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NEW GOLDEN MOLES (AFROTHERIA, CHRYSOCHLORIDAE) FROM THE EARLY PLIOCENE OF SOUTH AFRICA

Robert J. Asher and D. Margaret Avery

ABSTRACT

We describe new material of fossil golden moles (Chrysochloridae) from the early Pliocene site of Langebaanweg, South Africa. This site has produced hundreds of isolated craniodental and postcranial elements, all of which are easily identifiable as chrysochlorid. Based on size and morphology, at least three species are represented in this assemblage, two of which are represented by material of sufficient quality to name. Based on relative abundance, humeral and mandibular types can be associated with other material. Craniodentally, the most common Langebaanweg species closely resembles the extant Cape golden mole, *Chrysochloris asiatica*, but differs in showing a relatively narrow distal humerus, proportionally similar to that of the extant *Eremitalpa granti*. A second, rarer species is represented by two well-preserved mandibles that exhibit a stout, enlarged lower second incisor, a robust mandibular corpus, and is associated with a less common humeral type that resembles living *Chrysochloris*. At least one additional species is represented by a small number of relatively large humeri, femora, and scapular fragments. Because it lacks any craniodental representation, it is not named in this paper. We tentatively suggest that the relatively narrow distal margin of the humerus of the new, *C. asiatica*-like species may have been adapted to a habitat similar to that of the modern *E. granti*, a "sand-swimming" golden mole currently known from northwestern South Africa and southern Namibia.

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INTRODUCTION

In the third edition of *Walker's Mammals of the World*, Bronner and Jenkins (2005) list 21 species of recent golden moles (Chrysochloridae, Afrotheria), all but three of which are known from the southern African mainland in the five countries at or below the 20th parallel. Two species (*Chrysochloris stuhlmanni* and *Calcochloris leucorhinus*) are known from equatorial localities in and near Cameroon, DRC, and the countries surrounding Lake Victoria. A third "northern" taxon, *Calcochloris tytonis*, is represented by a jaw and partial skull from a single owl pellet from Somalia (Simonetta 1968).

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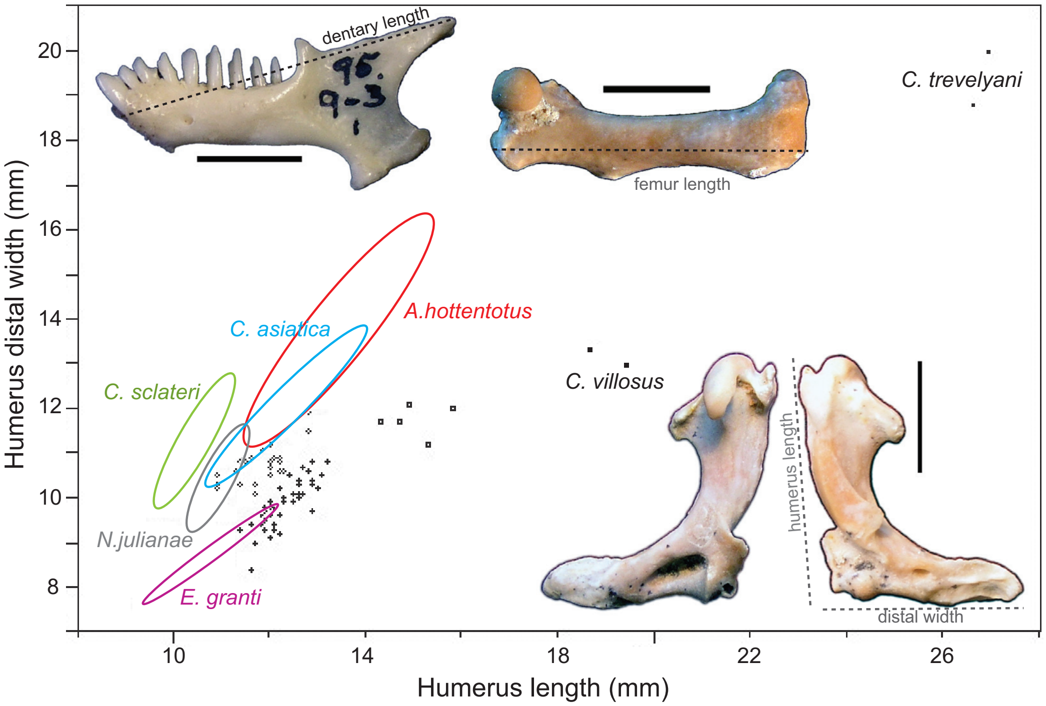

FIGURE 1. Humerus lengths and widths across golden moles. Modern taxa (except for *Chrysospalax*) are represented by 95% confidence circles encompassing each color-coded distribution (individual data points not shown). Solid crosses represent *C. arenosa*; open crosses represent *C. bronneri*; open squares represent unnamed, large humeral morphotype from Langebaanweg. Measurements are indicated by left dentary of *C. asiatica* (BMNH 95.9.3.1), right femur of indeterminate Langebaanweg chrysochlorid (SAM-PQL 28549), and humerus of *C. bronneri* (SAM-PQL 70258). Scale bars indicate 5 mm.

Extinct golden moles of unquestionable family-level affiliation are limited to just four named species: *Prochrysochloris miocaenicus* (Butler 1984), *Proamblysomus antiquus, Chlorotalpa spelea* (Broom 1941), and *Amblysomus hamiltoni* (De Graaff 1957). The former is from early Miocene localities in Kenya, and the latter three are from the Plio-Pleistocene of South Africa. Mein and Pickford (2003) referred additional remains from the middle Miocene of Namibia to *Prochrysochloris sp.* Golden mole fossils are not uncommon from late Miocene to Recent fossil localities in southern Africa (cf. Avery 2000). However, they are rarely assigned to an explicit, named species due to the fragmentary condition of their remains.

