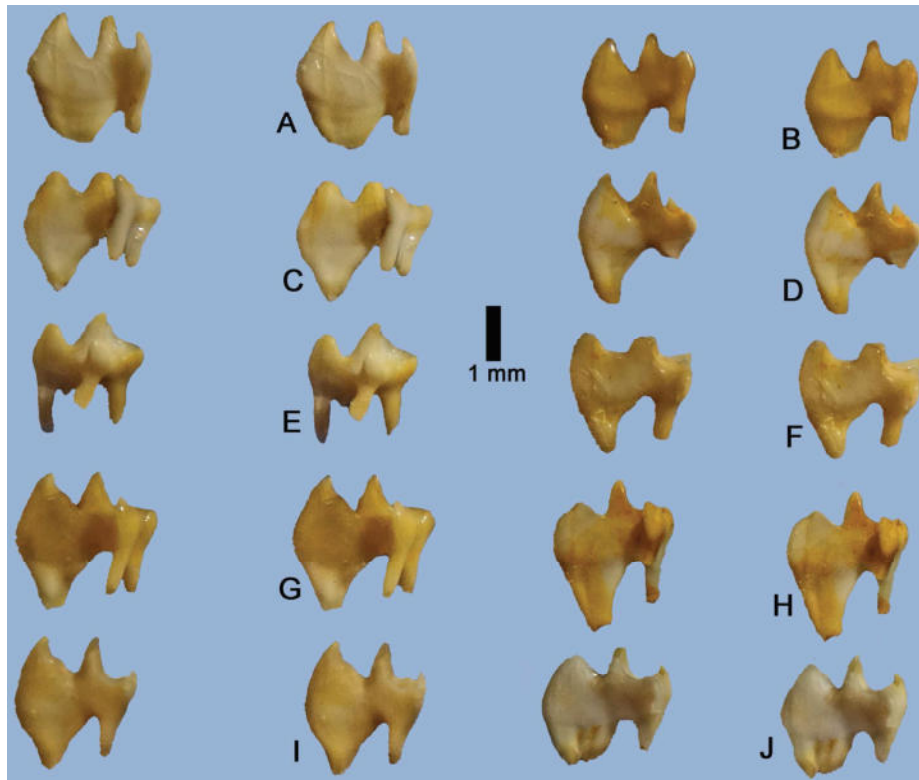


Figure 24. GSN Na 6.2 – 6.11, stereo mesial and distal views of P4/ (E) and upper molars (A-D, F-J) of *Namachloris arenatans* from Eocliff EC 7 (scale: 1 mm).

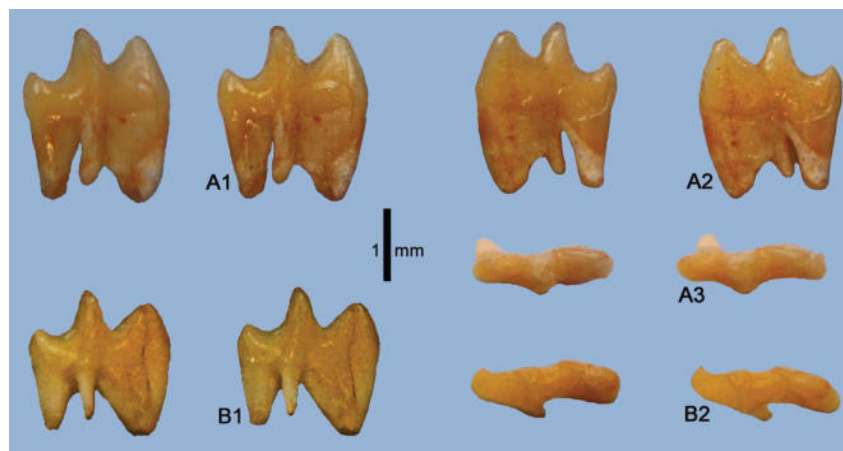


Figure 25. *Namachloris arenatans* right M3/s from Eocliff, EC 9, A) GSN Na 34, A1 – stereo distal view, A2 – stereo mesial view, A3 – stereo occlusal view; B) GSN Na 32, B1 - stereo distal view, B2 - stereo occlusal view (scale: 1 mm).

The upper third molar differs from the anterior ones by its highly mesio-distally compressed morphology resulting in a transverse undulating blade-like crown. The metacone and the root which supports it are reduced in dimensions. The parastyle is in line with the protocone and paracone, the metastyle is obsolete. The M3/ of *Namachloris* is not reduced in bucco-lingual dimensions relative to the other molars, unlike extant chryso-

chlorids such as *Eremitalpa*, *Amblysomus* and *Chrysochloris* which have M3/s that are considerably smaller than the M2/ (Asher & Sanchez-Villàgra, 2005; Butler, 1984).

The lower dental formula comprises three incisors, a canine, three premolars and three molars. The first lower incisor is tiny, the second one large, the third one small. The lower canine is large, the anterior premolars small and peg-like. The p/4 and the three

molars are subequal in length. The lower molars have a vestigial paraconid located close to the metaconid, but well developed blade-like protoconid and metaconid arranged such as to form a transverse blade with a v-shaped

notch in its apical edge corresponding to the junction between the two cusps (Fig. 26, 27). In the molars of *Namachloris* there is a prominent talonid about half as tall as the trigonid.

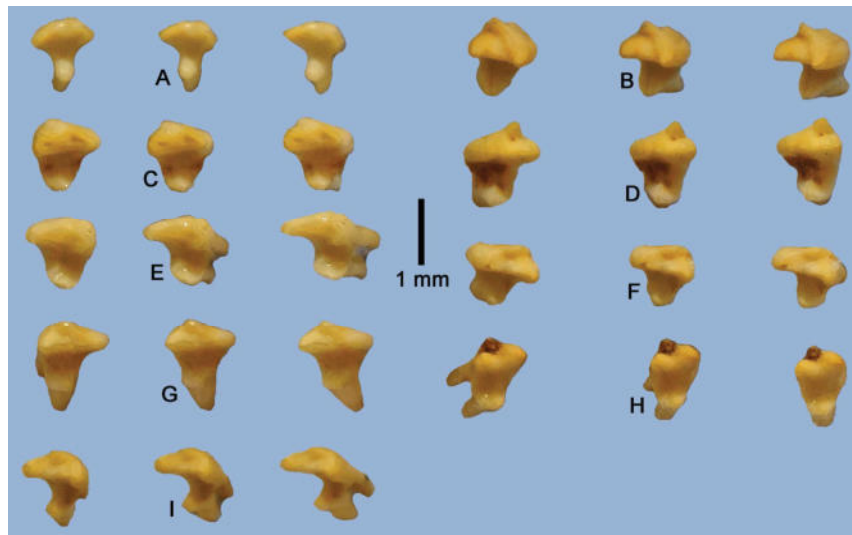


Figure 26. GSN Na 6, stereo triplet occlusal views of lower molars of *Namachloris arenatans* from Eocliff, EC 7 (scale: 1 mm).



Figure 27. A-C) GSN Na 6, stereo views of left lower molariform teeth of *Namachloris arenatans* from Eocliff, EC 7, 1 – distal, 2 – buccal, 3 – lingual, 4 – mesial views (scale: 1 mm).

Discussion

The dentition of *Namachloris arenatans* is zalambdodont, but unusual among mammals with such teeth, including extant chrysochlorids, the protocone is much the largest of the cusps of the upper molars. The protocone apex is as high as that of the paracone, and it is much broader bucco-lingually, and deeper apico-cervically than in molars of the potamogalid *Namagale* for example, and its root usually shows a bifid apex (rarely trifid) and is scored by a groove (or two grooves) indicating an incipient double-rooted underlying structure. The protocone root is however, not very tall and it tapers rapidly which gives it a triangular profile in mesial and distal views. The roots beneath the metastyle and parastyle are smaller and shorter than the protoconal root, and are rounded in section, pillar-like in form and vertical.

The dentition of *Namachloris* retains several primitive characters when compared to those of extant chrysochlorids. The upper third molars are not greatly reduced in dimensions compared to the M1/ and M2/, and the

protocones are large, not reduced or absent as in extant chrysochlorids. The metacone is present in M1/ and M2/ but is reduced in dimensions and is positioned close to the paracone. In the lower molars the talonids of *Namachloris arenatans* are well developed, contrasting strongly with the much reduced, or even absent talonids in extant *Chrysochloris* and *Eremitalpa*.

The upper central incisors of *Namachloris*, which are in contact inter-proximally, are large and point downwards and slightly backwards, as in extant chrysochlorids. The lower second incisor is much larger than the tiny i/1 and the small i/3, again as in extant forms. Thus the anterior dental battery was functionally quite similar to that of living golden moles which indicates that *Namachloris* probably had a comparable diet to that of extant chrysochlorids (termites, beetle larvae, small vertebrates). The posterior cheek teeth, with their combination of relatively large talonids (a primitive feature) and taller transverse blades formed of the protoconid and metaconid with vestigial paraconid, appear to have been suited to a diet similar to that of extant golden moles.

Post-cranial skeleton *Manubrium*



Figure 28. Manubria of *Namachloris arenatans* from Eocliff, EC 7, A) GSN Na 10, B) GSN Na 9, 1) stereo ventral views, 2) stereo dorsal views (scale: 5 mm).

The manubrium of *Namachloris arenatans* has an elongated anterior process, a strong ventral keel and is not overly concave dorsally (Fig. 28). It resembles that of *Chrysochloris* in most features but a significant difference consists of the less concave dorsal surface (Asher & Avery, 2010).

Synsacrum

The only synsacrum available from Eocliff consists of four vertebrae fused together with signs that a fifth was originally present, perhaps only partly fused at the time of death (Fig. 29). The morphology of the bone resembles that of *Chrysochloris* (Asher &

Avery, 2010). The dorsal processes of the synsacral vertebrae are fused together, leaving only small to tiny foramina between them. The

dorsal ridge of the synsacrum curves ventrally at the 4th and 5th vertebra, indicating that the tail was probably reduced in length.

