Origin and evolution of *Heterocephalus* from East Africa (Rodentia: Heterocephalidae)

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Abstract. Known today by a single species only in the Horn of Africa, rodents of the *Heterocephalus* genus displayed through Neogene times a larger geographical distribution and a higher diversity. Here we present the state of art of the knowledge of the described fossil *Heterocephalus* species and follow the different described lineages through time and space. We also present some morphological and classical morphometric analyses upon the skulls and teeth of the modern representative of the genus compared with the fossil ones. This allowed to find some cranio-dental criteria allowing to validate the probable presence of two to three modern species in the horn of Africa and define and discuss some dental trends of evolution of the fossil lineages through time and space. Finally, by gathering the paleoclimatic conditions and collecting environmental parameters of each site were *Heterocephalus* remains were collected we propose a scenario of evolution of the genus.

Key words. Morphology, classical morphometry, fossil record, Plio-Pleistocene, taxonomy.

INTRODUCTION

Among the endemic rodents of Africa, the African mole rats are represented by two families, including six genera and 29 species. This group of hystricognath rodents is constituted only by subterranean taxa that have developed unique adaptations to life under ground. Among the most outstanding adaptations, the naked mole rat (*Heterocephalus*) has developed a remarkable physiology as well as eusociality (BURDA et al. 2000, JARVIS & SHERMAN 2002). Initially, all the African mole-rats were classified in a single family but a recent molecular revision of the Ctenohystrica clade by PATTERSON & UPHAM (2014) found the *Heterocephalus* lineage as diverging very early from the other Bathyergidae and despite morphological similarities, these authors followed LANDRY (1957) in rehabilitating the Heterocephalidae family with a monotypic genus. According to these authors the divergence time would have occurred during the Oligocene times at around 32 Ma and the molecular divergence is accompanied by numerous morphological and ethological traits.

   The taxonomic study of the genus *Heterocephalus* started when RÜPPELL (1842) described it for the first time and named the species *H. glaber* from the type locality "die Wiesen-Thäler in Schoa, südlich von Abyssinien," Schoa, Ethiopia. Then THOMAS (1885a) added a new species description within the genus *Heterocephalus phillipsi* from "Gerlogobie, Ogardain, Central

Somaliland". Later, *Heterocephalus ansorgei* Thomas, 1903 was described from "Between Ngomeni and Kjinani, Makindu country, British East Africa". In the same times THOMAS (1904) created the genus *Fornarina* with the species *F. phillipsi* Thomas, 1903 for a specimen collected in Mogadishu, Italian Somaliland. Finally the latter author created a last species named *Heterocephalus dunni* Thomas, 1909 whose holotype was coming from "Wardairi, Central Somaliland."

Further, a Swedish expedition through British East Africa allowed LÖNNBERG (1912) to describe a new subspecies called *H. glaber progrediens* from North Guaso Nyiro. By the same times, *Heterocephalus stygius* Allen, 1912 was named from the type locality "Neuman's Boma, on the northern Guaso Nyiro River, British East Africa". Finally, a last subspecies was published at the occasion of the publication of an Italian Expedition to Somalia: *Heterocephalus glaber scorteccii* de Beaux, 1934 from Gardo, northern Italian Somalia.

Today, following HOLLISTER's revision (1919), only a single species is recognized in the genus, *H. glaber* which is distributed in the arid regions of the Horn of Africa, from Djibouti, eastern and southern Ethiopia and north-eastern Kenya (MONADJEM et al. 2015). But, a recent analysis of the genetic diversity of *Heterocephalus* on its whole distribution has shown the existence of two deeply divergent lineages that may correspond either to subspecies or even represent valid species. Their divergence would date from 1.4 to 0.8 Ma and be related to the mid Pleistocene climate change (ZEMLEMEROVA et al. 2021). Moreover, in the past, DENYS & JAEGER (1986) described two lineages of fossil *Heterocephalus* with a distinction between northern Rift (modern *H. glaber* whithout fossil representatives) and a southern Rift lineage with three extinct species (*H. atikoi*, *H. manthi*, *H. jaegeri*) found in northern Tanzania and southern Ethiopia.

These works allow to ask new questions about the genus diversification and evolution of *Heterocephalus*. Is there only one or two species in the genus? Are the molecular lineages corresponding to the fossil ones and how can we relate them to draw an evolutionary history? Can we find paleoecological or tectonics causes driving this split or constraining the species morphological evolution?

To answer these questions of the probable presence of various subspecies or valid species inside the genus and retrace its evolution through time and space in East Africa, we have performed a comparison of the cranio-dental characters of the whole described modern and fossil taxa of *Heterocephalus*. Then we have attempted to retrace the morphological evolution of the genus with regards to climate change proxy and biogeography as well as the rift valley tectonics events.

MATERIAL AND METHODS

For taxonomic comparisons, the specimens were examined under a binocular microscope and dental patterns were drawn thanks to a camera lucida. Pictures of the specimens were captured with a SEM HITACHI SV 3500 and a Dinolite MS 36B. The cranio-dental distances were taken at 0.01 mm precisions with a Mitutoyo calliper (Absolute Digimatic) while the dental measurements were taken with a measuroscope and the Dinolite.

Eight skull distances were taken as follows: LGT – total length of the skull from the nasal anterior extremity to the condyle foramen; WZYG – maximum bizygomatic width; CIO – interorbital constriction at the narrowest width; LBT – maximum tympanic bullae length; LFOPAL – length of the palatal foramen; Diast – length of the diastema between the basis of the upper incisor and the basis of the M^1 crown; LS^{1-3} – upper toothrow length; LI_{1-3} – lower toothrow length.

The dental nomenclature is adapted from DENYS (1987) and figured here (Fig. 1). For each upper and lower molar, the maximum length and width of the occlusal surface were taken. An attempt to evaluate the relative age of the specimens was made but due to the low samples analysed here was difficult to interpret.

Similarly, few information on the breeding status or social rank of the modern specimens in collections prevented us to look at as sexual or "social" dimorphism.

Basic univariate statistics (mean, max, min, SD) were employed on each cranio-dental measurement for comparisons purposes between the different modern and fossil populations. Bivariate plots were used to visualize size and proportions differences while PCA (principal component analyses) on the skull distances were used to observe the whole variability of the modern representatives of the genus. All statistical analyses were done using the software XLSTAT 10 (Addinsoft).

We compared our fossil material with holotypes and various modern representative specimens arising from the whole distribution of the taxon in East Africa. These specimens were housed in various institutions like the Mammalogy Department of the Museum national d'histoire naturelle (MNHN, Paris, France), the Mammalogy section, Natural History Museum (BMNH, London, UK); the reference collection of the Paleoanthropological Department of the National Museum of Ethiopia (Addis Ababa). The holotype picture of *Heterocephalus glaber* was provided by the Senckenberg Museum (SMF, Frankfurt am Main, Germany).

The details of the modern specimens used in this study accompanied with their geographic origin are provided in Supplementary Table 1. We used in total 34 modern specimens among which 14 from Somalia, 3 from Ethiopia, 12 from Kenya and included the holotypes of *Heterocephalus glaber*, *H. ansorgei*, *H. phillipsi*, and *H. dunni*. For all modern specimens employed we used labels of the voucher specimens at the exception of the Kenyan specimens labelled as glaber that could either belong to *H. g. glaber* or to *H. g. ansorgei*. The latter specimens have been treated separately in the multivariate analyses in order to precise the identifications.
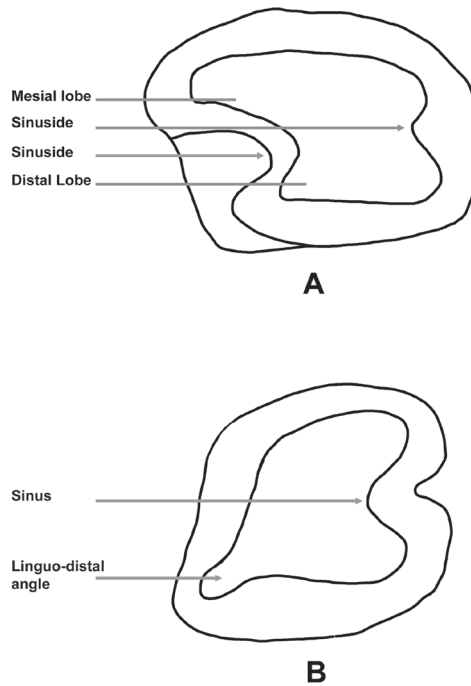

Fig. 1. Dental nomenclature of *Heterocephalus* molars; A – left lower M_2; B – left upper M^2 (after DENYS 1987).

Comparisons with fossil taxa have been performed with specimens from literature data as well as from various Neogene east African sites. Specimens from Laetoli and Olduvai (N Tanzania) were described in DENYS (1987, 1989, 2011), those from the Omo Shungura deposits (S Ethiopia) came from WESSELMAN (1984) and from Goda Buticha (E Ethiopia) (STOETZEL et al. 2018). The specimens from Fejej (Ethiopia) was presented in ECHASSOUX et al. (2004). The Laetoli specimens are housed in the Palaeontology Department of the Dar Es Salaam Museum. The Omo Shungura, Fejej, and Goda Buticha specimens are housed in the Palaeontological collections of the National Museum of Ethiopia (Addis Ababa). The Olduvai specimens are housed in both Kenya Museums and Palaeontological collection of the Montpellier II University (France).

Because most of the preserved fossil material is constituted of isolated molars or broken maxillaries and mandibles, we focused here on dental characters for comparisons between modern and fossil specimens.

RESULTS

First, we recapitulate the various skulls and dental characters of the modern whole named specimens of *Heterocephalu*s based upon original diagnoses and then present our observations in order to find diagnostic characters. We then explore the size variability of the modern *Heterocephalus* representatives. Finally, we present the cranio-dental characters of the fossil species and their size variability compared to the modern ones.

Cranio-dental characters of modern *Heterocephalus*

When he described the holotype of *Heterocephalus glaber* Rüppell, 1842 mentioned the presence of two procumbent incisors and three cylindric simple molars per jaws. Then, THOMAS (1885b) described *H. phillipsii* with two molars and created the genus *Fornarina* that was later considered as not valid due to the variability in the number of cheek teeth of the various specimens of that species. According to THOMAS (1885), *H. phillipsii* is diagnosed compared to *H. glaber* holotype, by a smaller incisor foramina, small face equal in length to the braincase, short nasals squared behind and smaller than the ascending process of the premaxillary. Molars round and simple, upper molars with one fold disappearing with wear and on lower molars two folds (internal plus external). By describing *H. ansorgei*, Thomas, 1903 remarked its very small size, the palate ending just after the M^3 and the small and narrow molars, the weaker incisors. Later THOMAS (1909) described *H. dunni* having the same size as *H. glaber*, a large muzzle and large nasals broad behind, thick and wide zygomatic anteriorly and posteriorly, a mandible with short low coronoid as in *H. phillipsi*. According to the last author, the incisors of *H. dunni* are broader than in other species of the genus and it is characterized by the M_3 being the smallest molar of the toothrow. ALLEN (1912) in describing *H. stygius* remarked its nasals making more than one-third the occipito-nasal length, the zygomata bowed out anteriorly as in dunni, the coronoid process short similar to *H. dunni* and *H. phillipsii*, the upper M^3 being the smallest molar and on the lower molars, the M_2 being the largest molar and the M_1=M_3 length, all having an internal and external fold.

LÖNNBERG (1912) described *H. glaber progrediens* characterized by a coronoid process higher and slender than in *H. dunni*, an incisor foramen different from *H. glaber* in being situated behind a line made behind the palate as a continuation of the peripheric contour of the zygoma arches (while this foramen is more anterior in *H. glaber*) and a difference in the premaxillary and maxillary sutures. No molar characteristics were mentioned in this description. The last described subspecies is due to DE BEAUX (1934) while creating *H. glaber scorteccii* characterized

by a narrow nasal, a small upper M^3, the lower M_2 being the largest one of the toothrow while in *H. glaber* it is the lower M_3.