Seiffert et al. (2007) described a fragmentary jaw that they argued might be the oldest relative of the group, *Eochrysochloris tribosphenus,* from the Eo-Oligocene of northern Egypt. They referred two specimens to this species, which (as the specific epithet implies, and in contrast to any known chrysochlorid) show basined talonids on p4 and m2 (other cheek teeth are incompletely known). No features of the highly derived coronoid or angular processes of chrysochlorids are adequately preserved in these specimens to unambiguously infer their anatomy. It is reasonable to expect that chrysochlorid fossils will be found at some point during the Paleogene and in some place on the African continent, such as the Eocene-Oligocene boundary in northern Egypt. Nevertheless, the anatomical basis for doing so is not yet definitive.

Biogeographically, it is even less surprising to document the occurrence of fossil chrysochlorids in the early Pliocene of Western Cape Province, South Africa. Here we describe isolated, but intact and numerous, cranioskeletal elements of golden moles from the site of Langebaanweg. Although without direct associations between elements, the numerically most common jaws, maxillae, ear ossicles, pelvic, fore- and hind-limb elements closely resemble in size and shape the living Cape golden mole, *Chrysochloris asiatica*. An exception to this generalization is that the most common humeral type shows a significantly narrower distal humerus (i.e., the distal margin from the tip of the medial epicondyle, including the trochlea and capitulum, to the supinator crest; see Figure 1) than that exhibited by *C. asiatica* and most other golden moles. In addition, two out of over 100 jaw fragments (including over 40 relatively complete dentaries) preserving anterior teeth and/or alveoli show an enlarged, very robust second lower incisor. Finally, a small number of limb elements (but no craniodental elements) represent a substantially larger golden mole than the extant *C. asiatica*. We argue that these differences justify the assignment of the Langebaanweg chrysochlorid fossils to at least three species, two of which are represented by sufficiently high-quality material to be named in this paper.

MATERIALS AND METHODS

Over the past several decades, work carried out at Langebaanweg by staff and volunteers at the Iziko South African Museum in Cape Town has resulted in the collection of thousands of vertebrate fossils. The majority of these specimens had been deposited under high-energy conditions and excavated as overburden by commercial mining operations. Although some excavations were undertaken, material was mainly collected opportunistically by, and under the direction of, Q. Brett Hendey, who was the original and long-time principle investigator of the site (e.g., Hendey 1967, 1974, 1981). Additionally, fossiliferous sediment was deposited in "dumps" to allow later hand recovery of specimens by paleontological teams. Micromammal remains were also recovered through screenwashing. Hence, individual localities at Langebaanweg generally are not in situ and likely represent at least some degree of time-averaging.

Chrysochlorids possess a highly distinctive skeleton, elements of which are easily distinguishable from other mammalian species present at Langebaanweg. Hundreds of catalogued chrysochlorid skeletal fragments are represented. We analyzed the majority of relatively complete dentaries, maxillae, premaxillae, mallei, humeri, radii, ulnae, femora, tibiae-fibulae, sacra, innominates, and sterna. We base our specific diagnoses on those elements that display clear variation in size and/or qualitative morphology, namely, dentaries, humeri, and femora. Other elements from Langebaanweg, such as maxillary and maxilla-premaxillary fragments and some postcrania, are homogeneous in anatomy and size, and based on comparisons with extant species are proportional to the individuals represented by the most common dentary and humeral morphotype. We therefore include them in the hypodigm for the more common of the two new species described here.

Abbreviations: AMNH, American Museum of Natural History, New York; **KM**, Amathole Museum, King Williams Town; **KNM**, National Museums of Kenya, Nairobi; **NRM**, Naturhistoriska Riksmuseet, Stockholm; **SAM,** All collections in the Iziko South African Museum (formerly the South African Museum) have this prefix, followed by a hyphen and the relevant sub-collection acronym. **SAM-PQL,** fossils described herein are housed in the Cenozoic Collections of Iziko South African Museum. At the time of collection the material was accessioned in the Department of Quaternary Palaeontology (hence, "PQ"), and each site was assigned an acronym, in this case "L" for Langebaanweg. **SAM-ZM,** Iziko South African Museum modern mammals. **TM**, Transvaal Museum, Pretoria.

ASSOCIATION OF ELEMENTS

Based on comparative anatomy and size, mandibles (discussed in more detail in the specific diagnoses), and femora can be divided into two morphotypes, humeri into three.

A distribution of length in all measured Langebaanweg humeri exhibits a clear break at 14 mm (Figure 1), with the majority (65 of 70 measured specimens) below this amount. Among these smaller humeri, there is another gap between those showing a length/distal width ratio near 1.39 (43 individuals) and those with one near 1.21 (22 individuals; see Figure 2). The five large humeri also show a length/distal width ratio of 1.39 (Figure 2). The only extant chrysochlorids we observed to approach the most common humeral dimensions among the Langebaanweg material are *Eremitalpa* and *Chrysospalax*, both of which have a relatively narrow distal humeral margin (for a chrysochlorid). The former overlaps slightly with the smaller size range of the most common humeral morphotype at Langebaanweg, whereas *Chrysospalax* is substantially larger than any of the fossil golden moles described here (see Discussion). If our assumption is correct that relative abundance is an accurate guide to the association of the most common mandibular and humeral morphotypes at Langebaanweg, then the ratio of dentary/humerus length resembles that of *Eremitalpa*, as does the ratio of humerus length/distal width of this new species (Table 1). Craniodentally, however, this taxon shows many differences and is clearly distinct from *Eremitalpa*, and more closely resembles *Chrysochloris asiatica* (see species diagnosis, below).