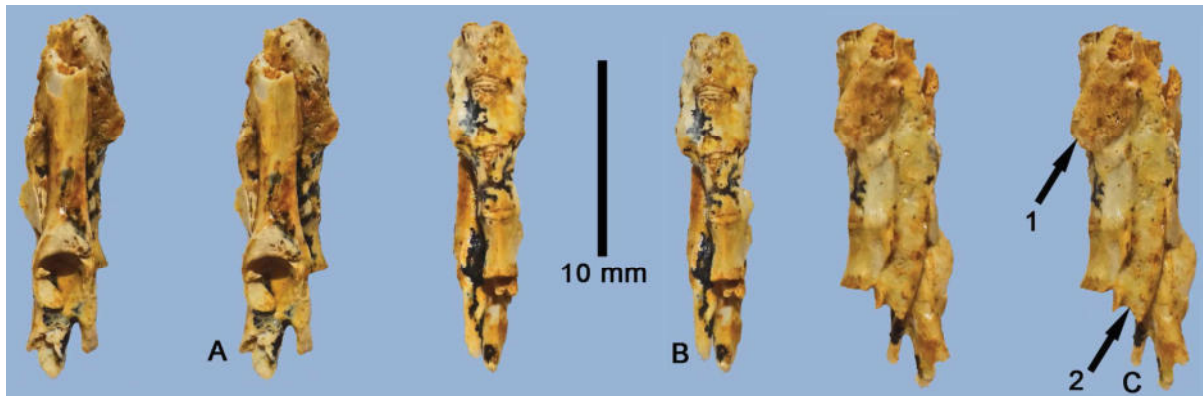


Figure 29. GSN Na 10, synsacrum of *Namachloris arenatans* from Eocliff, EC 7, A) lateral stereo view of os coxa attached to synsacrum but rotated at an angle of ca 45° from its natural position (see part of the auricular surface beneath the os coxa), B) ventral stereo view, C) lateral stereo view of synsacrum; 1) auricular surface for attachment of the os coxa, 2) fused dorsal processes of the synsacral vertebrae (anterior to the top of the image for the synsacrum) (scale: 10 mm).

1st Rib

The first rib of *Namachloris arenatans* resembles that of *Chrysochloris* (Asher & Avery, 2010) (Fig. 30). It has a bulbous

vertebral articulation, a somewhat narrower, but strongly developed neck, and a broad spatulate, concave, paddle-shaped distal end which articulates with the manubrium.

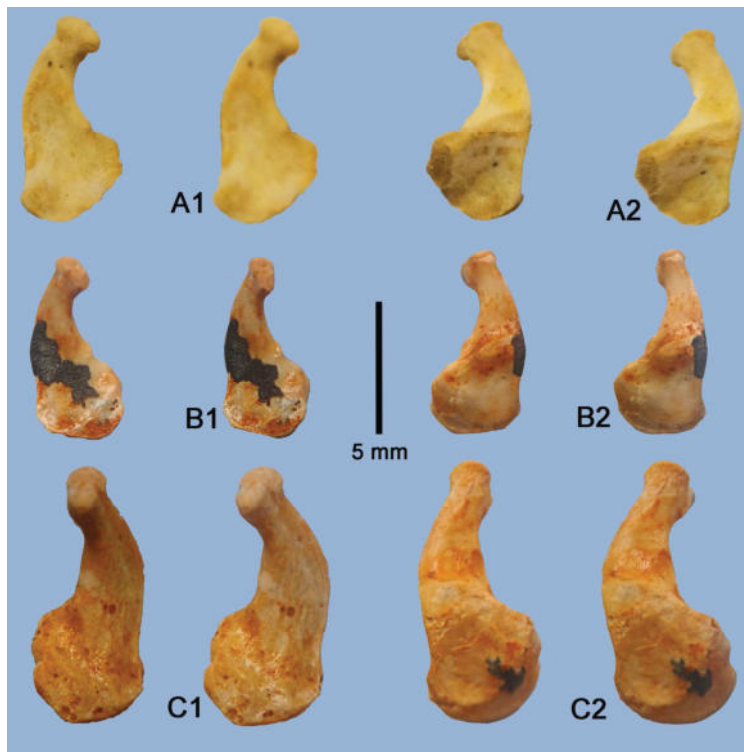


Figure 30. GSN Na 14, first ribs of *Namachloris arenatans* from Eocliff, EC 7. A) left rib B) left rib, C) right rib; 1- stereo medial views, 2- stereo lateral views (scale: 5 mm).

Pectoral girdle and limb
Scapula

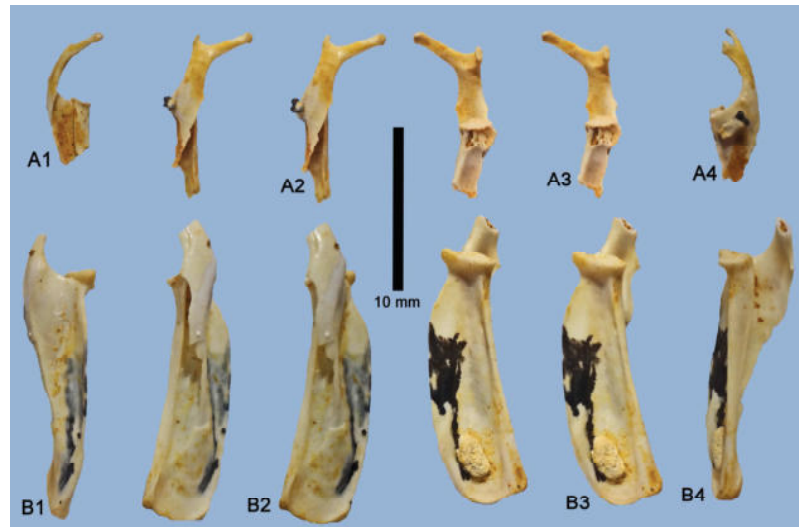


Figure 31. GSN Na 71, scapulae of *Namachloris arenatans* from Eocliff, EC 8, A) glenoid and acromion of right scapula, A1 – posterior view, A2 – stereo lateral view, A3 – stereo medial view, A4 – posterior view, B) left scapula blade with glenoid, spine and base of acromion, B1 – anterior view, B2 – stereo lateral view, B3 – stereo medial view, B4 – posterior view (scale: 10 mm).

The scapula of *Namachloris arenatans* has an elongated but narrow blade, a tall recurved spine, with an enormous extension of the acromion overhanging and extending well beyond the glenoid cavity (Fig. 31). The acromion bifurcates into two tines, a shorter one in line with the scapular spine (acromion) which articulated with the clavicle via a cartilaginous joint, and a longer one (the metacromion) that diverged posteriorly. The neck of the scapula is clearly defined with the base of the glenoid process flaring outwards all round. The posterior border of the blade is quite straight and has a reinforced beaded margin visible on both the lateral and the medial sides. The medial surface of the blade is concave but not very deep, even at its deepest opposite the spine. The scapular spine,

in contrast, is tall and curved posteriorly, thereby overhanging a substantial posterior scapular fossa. The vertebral end of the spine fades into the blade well before the vertebral border is reached. The vertebral border is flat, short and straight in its posterior part, slightly convexly curved anteriorly.

Clavicle

The clavicle of *Namachloris arenatans* has a rod-like proximal part that articulates (via a cartilaginous joint) with the shorter of the two acromial tines of the scapula, and a blade-like distal part that extends to the manubrium (Fig. 32). In overall shape the clavicle resembles an old-fashioned barber's razor.

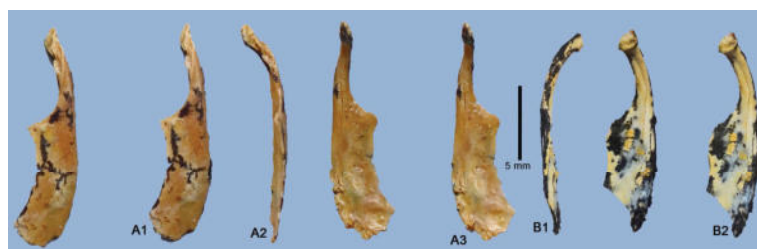


Figure 32. Clavicles of *Namachloris arenatans*, A1) GSN Na 64 from Eocliff, EC 1, stereo dorsal view, A2) lateral view, A3) stereo ventral view; B1) GSN Na 71 from Eocliff, EC 8, lateral view, B2) stereo ventral view (scale: 5 mm).

Humerus

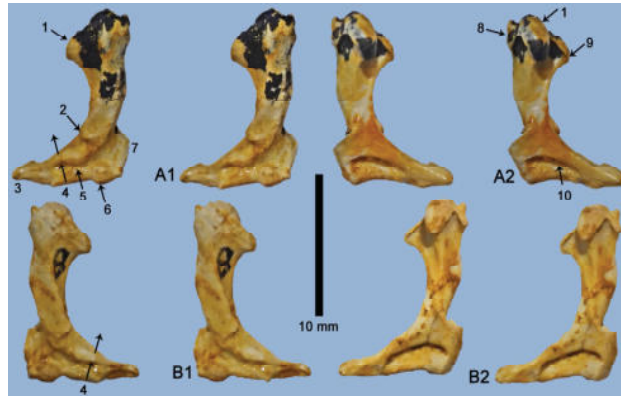


Figure 33. GSN Na 11, humeri of *Namachloris arenatans* from Eocliff, EC 7, A) left humerus, B) right humerus. A1 and B1) stereo cranial views, A2 and B2) stereo caudal views. 1 – Head, 2 – Pectoral tubercle at base of humeral crest, 3 – Entepicondyle, 4 – Entepicondylar foramen, 5 – Supratrochlear fossa, 6 – Trochlea, 7 – Ectepicondyle, 8 – Lesser tuberosity, 9 – Greater tuberosity, 10 – Olecranon fossa (scale: 10 mm).

