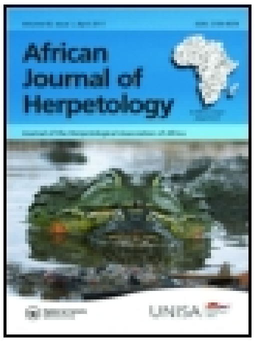

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Comparative skull osteology and preliminary systematic revision of the African lizard genus *Heliobolus* (Squamata: Lacertidae)

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ABSTRACT
The anatomy of African lacertid lizards (Lacertidae: Eremiadini) is poorly known, which has hindered a better understanding of their evolutionary relationships. This applies especially to the East African clade, which includes the genera *Nucras*, *Latastia*, *Philochortus*, *Pseuderemias* and *Heliobolus*. We present a detailed description of the skull osteology of the genus *Heliobolus* using X-ray microcomputed tomography and compare its morphology to the above lacertid taxa. Because the genus *Heliobolus* includes species of doubtful validity and affinities (*Heliobolus neumanni* and *Heliobolus nitidus*), we also present a detailed intrageneric comparison and construct a morphological character matrix that we analyse against a phylogenetic backbone derived from previous molecular studies. *Heliobolus lugubris* and *Heliobolus spekii* can be well characterised as a monophyletic group on the basis of a short postorbital and a continuously broad posterior margin of the parietal, differing from *H. nitidus* and other members of the East African clade in an overall low degree of ossification and reduced ventral extension of the frontal bone. Our preliminary phylogenetic analysis suggests that the genus *Heliobolus* is currently polyphyletic. We propose that the name *H. neumanni* be officially retracted, because specimens assigned to this species show very different morphologies relative to each other and are placed in different parts of the tree in our analysis. Also, the type specimen is lost and no specimens were collected from the type locality. *H. nitidus* shows a signal towards the genus *Latastia*. A definitive, new generic assignment of *H. nitidus* must await further investigations based on molecular data.

KEYWORDS
computed tomography; cranial osteology; systematics

Introduction

The Lacertidae is an Old World squamate family that comprises more than 320 species of lizards inhabiting various ecoregions and climatic zones of Eurasia and Africa (Arnold *et al.* 2007; Uetz & Hošek 2016). The "African" radiation of the subfamily Lacertinae is represented by the tribe Eremiadini, also referred to as the "Ethiopian and Advanced Saharo- Eurasian forms" in Arnold's (1989) morphology-based phylogeny. According to

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Hipsley *et al.* (2014), the Eremiadini evolved approximately 35–30 Mya (million years ago) and comprises 22 genera (Edwards *et al.* 2013a). The Eremiadini can be further divided into two distinct groups, the so-called Saharo- and Ethiopian (sub)clades, based on phylogenetic analyses using molecular data (Mayer & Pavlicev 2007; Kapli *et al.* 2011; Hipsley *et al.* 2014; Baeckens *et al.* 2015). Whereas the Ethiopian subclade is almost exclusively distributed in Africa, the Saharo-Eurasian subclade, as the name suggests, has a transcontinental distribution. According to Hipsley *et al.*'s (2014) time-calibrated molecular phylogeny, these subclades diversified in the late Oligocene. The Ethiopian subclade of the Eremiadini can be further subdivided into two sister clades, a South African and a North/East African group (Engleder *et al.* 2013), which separated 27–20 Mya (Hipsley *et al.* 2014). Morphological and osteological descriptions are scarce for most African lacertids, and particularly for the latter group, comprising the genera *Nucras*, Gray 1838, *Philochortus*, Matschie 1893, *Pseuderemias*, Boettger 1883, *Latastia*, Bedriaga, 1884, and *Heliobolus*, Fitzinger 1843 (but see Edwards *et al.* 2013b; Hipsley & Müller 2017). The general relationships among these genera based on molecular evidence (see above) is provided in Fig. 1.