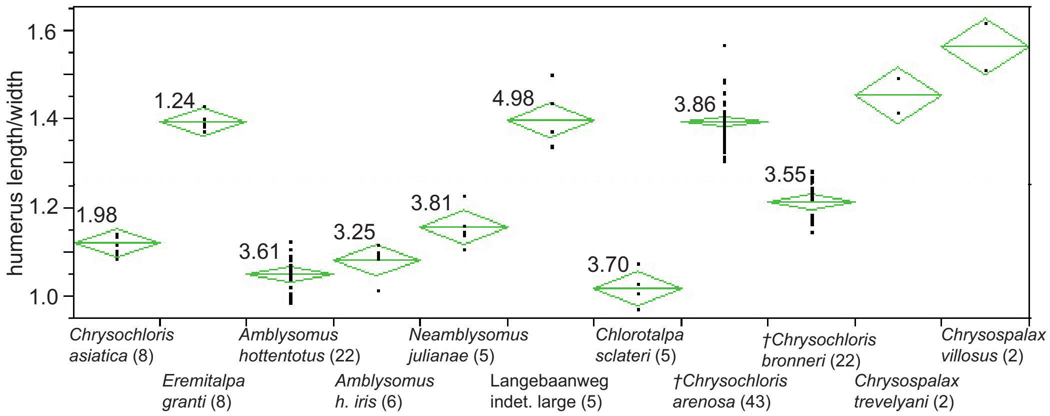

FIGURE 2. Ratio of humerus length/width across golden moles. Diamonds indicate 95% confidence interval of the mean; coefficients of variation for humerus length/width ratio are listed above each diamond; sample size in parentheses after each taxon name.

FIGURE 3. Partial scapula (left, SAM-PQL 35122), femur (middle, SAM-PQL 33197), and humerus (right, SAM-PQL 67132) of unnamed, large fossil chrysochlorid from Langebaanweg. Scale bar indicates 5 mm.

Femora show size variation indicative of multiple species (Table 1). Based on comparisons with extant species, some femora and the few preserved scapular fragments represent individuals larger than those represented by the most common dentaries and humeri at Langebaanweg, and cannot confidently be associated with any craniodental remains. We therefore do not assign these elements to any novel species. Five of the measured femora show an average length of 15.6 mm (Figure 3), similar to that of extant *Amblysomus hottentotus*. All of the other femora are below 14 mm in length, averaging 12.9 mm, statistically indistinguishable from *C. asiatica* and *Neamblysomus julianae*. Femora have a round, globular condyle proximally and a scar for the fovea capitis interrupting the articular surface of the femoral head from its midpoint to the femoral neck. Greater and lesser trochanters are present, but small, and without any concavity for attachment of obturator musculature. A third trochanter is situated near the midpoint of the shaft. A shallow articular surface for the patella marks the distal femoral margin. The femoral condyles are slightly displaced medially, reflecting the presence of a flange for muscle attachments on the lateral margin of the distal femur.

Intact scapulae are lacking. However, several fragments exist with a diagnostically chrysochlorid glenoid region and scapular spine that extends far lateral to the glenoid articular surface (Figure 3). In the two specimens with at least a partially intact distal spine (SAM-PQL 35122, 35106), the metacromion process is narrow and elongate, pointing caudally away from the glenoid. These appear to be proportional in size to the larger morphotype represented by a small number of humeri and femora.

Here, we name two new chrysochlorid species using the most diagnostic elements of their skeletons as types. Furthermore, we add to the referred specimens of the two new species those elements that, based on relative abundance and

TABLE 1. Average element lengths in mm and proportions, with sample size and coefficient of variation (CV, or standard deviation expressed as a percentage of the mean) in parentheses. CVs reported only for sample sizes above 2. Proportions for extant species represent values averaged across each individual in the sample; dentary/humerus proportions for fossils are calculated using the average value for each element. Raw data are available in .xls format in Appendix 1.

Taxon	Dentary Length	Humerus Length	Femur Length	Dentary/ Humerus	Dentary/ Femur
Amblysomus hottentotus	17.08 (23, 4.1)	13.54 (22, 6.41)	15.61 (21, 7.02)	1.26 (22)	1.10 (21)
Amblysomus hottentotus iris	16.7 (7, 2.59)	13.03 (6, 2.15)	15.03 (4, 3.45)	1.28 (6)	1.13 (4)
Neamblysomus julianae	14.13 (6, 2.03)	10.90 (5, 2.34)	12.6 (1)	1.30 (5)	1.12 (1)
Chrysochloris asiatica	15.51 (20, 3.05)	12.34 (8, 5.55)	13.8 (8, 8.8)	1.25 (8)	1.12 (8)
Chlorotalpa sclateri	13.76 (5, 2.22)	10.46 (5, 3.35)		1.32 (5)	
Eremitalpa granti granti	12.29 (8, 4.25)	10.74 (8, 5.31)	11.23 (8, 4.87)	1.15 (8)	1.10 (8)
Chrysospalax villosus	19.6 (1)	19 (2)	22.1 (1)	1.05 (1)	0.89 (1)
Chrysospalax trevelyani	26.75 (4, 1.38)	26.75 (2)	32.9 (1)	1.00 (2)	0.8 (1)
†*Chrysochloris arenosa*	14.63 (41, 4.4)	12.29 (43, 3.68)		1.19	
†*Chrysochloris bronneri*	15.6 (2)	11.79 (20, 4.58)		1.32	
† *Langebaanweg* indet. large taxon		15 (5, 3.83)	15.58 (5, 7.39)		
† *Langebaanweg* indet. small taxon			12.92 (17, 4.01)		

proportions among living chrysochlorids, match those of our proposed type specimens. In addition, given our proposed species limits, coefficients of variation (the standard deviation expressed as a percentage of the mean) for dentary and humerus lengths are under 5 and comparable to those for modern taxa (Table 1). We leave unnamed a third Langebaanweg chrysochlorid morphotype, represented by relatively large humeri, femora, and scapular fragments, which cannot yet be associated with any craniodental remains.