As early as HOLLISTER (1919) made a revision of the Kenyan known forms of *Heterocephalus* and demonstrated the synonymy of *H. ansorgei*, *H. stygius*, *H. g. progrediens* with *H. glaber* based upon their high individual variability observed. He mentioned the variability of the mandibular coronoid process and the nasal development with age as well as changes in size and shape of the molars and incisors morphology with age. Following that, we keep here the trinomial designation for each of the described taxa of the genus, except for the holotype of *H. glaber* description.
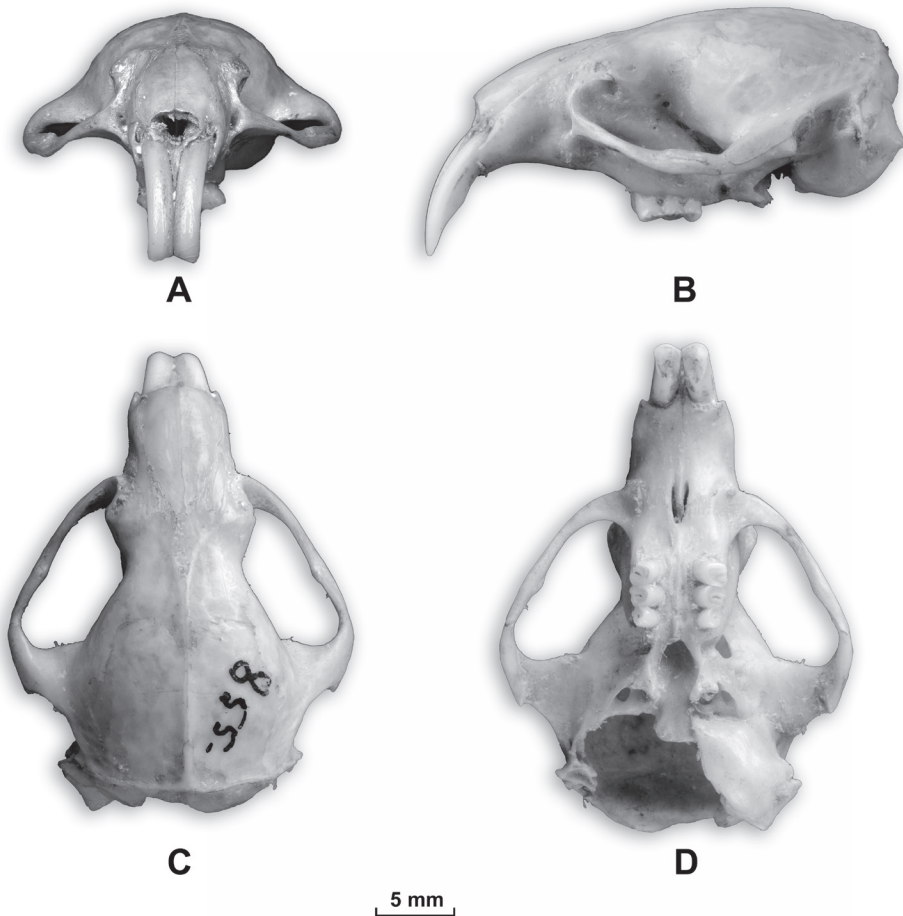

5 mm

Fig. 2. Holotype of *Heterocephalus glaber*, SMF 855; A – anterior view of the skull; B – lateral view; C – dorsal view; D – ventral view. The mandible is absent.

Skull of the holotype of *Heterocephalus glaber*

Thanks to the courtesy of the Senckenberg Museum we could redescribe the holotype of *Heterocephalus glaber* (Fig. 2). The holotype displays a massive skull with two large proodont incisors (Fig. 2). The parietal and zygomatic width are large and sagittal and occipito-parietal crests well marked. The muzzle is wide and the nasal enlarged anteriorly. There are two marked bumps at the back of the zygomatic plate which is narrow with a groove and a small infraorbital foramen. The zygomatic arch is thin in maxillary part and thicker in the jugal one. In ventral view, the incisor foramina are small, three molars of decreasing size from front to back are disposed in parallel. The palate is ending just after the molar rows. The tympanic bulla is not inflated and narrow. The auditive meatus is small and there is a rectilinear end of the auditory bulla (in ventral view). The mandible of the holotype is lost.

In order to precise the description of a typical *H. glaber* and provide illustration of its variability, we complete the holotype description by adding specimens from Ethiopia of the Paris Museum. We examined two specimens of *H. glaber glaber* of Ethiopia (MNHN CG-1901-72 and MNHN 1901-573) which display the same characteristics than the holotype but with a more marked and enlarged occipital crests and narrow tympanic bullae with rectilinear posterior parts and two marked tubercles in the extremities. In dorsal view the nasal is not enlarged anteriorly but all other holotype characteristics are kept here (Fig. 3). In these Ethiopian specimens, the foramen magnum is entering between the bullae and two condyles are well developed. There is an important size difference between the two skulls that come from Harar.

The skulls of *H. g. phillipsi* are small and display the same skull characters than in *H. glaber* holotype except the nasal is relatively narrower anteriorly and tympanic bullae are large. There are three to two upper cheek teeth and two lower ones displaying narrow lower molars with well marked labial and lingual sinusides. The molars are small compared to *H. glaber glaber*.

Molars of Ethiopian *Heterocephalus glaber glaber*

The mandible of the Ethiopian specimens displays an hystricognath pattern and three cheek teeth with the first molar smaller than the two others and an internal and a labial sinus present on the M_{2-3}. The lower M_3 is the largest of the molar row and it has an elongated narrow aspect (Fig. 4).

On the holotype the three upper cheek teeth (not figured) are low crowned as well as in the MNHN Paris specimens. In the upper molars of the holotype the upper M^3 is smaller compared to the M^{1-2} and there is a labial sinus but no lingual one (Fig. 2).

The cusp disposition of the Ethiopian representatives of *H. g. glaber* display some variability in morphology (Fig. 4). In a juvenile (or a non-reproducing) modern specimen from East Ethiopia (DDW 24) one can see a well marked labial sinus on upper molars and the upper M^3 is the smallest tooth. The labial sinus is absent in the two other specimens except on an upper M^2 were we distinguish a small lingual one.

Comparisons of holotypes of *Heterocephalus*

We compared the molars of some types and specimens of *Heterocephalus* from the whole East African distribution and because all described taxa of the genus have been synonymized, we keep in the following lines the trinomial designation. At the first glance, the modern upper and lower molars look larger and wider in *H.glaber glaber* from Somalia, Ethiopia than those of *H. glaber philippsi*, *H. glaber dunni* (both from Somalia) and *H. glaber ansorgei* from Kenya (Fig. 5). In *H. glaber glaber* the upper M^3 is the smallest molar like also in *H. glaber dunni*. In the holotype of *H. ansorgei* all the three molars are equal in size. On other *H. g. ansorgei* of Kenya the upper M^3 is the smallest molar but looks less reduced than in *H. glaber glaber*

representatives (Fig. 6). For the lower molars, the lower M_3 is the largest one in *H. glaber ansorgei* while it is equivalent in length and width in *H. glaber glaber*. In *H. g. dunni* it is the M_2 which is the largest molar. The labial sinuside is always present in M_{2-3} in all forms. At the present we can observe some variability in those dental characters and we were not able to verify weather they are related to age and wear stages, or have specific value, due to the absence of developmental series of this species.

Dental variability in *Heterocephalus glaber ansorgei*

We detail here the dental variability in *H. glaber ansorgei* (Fig. 6), we can observe that the upper M^3 is the smallest tooth of the molar row and there is a labial sinus present in the upper M^1. The enamel basin keeps traces of some lophs. On the lower molars, the three teeth display about the same length and are relatively narrow and elongated. Both labial and lingual sinusides are well marked on all molars. The M_3 is long, narrow and bi-lobed on all specimens.
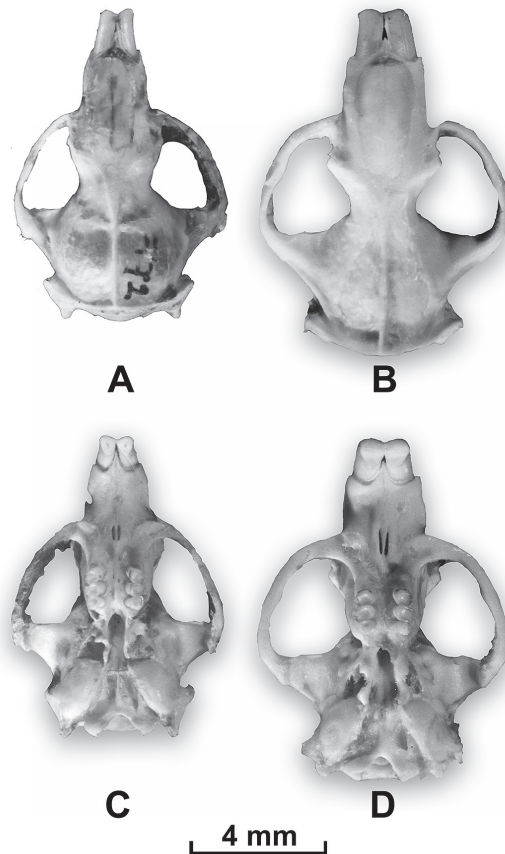

Fig. 3. *Heterocephalus g. glaber* MNHN-CG-1901-572 (A , C) and 1901-573 (B, D) from Harar (Ethiopia).

Table 1. Standard statistics for skull dimensions in mm of 42 specimens of modern *Heterocephalus*; N – number of individuals; min, max – minimum and maximum values; SD – standard deviation

statistics	LGT	WZYG	CIO	LBT	LFOPAL	Diast	LS$^{1-3}$	LI$_{1-3}$
N	42	42	42	42	42	42	42	42
min	18.700	13.400	5.000	5.000	1.300	5.600	2.400	2.700
max	29.520	21.750	7.300	8.000	2.210	10.000	4.300	4.200
mean	22.966	16.919	5.710	6.541	1.778	7.139	3.440	3.647
variance	7.176	3.500	0.201	0.466	0.075	1.006	0.101	0.130
SD	2.679	1.871	0.448	0.682	0.273	1.003	0.317	0.360

Modern skull and molar variability

Skull morphometrics

The skull variability of 42 specimens of *Heterocephalus* from Kenya, Ethiopia, Somalia has been examined (Table 1) but we could not incorporate to the analyses all the type specimens due to their bad state of preservation for some. The PCA performed on skull distances provides a clear size axis probably resulting from age variation (Fig. 7) but no clear geographic distinction. By the fact on the PCA, we can see the two most contributing variables being the total length of the skull (LGT) and the bizygomatic width (WZYG). The smallest specimens being *H. g. ansorgei* from Kenya and *H. glaber phillipsi* from Somalia. The largest are the Ethiopian specimens of MNHN (Fig. 7).

Molar morphometrics

We provide here the standard statistics for the length and width of the modern *Heterocephalus glaber* sensu lato upper and lower molars . We confirm here that the M^3 is the smallest molar of the upper tooth row and the M$_1$ for the lower tooth row. In average the upper molars are wider than long while the lower molars are longer than wide (Table 2).