Heliobolus, which we especially address in the current study, comprises four species: *Heliobolus lugubris* (Smith, 1838), distributed in southwestern Africa (Branch 1998); *Heliobolus spekii* (Günther, 1872) of East Africa (Spawls *et al.* 2004) consisting of 3 recognised subspecies (*H. s. spekii, H. s. scorteccii* (Arillo *et al.* 1965), and *H. s. sextaeniata* (Stejneger, 1894)) with largely overlapping distribution ranges; *Heliobolus nitidus* (Günther, 1872), which has been recorded from several isolated localities across West Africa (Ineich & Chirio 2008), officially consisting of three subspecies, *H. n. nitidus* from West Africa, *H. n. garambensis* (Schmidt, 1919) from the Democratic Republic of Congo, and *H. n. quadrinasalis* from Chad (Chabanaud, 1918); and *Heliobolus neumanni* (Tornier,

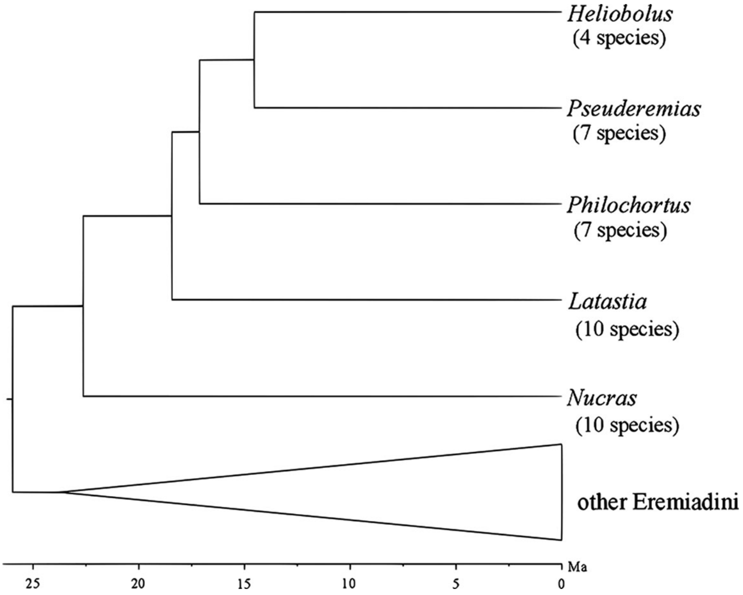

Figure 1. Phylogenetic relationships of the genera of the "North/East African group within Eremiadini", according to Hipsley *et al.* (2014). Scale bar refers to millions of years.

1905), originally described from the Barssa Valley in southern Ethiopia and now purportedly distributed in Ethiopia, Kenya and Tanzania (Spawls *et al*. 2004). Fitzinger (1843) coined the genus name and designated *Eremias lugubris*, described by Duméril and Bibron (1839) as the type species of the genus.

Additional genera of the North/East African group investigated in the current study are *Latastia*, *Philochortus*, and *Pseuderemias*. *Latastia* comprises ten species and is distributed across Sahelian Africa along the southern border of the Sahara, with its further distribution reaching southwards to Tanzania via the Horn of Africa, along Lake Victoria, Lake Tanganyika and Lake Malawi (Uetz & Hošek 2016). *Pseuderemias* contains seven species, which are distributed at the Horn of Africa and along the western shore of the Red Sea (Uetz & Hošek 2016). P*hilochortus* also comprises seven species and is primarily found at the Horn of Africa and the south-western tip of the Arabian Peninsula. An exception is *Philochortus zolii*, Scortecci, 1934, which occurs in five isolated areas in Egypt, Libya, Mali, and Niger (Uetz & Hošek 2016). A distribution map of the genera, as well as localities of specimens analysed are provided in Fig. 2.