SYSTEMATIC PALEONTOLOGY

Afrotheria Stanhope et al. 1998
Chrysochloridae Gray 1825
Chrysochloris Lacépède 1799
Chrysochloris arenosa sp. nov.

Type locality: Langebaanweg, South Africa

Derivatio nominis: *arenosa* is the Latin adjective for "sandy", based on the relatively narrow distal humerus, which converges on the morphology seen in the "sand swimming" golden mole *Eremitalpa*.

Holotype: SAM-PQL 20177 right humerus (Figure 4).

Age: early Pliocene

Diagnosis: Humeri show a significantly narrower distal margin (Figure 2) than those of extant *C. asiatica*. Based on relative abundance, humeri are associated with well-preserved maxillae and dentaries (Figure 4), containing 10 teeth in each dental quadrant and P3 protocones, similar in morphology to *C. asiatica*.

Material: All specimens have the acronym SAM-PQL. The following are dentaries assigned to this species and sufficiently complete to measure mandibular condyle to the symphysis: 20261, 35070, 35074, 35397, 57981, 67943, 69712, 69713, 69714, 69715, 69716, 69717, 69718, 69719, 69720, 69721, 69722, 69723, 69725, 69728, 69729, 69731, 69732, 69733, 69734, 69735, 69736, 69737, 69738, 69739, 69740, 69741, 69742, 69744, 69748, 69749, 70253, 70254, 70266, 70267, 70268, 70269, 70270.

Rostral fragments include SAM-PQL 35073 (left maxilla with C, P2, P4-M1), SAM-PQL 43200 (left maxilla with P3-P4), and SAM-PQL 69726 (right rostral fragment with I1-2, C, P3-4).

Based on relative abundance, we assign a representative malleus (SAM-PQL 13337), ulna (SAM-PQL 70250), radius (SAM-PQL 35208), terminal phalanx (SAM-PQL 23776), innominate (SAM-PQL 70252), and tibia-fibula (SAM-PQL 70251) to this species.

Description: Relatively complete dentaries and maxillae (Figure 4) show alveoli and/or teeth corresponding to a dental formula of 3.1.3.3, with a total of 10 teeth in each dental quadrant. In addition, all maxillary fragments that preserve cheek teeth show protocones on M1-2 and P3-4, but not on P2 or farther anteriorly. No specimen preserves M3, but alveoli for this locus are present. P2 exhibits a posterobucally extending mesostyle (e.g., SAM-