In order to see eventual differences between the sub species of *H. glaber* we first performed a PCA on 22 specimens with 12 dental measurements. In the plot of axis 1×2 we see that *H. g. ansorgei* and *H. g. dunni* are opposed to *H. g. glaber* from Somalia and Ethiopia along the axis 1 whose M^{2}W, M^{3}L, M^{3}W, and M$_3$W have the greatest contribution (Fig. 8). The M$_1$L and M$_1$W plus M$_2$L contribute to explain the axis 2. By the fact the M$_3$W of specimens labelled *H.*

Table 2. Length and width in mm of the upper and lower molars for modern *Heterocephalus glaber* s.l.; N – number of individuals; min, max – minimum and maximum values; SD – standard deviation

	M^{1}L	M^{1}W	M^{2}L	M^{2}W	M^{3}L	M^{3}W	M$_1$L	M$_1$W	M$_2$L	M$_2$W	M$_3$L	M$_3$W
N	25	25	25	25	22	22	25	25	25	25	22	22
min	1.08	1.10	0.95	0.90	0.40	0.70	1.05	0.90	1.10	0.95	1.20	1.05
max	1.50	1.95	1.40	1.95	1.25	1.75	1.53	1.35	1.60	1.65	1.80	1.75
mean	1.31	1.43	1.22	1.52	1.05	1.26	1.30	1.14	1.35	1.36	1.44	1.39
variance	0.015	0.037	0.012	0.063	0.036	0.043	0.018	0.014	0.016	0.030	0.022	0.039
SD	0.121	0.191	0.110	0.252	0.191	0.208	0.134	0.118	0.125	0.173	0.148	0.198

g. ansorgei in the BMNH (mean=1.14, N=4) is significantly smaller than the M_3W of other *H. g. glaber* specimens (mean=1.47, N=17). *Heterocephalus g. dunni* has the smallest M_3. This difference in the width of the M_3 and on dental proportions may represent a valid character to distinguish a second species within the genus *Heterocephalus*. We could not incorporate *H. g. phillipsi* to the analysis due to the absence of $M^3/_3$.

We then compared the molar dimensions of each sub species in function of our sample. We can see that *H. g. dunni* has the smallest molars for M^1L, M^2L, M^3L, M^3W, M_1L, M_3L, and M_3W; *H. g. phillipsi* has the smallest molars for M^1W and M^2W; *H. g. glaber* has the largest molars
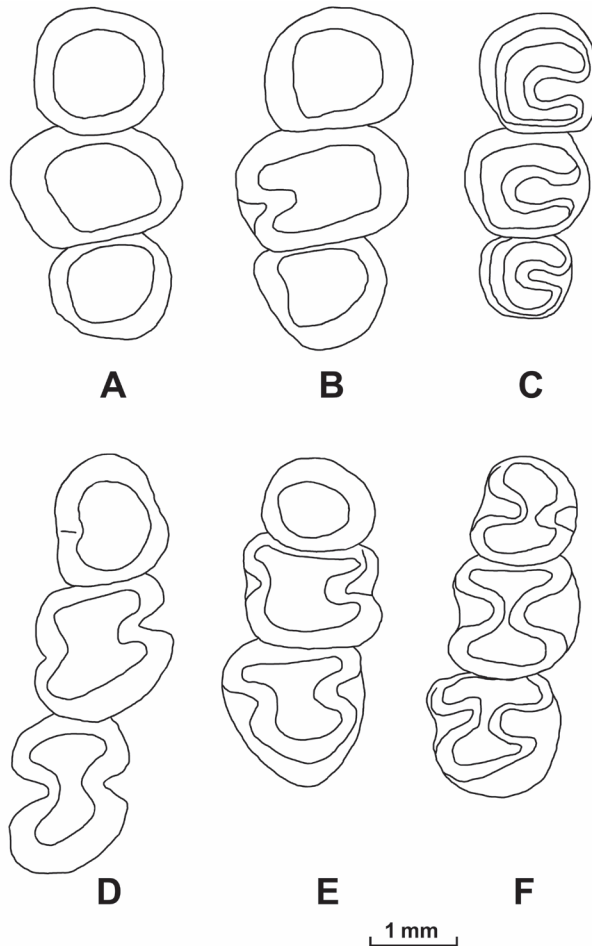

Fig. 4. Modern *Heterocephalus g. glaber* from Ethiopia – upper (top) and lower (bottom) molar rows. A & D – BMNH 97.8.9.22; B & E – MNHN ZM-MO 1978-268; C & F – DDW24.
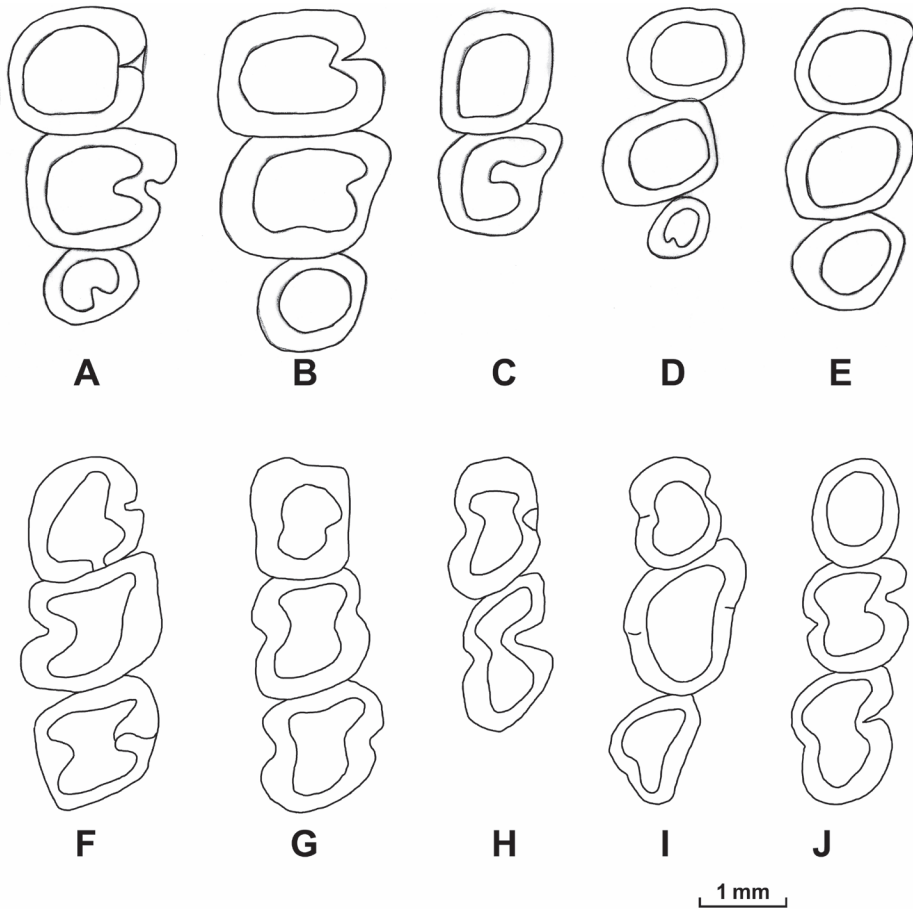
Fig. 5. Molar rows of various *Heterocephalus glaber* s.l. type specimens: top – right upper molars; bottom – right lower molars. A & F – BMNH 74.1.12 *H. g. glaber* Somalia; B & G – BMNH 99.5.31.1 *H. g. glaber*, Somalia; C & H – BMNH 85.12.10.11 holotype *H. phillipsi* (type *Fornarina*) Somaliland; D & I – BMNH 4.5.9.23 Holotype *H. dunni*, Waidiri Somalia; E & J – BMNH 98.9.25.3 holotype *H. ansorgei*, Kenya.

for all dimensions except for M_1L and M_2L; *H. g. ansorgei* has generally smaller molars than *H. g. glaber* (Table 3).

Cranio-dental characters of the fossil record

Miocene ancestors

STROMER (1926) has described a bathyergid named *Bathyergoides neotertiarius* from the Namibian Lower Miocene sites of Bohrloche and Langental which was also recovered by LAVOCAT

(1973) in East African Lower Miocene sites. *Paracryptomys mackennae* from Namib during the Neogene time, few bathyergids remains have yet been described. LAVOCAT (1973) described *Proheliophobus leakeyi* from Rusinga island site (around 18–16 Ma) and in 1988 *Richardus excavans* from Fort Ternan (around 14 Ma). By describing carefully the skull morphology of *Richardus excavans* he found that the species has close affinities with *Heterocephalus*. According to LAVOCAT (1988, 1989), *Richardus* differs from all modern and fossil Bathyergidae by the association of a small infraorbital foramen with a muscular insertion print large and well marked on the anterior part of the masseteric plate and muzzle. *Richardus* differs from *Proheliophobius*
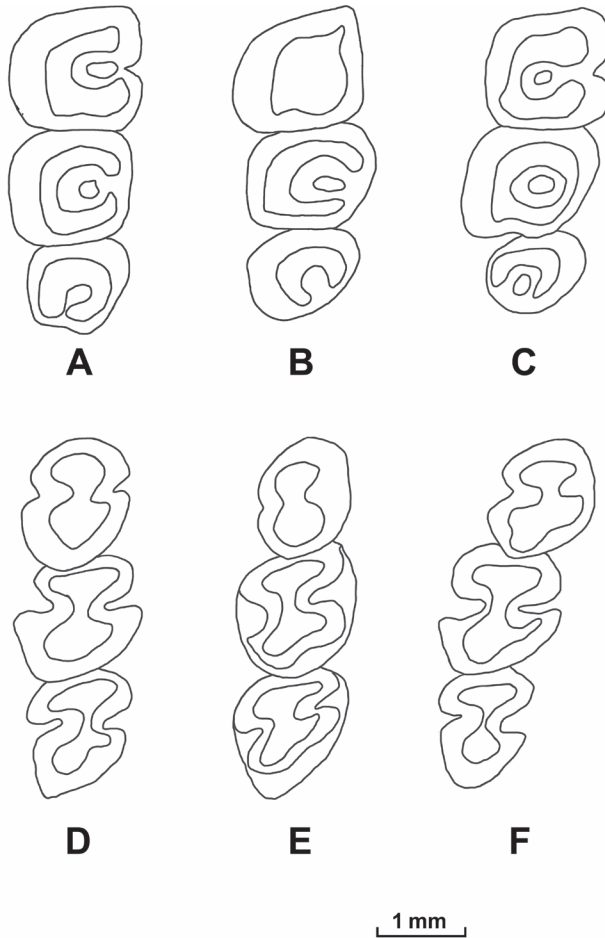

Fig. 6. Modern *Heterocephalus glaber ansorgei* from Juba River, Alexandria Kenya. Upper (top) and lower (bottom) right molar rows. A & D – BMNH 15.10.12.2; B & E – BMNH 15.10.12.1; C & F – BMNH 15.10.12.3.

Table 3. Length and width in mm of the upper and lower molars for modern *Heterocephalus glaber* subspecies; N – number of individuals; min, max – minimum and maximum values; SD – standard deviation. Note that all specimens designed as *H. g. glaber* in collections from Kenya, Ethiopia and Somalia have been grouped together here. The Kenyan specimens attributed to *H. g. glaber* in the BMNH should be further revised

ansorgei	M^{1}L	M^{1}W	M^{2}L	M^{2}W	M^{3}L	M^{3}W	M$_1$L	M$_1$W	M$_2$L	M$_2$W	M$_3$L	M$_3$W
N	4	4	4	4	4	4	4	4	4	4	4	4
min	1.180	1.250	1.150	1.300	0.850	1.100	1.200	0.950	1.250	1.100	1.250	1.050
max	1.350	1.500	1.350	1.450	1.050	1.250	1.500	1.250	1.450	1.450	1.550	1.300
mean	1.283	1.388	1.238	1.375	0.988	1.175	1.325	1.125	1.388	1.313	1.400	1.138
SD	0.072	0.111	0.085	0.065	0.095	0.065	0.126	0.132	0.095	0.155	0.147	0.111
dunni												
N	1	1	1	1	1	1	1	1	1	1	1	1
	1.080	1.400	1.100	1.300	0.400	0.700	1.250	1.000	1.500	1.300	1.200	1.050
glaber												
N	17	17	17	17	17	17	17	17	17	17	17	17
min	1.150	1.150	1.050	1.230	0.900	1.000	1.050	1.050	1.100	1.200	1.200	1.200
max	1.500	1.950	1.400	1.950	1.250	1.750	1.530	1.350	1.500	1.650	1.800	1.750
mean	1.341	1.489	1.247	1.627	1.097	1.315	1.283	1.174	1.306	1.425	1.468	1.468
SD	0.116	0.190	0.101	0.209	0.128	0.177	0.142	0.103	0.112	0.134	0.141	0.140
phillipsi												
N	3	3	3	3	0	0	3	3	3	3	0	0
min	1.100	1.100	0.950	0.900	–	–	1.250	0.900	1.300	0.950	–	–
max	1.350	1.250	1.250	1.300	–	–	1.500	1.100	1.600	1.250	–	–
mean	1.233	1.183	1.117	1.167	–	–	1.383	1.010	1.467	1.083	–	–
SD	0.126	0.076	0.153	0.231	–	–	0.126	0.101	0.153	0.153	–	–

by the presence of a deep groove between the angular apophysis and the mandibular corps. Such groove is a shared character with modern *Bathyergus* and *Heterocephalus*.