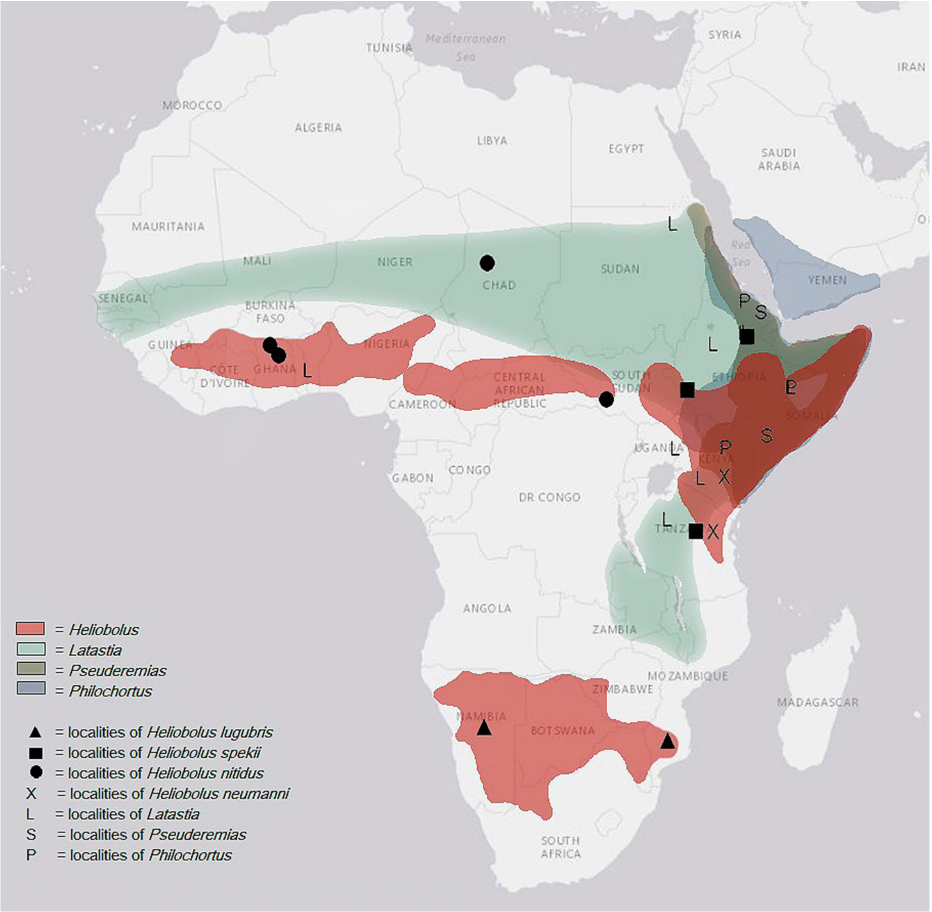

Figure 2. Map of Africa showing the collection localities of the specimens investigated in the current study, as well as the areas of distribution of the respective genera (modified from lacerta.de). For details see Table 1.

To date, most molecular studies agree that phylogenetic relationships within the North/East African group follow the branching pattern of *Nucras* (*Latastia* (*Philochortus* (*Heliobolus*, *Pseuderemias*))) (Fu 1998; Mayer & Pavlicev 2007; Kapli *et al.* 2011; Baeckens *et al*. 2015; see also Fig. 1). However, these relationships are complicated by a lack of data and taxonomic uncertainty for two of the four species in *Heliobolus*. The first is *"H." neumanni*, whose type specimen is lost (Bauer & Günther, 1995), and no genetic samples are available. Only recently has the name been applied to photographs (Spawls *et al*. 2004), although it is still unclear whether the photographed lizards are conspecific with the now-lost type. The second problematic species, *"H." nitidus* from West Africa (Ineich & Chirio 2008), has a markedly different distribution to the other members of the genus, and its assignment to the *Heliobolus* was not based on any detailed taxonomic assessment. Because there are no genetic samples available for these species, the only option currently to assess the systematic status of *"H." nitidus* and *"H." neumanni* is to perform comparative morphological analyses.