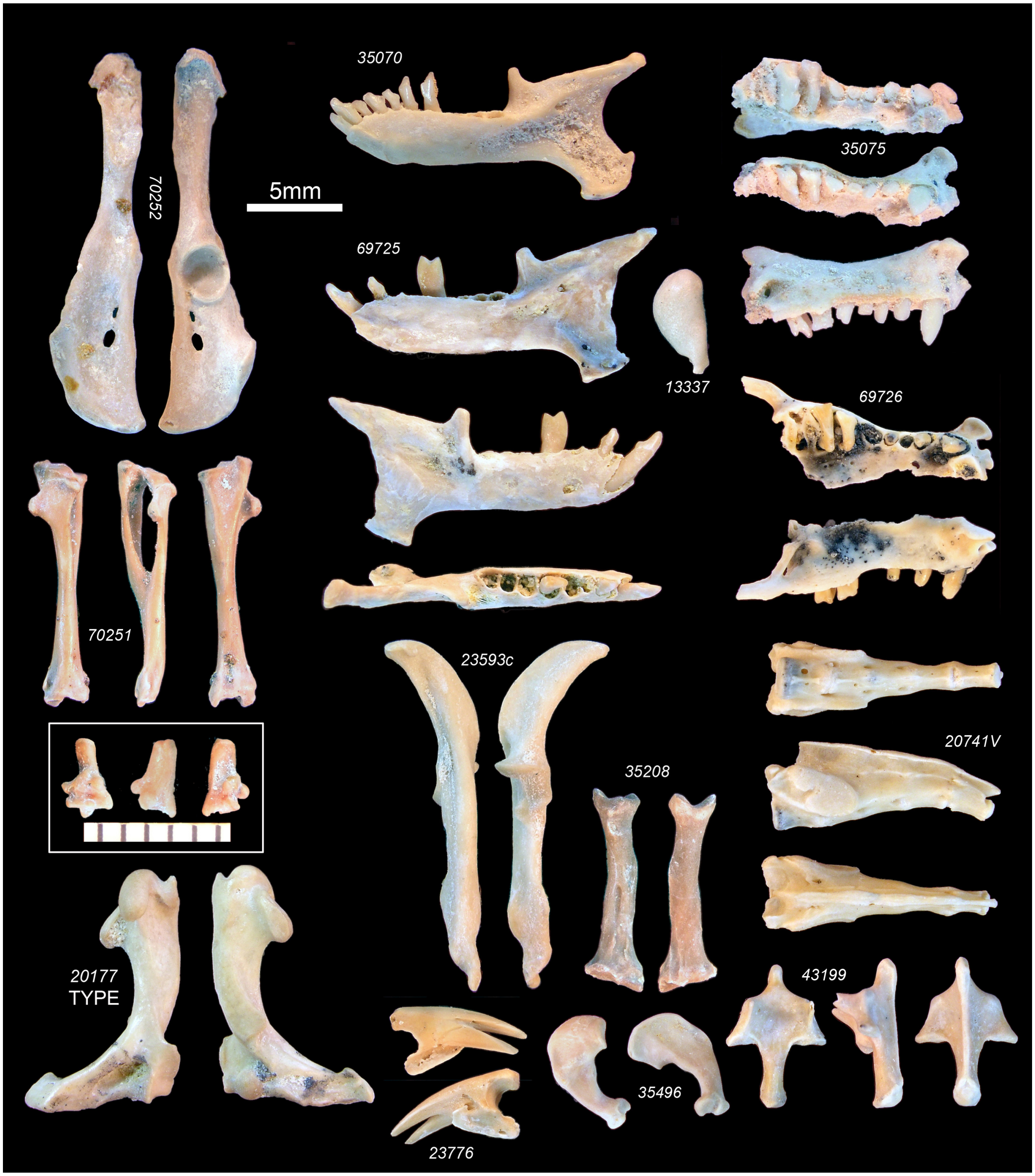

FIGURE 4. Remains of *Chrysochloris arenosa*, including (clockwise from top left) left innominate in internal and external views (SAM-PQL 70252); internal view of right dentary with i1-p4 (SAM-PQL 35070); internal, external, and occlusal views of right dentary with i2, c, p4 (SAM-PQL 69725; p4 slightly twisted postmortem); malleus (SAM-PQL 13337); rostrum fragment in ventral, ventrolateral, and lateral views (SAM-PQL 35075); rostrum fragment in ventral and lateral views (SAM-PQL 69726); synsacrum in ventral, lateral, and dorsal views (SAM-PQL 20741V); manubrium sternae in dorsal, lateral, and ventral views (SAM-PQL 43199); first rib in dorsal and ventral views (SAM-PQL 35496); radius in posterior and anterior views (SAM-PQL 35208); ulna in posterior and anterior views (SAM-PQL 70250); terminal phalanx of digit III in dorsal and ventral views (SAM-PQL 23776); humerus in posterior and anterior views (SAM-PQL 20177, type specimen); calcaneus in dorsal, plantar and lateral views (SAM-PQL 70251; note different scale); tibia-fibula in posterior, lateral, and anterior views (SAM-PQL 70251). All elements except for the calcaneus are photographed at the same 5 mm scale.

PQL 35073). The canine is small and conical, as are I2-3. As in *C. asiatica* and other golden moles, I1 is the largest of the incisors and is rooted in the premaxilla at an angle, so that it points into the oral cavity when viewed laterally (Fig. 4). Similarly, premaxillary remains exhibit two prongs jutting out anterolaterally from either side of the external nares. In addition, M1 is situated just medial to the anterior root of the zygomatic arch, immediately ventral to the short, bridge-like infraorbital canal, evident in dorsolateral aspect. No basicranial remains have yet been identified as chrysochlorid. However, hundreds of ear ossicles recovered from Langebaanweg are easily recognizable and resemble those of modern *C. asiatica.* They are elongate, ovoid, and tear-drop shaped (Figure 4), rather than the distinctive pea-shape of *Eremitalpa* or *Chrysospalax*. Relative abundance and size justifies their association with the most common humeral and mandibular morphotype, i.e., *Chrysochloris arenosa*.

All of the dentaries assigned to *C. arenosa* are similar in overall size and show little variation in qualitative morphology (Figure 4). As in the modern Cape golden mole (*C. asiatica*), they have 10 teeth and/or alveoli, molariform p3-m3, and molars and premolars without talonids. As for all known chrysochlorids, the Langebaanweg dentaries also show an i2 larger than adjacent incisors and a reduced coronoid process, projecting dorsally towards the transverse level of the mandibular condyle. Variation exists in the presence of a 2-rooted p4; specimens that are otherwise identical may differ in this respect (e.g., SAM-PQL 69720 with a 2-rooted p4 vs. SAM-PQL 69737 without). We observed similar variation in modern *C. asiatica*: e.g., SAM-ZM 39362 with a 2-rooted p4 vs. SAM-ZM 37130 without. In addition, some specimens preserving the mandibular angle, known in chrysochlorids to articulate with the hyoid apparatus (Bronner 1991), show a flat hyoid articular surface (e.g., SAM-PQL 69725); in other specimens this surface is curved (SAM-PQL 35070; see Figure 4). We also attribute these differences to intraspecific variation.

Humeri (Figure 4) show the characteristic chrysochlorid shape of the proximal humeral condyle, i.e., dorsoventrally elongate and somewhat teardrop-shaped. The greater tuberosity, just lateral to the humeral head, is smaller than the lesser tuberosity, which extends medially from the condyle. The shaft of the humerus shows a slight, medially concave curvature, culminating in the extremely elongate distal humeral margin, the medial tip of which would have articulated with an elongate, ossified flexor tendon, or third bone of the forearm. While no ossified flexor tendons have been identified from the Langebaanweg material, great similarity in other aspects of forelimb morphology makes it likely that these fossil chrysochlorids also possessed this structure. Along the anteromedial surface of the humeral shaft, towards the distal end of the diaphysis, a small flange is evident that contributes to a medial concavity of the distal humeral shaft, adding yet more surface area for forearm musculature.

In the extant *C. asiatica* and *A. hottentotus*, humeri have a distal margin that is nearly as large as the humerus itself, showing a ratio of humeral length/distal width close to 1, and not exceeding 1.15 (Figure 2). In contrast, humeri from Langebaanweg assigned to *C. arenosa* (e.g., SAM-PQL 20177), have a shorter distal margin, yielding ratios of humeral length/distal width between 1.3 and 1.5, averaging 1.39 (Figure 2). This is the key feature distinguishing *C. arenosa* from modern *C. asiatica*. As discussed above, craniodental features clearly distinguish *C. arenosa* from other chrysochlorids with a relatively narrow distal humerus, such as *Eremitalpa* and *Chrysospalax*.

Isolated synsacra (Figure 4) consist of 2–5 vertebrae, the neural spines of which fuse to form a dorsal, craniocaudally running ridge. Sacral centra also tend to fuse to one another. More variable is the position of the articular scar for the ilia. Most specimens (e.g., SAM-PQL 35108) show an articular surface on the lateral aspect of both S1 and S2 (Figure 4). However, in some specimens (e.g., SAM-PQL 35239) this surface is caudally displaced, comprised of S2-3 with no contribution from S1. These variations match intraspecific variability observed in recent specimens of *C. asiatica*.