Both *Richardus* and *Heterocephalus* share the same zygomatic arch disposition with a short backward jugal, short angular apophysis, narrow and high coronoid apophysis, same disposition of the zygomatic plate and presence of three jugal teeth (LAVOCAT 1989).

No *Heterocephalus* like specimen has yet been recorded in the well-documented Kenyan and Ethiopian Upper Miocene and Lower Pliocene sites of Lukeino (MEIN & PICKFORD 2006), Kanapoi (MANTHI & WINKLER 2020), Ibole (WINKLER 1997), Lemudong'o (MANTHI 2007), Tabarin Chemeron (WINKLER 2002), Aramis (LOUCHART et al. 2009), Adu Asa (WESSELMAN et al. 2009), Chororoa around 8 Ma (GERAADS 1998) and the meaning of this lacunae is not clear (Table 4).

Plio-Pleistocene records
During the Pliocene in East Africa, fossil *Heterocephalus* are found only in North Tanzania and are absent from contemporaneous Ethiopian and Kenyan sites. The oldest representative of the genus *Heterocephalus* would be *H. manthii* Denys, 2011 from Kakesio Beds at Laetoli (northern Tanzania) dated at about 4.3 Ma. Then, *H. quenstedti* Dietrich, 1942 has been described only

in the Upper Laetolil Beds at Laetoli (DENYS 1987, 2011). During the Lower Pleistocene, only three sites have yielded naked-mole rats remains represented by two extinct species: *H. atikoi* Wesselman, 1976, Omo Shungura (Ethiopia, 2.4–2.3 Ma), *H.* cf. *atikoi* Fejej (Ethiopia, 1.96 Ma; ECHASSOUX et al. 2004), and *H. jaegeri* Denys, 1989 from the Olduvai Bed I (N Tanzania, 1.7–1.6 Ma). *Heterocephalus* is absent of the well documented sites of Peninj (W Natron, S Kenya, 1.3 Ma) and from East Turkana Koobi Fora (N Kenya, 1.6 Ma). The species is absent from Hadar (AL 894) and Dikika (SABATIER 1982, BOBE et al. 2022, REED & GERAADS 2012). In the Middle and Upper Pleistocene the species is encountered in the Upper Pleistocene levels (A1C-70-80) at Goda Buticha (Ethiopia; STOETZEL et al. 2018) and is absent from the Ngaloba Beds (Laetoli, Tanzania; DENYS 2022; Table 4).

Heterocephalus manthii is characterized by a small skull and small molars and is a small hypsodont *Heterocephalus* species with a long, bilobed M^3, well marked anterior and posterior depressions on M^1, presence of elongated distolingual angle on M^1; *H. manthi* is distinguished from *H. quenstedti* by the bilobed, longer M^3. It has smaller molars than *H. atikoi*, and *H. jaegeri*. It is less hypsodont than *H. quenstedti* and *H. jaegeri*, but it is much more hypsodont than modern *H. glaber*. This species differs from modern *H. glaber* in the proportions and size of the molars, and greater hypsodonty. The M^3/$_3$ are narrow and longer than wider which looks similar to modern *H. glaber ansorgei* specimens.

Heterocephalus quenstedti Dietrich, 1942 is characterized by a small skull, very divergent tympanic bullae, inflated on their ventral side up to the auditory canal (Fig. 9). The paroccipital processes are joined to the bullae. The molars are smaller compared to any other modern
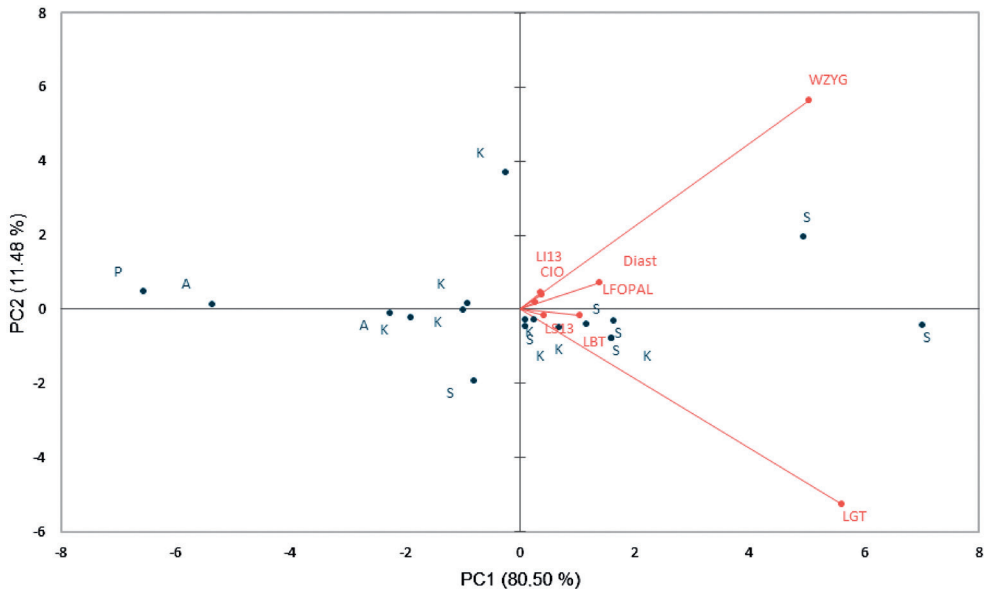

Fig. 7. Results of the Principal Component Analysis on 8 skull dimensions and 18 modern *Heterocephalus glaber* s.l. specimens; PC1 and PC2: 91.98%; A – *ansorgei*, K – Kenya, S – Somalia, E – Ethiopia, P – *phillipsi*.
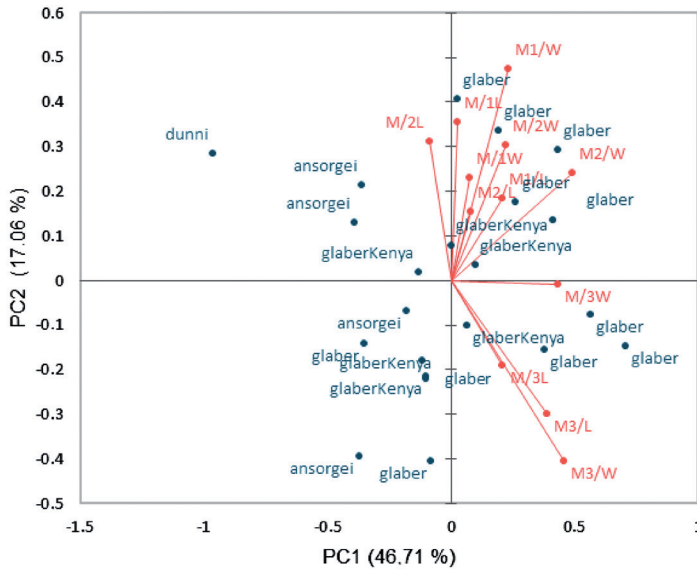
Fig. 8. Results of the Principal Component Analysis on 12 molars length and width dimensions, whithout *Heterocephalus glaber phillipsi* due to the absence of M³/₃ in these specimens. glaber: *H. g. glaber* Ethiopia,Somalia, glaber, Kenya: *H. g. glaber* from Kenya (subspecies *ansorgei* or *glaber* indeterminate), ansorgei: specimens labelled *ansorgei* at the BMNH, dunni: specimen labelled *dunni* at the BMNH.

species. The M³/₃ are not reduced in their distal width and the M₃ is larger than in *H. glaber*. Molar crowns are semi-hypsodont (higher than in *H. glaber*) and roots incompletely fused. *H. quenstedti* can be distinguished from *H. glaber* by a broader interorbital region, longer pterygoidal and basioccipital region, more divergent and inflated tympanic bullae. *Heterocephalus quenstedti* has relatively small and wide M³/₃ which is closer to modern *H. glaber glaber* from Ethiopia and Somalia.

Heterocephalus atikoi is similar to modern *H. glaber* in terms of molar morphology and dimensions (WESSLMAN 1984). It differs in exhibiting a higher crown. It has smaller molars than *H. quenstedti* and *H. jaegeri*. *Heterocephalus jaegeri* is characterized by more hypsodont molars, elongation of the disto-lingual enamel angle on upper M¹⁻². Absence of sinuside and sinus on M¹/₁. M³/₃ are large but small like in *H. glaber glaber* (Fig. 10) .

Cranio-dental size among Plio-Pleistocene fossil record

Cranio-dental dimensions
Very few complete skulls have been recovered from the fossil record. Only one specimen (LAET 75-2808) can be added to the PCA on skull distances and in order to incorporate the type specimens only three cranial distances were incorporated to the analyses (LGT, WZYG, CIO). Axis one is a size axis which separates smaller forms (*H. g. ansorgei*, *H. g. philippsi*, *H. g. stygius*) from larger ones like *H. g. dunni*, *H. g. glaber* and the Somalian specimens (Fig. 10). The skull

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Table 4. Distribution through time and space of the main Plio-Pleistocene *Heterocephalus* fossil record. We have associated here *Tachyoryctes* fossil record in order to discuss eventual competition between the two fossorial rodents

site	age	N Tanzania	Kenya	S.Ethiopia	N & E Ethiopia	reference
GJw22+ GB	43–26 ka	—	*Tachyoryctes*	—	—	TRYON et al. (2015)
Goda Buticha	63–25 ka	—	—	—	*Tachyoryctes, Heterocephalus*	STOETZEL et al. (2018)
Ngaloba Beds	120 ka	*Tachyoryctes*	—	—	—	DENYS (2022)
Garba VIII	200–300 ka	—	—	—	*Tachyoryctes*	SABATIER (1978, 1982)
Isenya	0.8 Ma	—	—	—	—	BRUGAL & DENYS (1989)
East Turkana	1.6 Ma	—	—	—	—	BLACK & KRISHTALKA (1986)
Olduvai Bed I	1.8–1.7 Ma	*Heterocephalus*	—	—	—	DENYS (1989)
Fejej	1.96 Ma	—	—	*Heterocephalus*	—	ECHASSOUX et al. (2004)
Omo F &G	2.4–2.3 Ma	—	—	*Heterocephalus*	—	WESSELMAN (1984)
AL 894	2.4 Ma	—	—	—	—	REED & GERAADS (2012)
Upper Ndolanya Beds	2.5–2.7 Ma	—	—	—	—	DENYS (2011)
Upper Laetolil Beds	3.7–3.5 Ma	*Heterocephalus*	—	—	—	DENYS (1987, 2011)
Hadar	3.5–3.3 Ma	—	—	—	*Tachyoryctes*	SABATIER (1978)
Dikika	3.6–3.2 Ma	—	—	—	—	BOBE et al. (2022)
Kanapoi	4.1 Ma	—	—	—	—	MANTHI & WINKLER (2020)
Lower Laetolil Beds	4.3 Ma	*Heterocephalus*	—	—	—	DENYS (2011)
Ibole	4.5 Ma	—	—	—	—	WINKLER (1997)
Tabarin/Chemeron	4.5–4.4 Ma	—	—	—	—	WINKLER (2002)
Aramis	4.4 Ma	—	—	—	*Tachyoryctes*	LOUCHART et al. (2009)
Lothagham	5.2–3.5 Ma	—	—	—	—	WINKLER (1999)
Adu Asa	5.7–4.9 Ma	—	—	—	*Tachyoryctes*	WESSELMAN et al. (2009)
Lemudon'go	6 Ma	—	—	—	—	MANTHI (2007)
Lukeino	6.1–5.8 Ma	—	—	—	—	MEIN & PICKFORD (2006)

of *H. quenstedti* (noted Q on Fig. 11) fit in the middle of the analysis with some Kenyan and Somalian *H. glaber glaber*.