The purpose of the current study is to present the first detailed comparative description of the skull osteology of *Heliobolus*, which will be compared to other taxa of the North/East African group. This information, together with additional details from external morphology, will be used to assess the systematic status of the different species of *Heliobolus*.

Materials and methods

External morphological analyses

A total of 61 specimens from the North/East African group, mainly from the collection of the Museum für Naturkunde Berlin (ZMB), were used in this survey (see Table 1 for specimen details, localities, and snout-vent lengths). Forty-one external characters listed in Table 2 were scored for all specimens to develop a morphological character matrix. The determination of character states was informed by Arnold (1989) and several identification keys, including Branch (1998), Spawls *et al.* (2004), and Largen and Spawls (2006). In addition to metric information (snout-vent length), we focused on features of squamation. These include number and position of scales surrounding the nostrils and other cranial shields, surface features of cranial, dorsal, ventral, and caudal scales, number and orientation of abdominal scales, presence and number of lamellae, and number of femoral pores. Because most specimens were collected decades ago and pigmentation has faded, because of preservation in alcohol, colour patterns were not used.

Osteological analyses

We performed osteological analyses on a subset of individuals, typically three specimens per species, using X-ray micro-computed tomography (CT). Specimens were CT scanned at the Museum für Naturkunde Berlin using a GE Phoenix nanotom at 70 kV, 150 µA for a duration of 750 ms, resulting in a resolution of 6–8 µm. The resulting three-dimensional volumes were analysed using the visualization software Volume Graphics Studio MAX 2.2. During analysis of the skull osteology of *H. lugubris/ spekii* and comparison with the other species *H. nitidus* and *H. neumanni*, as well as the other genera of the North/East African group, we defined and recorded character states of the skull (Table 3).

Table 1. Localities, inventory numbers and type status of specimens examined in the current study. Snout-vent length, measured using callipers, is shown in millimetres. Official abbreviations: AMNH = American Museum of Natural History; BMNH = Natural History Museum London; CAS = California Academy of Sciences; MNHN = Muséum National d'Histoire Naturelle Paris; ZMB = Museum für Naturkunde Berlin.