Isolated innominate bones (Figure 4) show typical chrysochlorid morphology. The pubis and ischium extend caudally from the acetabulum, parallel to one another, framing a minute obturator foramen that is smaller than the acetabulum. Occasionally the obturator foramen is partially fused, leading in some cases to two small foramina in this region. An articular surface for the sacrum is evident towards the cranial end of the ilium, but does not extend to the cranial tip of the ilium, which shows a slight lateral flare.

The tibia-fibula is fused both proximally and distally (Figure 4). Proximally, the fibula shows a laterally projecting condyle, typical for all extant golden moles. Also typical is the concave facet at the base of the fibula for articulation with a ball-like process extending dorsally from the ectal facet of the calcaneus. A single calcaneus was attached in matrix to the distal end of SAM-PQL 70251 (Figure 4). Distolaterally it shows a prominent, dorsally projecting condyle that articulates with the aforementioned facet of the distal fibula. Its distal margin for articulation with other tarsal elements is relatively flat; a small peroneal process is present that extends slightly past the distal calcaneal articular surface. The sustentaculum tali is present but poorly defined, with little indication of the contour of the articulation with the astragalus.

The manubrium sternae exhibits a sharp keel that juts anteroventrally (Figure 4). The keel grades in a straight line to form posteriorly a prominent condyle for articulation with the adjacent sternebra. The first rib articulates into the angle created by the caudally jutting condyle as it turns laterally to define alae on each side of the midline.

The first rib (Figure 4) has a typical chrysochlorid appearance, i.e., it is flattened and expands distally to form a paddle-shape, with articular surfaces distally for the sternum and proximally for T1.

Radii are distinguished proximally by a single, concave facet for articulation with the humeral capitulum (Figure 4). Distally the radius shows two facets for articulation with the scaphoid and lunate. Several specimens preserve a narrow bridge of bone near the radial distal margin that presumably enclosed a sheath of extrinsic digital flexors, often accompanied by a conspicuous trough. Most specimens that lack this bridge show evidence of postmortem abrasion on the distal radius and probably had one in life. Modern *C. asiatica* also shows this structure (e.g., SAM-ZM 37130).

Ulnae also match closely the morphology and size seen in *C. asiatica* (Figure 4). Both have an elongate, medially curved olecranon process, nearly as long as the shaft of the ulna distal to the humeral articular surface. The proximal articular facet for the humerus extends farther laterally than does the distal facet. The styloid process is narrow and pointed; articulations with the carpus are not limited to the styloid itself but are also present along the distal ulnar shaft.

The enlarged, terminal phalanx closely resembles that of digit III in modern *C. asiatica* (Figure 4). The phalanx ends in two points, both of which would have been covered in life with a large, keratinous claw. Proximally, the lateral articular facet for the adjacent, intermediate phalanx is dorsoventrally longer but mediolaterally shorter than the medial articular facet. Other carpal elements have yet to be identified.

Chrysochloris bronneri sp. nov.

Type locality: Langebaanweg, South Africa

Derivatio nominis: In honor of Prof. Gary Bronner of the Department of Zoology at the University of Cape Town, an internationally respected mammalogist who has made major contributions to chrysochlorid biology.

Holotype: SAM-PQL 28291 left dentary with i2-3, c, p2-m2 (Figure 5).

Age: early Pliocene

Diagnosis: The dentary is more robust than that of extant *C. asiatica* or contemporaneous *C. arenosa*, and shows a stout, enlarged lower i2 without a distinct posterior cusp and with a root that broadens as it enters the mandibular corpus. Based on relative abundance, we associate the second most common humeral morphotype (Figure 1) with the type dentary. These show a humerus length/distal width ratio significantly smaller than that of *C. arenosa*, close to that of extant *N. julianae* and *C. asiatica* (Figure 2).

Material: SAM-PQL 69724 (right dentary with i2, p2-m1). Humeri include SAM-PQL 32817, 66814, 70255, 70256, 70256, 70257, 70258, 70259, 70260, 70261, 70261, 70262, 70263, 70264, 70265, 70271, 70272, 70273, 70274, 70275, 70276, 70277, 70278, 70279, 70280.

Description: SAM-PQL 28291 and 69724 (Figure 5) show a broad, squat i2 without a posterior cusp and with a root that does not begin to narrow until it is well into the mandibular corpus, and which shows more curvature as it descends into the corpus than does the i2 of *C. arenosa*. The lack of a posterior cusp may be accentuated by wear in both specimens. However, the size and robustness of the tooth clearly indicate a marked difference from the gracile i2 of the many dentaries that preserve either the alveolus or the tooth itself, including 43 other specimens complete enough to measure condyle-symphysis distance. Deciduous teeth in golden moles, as with other afrotherians, may remain unreplaced for some time into adulthood (Leche 1907; Asher and Lehmann 2008). However, the possibility that these enlarged teeth represent deciduous precursors is unlikely, given the lack of erupting or unworn teeth at other loci, and since deciduous anterior teeth of chrysochlorids are generally similar in size or smaller than their permanent replacements. Enlarged, deciduous incisors that function throughout adulthood do occur among