The humerus of *Namachloris arenatans* is almost as broad distally as it is long due to the extreme elongation of the medial epicondyle and the broadening of the lateral condyle (Fig. 33). The summit of the head lies above the levels of the medial and lateral tuberosities, both of which are thickened and extend distally, the medial one forming a flange which significantly broadens the proximal end of the bone. In caudal view, the humeral head shows a prolongation resembling a “beak” which overhangs the femoral neck. The deltoid tuberosity is located low down on the shaft at the lower end of an elongated

deltoid crest. The shallow bicipital groove is high up on the shoulder of the bone. The medial condyle or caput of the distal articulation is rounded, hemispherical and is set off from the lateral condyle by a clear intercondylar groove. The lateral epicondyle is tall, forming a steep wall above and slightly lateral to the caput. The tiny entepicondylar foramen is located at the root of the medial epicondyle and above the lateral condyle. The olecranon fossa is medio-laterally broad, but does not have a fenestra. Indeed the bone flooring the fossa appears to be thick and compact.

Ulna

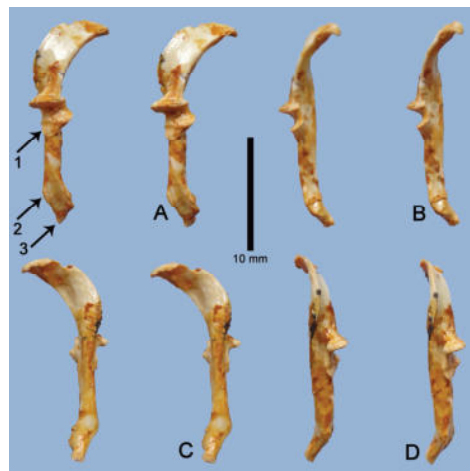


Figure 34. GSN Na 15, right ulna of *Namachloris arenatans* from Eocliff, EC 7, A) dorsal stereo view, B) medial stereo view, C) palmar stereo view, D) lateral stereo view. 1 – facet for proximal end of radius, 2 - flange from which the interosseus ligament originates which inserts into a depression in the distal end of the radius, 3 – styloid process (scale: 10 mm).

The ulna of *Namachloris arenatans* possesses an extremely elongated, compressed and curved olecranon process which is as long as the subsigmoid portion of the bone (Fig. 34). It curves medially and forms a broad blade-like surface. The sigmoid notch has a prominent lateral projection proximally and a medial extension distally. The articulation for the proximal end of the radius is small and is positioned on the dorsal aspect of the bone immediately beneath the sigmoid notch. The diaphysis of the ulna is straight and robust. The

ulna shaft broadens slightly at its distal end, forming a low, rounded flange from one side of which the interosseous ligaments originate which insert into a vertical depression in the distal end of the radius shaft. Distally, the ulna ends in a styloid process which is offset medially from the axis of the shaft. The styloid process at the distal end of the ulna may fit into a rounded articular facet on the triplex bone which suggests that a carpal bone may have become fused to the distal epiphysis of the ulna.

Radius

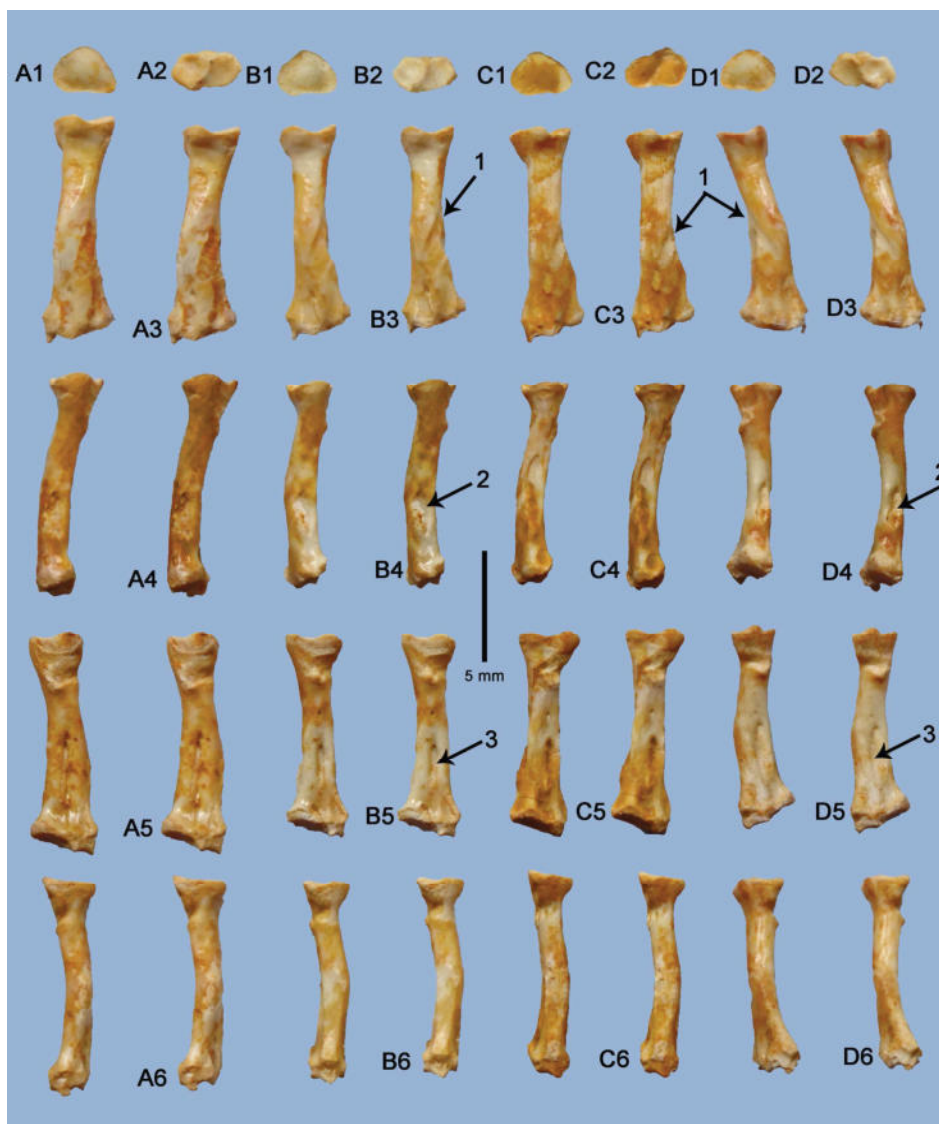


Figure 35. GSN Na 16, radii of *Namachloris arenatans* from Eocliff, EC 7, A-C) right D) left. A1-D1) proximal views, A2-D2) distal views, A3-D3) stereo cranial views, A4-D4) stereo medial views, A5-D5) stereo palmar views, A6-D6) stereo lateral views. 1 – Oblique groove on cranial surface of diaphysis, 2 – depression for the interosseous ligament emanating from the flange on distal end of the ulna, 3 – vertical groove in distal surface of diaphysis (scale: 5 mm).

The radius of *Namachloris arenatans* is a robust bone, slightly cranially convex with a prominent groove along the distal half of the diaphysis on its palmar side (Fig. 35). Unlike *Eremitalpa* and *Chrysochloris* (Asher & Avery, 2010) in *Namachloris* there is no distal bone bridge over this groove. The proximal articular facet for the ulna is small and is accompanied by a basal swelling in the neck. The proximal facet for the humerus is a slightly concave, round-cornered triangle. The distal facet for the carpal bones has two

concave surfaces separated by an oblique crest. Low down on the medial side of the diaphysis there is a vertical depression into which the interosseous ligament from the flange on the distal end of the ulna inserted. The cranial surface of the diaphysis shows an oblique groove descending the distal half of the bone starting just above the depression for the interosseous ligament – a similar groove occurs in *Eremitalpa* and *Chrysochloris* and is due to pressure from a tendon, possibly the *extensor carpi radialis*.

Flexor Bone

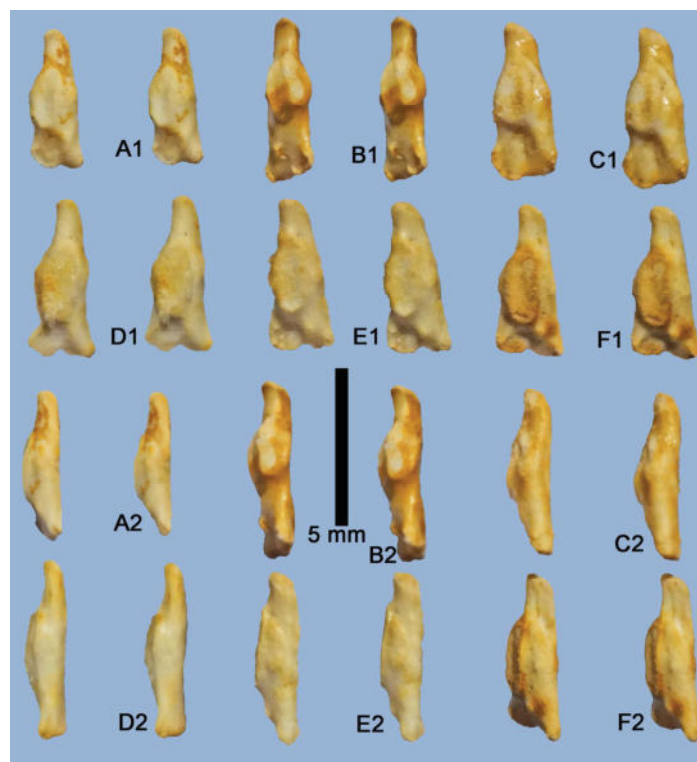


Figure 36. GSN Na 17 flexor bones of *Namachloris arenatans* from Eocliff, EC 7. A-F) stereo images of 1 - articular face, 2 – lateral surface (scale: 5 mm).