Species	Locality	Reference-No.	SVL (mm)
Heliobolus lugubris	Maconjo, Mozambique	ZMB 7774	59.2
Heliobolus lugubris	Namibia	ZMB 17951	53.16
Heliobolus lugubris	Namibia	ZMB 17951a	49.93
Heliobolus lugubris	Namibia	ZMB 17951b	53.01
Heliobolus lugubris	Namibia	ZMB 18328	55.8
Heliobolus neumanni	Dar es Salaam Region, Tanzania	CAS 245014	36.09
Heliobolus neumanni	Wema, Ngatana, Tana R, Kenya	MCZ 40203	40.82
Heliobolus neumanni	Wema, Ngatana, Tana R, Kenya	MCZ 40207	43.08
Heliobolus neumanni	Wema, Ngatana, Tana R, Kenya	MCZ 40216	41.39
Heliobolus nitidus	West Africa	BMNH 1946.8.6.51	39.98
Heliobolus nitidus	West Africa	BMNH 1946.8.6.52	33.46
Heliobolus nitidus	Kete, Togo	ZMB 16603	48.35
Heliobolus nitidus	Kuntja, Ghana	ZMB 78926	48.28
Heliobolus nitidus	Ulango, Togo	ZMB 78927	45.13
Heliobolus nitidus	Ulango, Togo	ZMB 78928	41.11
Heliobolus nitidus garambensis	Garamba, Belgian Congo	AMNH R-10686	59.88
Heliobolus nitidus quadrinasalis	Fort Arschambo, Chad	MNHN 1904161	66.69
Heliobolus spekii sextaeniata	Harar, Ethiopia	ZMB 19807	51.9
Heliobolus spekii sextaeniata	Harar, Ethiopia	ZMB 19807a	47.12
Heliobolus spekii sextaeniata	Harar, Ethiopia	ZMB 19807b	54.29
Heliobolus spekii sextaeniata	Barssa river, Ethiopia	ZMB 19796	47.79
Heliobolus spekii spekii	Mazimbu, Morogoro, Tanzania	ZMB 48324	45.94
Heliobolus spekii spekii	Mazimbu, Morogoro, Tanzania	ZMB 48325	39.27
Heliobolus spekii spekii	Mazimbu, Morogoro , Tanzania	ZMB 48327	41.09
Latastia boscai	Dire-Dawa, Ethiopia	ZMB 29460	43.23
Latastia carinata	Tekoscha, Somalia	ZMB 18202	36.58
Latastia carinata	Djildessa, Sheik Serbej, Ethiopia	ZMB 19793	42.49
Latastia johnstonii	Mozambique	ZMB 27552	52.8
Latastia johnstonii	Mozambique	ZMB 27552a	55.26
Latastia johnstonii	Mozambique	ZMB 27570	48.91
Latastia johnstonii	Mozambique	ZMB 27570a	52.08
Latastia johnstonii	Mozambique	ZMB 27570b	53.53
Latastia johnstonii	Mozambique	ZMB 27570c	56.56
Latastia johnstonii	Mozambique	ZMB 27570d	47.77
Latastia longicaudata	Kibwezi, “British East Africa“	ZMB 22443	86.49
Latastia longicaudata	Kibwezi, “British East Africa“	ZMB 74545	84.41
Latastia longicaudata	Lake Awasa, Ethiopia	ZMB 19784	51.57
Latastia longicaudata	Lake Awasa, Ethiopia	ZMB 19784a	39.56
Latastia longicaudata	Lake Awasa, Ethiopia	ZMB 19787b	38.74
Latastia longicaudata	Tanzania	ZMB 24329	89.62
Latastia siebenrocki	Porto Novo, Benin	ZMB 17954	37.36
Latastia siebenrocki	Eldama Ravine, Kenya	ZMB 18642	48.02
Latastia siebenrocki	Eldama Ravine, Kenya	ZMB 18643	43.07
Latastia siebenrocki	Eldama Ravine, Kenya	ZMB 18644	47.66
Latastia siebenrocki	Eldama Ravine, Kenya	ZMB 18645	39.98
Nucras boulengeri kiliosae	Kilosa, Tanzania	ZMB 29823	45.31
Philochortus hardeggeri	Dadab near Zeila, Somalia	ZMB 18200	53.87
Philochortus hardeggeri	Dadab near Zeila, Somalia	ZMB 19817	63.68
Philochortus hardeggeri	Dadab near Zeila, Somalia	ZMB 79709	63.84
Philochortus spinalis	Adali County, Ethiopia	ZMB 10270	50.91
Philochortus spinalis	Odamuda, Arussi Galla, Ethiopia	ZMB 19752	44.4
Philochortus spinalis	Odamuda, Arussi Galla, Ethiopia	ZMB 19791	60.45
Pseuderemias brenneri	Brava, Somalia	ZMB 6443	46.49
Pseuderemias brenneri	Brava, Somalia	ZMB 76539	50.42
Pseuderemias brenneri	Brava, Somalia	ZMB 76540	44.04
Pseuderemias mucronata	Tokosha, Somalia	ZMB 19803	33.34

(*Continued*)

Table 1. Continued.

Species	Locality	Reference-No.	SVL (mm)
Pseuderemias mucronata	Tokosha, Somalia	ZMB 19803a	26.93
Pseuderemias mucronata	Tokosha, Somalia	ZMB 19803b	23.08
Pseuderemias mucronata	Warabot, Somalia	ZMB 19804	28.46
Pseuderemias mucronata	Warabot, Somalia	ZMB 19804a	24.16
Pseuderemias mucronata	Tokosha, Somalia	ZMB 79701	46.15

Table 2. Character numbers, descriptions and states used in this survey.