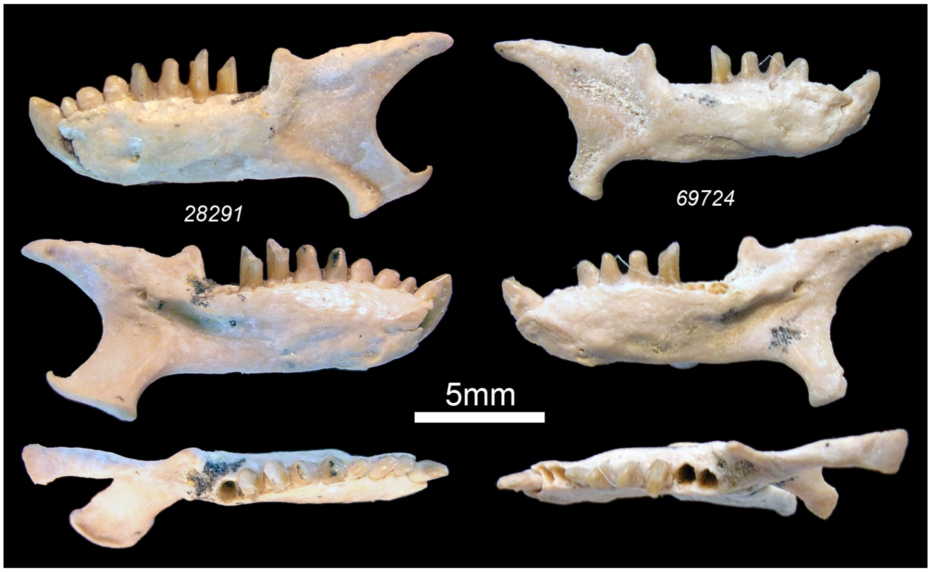

FIGURE 5. Dentaries of *Chrysochloris bronneri*: left dentary with i2-m2 (left, SAM-PQL 28291, type specimen) and right dentary with i2, p2-m1 (right, SAM-PQL 69724). From top to bottom, both show external, internal, and occlusal views.

mammals (e.g., rodents and lagomorphs); we cannot rule out the possibility that this has occurred in a golden mole. If so, it would be a first for the group and would further comprise morphological support for the existence of a new species. Whatever the identity of the enlarged i2, we interpret the two Langebaanweg individuals that have it as a second, *C. asiatica*-sized species of early Pliocene golden mole, here named *Chrysochloris bronneri*.

One of these dentaries (SAM-PQL 69724) appears at first glance to lack an alveolus for i1, suggesting only nine teeth in each dentary. SAM-PQL 69724 also seems to have a narrower angular process than SAM-PQL 28291. However, we believe both the dental formula and the angular process morphology in these specimens are in fact the same as in other specimens. SAM-PQL 69724 shows evidence of postmortem abrasion along the mandibular symphysis and angular process (Figure 5). Furthermore, dental reduction among living chrysochlorids, from 10 to 9 teeth in each quadrant, results from loss of the third molar, not the first incisor. Hence, as for all other chrysochlorid dentaries from Langebaanweg that preserve the relevant anatomy, it is likely that this specimen also had 10 teeth in each jaw and a relatively broad angular process.

DISCUSSION

All extant golden moles examined here except for *Chrysospalax* show dentaries that are slightly longer than their femora, comprising an average dentary length/femur length ratio near 1.1, one that is statistically indistinguishable in *Neamblysomus, Amblysomus, Chrysochloris,* and *Eremitalpa*. Association of the smaller femoral morphotype with dentaries assigned to either of the two *C. asiatica*-sized species named here also yields jaw-femur length ratios slightly over 1.1 (Table 1). The two extant species of *Chrysospalax* have femoral lengths between 40-120% larger than the largest chrysochlorid fossil recovered from Langebaanweg (Table 1). Due to its large size and the fact that larger mammals tend to have relatively smaller heads, *C. trevelyani* shows a dentary/femur length ratio below 1.0.

Dentaries are substantially longer than humeral shafts in extant *Chrysochloris, Amblysomus, Neamblysomus,* and *Chlorotalpa*, exceeding a dentary/humerus length ratio of 1.24. This ratio is smaller in extant *Eremitalpa* and *Chrysospalax*, about 1.14 in the former and just over 1.0 in the latter. The associations of dentaries with humeri for the two species named here yield ratios of 1.19 for *C. arenosa* and 1.32 for *C. bronneri*. These ratios underscore our interpretation that *C. arenosa* is convergent on *Eremitalpa* and that *C. bronneri* more closely resembles other, similarly sized chrysochlorids in skeletal proportions (Table 1).

Given that individual collecting sub-localities at Langebaanweg result from many years of opportunistic excavation and invariably represent a substantial amount of temporal and geographic

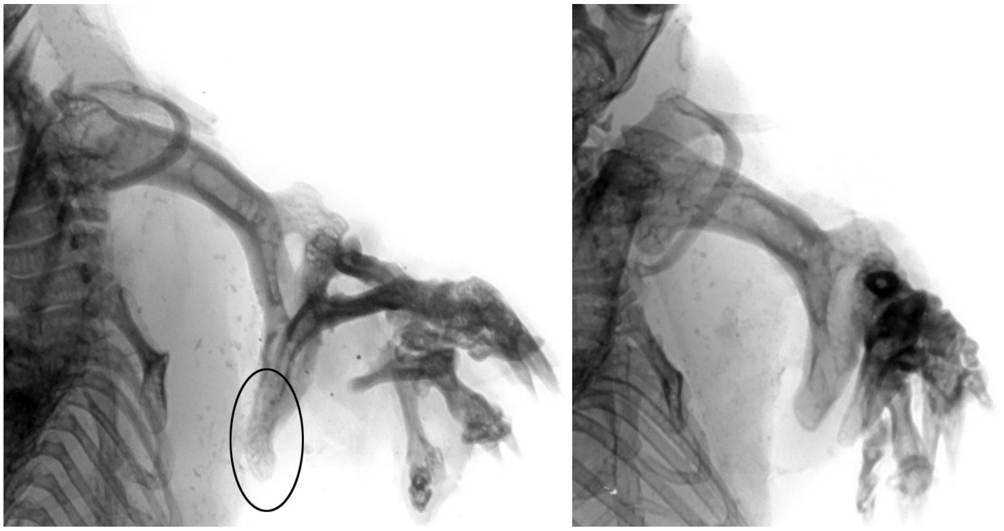

FIGURE 6. Radiographs of the forelimb in *Cryptochloris wintoni* (left, NRM Eg28) and *Eremitalpa granti* (right, NRM Eg32), showing the elongate distal humerus in *Cryptochoris* (circled).

averaging, we hesitate to ascribe much significance to the distribution within Langebaanweg of the chrysochlorid material described here. However, it is worth pointing out that the Langebaanweg "TCCW" sub-locality has produced two of the five large femora and three of the five large humeri. Other elements assigned to both new species described here derive from about 16 distinct sub-localities.