The flexor bone of *Namachloris arenatans* is slightly shorter than the radius, is narrow proximally and broader distally where it has a tall narrow articular surface with three rounded swellings, possibly sesamoids that have been incorporated into it (Fig. 36). On its internal side, the “diaphysis” of the flexor bone has a swelling which contacts the radius and ulna, thereby producing two confluent articular surfaces, one for each of the forearm bones. The form and extent of this articular swelling

appears to be quite variable in the available sample, but it is always present. In extant chrysochlorids the flexor bone is the ossified part of the *tendon flexor digitorum communis profundus* and it has a simple distal termination, highly divergent from the expanded form in *Namachloris*, and it doesn’t possess the central swelling with articular surfaces for the radius and ulna which occurs in the latter genus.

Trapezium-trapezoid-metacarpal II Complex (the “ttm” or “Totem” bone)

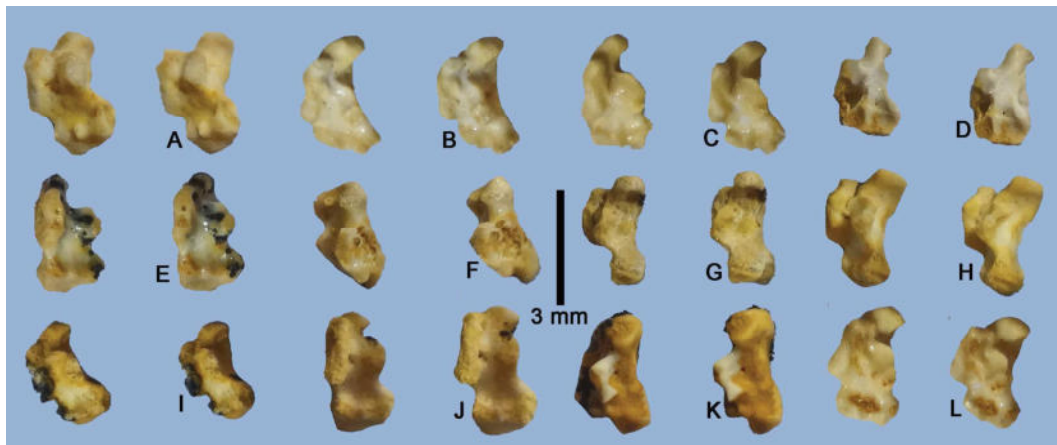


Figure 37. GSN Na 74, stereo views of bones of *Namachloris arenatans* from Eocliff, EC 7, interpreted to be a complex bone comprised of carpals 1 and 2 fused with metacarpal II (scale: 3 mm).

The second metacarpal of the extant dune shark, *Eremitalpa*, is fused with carpals 1 and 2 (trapezium and trapezoid) (Kindahl, 1949) here called the “ttm” (totem) bone Fig. 37). The equivalent bone from Eocliff has a

complex surface morphology with knobs and depressions that fit into corresponding topography in the triplex bone, thereby forming an interlocking mass of bone supporting digits II and III.

Triplex Bone

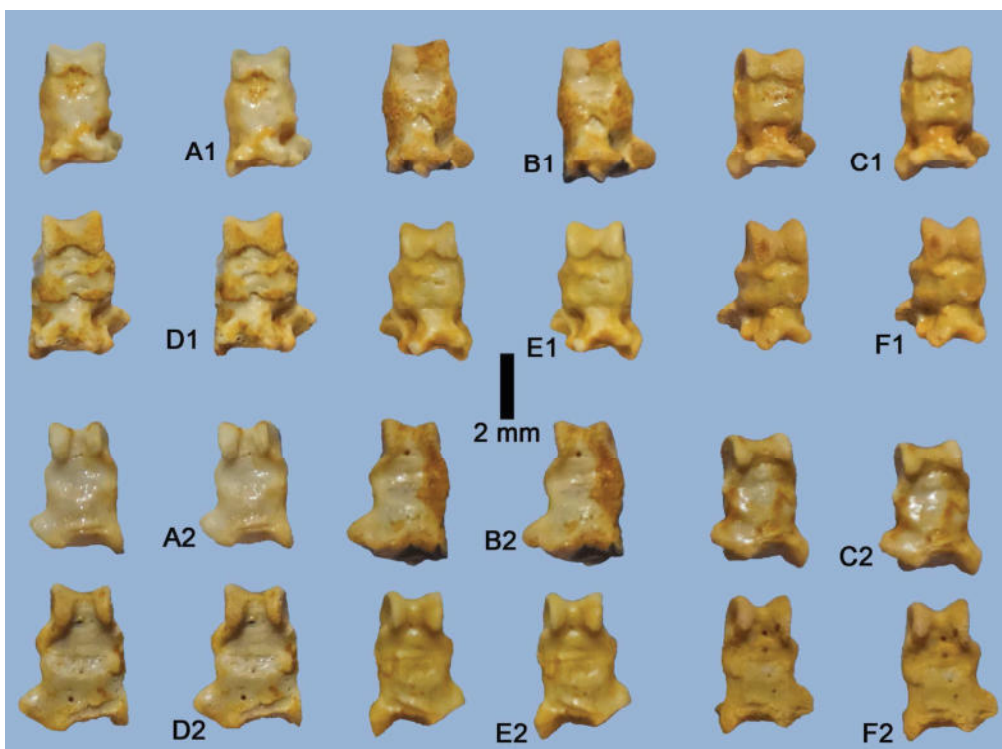


Figure 38. GSN Na 18, triplex bones of *Namachloris arenatans* from Eocliff, EC 7, 1 – stereo dorsal views, 2 – stereo palmar views (scale: 2 mm).

The triplex bone of *Namachloris arenatans* is an extraordinary example of functional fusion of foot bones in a mammal. It comprises metacarpal III, and the first and second phalanges of digit III (Fig. 38). Its name “triplex” bone derives from the fact that three bones are fused together into a single complex, just as the name “duplex” bone of chalicotheres derives from the fact that two bones are fused together, in the latter case the first and second phalanges.

The zones of fusion between the three bones are clearly discernible in some specimens where rough ridges undulate across the dorsal surface of the shaft. The proximal end of the triplex bone (ie metacarpal III) has a complicated three-dimensional zone of articular facets for the styloid process of the ulna and the distal articular complex of the flexor bone. There may also be an articular contact with the totem bone. The result is an interlocking

Third phalanges

There are two kinds of terminal phalanges in *Namachloris arenatans*. The most obvious ones and the most commonly preserved are the large terminal phalanges of manual digit III. The second type comprises smaller versions of the first which are quite common and probably come from digits II and IV, or from the foot.

The terminal phalanges of digits II, III and IV are bifid apically, with a prominent deeply concave proximal articular surface with a central ridge corresponding to the groove and

articulation between the forearm and the hand. The “diaphysis” of the triplex bone (in reality the first phalanx) is medio-laterally broader than its distal end (in reality the second phalanx). The distal articular surface comprises a pulley with two well defined parallel lips spaced far apart. The form of the distal pulley indicates that movement of the third phalanx was strictly confined to the extension / flexion plane, and that radial or ulnar deviation movements were minimised. The lips of the pulley extend well over 180°, meaning that the third phalanx could rotate on the second one over a large angle.

In *Eremitalpa*, the triplex bone is shortened to such an extent that the part comprising the first phalanx is vestigial (Kindahl, 1949). In *Namachloris* the part comprising the first phalanx is subequal in dimensions to the MC III and is larger than the part comprised of the second phalanx.

lips of the second phalanx (or triplex bone in the case of digit III). The base of the phalanges on the volar side has a prominent bony pad pierced by foramina laterally and medially. The volar surface of this swelling is concave. In lateral view these phalanges show a dorsal articular beak that overhangs the proximal articulation of the bone. On the dorsal side of these phalanges, there are narrow, shallow grooves which run from the base of the split in the phalanx backwards both medially or laterally. Similar grooves occur in the terminal phalanges of *Chrysochloris* and *Eremitalpa*.

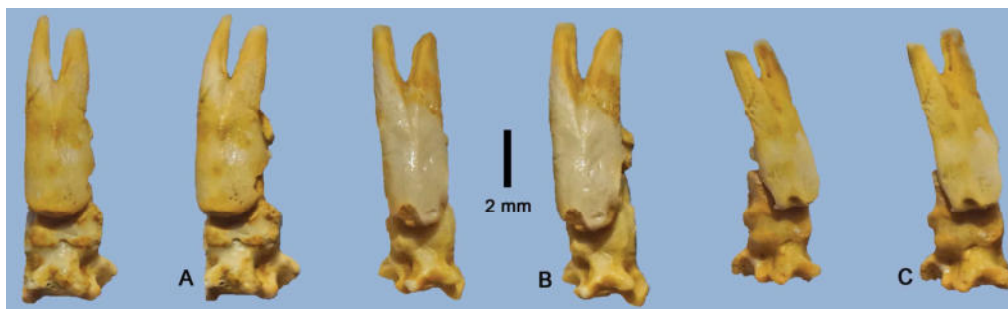


Figure 39. GSN Na 18, triplex bones and GSN Na 19, 3rd phalanges of manual digit III of *Namachloris arenatans* from Eocliff, EC 7, in articulation, dorsal stereo views (scale: 2 mm).