Molars dimensions

Because most of the fossil record is constituted by isolated molars we have compared all data. We can observe that the fossil specimens also display a high variability in size of the molars (Fig. 12). *H.manthii* has always a very small size. *Heterocephalus quenstedti* has always smaller molars than *H. jaegeri* which means that if the three fossil species are phylogenetically related there is an increase of the molar sizes through times. For the upper M^{1-2} all fossil molars are smaller than the modern *H. g. glaber* from Somalia and fit within the Kenyan, ansorgei specimens size except for the M_2 and M_3 where *H. jaegeri* has similar size compared to Somali *H. g. glaber*. *Heterocephalus quenstedti* has a small $M^1/_1$ and $M^3/_3$ compared to other fossil and modern species as well as the smallest M_1 and M_3. *Heterocephalus atikoi* from Fejej keep the
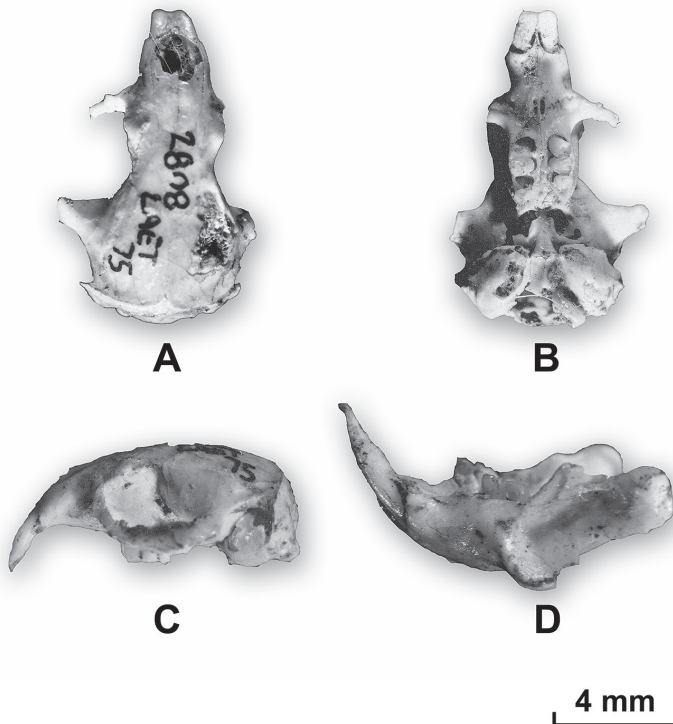

Fig. 9. Skull and mandible of *Heterocephalus quenstedti* (Upper Laetolil Beds, Laetoli) LAET75-2808; A – dorsal view; B – ventral view; C – lateral view; D – lateral view of the mandible.
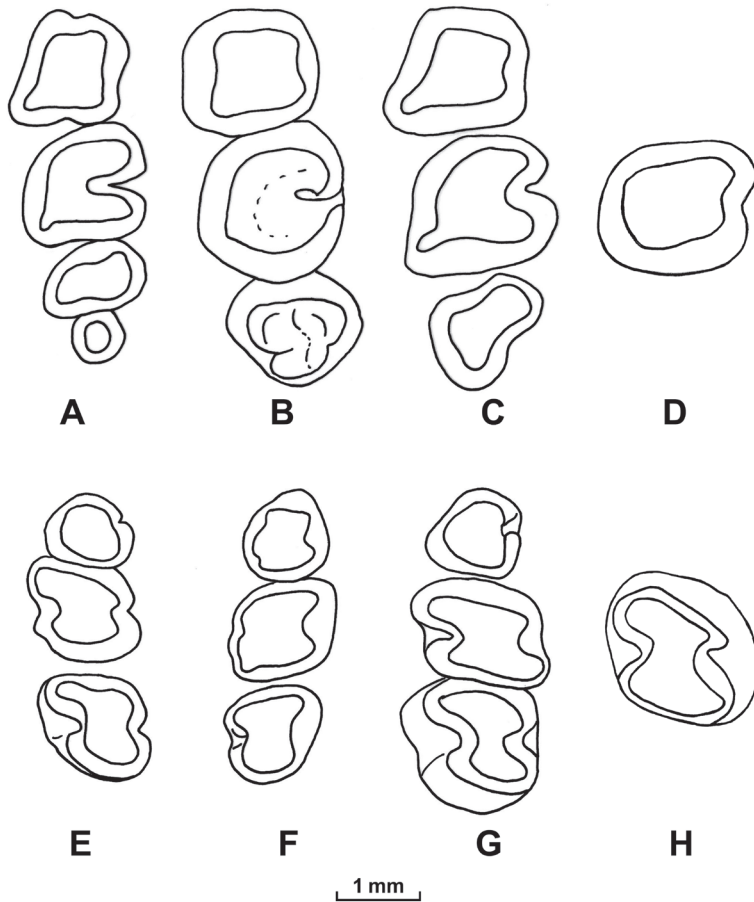
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Fig. 10. Dental morphology of fossil *Heterocephalus* species; top – upper right molar row; bottom – lower right molar row. A & E – *Heterocephalus manthii* holotype Kakesio; B & F – *H. quenstedti* LAET75-2808; C & G – *H. jaegeri* FLKN1 M3 Olduvai Bed I; D & H – *H. atikoi* M^2/$_2$ Omo Shungura 141-73-9084 & 28-165.

same size of the M^2 than in *H. quenstedti* from Laetoli and modern *H. g. ansorgei*, *H. g. phillipsi* and is smaller than *H. jaegeri* and the Somalian *H. g. glaber* specimens (Fig. 12).

Molar rows lengths
The plot of the Upper teeth row length versus the lower one shows that the available fossil specimens fit within the variability of the modern *H. glaber* s. l. (Fig. 13); *H. g. dunni* has the smallest molar rows like *H. g. phillipsi*.

DISCUSSION

Is there more than one species?

ZEMLEMEROVA et al. (2021) recently performed the first phylogenetic study of the whole genus in nearly all its distribution range and found a strong phylogeographic structuration for the whole genus. Two very divergent lineages that could be considered as distinct species were highlighted. The first clade named *H. glaber glaber* was found only in eastern Ethiopia and Djibouti, while the second has a larger distribution in Somali-Masai savanna in southern Ethiopia and Kenya (and probably southern Somalia) and it was named provisionnaly as *H. glaber ansorgei* according to ZEMLEMEROVA et al. (2021) pending the observation of *H. g. phillipsi* which has priority as the senior synonym.

If we refer to the biological concept of species, despite their high divergence percentage, both lineages are constituting valid subspecies because it was related that in captivity, naked mole-rats from northern and southern Kenya readily interbreed and produce healthy young (JARVIS & SHERMAN 2002). Moreover, the estimated date of divergence between the eastern and southern clades of *Heterocephalus* is quite recent (1.4–0.8 Ma) compared to the long fossil history of the genus.

However, morphologically we find some discriminant criteria (see below) that may allow to validate the two molecular clades pending further examination of the whole variability of modern collections of the genus including external and post-cranial characters. In addition, a sympatric zone or a contact one can be hypothetised for Somalia region for which no mole-
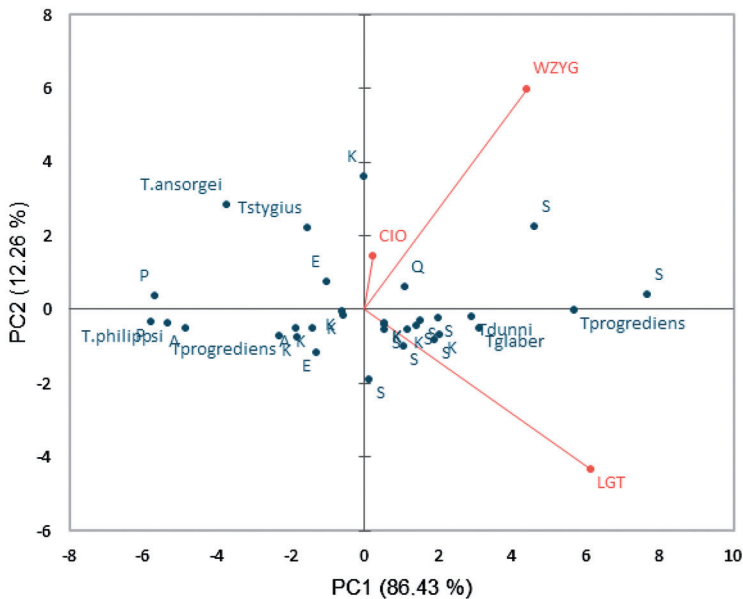
Fig. 11. Results of the Principal Component Analysis on three skull distances and 32 individuals; T – holotype; S – Somalia; E – Ethiopia; K – Kenya; P – *philippsi*; A – *ansorgei*; Q – *quenstedti*.

Fig. 12. Scatter plots of molars width versus length for fossil (triangles) and modern (points) *Heterocephalus* species; A – *H. g. ansorgei*, ATK – *H. atikoi*; D – *H. g. dunni*; E – Ethiopian *H. g. glaber*; J – *H. jaegeri*; K – Kenyan *H. g.* cf. *glaber*; KK – *H. manthii*; Q – *H. quenstedti*; S – Somalian *H. g. glaber*.