Functional inferences based on the distal humerus. All golden moles, and many other clades of small, burrowing mammals (cf. Rose and Emry 1981), show a hyper-developed medial epicondyle of the distal humerus. This process contributes to a distal humeral margin that exceeds the length of the humeral shaft in some taxa. In *Eremitalpa* the distal humeral margin is also very robust compared to non-chrysochlorids, but is significantly narrower than the distal margin of other golden moles (Figures 2, 6). The morphology of this region may be influenced by the peculiar "sand-swimming" locomotor technique of *Eremitalpa* (Gasc et al. 1986). In much of its habitat, this taxon does not construct permanent burrows, but moves through non-indurated sands that collapse immediately behind the animal, leading to its "sand-shark" moniker (Fielden et al. 1992). The habitat of the South African subspecies (*E. g. granti*; the subspecies measured for this study) is also composed of relatively large dune fields (Nowak 1999). The resistance of these sands as a burrowing substrate is lower than that of the more indurated soils in which *Chrysochloris* and *Amblysomus* (for example) dwell, possibly necessitating less muscle mass and therefore less development of the distal humeral margin in *Eremitalpa.*

The distal humeral margin in the largest genus of golden mole, *Chrysospalax*, is also narrower relative to humerus length than it is in other chrysochlorids (Figure 2). This is consistent with the less fossorial and more terrestrial habitat of this golden mole relative to other genera (Nowak 1999). Furthermore, *Chrysospalax* humeral dimensions reflect the fact that longbones scale with positive allometry relative to most other body indices (Christiansen 2002). By virtue of its more terrestrial habitat and relatively large size, *Chrysospalax* shows a lower ratio of humerus length/distal width.

We hypothesize that *C. arenosa* represents a distinctive early Pliocene chrysochlorid, closely related to the extant *C. asiatica*. Like modern *Eremitalpa*, this extinct golden mole was adapted to an arid environment in which it regularly burrowed in poorly-indurated sands and/or spent relatively more time aboveground. While remains of *Eremitalpa* have recently been recorded from the nearby West Coast National Park (Avery et al. 2005), the possibility that the Langebaanweg fossils represent a population of *Eremitalpa* can be ruled out by the fact that none of the cranial remains (e.g., mallei, maxillae, dentaries) resemble the distinctive morphology of that taxon (e.g., short palates, absent protocones on P3, ovoid mallei). Another genus of golden mole, *Cryptochloris*, is sympatric with some *Eremitalpa* populations (Meester et al. 1986). Indeed, specimens of *Cryptochloris* are frequently mislabeled as *Eremitalpa* in museum collections as the two are externally very similar in appearance. Unfortunately, properly macerated skeletons of *Cryptochloris* are nonexistent in museum collections, and we therefore lack comparative data on their humeral proportions. However, radiographic images (Figure 6) show that the distal humeral width is not as reduced in *Cryptochloris wintoni* as it is in *Eremitalpa* or our hypodigm of *C. arenosa*. Otherwise, *Cryptochloris* is anatomically similar to *Chrysochloris*, showing 10 teeth in each molar quadrant, no talonids on its molars or premolars, and a club-shaped malleus. It differs from *C. asiatica* in that its temporal bulla is smaller, and the maxillae are more expanded dorsally on the rostrum than on the alveolar margins of the palate. *Cryptochloris* also shows similarly sized upper incisors and a larger first digit than *C. asiatica* (Helgen and Wilson 2003). We believe the morphology of the maxilla, premaxilla, incisors, and humerus of the Langebaanweg chrysochlorids rule out their possible membership in *Cryptochloris.*

No craniodental material is yet known that fits the size range expected for the large morph, which also exhibits a relatively narrow distal humeral margin. This taxon is significantly smaller than extant *Chrysospalax*, and as in the small Langebaanweg morph may have been adapted for sand-swimming and/or spending relatively more time aboveground than extant golden moles in its size range.

CONCLUSIONS

Based on metric comparisons with extant golden moles, fossil chrysochlorids from Langebaanweg show limited morphological variation and fit into three morphotypes, one similar in size to the extant *Amblysomus hottentotus* and two smaller ones closer to *Chrysochloris asiatica* (Figure 1). All craniodental material fits into the smaller groups. Specimens in the smaller size-morph resemble *C. asiatica* in showing an enlarged, club-like malleus, 10 teeth in each dental quadrant, protocones evident on upper P3 through M3, and lower molars without talonids. Specimens in the smaller size morph differ from one another in two respects that, in our view, justify assignment to two different species.

Chrysochloris arenosa sp. nov. is characterized by a relatively narrow distal margin of the humerus, with a length/distal width ratio of ca. 1.4, similar in proportion but absolutely larger than humeri of the extant *Eremitalpa granti* (Figure 2). It is further associated with *C. asiatica*-like maxillae and dentaries with an i2 that is only slightly larger than adjacent incisors and with a posterior cusp (Figure 4).

Chrysochloris bronneri sp. nov. is defined by two dentaries that show an enlarged, curved i2 without a posterior cusp and with a robust mandibular corpus (Figure 5). These dentaries are likely associated with the second most-common humeral morphotype that shows a wider distal humeral margin and correspondingly lower length/distal width ratio averaging ca. 1.2 (Figure 2). This is slightly greater than but close to the ratios present in *N. julianae* and *C. asiatica*.

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APPENDIX

Electronic spreadsheet with measurements and specimens observed (see palaeo-electronica.org/2010_1/index.html).