No.	Character	Character states
1	elongated temporal shield	0 = no, 1 = relatively long, 2 = long
2	dorsal scales keeled	0 = not keeled, 1 = slightly keeled, 2 = strongly keeled
3	caudal scales keeled	0 = not keeled, 1 = slightly keeled, 2 = strongly keeled
4	lateral scales keeled	0 = not keeled, 1 = slightly keeled, 2 = strongly keeled
5	surface of cranial shields	0 = smooth, 1 = ornamented
6	granular scales between supraoculars and frontal	0 = absent, 1 = present
7	notched frontal shield	0 = not notched, 1 = slightly notched, 2 = strongly notched
8	occipital shield	0 = absent, 1 = present
9	circular mark on interparietal shield	0 = absent, 1 = present
10	labial in contact with nostril	0 = absent, 1 = present
11	postnasal in contact with rostral	0 = not in contact, 1 = in contact
12	supraciliary granules	0 = absent, 1 = present
13	disoriented scales on chest	0 = absent, 1 = slightly disoriented, 2 = present and well visible
14	dorsal scales at midline	0 = not enlarged, 1 = enlarged
15	subocular reaching oral fissure	0 = not reaching fissure, 1 = reaching fissure
16	femoral pores	0 = few (<10), 1 = moderate (between 10–16), 2 = many (>16)
17	no. of keels on lamellae	0 = 0, 1 = 1, 2 = 2
18	no. of shield embracing nostril	0 = 2, 1 = 3, 2 = 4 (Fig. 3)
19	nasal length	0 = short (ratio of nasal length/ total skull length <0,17), 1 = long
20	nasal convexity	0 = moderate (e.g. Fig. 9), 1 = distinct (e.g. Fig. 4)
21	frontals	0 = not fused, 1 = fused
22	extent of ventral frontal descent	0 = no descent (e.g. Fig. 13A), 1 = descending moderately (e.g. Fig. 13E), 2 = descending deeply (e.g. Fig. 13F)
23	parietal shape	0 = rectangular (e.g. Fig. 5), 1 = elongated (e.g. Fig. 7)
24	pineal fontanelle	0 = absent, 1 = present
25	posterior margin of parietal	0 = small (e.g. Fig. 6), 1 = tapered (e.g. Fig. 10), 2 = broad (e.g. Fig. 9)
26	posterior end of squamosal	0 = slender (e.g. Fig. 11), 1 = moderately deep (e.g. Fig. 8), 2 = distinctly deep (e.g. Fig. 5)
27	no. of anterior projections on postfrontal	0 = 1, 1 = 2
28	postfrontal and postorbital	0 = separated, 1 = fused
29	shape of postorbital	0 = short and broad (e.g. Fig. 6), 1 = long and slender (e.g. Fig. 7)
30	temporal opening	0 = not closed, 1 = closed
31	zygomatic process on jugal	0 = absent (e.g. Fig. 9), 1 = weakly developed (e.g. Fig. 5), 2 = distinct (e.g. Fig. 10)
32	lacrimal bone length	0 = relatively short (e.g. Fig. 7), 1 = long (e.g. Fig. 9)
33	lacrimal bone width	0 = slender (e.g. Fig. 9), 1 = comparatively broad (e.g. Fig. 8)
34	lacrimal descending into orbital cavity	0 = not descending into cavity, 1 = descending into cavity
35	palpebral ossifications	0 = hardly present, 1 = strongly developed
36	posterior projections of the vomer	0 = average size , 1 = elongated
37	shape of anterolateral process of septomaxilla	0 = absent , 1 = present as hump, 2 = distinctly turned medially, 3 = complexly developed
38	alar process of prootic	0 = single alar process (e.g. Fig. 6), 1 = subdivided alar process (e.g. Fig. 5)
39	ventromedial flange on retroarticular process	0 = absent (e.g. Fig. 5), 1 = distinctly developed (Fig. 7)
40	orbitosphenoid shape	0 = simple funnel, 1 = additional appendages
41	frontal bone width	0 = narrow (ratio frontal width/ total skull length <0.7), 1 = moderate, 2 = broad (ratio frontal width/ total skull length >0.8)

Table 3. Character matrix corresponding to characters in Table 2. An asterisk (*) indicates specimens included in the second phylogenetic analysis with reduced taxon sampling.