cular data are yet available and due to strong morphological differences we prefer to keep some Somalian forms as a separate sub species and not put *H. g. phillipsi* as senior synonym of *H. g. ansorgei* for the moment.
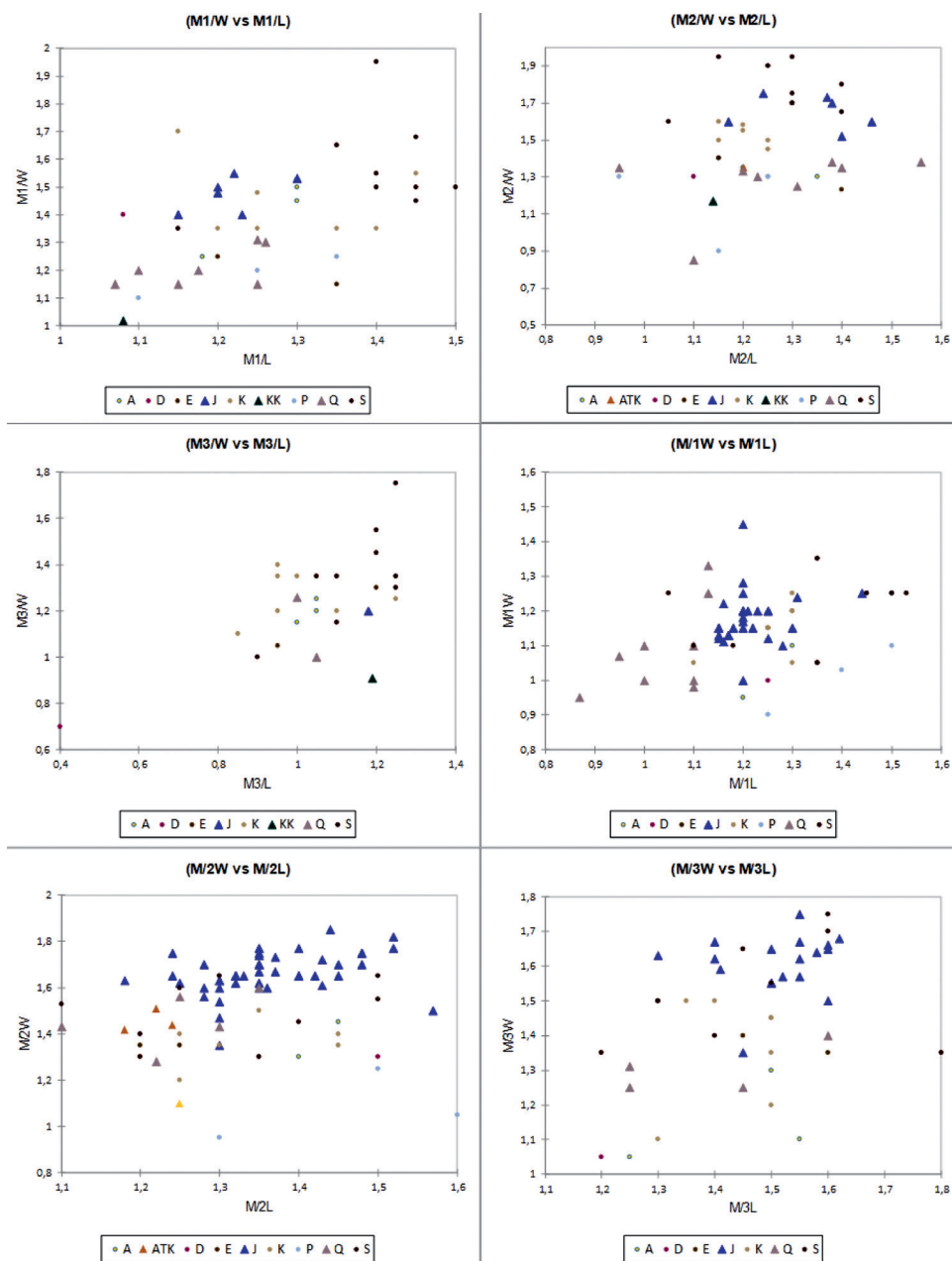
We provide below some new cranio-dental diagnostic characters for each sub-species and add a third geographical sub-species as a result of this work because *H. g. philippsi* and *H. g. dunni* are similar but share very different morphological patterns from *H. g. ansorgei* and *H. g. glaber*. By describing *H. dunni*, Thomas (1909) noticed its shared characters with *H. phillipsi*. We could not place here the other species like *H. g. progrediens* in synonymy, but in the PCA including type specimens showed that *H. g. stygius* is very close to *H. g. ansorgei* and both could be synonym (Fig. 7). *Heterocephalus g. scorteccii* may be synonymous with *H. g. phillipsi* because de Beaux (1912) diagnosed it as small, narrow nasal, small molars among which small upper M³. Moreover, due to low available samples for some taxa we cannot here revise their specific status.

Subspecies diagnoses of *Heterocephalus glaber*

Heterocephalus glaber glaber Rüppell, 1842

Distribution. East Ethiopia, Somalia, Djibouti, ?Kenya.
Cranio-dental characters. Large size of the skull (21.4–29.5 mm), large and wide molars especially the M_3. The upper and lower molar rows are large (M^{1-3} 3.3–3.7 mm, M_{1-3} 3.1–4.2 mm, N=16). Sinus and sinusid poorly marked. On average $M^2/_2$ width measure 1.63 and 1.43 mm, and $M^3/_3$ width 1.32 and 1.47 mm.

Heterocephalus glaber ansorgei Thomas, 1903

Synonym. *H. stygius* Allen, 1912
Distribution. Kenya.
Cranio-dental characters. Small skull (19.0–22.3 mm), small and narrow lower M_3 and upper M^3, labial and lingual sinus and sinuside well marked. Large upper and lower molar rows (M^{1-3} 3.4–3.8 mm, M_{1-3} 3.5–4.2 mm, N=4). On average $M^2/_2$ width measure 1.38 and 1.21 mm, $M^3/_3$ width 1.18 and 1.14 mm.

Heterocephalus glaber phillipsi Thomas, 1885

Synonyms. *H. dunni* Thomas, 1909; *H. scorteccii* de Beaux, 1934
Distribution. Somalia, eastern Ethiopia.
Cranio-dental characters. Small to medium size of the skull (18.6–26.0 mm), low coronoid process of the mandible, small molars rows (*H. g. phillipsi*: M^{1-3} 2.4–2.84 mm, M_{1-3} 2.7–2.8 mm, N=2; *H. g. dunni*: M^{1-3} 4.0 mm, M_{1-3} 2.95 mm, N=1), small or absent upper M³, long but narrow molars especially the M_2, and also M_3 when present, labial and lingual sinus and sinuside well marked. On average $M^2/_2$ width measure 1.17 mm for *H. g. phillipsi* and $M^3/_3$ width 0.7 and 1.05 mm for *H. g. dunni*.

Morphological evolutionary trends

The relationships between the Miocene Kenyan *Richardus* and the earliest recognized *Heterocephalus* have not yet been clarified due to a gap of nearly 10 Ma in the fossil record of this taxon. However, this means that Heterocephalidae family is old and the fossorial way of life in this taxon appeared probably very early in time. However, *Richardus* and *Heterocephalus* lineages differ from the *Proheliophobius* and *Cryptomys*, *Bathyergus* lineages by the reduction

of masseter muscular insertion and many characters from the mandible and the molars, among which the reduction of the dentition to three and even two molars.

Concerning the Plio-Pleistocene *Heterocephalus* species one can see the Tanzanian lineage (*H. manthii*, *H. quenstedti*, *H. jaegeri*) displays a size increase of the molars through time (especially the $M^1/_1$ and $M^3/_3$) and a tendency to increase the height of the crowns (hypsodonty).

None of the modern specimens examined displayed a long bilobed M^3 like in *H. manthii* or a large upper M^3 except MNHN 1884-1572 of unknown origin and which has a very large skull, strong jugal archs (dominant adult individual?) .

Finally there is a decrease of the size of the upper M^3 between the fossil and modern *H. glaber glaber* and *H. glaber philippsi* but not in *H. glaber ansorgei*. Such tendency to reduce the size of the $M^3/_3$ is found in many African rodent lineages like in *Mus* (*Nannomys*) or in Dendromurinae. The causes of the modifications of molars size is not fully known, but in the case of shrew-rats of Sulawezi (Indonesia), the loss of molars in *Rhynchomys* and *Paucidentomys* is accompanied by an adaptation to soft-bodied preys which is not the case here (ESSELSTYN et al. 2012). In the gerbil *Desmodilliscus braueri* there are three upper molars and only two in the mandible against the classical formula in other Gerbillinae. The diet of *D. braueri* is similar to those of other members of the Gerbillinae (granivory), so such loss of the third molar could not be adaptive and result from genetic cause. *Heterocephalus* and most of other Bathyergidae have developed a simple pattern of molar occlusal surface with low enamel proportions compared to dentine which is also found in Pedetidae (grazer) and primitive Geomyidae. In the Tsavo East National Park, BRETT (1986, 1991a, b) showed that *Heterocephalus* is a specialist feeder on underground plants with a large diversity of geophytes for which it consumes only rhizomes, roots and tubercles as deep as 70 cm below the surface and there is a non-random distribution
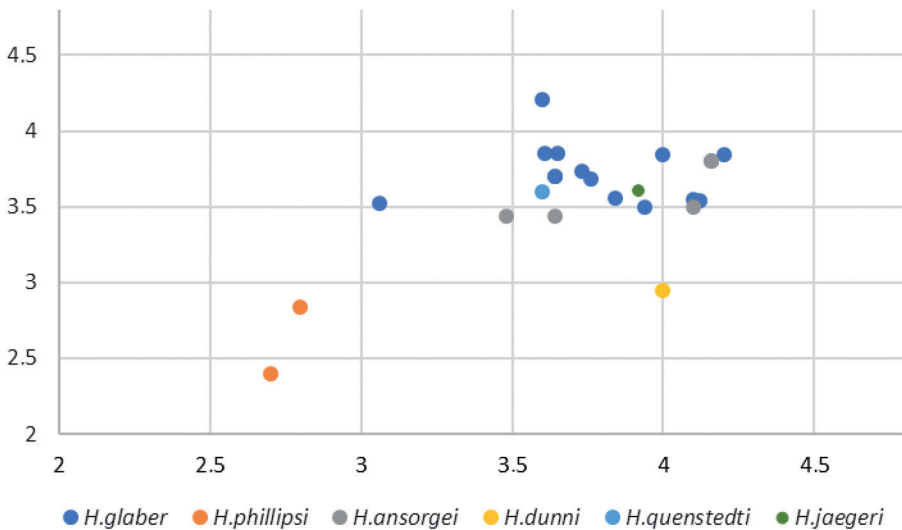

Fig. 13. Scatter plot of the length of the upper M^{1-3} versus lower M_{1-3} in mm.

of burrows system with patches of such vegetation. Is there a difference in food hardness that allowed the reduction of the M^3/$_3$ between the different lineages of *Heterocephalus* accompanied or not by the increase of the skull length as well as dental rows? According to Samuels (2009) the surface of cheek tooth area increases with herbivory as well as the length of the upper tooth row in rodents. Other parameters like size of the M^3/$_3$ may be relevant with diet adaptation in rodents but none of these studies attempted to combine diet and occlusal surface area or molar morphology in mole rats or even in other burrowing rodents (Martin et al. 2016).

It has also been suggested that the development of hypsodonty may be related to the increase of abrasion resulting from soil particles swallowed during ingestion of underground plants (Rensberger 1975). The fossil *H. jaegeri* displays the highest hypsodonty, largest size of the molars and enlargement of the tooth surface with the elongation of the linguo-distal angle of the tooth. Their teeth morphology do not correspond to any modern *Heterocephalus* taxon and we may hypothethize that the Tanzanian lineage was extinct after 1.6 Ma. By the fact no *Heterocephalus* live presently in the Serengeti. The development of hypsodonty and increase of the size of the cheek teeth observed in the Tanzanian lineage may result also from an increase in aridity of that region.

It appears from this work, that the different modern geographical subspecies of *Heterocephalus* have a relative plasticity in terms of molars size and morphology that were already remarked by Thomas in his earliest descriptions and we confirm it here.

Plio-Pleistocene diversification

In the Tanzanian rift basin, *Heterocephalus* is found since 4.3 Ma while in Ethiopia it is not recovered before 2.3 Ma despite the existence of various sites having yielded rodents (Table 4). It is absent from all Kenyan sites having yielded rodents. Today *Heterocephalus* is no longer living in Tanzania but is known in Kenya and Ethiopia, Somalia.