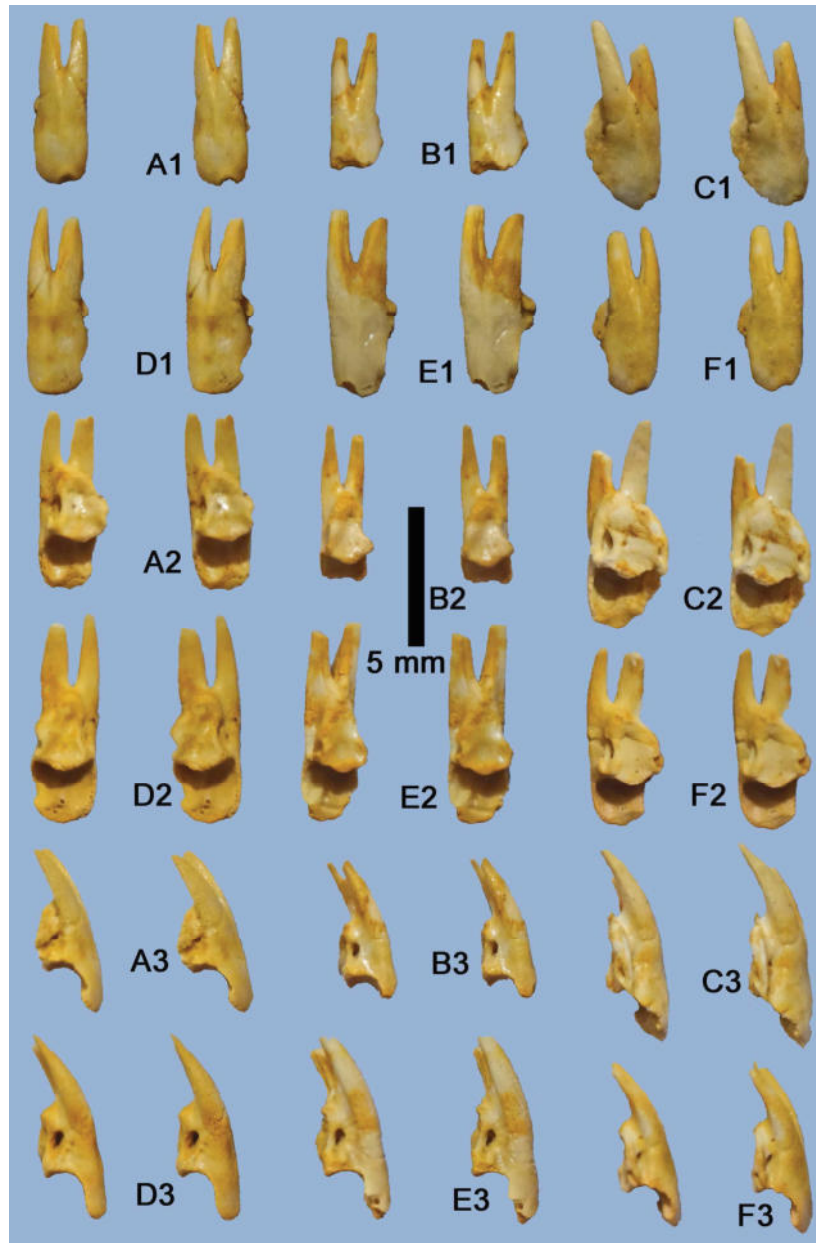


Figure 40. GSN Na 31, 3rd phalanges of manual digit III, *Namachloris arenatans* from Eocliff, EC 9, 1 – stereo dorsal, 2 – stereo palmar, 3 – stereo lateral views (scale: 5 mm)

Small 3rd phalanges



Figure 41. GSN Na 29, small third phalanges of *Namachloris arenatans* from Eocliff, EC 7, 1 – stereo dorsal views, 2 – stereo lateral views (scale: 3 mm).

Pelvic girdle and limb
Os coxa

The os coxa of *Namachloris arenatans* is in most features like that of extant *Chrysochloris* (Asher & Avery, 2010) but it differs from it in one important respect (Fig. 42). A roughened ovoid cranio-caudally elongated surface at the cranial end of the os coxa (ilium) articulates with the auricular surface of the synsacrum, as is usual in

mammals, but there is in addition a large rugose area on the inner surface of the ischium at the level of the acetabulum which is absent in extant *Chrysochloris*, probably for insertion of an enlarged supraspinosus ligament, a highly unusual structure for such a small mammal.

The obturator foramen is relatively small, and in some specimens is partly infilled with bone, leaving small fenestra.

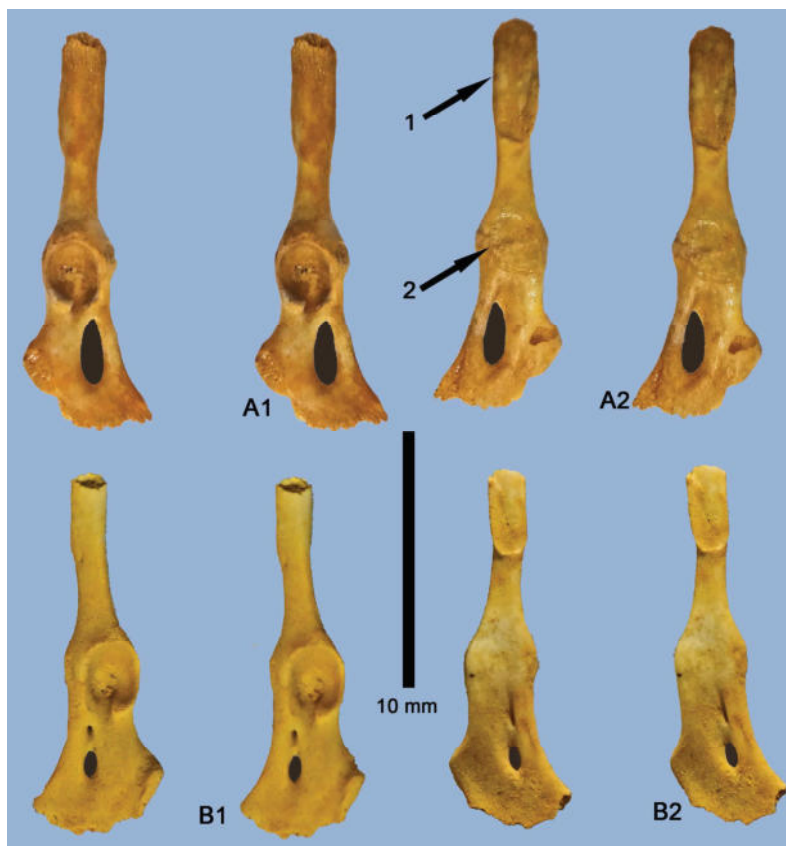


Figure 42. GSN Na 45, os coxae of *Namachloris arenatans* from Eocliff, EC 9, A1) lateral stereo view, A2) medial stereo view, B1) lateral stereo view, B2) medial stereo view. 1) roughened surface of the ilium which contacts the auricular surface at the anterior part of the synsacrum, 2) roughened area on the inner surface of the ischium probably for attachment of the supraspinosus ligament (scale: 10 mm).

Femur

The femur of *Namachloris arenatans* is cranio-caudally rather flat, and there is a marked bend in the middle of the diaphysis (Fig. 43). The apex of the greater trochanter is at about the same level as the head of the femur, and the digital fossa is small but quite deep. The neck is short and the lesser trochanter is strongly developed, contributing to the relatively great width of the bone. The third trochanter is well developed and is

located in the middle of the shaft just beneath the bend in the diaphysis and it extends well down the shaft, thereby broadening the distal part of the bone to a significant extent. The distal condyles of the femur are cranio-caudally flattened and the patellar groove is slightly oblique. Even though the distal epiphysis in *Namachloris* is flattened, it is not nearly as flat as that of *Eremitalpa*, and thus in the former taxon it represents an incipient stage of flattening.