The first east African *Heterocephalus* occurs at 4.3 Ma in Kakesio (Lower Laetoli Beds, N Tanzania). This locality has yielded a low abundance of fossils and only three rodent taxa among which *Petromus* sp. which could indicate rocky areas in dry conditions and presence of the extinct species *Saccostomus major* whose modern relatives make burrows in soft soils, black cotton soils and old termitaries mounts. The genus has not been recorded from other well-documented contemporaneous sites of East Africa (Lukeino, Kanapoi) for unknown taphonomic or paleoenvironmental reasons. By that times, the spreading of C4 grasslands starting at around 10 Ma and major atmospheric circulation changes in Indian Ocean and the onset of glacial-interglacial cycles have deeply transformed the vegetation and mammalian communities (Cerling et al. 1997, Bonnefille et al. 2004, Bobe & Behrensmeyer 2004, Uno et al. 2016, de Menocal 2004). It is known also that the East African Rift system began to uplift (in southern Ethiopia and Turkana depression in nortern Kenya) during the Eocene-Oligocene times and uplifting reached its maximum around 2.5 Ma. As early as 20 Ma there was the development of the main Ethiopian and Kenya rifts when after a major tectonic episode around 5 Ma in the Tanganyka and Malawi Rifts, the North Tanzanian divergence appeared at that time (Fig. 14). The major Tanzanian escarpments were present by 3 Ma and with crests between 1500 and 5000 m and it was recently shown that rifting is associated with drastic reorganisation of atmospheric circulations and aridification (Sepulchre et al. 2006).

According to de Menocal (2004), the Plio-Pleistocene period in East Africa is characterized by a long trend towards a general increase of aridity but with some peaks of higher intensity

related to the amplification of high latitude glacial cycles. Three major periods of aridity increase can be recognized between 2.8–2.4 Ma, 1.8–1.6 Ma and 1.2–0.8 Ma. Because *Heterocephalus glaber* is today living in arid and semi-arid environments (KINGDON 1974, JARVIS & SHERMAN 2002), we may hypothethise that the Pleistocene diversification of this taxon may be driven by these climate changes. By the fact *H. atikoi* and *H. jaegeri* are found in southern Ethiopia and northern Tanzania around 2.4–1.7 Ma during arid periods. Fejej FJ-1 is a contemporaneous from Omo F and G sites and the large mammal assemblages indicate an open savanna environment and also probable woodlands and gallery forest habitats were permanent water was found while the small mammals represent a more steppic arid environment (WESSELMAN 1984). According to ECHASSOUX et al. (2004), the small mammals coming from the C1 level of the site FJ-1a are similar to those of Omo Shungura members F & G and are contemporaneous of the climatic arid episode occurring at 2.4 Ma. In Goda Buticha during upper Pleistocene times, the arid grassland habitat was present around the cave but the rodent fauna do indicate also the presence of montane forest and woodlands in the vicinity (STOETZEL et al. 2018).

Further it has recently been demonstrated that the long term C4 grassland expansion trend was punctuated by a C3 grass increase during a warm episode characterized by more woody vegetation at the Mid Pleistocene transitions (1.3–0.7 Ma) in the Turkana Basin (QUINN & LEPRE 2021). This period corresponds to a gap in our *Heterocephalus* record, the possible extinction of the Tanzanian lineage and the estimated period of divergence of the Kenyan lineage of *H. ansorgei* (Fig. 14).
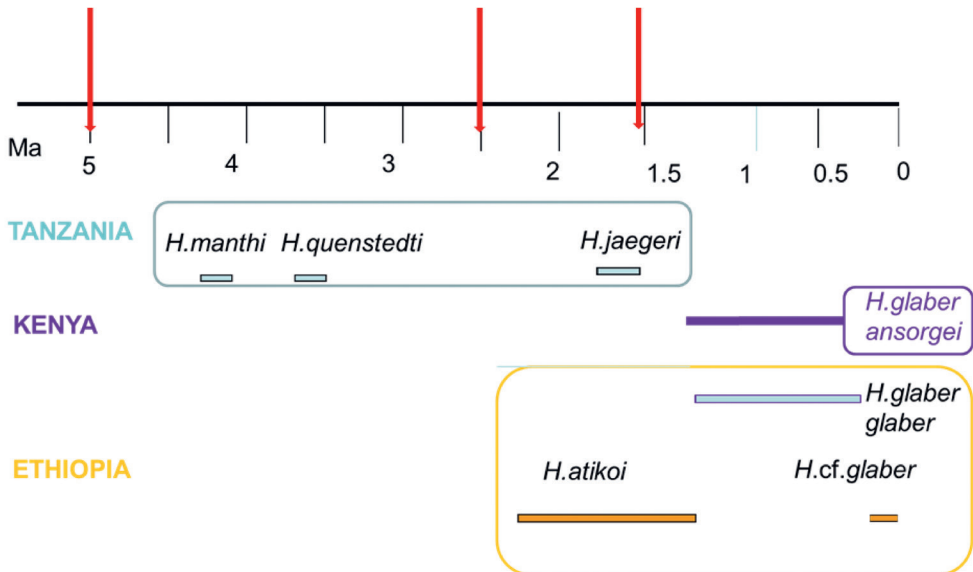

Fig. 14. Diversification through time and space of the Plio-Pleistocene and modern *Heterocephalus*. The red arrows indicate important climatic and tectonic pulses. The divergence between *H. ansorgei* and *H. glaber glaber* was estimated at 1.4–0.8 Ma (ZEMLEMEROVA et al. 2021).

Plant Underground Storage Organs (USO) are geophytic structures (corms, bulbs, rhizomes, tubers) that are relatively common in xeric habitats and consumed in great quantities by mole rats (YEAKEL et al. 2007). We do not know wether *H. glaber* prefers C3 or C4 plants USO or if it consumes both, but such changes in the vegetation may explain some pattern of diversification in the Rift Valley of the naked mole rat and its arrival in southern Ethiopia at around 2.4 Ma at the favour of a more arid episode (DE MENOCAL 2004).

Because *Heterocephalus* remains are absent from well-documented Kenyan and Ethiopian sites during 6–2.4 Ma we can hypothethize their ancestral populations were living in northern Tanzania (and may be more southerly than today) in an isolated basin of the tectonically active forming southern Rift. Later populations spread slowly to the north and isolation in the rift valley basins lead to the differentiation of two main lineages (Ethiopian and Kenyan ones) and possibly a Somalian one.

The late arrival of *Heterocephalus* in Ethiopia may be also related to the hypothesis of competition for subterranean fossorial niche with *Tachyoryctes* as expressed by KINGDON (1974) and discussed in ŠUMBERA et al. (2018) (Table 4). The latter authors indicated that the centre of diversification of the root rats is probably Ethiopian and the first radiation occurred in 3.1–0.9 Ma. By the fact, the first occurrence of *Tachyoryctes* in East Africa dates from 5.7 Ma in Adu Asa site situated in the Middle Awash (Ethiopia) and the paleoenvironment is qualified of moist grassland (WESSELMAN et al. 2009, LOPEZ-ANTONANZAS & WESSELMAN 2013). If root rats prefer cold and humid habitats, the naked mole rats prefer arid open grasslands with unpredictable rainfall. The alternate presence of both taxa may reflect the climatic oscillations occurring in the rift valley and explain the pulses of evolution of the taxa.

However, the rarity and alternance of *Heterocephalus* and *Tachyoryctes* in the East African Plio-Pleistocene sites may also be due to a taphonomic predation bias. By the fact it is well known that rodents and other small mammals originate from avian and carnivore predation in fossil sites (ANDREWS 1990, FERNANDEZ-JALVO et al. 1998, STOETZEL et al. 2022). *Heterocephalus* is preyed upon by small carnivores, raptorial birds and snakes. *Tachyoryctes* is mostly hunted by small carnivors like *Ictonyx* and *Poecilogale* and occasionally by *Leptailurus serval* and *Canis simensis*. It is also found in eagle, augur buzzard and large owl pellets (DENYS 2022).

CONCLUSIONS

Based upon our modern reference sample, which is limited in terms of geographic and population coverage, we confirm the existence of a high morphological and size variability among modern representatives of the genus *Heterocephalus*. By incorporating some type specimens to the descriptions and analyses we confirm that the *H. g. ansorgei* specimens from Kenya and *H. g. phillippsi* from Ethiopia, Somalia examined here are distinct from those attributed to *H. glaber* s.s. from Ethiopia and Somalia mostly based upon the dental morphology and cranio-dental size. This could confirm partly the molecular study of ZEMLEMEROVA et al. (2021). However, further works including larger samples and integrating sexual and social dimorphism are necessary to rehabilitate *H. g. ansorgei* and *H. g. philippsi* as valid species. There is also the need to study size and morphology structure of wild colonies corresponding to molecular lineages named ansorgei, philippsi and true glaber.

We could define morphological trends between the fossil Tanzanian lineage that appears now extinct and highlight that each named subspecies has a different pattern in the relative proportion and size of the molars. The meaning of these differences is not clear due to the absence of solid

informations on the adaptative versus genetic value of molar patterns among these and other groups of burrowing rodents.

The comparative study of the modern and fossil *Heterocephalus* shows that they were present first in Tanzania and then are recovered further north in the Horn of Africa. We can put in relation some episodes of this dispersal with arid climatic events as well as tectonic periods and document the ability of the species to track arid and open habitats whithout much morphological changes since about 5 Ma.

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APPENDIX 1

Voucher list of the *Heterocephalus glaber sensu lato* specimens employed in this work, in bold are type specimens; label – name associated to the voucher; abb – designation employed through various statistical analyses here; name – name proposed here after this revision. However due to the low sample some attributions remaied indetermined. The Kenyan specimens may belong either to *H. g. ansorgei* or to *H. g. glaber*

museum ID	country	locality	label	abb	name
BMNH 4.5.9.22	Somalia	Hargeisa	*glaber*	S	*g. glaber*
BMNH 99.5.31.1	Somalia	Goolis Mountains	*glaber*	S	*g. glaber*
BMNH 93.11.30.1	Somalia	Errer (Erru region)	*glaber*	S	*g. glaber*
BMNH 1907.4.1.12	Somalia	Hargeisa	*glaber*	S	*g. glaber*
BMNH 97.8.9.22	Somalia	Sik	*glaber*	S	*g. glaber*
BMNH 6.3.4.10	Somalia	Sheik	*glaber*	S	*g. glaber*
BMNH 9.5.31.1	Somalia	–	*glaber*	S	*g. glaber*
BMNH 4.5.9.24	Somalia	–	*phillipsii Fornarina*	P	*g. phillipsi*
BMNH 3.12.3.1	Somalia	Mogadishu	*phillipsii Fornarina*	P	*g. phillipsi*
BMNH 1904.5.9.23[?]	Somalia	Wardain	*dunni*	D	*g. phillipsi*
BMNH 32.2.19.10	Kenya		*glaber*	K	indet.
BMNH 32.2.19.9	Kenya	Gaba Tula	*glaber*	K	indet.
BMNH 74.169	Kenya	Kipsing R., 60 mi north	*glaber*	K	*g. glaber*
BMNH 15.10.12.1	Kenya	Juba R., Alexandria	*ansorgei*	A	*g. ansorgei*
BMNH 15.10.12.2	Kenya	Juba R., Alexandria	*ansorgei*	A	*g. ansorgei*
BMNH 15.10.12.3	Kenya	Juba R., Alexandria	*ansorgei*	A	*g. ansorgei*
BMNH 9.6.1.28	Kenya	Barissa, Boran	*glaber*	K	cf. *g. glaber*
BMNH 74.173	Kenya	Kipsing R., 60 mi north	*glaber*	K	cf. *g. glaber*
BMNH 11.12.1.122	Kenya	Ngama Nyango, Eusso Nyiro	*glaber*	K	cf. *g. glaber*
BMNH 1951.703	Kenya	Sankuri, Tana R.	*glaber*	K	*g. glaber*
BMNH 1951.702	Kenya	Sankuri, Tana R.	*glaber*	K	*g. glaber*
BMNH 74.170	Kenya	Kipsing R., 60 mi north	*glaber*	K	*g. glaber*
MNHN ZM-MO 1884-1572	Somalia	–	*glaber*	S	*g. glaber*
MNHN ZM-MO 1901-572	Ethiopia	Harrar	*glaber*	E	*g. glaber*
MNHN ZM-MO 1978-269	Somalia	Genale	*glaber*	S	*g. glaber*
MNHN ZM-MO 1978-268	Somalia	Afmadu	*glaber*	S	*g. glaber*
DDW24	Ethiopia	Goda Butisha	*glaber*	E	*g. glaber*
Omo	Ethiopia	Omo River	*glaber*	E	*g. glaber*
BMNH 85.12.10.1	Somaliland	Gerlogobie, Ogardain, Central Somaliland	*phillipsii*	T P	*g. phillipsi*
SMNS 855	Ethiopia	Schoa	*glaber*	T G	*g. glaber*
BMNH 4.5.9.23	Somaliland	Wardairi	*dunni*	T D	*g. phillipsi*
BMNH 98.9.25.3	Kenya	betw. Ngomeni and Kjinani, Makindu C.	*ansorgei*	T A	*g. ansorgei*