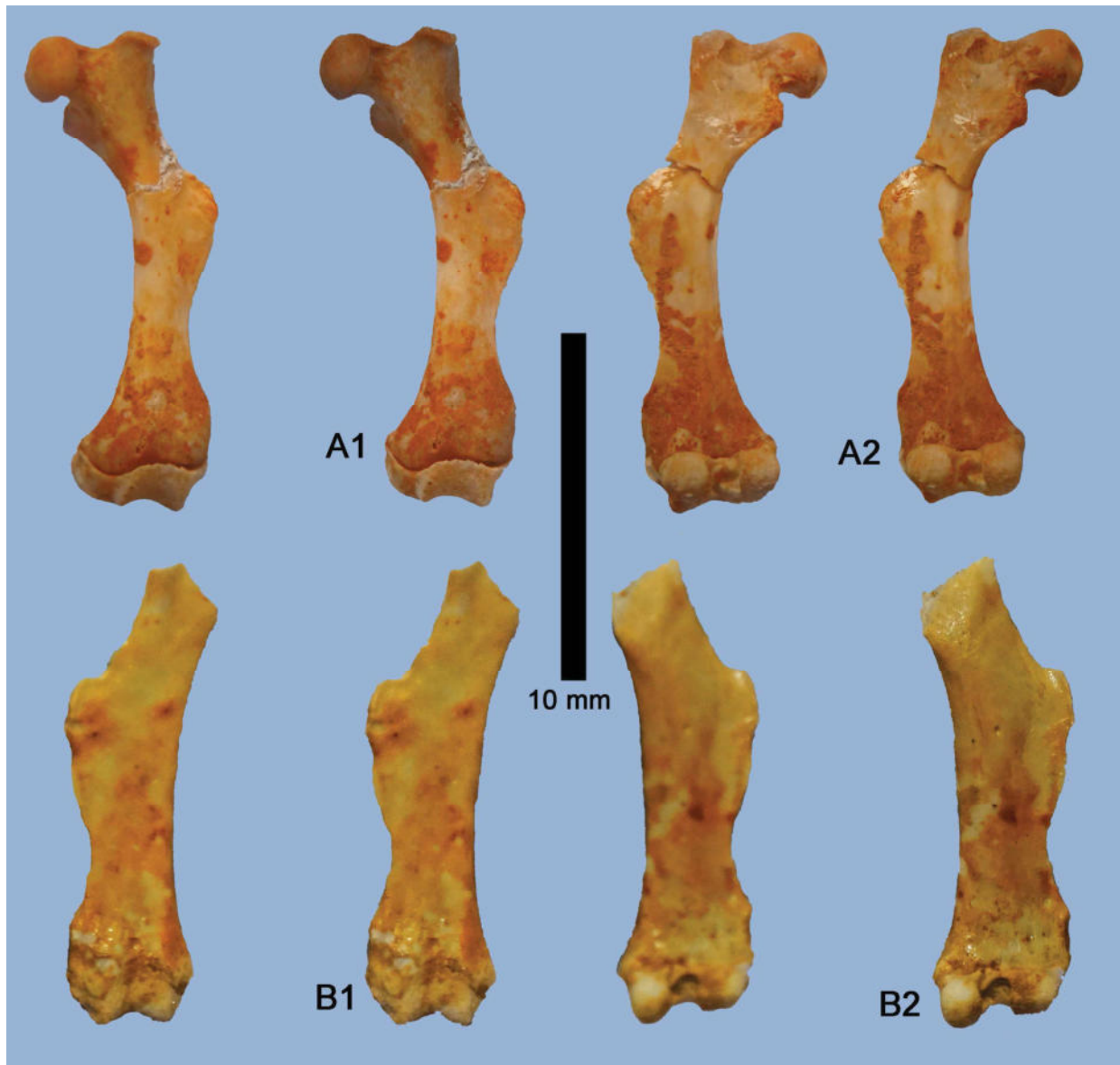


Figure 43. Femur of *Namachloris arenatans*. A) GSN Na 25.1, left femur, B) GSN Na 25.2, right femur lacking the head, neck and greater and lesser trochanter; 1 – stereo cranial views, 2 – stereo caudal views (scale: 10 mm).

Patella

The patella of *Namachloris arenatans* is a robust bone with short proximal and distal

beaks, which gives it a short oval outline (Fig. 44). The articular surface is only slightly curved and the body of the bone is thick.

Tibio-Fibula

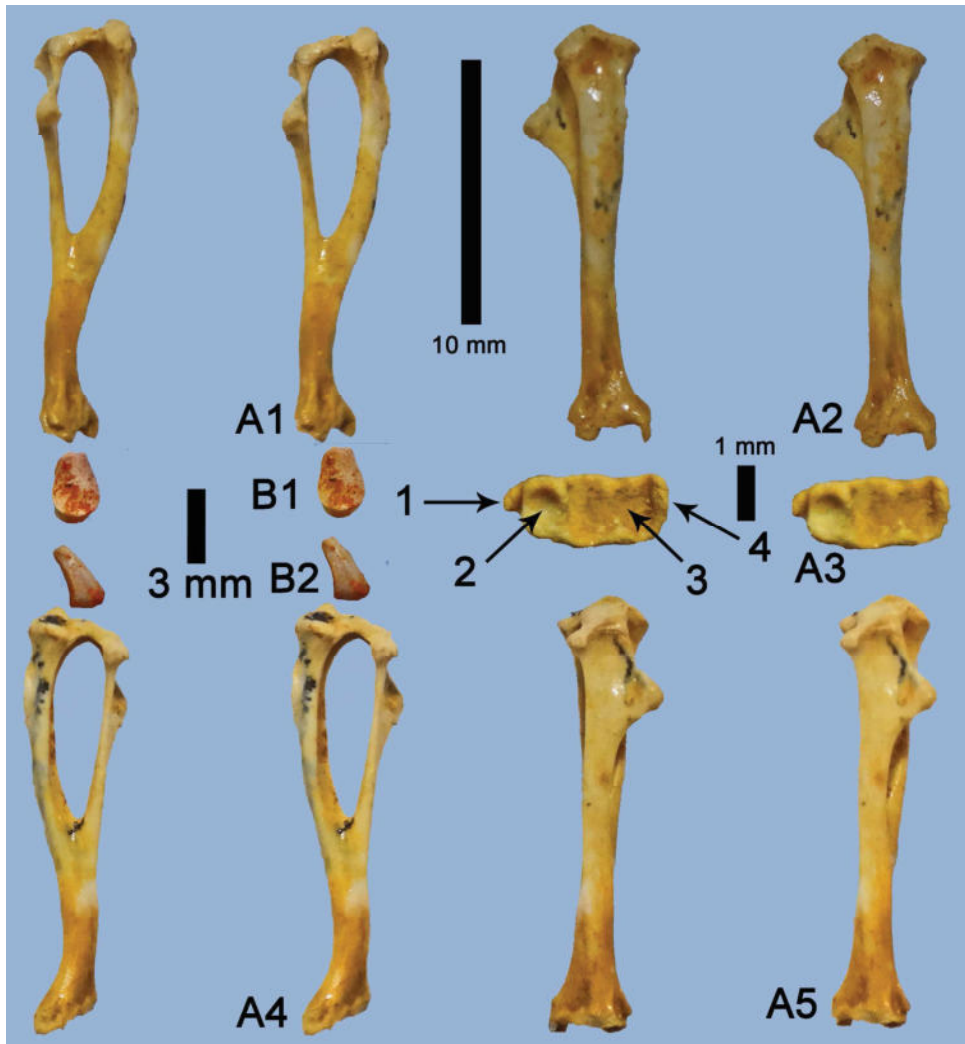


Figure 44. A) GSN Na 73, left tibia and fibula of *Namachloris arenatans* from Eocliff, EC 8, A1) stereo medial view, A2) stereo cranial view, A3) stereo distal view, A4) stereo lateral view, A5) stereo caudal view. 1) flange on fibula bordering the groove for tendons, 2) calcaneal facet, 3) talar facet, 4) medial malleolus of the distal tibia (scales : 10 mm and 1 mm). B) GSN Na 74, patella of *Namachloris arenatans* from Eocliff, EC 7, B1) stereo articular view, B2) stereo lateral view (scale: 3 mm).

The tibia and fibula of *Namachloris arenatans* are fused proximally and distally, with a prominent inter-osseous space between the two bones in the proximal half (Fig. 44). The tibia is convexly curved in its proximal half but straightens out in the distal half where it is fused with the fibula. The tibial crest on the cranial aspect of the bone is low and short. The proximal half of the fibula has a large triangular process that points medially.

The lateral malleolus at the distal end of the fibula has a low but sharp flange of bone

that borders the groove for the tendons, and the distal end of the lateral malleolus has a hemispherical depression which articulates with a ball-like articular facet in the calcaneum. The relatively shallow talar facet has a low central ridge with rounded pulley margins and a low medial malleolus. Evidently the ankle joint could permit small eversion and inversion movements as well as the more important extension and flexion movements.

Talus

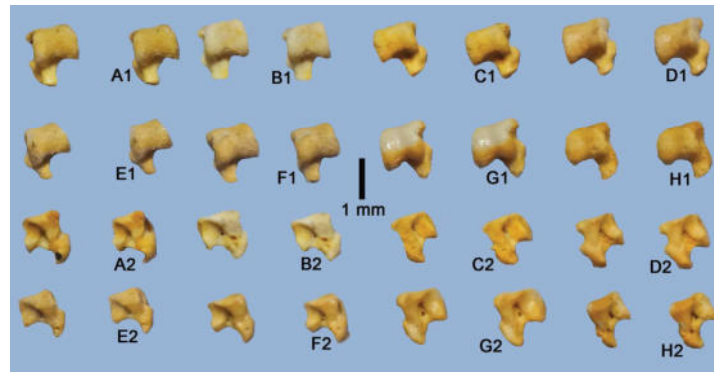


Figure 45. GSN Na 27, tali of *Namachloris arenatans*. 1 – stereo tibial views, 2 – stereo calcaneal views (scale: 1 mm).

The talus of *Namachloris arenatans* is notable for its short neck and reduced head (Fig. 45). The pulley-like articulation for the distal tibia has a low central groove and the lips of the pulley are low and rounded, a conformation that would permit significant inversion and eversion movements. There are shallow depressions on the medial and lateral sides of the trochlea, indicating the same possibility of inversion and eversion movements. The calcaneal aspect of the talus shows two articular facets, one concave, the other slightly convex for the sustentaculum of

the calcaneum. These two facets are separated by a groove at the base of which is a deep fossette (probably a remnant of the astragalar foramen) which does not however pierce through the bone (unlike *Eremitalpa* in which it does). The lightly convex tibial facet extends slightly onto the short neck of the talus but is separated from the head by a rough patch of bone. The head of the talus is small and is medio-laterally compressed which results in a tall ovoid articular facet for the navicular.

Calcaneum



Figure 46. GSN Na 26, calcanea of *Namachloris arenatans*. 1 – stereo talar views, 2 – stereo caudal views (scale: 4 mm).

The calcaneum of *Namachloris arenatans* is remarkable for the presence of a ball-like articular facet on its dorsal side (talar side) which articulates with the distal end of the fibula (Fig. 46). This articular facet is slightly more distally positioned than the talar facets are. There is a relatively open, flat sustentaculum for the talus, a tuber calcis which is about as tall as the body of the calcaneum and a short part for the navicular. The apex of the tuber calcis is not swollen, usually being narrower than its base. The peroneal process is distally positioned. The open morphology of the talar articulation and

the hemispherical articulation for the distal fibula indicates that the ankle joint was capable of eversion and inversion movements as well as the more important rotatory movements associated with flexion and extension of the foot. The brevity of the body of the calcaneum, especially of the part that articulated with the navicular indicates that the ankle and foot were compact, and not proximo-distally elongated. The overall impression is that the ankle was functionally similar to that of extant *Chrysochloris*, a committed sand-swimmer.

Metatarsals

Metatarsals attributed to *Namachloris arenatans* are short and stout, the proximal ends of some of them have a lateral projection as in *Eremitalpa* (Kindahl, 1949) and the distal

end is robust (Fig. 47). On the plantar surface of the diaphysis there is a distal ridge which blends into a subtle rounded ridge on the lower surface of the distal epiphysis. Dorsally there is no trace of a ridge on the distal articulation, the articular surface being smooth and rounded.

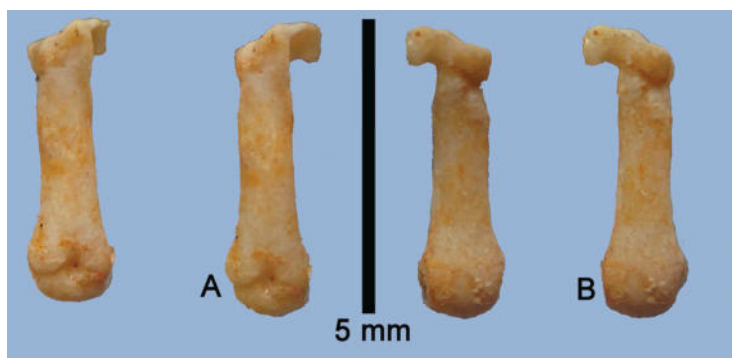


Figure 47. GSN Na 89, metatarsal attributed to *Namachloris arenatans* from Eocliff, EC 8. 1 – stereo dorsal view, 2 – stereo plantar view (scale 5 mm).

Discussion

Given their Eocene age, the most striking aspect of the chrysochlorids from Eocliff is their highly derived skeletal morphology, many of the post-cranial bones superficially resembling those of extant golden moles such as *Eremitalpa* Roberts, 1924, and *Chrysochloris* Lacépède, 1799. However, closer inspection reveals the presence of a suite of primitive features in most of the skeleton and dentition of *Namachloris*. Nevertheless, there can be little doubt that the Eocliff chrysochlorids were fully adapted to sand-swimming and to a diet requiring a zalambdodont dentition, probably had a mandibular-hyoid contact and possessed a seismic acoustic system. The nose pad was

already developed; inferred from the presence of a narial flange on the premaxilla.

Furthermore the terminal phalanges of the hands and feet are bifid apically and supported claws in which the volar surfaces are concave and overlap slightly to produce a concave spade-like surface for “sand-compression” during the flexion phase of locomotion, combined with sharp forward edges for “cutting through sand” during the extension phase when the hands are pushed forwards, terminal phalanges pointing directly anteriorly, in preparation for the next flexion phase of movement - in other words, the hands of *Namachloris* were adapted for “swimming” through loose or poorly consolidated sand, much as in the extant “Namib Sand Shark” *Eremitalpa granti* (Gasc *et al.*, 1986). They

were not burrowers in the sense that mole-rats, moles, armadillos and other strictly fossorial mammals are, which can dig through compact or consolidated substrates such as soil. Chrysochlorids can “swim” or “burrow” through loosely consolidated or friable substrates but are defeated by consolidated ones (Jackson, 2007). The musculo-skeletal modifications of sand swimmers are, as a consequence, radically divergent from those of truly fossorial mammals such as talpids and armadillos which can burrow through compact soils.

For the first time, fossil clavicles and flexor bones of chrysochlorids are described. These bones possess an extraordinary morphology, the clavicle of *Namachloris* is rod-like in its proximal part where it articulates via a cartilaginous joint with the shorter of the two scapular acromial apophyses and distally it flattens out into a razor-like form that likely extended to the suitably modified manubrium,

probably providing increased surface for muscle insertions. The 1st rib is massive and short with a broad, thick, paddle-shaped distal part, as in extant chrysochlorids, indicating that the front of the rib cage was already reduced in volume (concave) as in extant forms of the family. The flexor bone of *Namachloris* differs from that of extant chrysochlorids in having a complex spatulate distal part showing articular facets for some of the carpal-metacarpals. Furthermore, in its middle it possesses a swollen bony pad sporting two facets where it pressed against the radius and ulna, a morphology unknown in extant chrysochlorids. Unlike *Eremitalpa* and *Chrysochloris*, both of which possess a raised bony bridge over the volar groove near the distal end of the radius (Fig. 48), *Namachloris* does not have such a structure. From this it is concluded that the divergence between *Eremitalpa* and *Chrysochloris* post-dates the age of *Namachloris*.

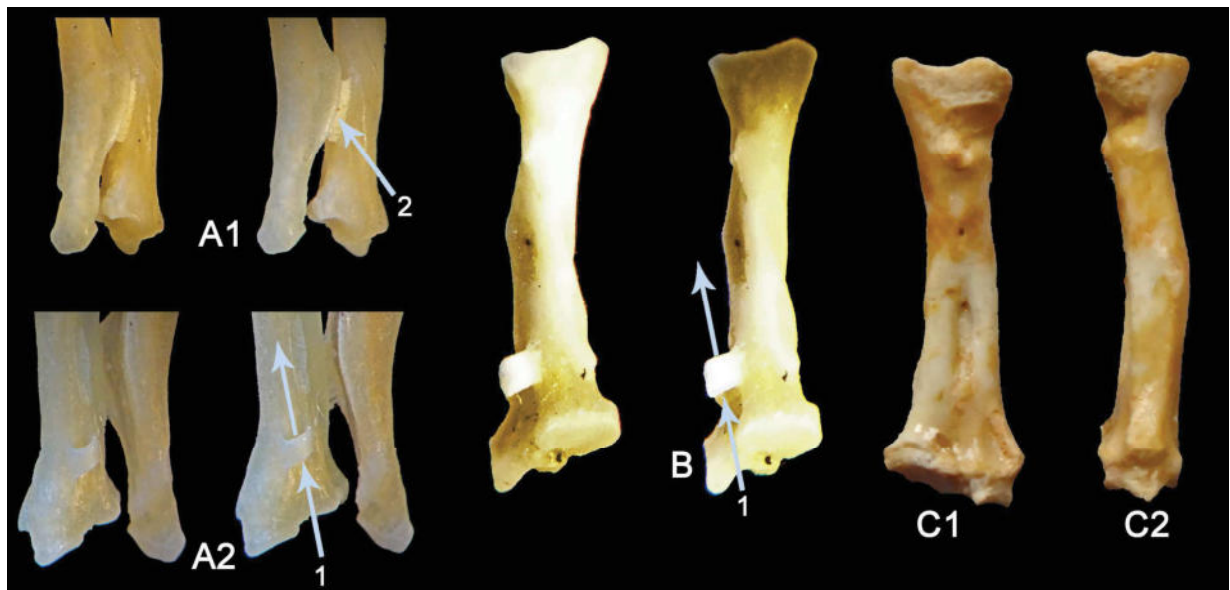


Figure 48. A-B) Stereo images of distal radius and ulna of extant *Chrysochloris asiatica*, arrows show 1 – the osseous bridge on the volar side of the radius near the distal end, and 2 – the interosseous ligament running between the lateral flange of the distal ulna and a depression in the distal end of the radius. C) radius of *Namachloris arenatans*, C1 – volar, and C2 – side view to show absence of bony bridge (not to scale).

The extraordinary features of the post-cranial skeleton of the Eocliff chrysochlorid do not end there. The distal humerus is medio-laterally broadened, the olecranon process of the ulna is elongated, medially curved and enlarged, and the distal part of the ulna has a flange from which the interosseous ligament extends towards the radius, inserting into a tall, narrow, depression on the distal radius, thereby binding the distal ends of the radius and ulna tightly together. As in extant chrysochlorids, *Namachloris* has a flexor bone forming the “third” bone of the forearm, first commented upon by Cuvier, 1817 in the Cape Golden Mole: it is the ossified *tendon flexor digitorum communis profundus* (D’Alton, 1831; De Blainville, 1839-1864; Kindahl, 1949; Vaughan, 1972; Vaughan *et al.*, 2000). The flexor bone in *Namachloris* is almost as long as the radius and shows a swelling in the middle with pressure facets where it pressed against the radius and ulna, and distally it possesses three small articular knobs possibly for the triplex bone and the “tm” (trapezium – trapezoid - second metacarpal) complex.

The third manual digit is an extraordinary osteological complex, comprised of two bones, a proximal one, here termed the “triplex” bone, and a distal one consisting of the enlarged terminal phalanx with a solid volar complex and a long bifid apex. The triplex bone comprises the IIIrd metacarpal and 1st and 2nd phalanges which have fused together (Kindahl, 1949). The “triplex” bone is so-called, not only because it is composed of three bones fused together but also to conform etymologically with the name of the “duplex” bone of chalicotheres (clawed perissodactyls) which comprise fused first and second phalanges. In both *Namachloris* and chalicotheres, the distal articulation for the bifid third phalanx has widely spaced, medio-laterally compressed medial and lateral pulley lips on the volar aspect. Even more peculiar is the concavity on the base of the triplex bone which possibly articulated with the flexor bone and the complex surface which articulates with a highly complicated bone comprised of the fusion of carpals 1 and 2 with metacarpal II. In brief, the humerus, radius, ulna, flexor bone, triplex bone and third phalanx of digit III, and the associated complex of digit II, combined to form

a robust articular chain running from the elbow joint to the claws, with its movements strongly constrained to the flexion-extension plane, and reducing the possibility of ulnar or radial deviation of the hand at the wrist joint and at the interphalangeal articulations, although pronation and supination of the ensemble would not have been greatly restricted.