APPENDIX 2

Detail of the molar dimensions of the modern and fossil specimens used in this work: M^{1-3} – upper molars, M_{1-3} – lower molars, L – length, W – width, A – *ansorgei*, D – *dunni*, P – *phillipsi*, S – Somalia, K – Kenya, E – Ethiopia, ab – abbreviation country/taxon; for a comlete ID see Appendix 1

subspecies	ID	ab	M^1L	M^1W	M^2L	M^2W	M^3L	M^3W	M_1L	M_1W	M_2L	M_2W	M_3L	M_3W
ansorgei	15.10.12.2	A	1.30	1.50	1.35	1.30	1.00	1.15	1.50	1.25	1.45	1.45	1.25	1.05
ansorgei	98.9.25.3	A	1.18	1.25	1.20	1.35	1.05	1.25	1.20	0.95	1.25	1.10	1.55	1.10
ansorgei	15.10.12.1	A	1.30	1.45	1.15	1.40	1.05	1.20	1.30	1.10	1.40	1.30	1.50	1.30
glaber	DDW24	E	1.35	1.15	1.40	1.23	0.95	1.05	1.25	1.15	1.25	1.35	1.45	1.40
glaber	1901-572	E	1.20	1.25	1.15	1.40	1.20	1.30	1.10	1.10	1.20	1.35	1.60	1.35
glaber	9.6.1.28	K	1.25	1.48	1.25	1.60	1.00	1.35	1.10	1.05	1.35	1.50	1.50	1.45
glaber	74.170	K	1.20	1.35	1.25	1.50	0.95	1.35	1.30	1.20	1.25	1.20	1.50	1.35
glaber	11.12.1.122	K	1.25	1.35	1.25	1.30	1.25	1.25	1.30	1.05	1.35	1.30	1.50	1.50
glaber	74.173	K	1.15	1.70	1.20	1.58	0.95	1.20	1.25	1.15	1.25	1.40	1.35	1.45
glaber	51.702	K	1.45	1.55	1.20	1.55	0.95	1.40	1.30	1.25	1.30	1.35	1.50	1.50
ansorgei	15.10.12.3	A	1.35	1.35	1.25	1.45	0.85	1.10	1.30	1.20	1.45	1.40	1.40	1.10
glaber	74.169	K	1.40	1.35	1.15	1.50	1.10	1.20	1.35	1.35	1.45	1.35	1.30	1.20
phillipsi	85.12.10.1	P	1.35	1.25	1.25	1.30	–	–	1.50	1.10	1.60	1.05	–	–
phillipsi	4.5.9.24	P	1.25	1.20	0.95	1.30	–	–	1.40	1.03	1.30	0.95	–	–
phillipsi	3.12.3.1	P	1.10	1.10	1.15	0.90	–	–	1.25	0.90	1.50	1.25	–	–
glaber	97.8.9.22	S	1.45	1.45	1.15	1.95	1.25	1.35	1.53	1.25	1.50	1.55	1.80	1.35
glaber	4.5.9.22	S	1.40	1.50	1.25	1.90	1.25	1.75	1.35	1.05	1.25	1.60	1.60	1.70
glaber	99.5.31.1	S	1.40	1.95	1.40	1.80	1.10	1.15	1.35	1.05	1.35	1.30	1.40	1.40
glaber	6.3.4.10	S	1.45	1.50	1.30	1.75	1.25	1.30	1.50	1.25	1.40	1.45	1.30	1.50
glaber	74.112	S	1.40	1.55	1.30	1.70	0.90	1.00	1.35	1.35	1.30	1.65	1.30	1.50
dunni	4.5.9.23	D	1.08	1.40	1.10	1.30	0.40	0.70	1.25	1.00	1.50	1.30	1.20	1.05
glaber	93.11.30.1	S	1.45	1.68	1.40	1.65	1.10	1.35	1.45	1.25	1.50	1.65	1.60	1.75
glaber	1884-1578	S	1.50	1.50	1.30	1.70	1.20	1.45	1.10	1.10	1.20	1.40	1.45	1.65
glaber	1978-268	S	1.35	1.65	1.30	1.95	1.20	1.55	1.05	1.25	1.10	1.53	1.50	1.55
glaber	1978-269	S	1.15	1.35	1.05	1.60	1.05	1.35	1.18	1.10	1.20	1.30	1.20	1.35
Kakesio	–	KK	1.08	1.02	1.14	1.17	1.19	0.91	–	–	–	–	–	–
quenstedti	–	Q	1.07	1.15	1.56	1.38	1.05	1.00	0.87	0.95	1.22	1.28	1.60	1.40
quenstedti	–	Q	1.26	1.30	1.10	0.85	1.00	1.26	1.10	1.00	1.30	1.43	1.25	1.25
quenstedti	–	Q	1.25	1.31	1.23	1.30	–	–	0.95	1.07	1.10	1.43	1.45	1.25
quenstedti	–	Q	1.25	1.15	1.20	1.33	–	–	1.10	0.98	1.35	1.60	1.25	1.31

subspecies	ID	ab	M^1L	M^1W	M^2L	M^2W	M^3L	M^3W	M_1L	M_1W	M_2L	M_2W	M_3L	M_3W
quenstedti	–	Q	1.18	1.20	0.95	1.35	–	–	1.13	1.33	1.25	1.56	–	–
quenstedti	–	Q	1.15	1.15	1.40	1.35	–	–	1.13	1.25	–	–	–	–
quenstedti	–	Q	1.10	1.20	1.38	1.38	–	–	1.10	1.10	–	–	–	–
quenstedti	–	Q	–	–	1.31	1.25	1.18	1.20	1.00	1.00	–	–	–	–
quenstedti	–	Q	–	–	–	–	–	–	1.00	1.10	–	–	–	–
jaegeri	–	J	1.20	1.50	1.46	1.60	–	–	1.20	1.25	1.30	1.63	1.62	1.68
jaegeri	–	J	1.22	1.55	1.38	1.70	–	–	1.31	1.24	1.48	1.70	1.40	1.67
jaegeri	–	J	1.23	1.40	1.17	1.60	–	–	1.17	1.13	1.45	1.70	1.55	1.67
jaegeri	–	J	1.20	1.48	1.24	1.75	–	–	1.20	1.28	1.35	1.77	1.60	1.66
jaegeri	–	J	1.15	1.40	1.40	1.52	–	–	1.23	1.20	1.37	1.67	1.52	1.57
jaegeri	–	J	1.30	1.53	1.37	1.73	–	–	1.22	1.15	1.44	1.85	1.60	1.65
jaegeri	–	J	–	–	–	–	–	–	1.15	1.12	1.45	1.65	1.50	1.65
jaegeri	–	J	–	–	–	–	–	–	1.20	1.18	1.57	1.50	1.40	1.62
jaegeri	–	J	–	–	–	–	–	–	1.25	1.12	1.40	1.77	1.30	1.63
jaegeri	–	J	–	–	–	–	–	–	1.20	1.45	1.43	1.61	1.58	1.64
jaegeri	–	J	–	–	–	–	–	–	1.25	1.20	1.30	1.60	1.55	1.57
jaegeri	–	J	–	–	–	–	–	–	1.20	1.20	1.28	1.60	1.55	1.75
jaegeri	–	J	–	–	–	–	–	–	1.20	1.00	1.30	1.63	1.41	1.59
jaegeri	–	J	–	–	–	–	–	–	1.28	1.10	1.32	1.65	1.60	1.50
jaegeri	–	J	–	–	–	–	–	–	1.44	1.25	1.52	1.77	1.50	1.55
jaegeri	–	J	–	–	–	–	–	–	1.15	1.15	1.25	1.62	1.50	1.55
jaegeri	–	J	–	–	–	–	–	–	1.21	1.20	1.52	1.82	1.45	1.35
jaegeri	–	J	–	–	–	–	–	–	1.16	1.22	1.35	1.75	1.55	1.62
jaegeri	–	J	–	–	–	–	–	–	1.20	1.20	1.35	1.70	–	–
jaegeri	–	J	–	–	–	–	–	–	1.20	1.17	1.35	1.70	–	–
jaegeri	–	J	–	–	–	–	–	–	1.30	1.15	1.28	1.56	–	–
jaegeri	–	J	–	–	–	–	–	–	1.15	1.13	1.36	1.60	–	–
jaegeri	–	J	–	–	–	–	–	–	1.15	1.15	1.40	1.65	–	–
jaegeri	–	J	–	–	–	–	–	–	1.20	1.15	1.42	1.65	–	–
jaegeri	–	J	–	–	–	–	–	–	1.20	1.20	1.30	1.54	–	–
jaegeri	–	J	–	–	–	–	–	–	1.18	1.15	1.48	1.75	–	–
jaegeri	–	J	–	–	–	–	–	–	1.25	1.20	1.30	1.47	–	–
jaegeri	–	J	–	–	–	–	–	–	1.20	1.20	1.28	1.70	–	–
jaegeri	–	J	–	–	–	–	–	–	1.17	1.13	1.48	1.75	–	–
jaegeri	–	J	–	–	–	–	–	–	1.16	1.11	1.40	1.65	–	–

APPENDIX 2

(continued)

subspecies	ID	ab	M¹L	M¹W	M²L	M²W	M³L	M³W	M₁L	M₁W	M₂L	M₂W	M₃L	M₃W
jaegeri	–	J	–	–	–	–	–	–	–	–	1.35	1.74	–	–
jaegeri	–	J	–	–	–	–	–	–	–	–	1.32	1.65	–	–
jaegeri	–	J	–	–	–	–	–	–	–	–	1.35	1.60	–	–
jaegeri	–	J	–	–	–	–	–	–	–	–	1.24	1.65	–	–
jaegeri	–	J	–	–	–	–	–	–	–	–	1.33	1.65	–	–
jaegeri	–	J	–	–	–	–	–	–	–	–	1.18	1.63	–	–
jaegeri	–	J	–	–	–	–	–	–	–	–	1.35	1.62	–	–
jaegeri	–	J	–	–	–	–	–	–	–	–	1.24	1.75	–	–
jaegeri	–	J	–	–	–	–	–	–	–	–	1.35	1.67	–	–
jaegeri	–	J	–	–	–	–	–	–	–	–	1.30	1.35	–	–
jaegeri	–	J	–	–	–	–	–	–	–	–	1.37	1.73	–	–
jaegeri	–	J	–	–	–	–	–	–	–	–	1.43	1.72	–	–
jaegeri	–	J	–	–	–	–	–	–	–	–	1.32	1.62	–	–
jaegeri	–	J	–	–	–	–	–	–	–	–	1.32	1.65	–	–
atikoi	–	ATK	–	–	–	–	–	–	–	–	1.24	1.44	–	–
atikoi	–	ATK	–	–	–	–	–	–	–	–	1.18	1.42	–	–
atikoi	–	ATK	–	–	–	–	–	–	–	–	1.22	1.51	–	–
cf. atikoi	–	ATK	–	–	1.20	1.35	–	–	–	–	–	–	–	–