The hind limbs of *Namachloris arenatans* were less spectacularly modified than the fore limbs, but there are nevertheless several intriguing skeletal modifications. The femur is flattened cranio-caudally with a well-developed third trochanter at about mid-length which is positioned where there is a distinct bend in the diaphysis of the femur, and the tibia and fibula are fused proximally and distally with a large inter-osseous space between them located in the proximal half of the bone. The distal end of the bone is peculiar in that the fibula has a small, sharp lateral apophysis or flange, and there is a hemi-spherical concavity in its distal aspect which articulates with a ball-like facet of the calcaneum. The talus has a tiny head and its tibial articulation has a shallow pulley groove and its margins are rounded and its side impressed, a combination which indicates that the ankle joint was free to move in many directions, mainly parasagittal (extension – flexion), but permitting significant eversion and inversion movements. The metatarsals of *Namachloris* possess a lateral flange on the proximal end similar to those of extant *Eremitalpa*. From all this evidence we conclude that the spectrum of skeletal modifications in *Namachloris* is compatible with a sand-swimming mode of locomotion.

Biogeography

The presence of abundant chrysochlorid fossils at Eocliff, Namibia, provides fuel for the debate about the biogeographic affinities of Southern African faunas (Pickford, 2008c). The domination of chrysochlorids, potamogalids, macroscelidids and tenrecids among the non-rodent terrestrial small mammals is a striking aspect of the Eocliff fauna, much as it still is today in the subregion (with the exception of tenrecids) (Roberts, 1951; Meester *et al.*, 1986). The abundance and diversity of these three

former families in the Eocene and at present (Bronner, 1991, 1996, 2000) indicates that Southern Africa was at the centre of their radiation, whilst their rarity and low diversity in Eastern and Northern Africa indicates that the septentrional part of the continent was peripheral to the stage on which their main evolutionary activity was played out.

The same applies to the Cape Flora, which, despite its small areal extent, comprises one of the world's six Floral Biogeographic Realms. Among the invertebrates, the terrestrial gastropod fauna of the Southwest African Region has been dominated by acavids since the Lutetian (*Dorcasia*, *Trigonephrus*) with little evidence of other groups dispersing into the region (Pickford, 2008b; Pickford *et al.*, 2008a) and none of this family dispersing to the rest of the continent, although it is known to occur in Madagascar. It is thus not fanciful to start speaking of a Cape Faunal Realm as an entity distinct from, but with some links to, the Ethiopian Realm in the same way that we employ the term Cape Floral Realm for the vegetation of the sub-region.

The environmental substrate that links the Cape Small Mammal Fauna, the Cape Terrestrial Gastropod Fauna and the Cape Flora together consists of juxtaposed subtropical and "mediterranean" conditions, spanning the winter rainfall to summer rainfall climatic transition zone, combined with long term semi-arid to arid palaeoclimates. These conditions have been present more or less continuously in South-western Africa since the Lutetian-Bartonian, although there is evidence that there were considerable latitudinal shifts in the position of the winter rainfall belt, sometimes hundreds of km further north than today, sometimes further south (Pickford *et al.*, 2014).

Relationships to other Chrysochloridae

Previously, the earliest supposed chrysochlorid fossil was *Eochrysochloris* from the Rupelian of the Fayum, Egypt (Seiffert *et al.*, 2007). However, the type species *Eochrysochloris tribosphenus* has a well developed paraconid in the lower molars, well separated from the metaconid, hence the specific name. In all the Namibian fossils, which are several

million years older than the Egyptian ones, the paraconid is vestigial and is close in front of the metaconid. This means either than *Eochrysochloris* is not a chrysochlorid, or that it is an extremely dentally primitive member of the family that persisted in Egypt long after other members of the family had developed the extant pattern of the trigonid morphology. Asher & Avery (2010) were of a similar opinion about the Egyptian fossils.

Prochrysochloris miocaenicus from the Early Miocene of East Africa (Butler & Hopwood, 1957) is still rather poorly known, but shows the fully derived trigonid morphology in the lower molars (Butler, 1984) typical of the family. *Namachloris* from Eocliff, Namibia, however, has large protocones in the upper molars, which are either small or absent in Miocene and younger forms.

Late Miocene and basal Pliocene Chrysochloridae from Langebaanweg, South Africa, reveal the presence of essentially modern forms, albeit with sufficient distinctions to be classified in different species from any of the extant forms, of which 21 species are currently accepted (Asher & Avery, 2010) arranged in nine genera (Asher *et al.*, 2010). Other Plio-Pleistocene fossil chrysochlorids from karst deposits of South Africa are also easily integrated into extant genera (Broom, 1941; De Graaf, 1957).

On the basis of the Bartonian, Early Miocene, Late Miocene and Plio-Pleistocene records of chrysochlorids from Southern Africa, it is concluded that this corner of the continent has been a centre of chrysochlorid distribution since at least the Bartonian, and that the supposed Rupelian form from Egypt (*Eochrysochloris*) is probably not relevant to understanding chrysochlorid evolution, the earliest known definite member of the family known outside southern Africa being early Miocene *Prochrysochloris* from Kenya and Uganda.

Systematics and Phylogeny

The realisation that "Insectivora" and "Lipotyphla" (Dobson, 1883; Butler, 1972, 1978, 1985, 1988) are not natural phylogenetic or systematic categories (Stanhope *et al.*, 1998) has resulted in a burst of debate concerning the

appurtenance of tenrecs, otter-shrews and golden moles which are now usually considered to be part of a mammalian clade of African origin, the Afrotheria (Asher, 2001, 2003; Asher *et al.*, 2003, 2010; Asher & Sanchez-Villagra, 2005; Douady *et al.*, 2002; Sanchez Villagra *et al.*, 2007; Seiffert, 2007, 2010; Seiffert *et al.*, 2007; Tabuce *et al.*, 2008).

Much of the recent debate has been based on molecular evidence with only a minor amount of data gleaned from comparative anatomy (Asher, 1999; Seiffert, 2010). Furthermore, anatomical characters in the various cladistic analyses are dominated by dento-gnathic features, with only a few post-cranial characters being taken into account. In addition, the molecular and anatomical characters are obtained predominantly from extant taxa. These restrictions have introduced a bias into the analyses which has rendered aspects of the debate somewhat contentious (Asher, 2003), but despite the shortfalls of the data bases, a consensus appears to have emerged that tenrecs and golden moles are more closely related to each other than either of them are to other afrotherians (Macroscelidea, Tubulidentata, Sirenia, Hyracoidea and Proboscidea) (Roca *et al.*, 2004; Seiffert, 2010). The hypothesis that tenrecs and golden moles are afrotherians has not seriously been challenged by any of the recent authors who have commented on the issue. The Eocliff evidence throws this consensus of opinion into doubt.

Namachloris arenatans from Eocliff is surprisingly modern in many aspects of its cranial, dentognathic and post-cranial skeleton, which indicates that Chrysochloridae is an extremely ancient family which diverged from

Conclusions

The Eocliff Limestone has yielded a rich and diverse small mammal fauna of Late Eocene age. Among the fauna is a new genus and species of Chrysochloridae, *Namachloris arenatans*.

All the post-cranial modifications observed in Late Eocene *Namachloris* indicate that it was well adapted for swimming through loose or poorly consolidated sand.

other afrotherians well before the Late Eocene. The other “insectivores” from Eocliff, show affinities to potamogalids (*Namagale grandis*) and tenrecids (*Sperrgale minutus* and *Arenagale calcareus*) which suggests that there was a separation between the African potamogalids and the Madagascan tenrecids substantially earlier than the age of the Eocliff deposits (Late Eocene : Bartonian).

Seiffert (2010) hypothesised a Late Cretaceous dichotomy between tenrecs and golden moles, but he had no evidence older than the Early Oligocene, which translates into the existence of lengthy ghost lineages (some 20 – 30 million years duration). The Eocliff deposits yield a great deal of evidence concerning early chrysochlorid and potamogalid and tenrecid anatomy but the fossils are only a few million years older than the earliest previously available samples from the Early Oligocene of the Fayum, Egypt, and thus they do not suffice to reduce the duration of the ghost lineages in a substantial way. Nevertheless, the Eocliff fossils do reveal that, by the Bartonian, the Potamogalidae, Tenrecidae and Chrysochloridae were remarkably divergent in cranial, dental and post-cranial anatomy, which in turn indicates ancient dichotomies between them, as postulated by Seiffert (2010).

The other conclusion is that the potamogalids, tenrecids and chrysochlorids may be less closely related to Afrotheria than current hypotheses suggest, raising the possibility that their inclusion in Afrotheria does not correctly reflect their phylogenetic positions nor their origins.

The narial flange of *Namachloris arenatans* indicates that it possessed a nose pad, the skull is sharp forwards and broad distally and the orbits are small, all of which are adaptations for swimming through loose or loosely consolidated sand (Gasc *et al.*, 1986; Rautenbach, 1982; Fielden *et al.*, 1990, 1992; Perrin & Fielden, 1999). The enlarged and bulbous incus indicate the possession of an acoustic apparatus based primarily on sensing

seismic signals (Mason, 2003a, 2003b; Narins & Willi, 2012). The dentition is extremely zalambdodont, even if it shows several primitive features when compared with extant chrysochlorids (large protocones dominating the upper molars and large talonids in the lower molars for example). This indicates that the prey of *Namachloris* was probably quite similar to that of extant Golden Moles, comprising mainly termites such as *Psammodermes* (Pickford, 2006, 2008a) or other soft invertebrates (beetle larvae) or even small vertebrates (young of geckos or lizards, for example).

The fact that *Namachloris arenatans* is older than *Eochrysochloris tribosphenus* and already had a fully zalambdodont dentition renders it unlikely that the latter taxon from the Fayum, Egypt, is a chrysochlorid. This means that, apart from Southwestern Africa, the family Chrysochloridae is unknown from Palaeogene deposits in the rest of the continent.

Finally, the fact that *Namachloris* skeletal remains are common in fossilised owl pellets at Eocliff, and that many of the individuals were juveniles when they died, indicate that the species was a frequently preyed

upon by owls, which in turn suggests that by the Late Eocene *Namachloris* was probably already adapted to a nocturnal or crepuscular daily activity rhythm, like most extant chrysochlorids (Rautenbach, 1982; Rathbun & Rathbun, 2006; Jackson, 2007).

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