Inventory no.	Species	Character states
ZMB 7774*	*H. lugubris*	10200110101100112111100122000010110121101
ZMB 19751	*H. lugubris*	10200111101100112111100122000010110121111
ZMB 17951a	*H. lugubris*	102001111011001121
ZMB 17951b	*H. lugubris*	102001111011001121
ZMB 18928	*H. lugubris*	11200111101100112111100122000020110121101
CAS 245014*	*"H. neumanni”*	10200001000000110101021010101121001001002
MCZ 40203*	*"H. neumanni”*	12200011110100112200111110101021011011001
MCZ 40207*	*"H. neumanni”*	12210011010100112211121111101011111031001
MCZ 40216*	*"H. neumanni”*	122100110101001122
BMNH 1946.8.6.51*	*“H.” nitidus*	22200021001100112100111110101011011011001
BMNH 1946.8.6.52*	*“H.” nitidus*	12200011101100112100111111101011011031001
MNHN 1904 161*	*"H.” nitidus quadrinasalis*	22200021101100112111121111101011011011001
AMNH 10686*	*“H.” nitidus garambensis*	12210011101100112100121111101011011031001
ZMB 16603*	*"H.” nitidus*	222000011011001121
ZMB 78926*	*"H.” nitidus*	22200021101100112111121110101011011031101
ZMB 78927*	*“H.” nitidus*	22200021101100112111121110101010111031001
ZMB 78928*	*“H.” nitidus*	22200011101100112111121111101110111031001
ZMB 48324*	*H. spekii spekii*	02201110001100112111100121000120010110001
ZMB 48325	*H. spekii spekii*	02201110101100112110100122000110010110001
ZMB 48327	*H. spekii spekii*	022011011011001121
ZMB 19807	*H. spekii sextaeniata*	022011011011000121
ZMB 19807a	*H. spekii sextaeniata*	02201101101100012111100122000020010110101
ZMB 19807b	*H. spekii sextaeniata*	022011001011000121
ZMB 19796	*H. spekii sextaeniata*	12201111001100012101100122000120010110111
ZMB 29458*	*L. boscai*	202000111101001022
ZMB 29460*	*L. boscai*	202000111101001022
ZMB 18202*	*L. carinata*	21200011110120102211111112101001100021001
ZMB 19793*	*L. carinata*	21200011110100102200121100101001011021001
ZMB 27552*	*L. johnstonii*	22200011010100112200111112101111101031001
ZMB 27552a*	*L. johnstonii*	22200011010100022210121112101111101031001
ZMB 27570*	*L. johnstonii*	12210011010100112201121102101110101021001
ZMB 27570a*	*L. johnstonii*	22220011010100112200121112101111101021001
ZMB 27570b*	*L. johnstonii*	22210011010100122200121112101110101011001
ZMB 27570c*	*L. johnstonii*	122000110101001222
ZMB 27570d*	*L. johnstonii*	112100111101001122
ZMB 22443*	*L. longicaudata*	22220021110120102211121111101011111031001
ZMB 74545*	*L. longicaudata*	12220021110120102211121111101011111031001
ZMB 19784*	*L. longicaudata*	21200011110120102210121111101011111031001
ZMB 19784a*	*L. longicaudata*	202000111101201022
ZMB 19784b*	*L. longicaudata*	212000111101201022
ZMB 24329*	*L. longicaudata*	112000110101201122
ZMB 19754*	*L. siebenrocki*	12200011010100112200111101101011001011001
ZMB 18642*	*L. siebenrocki*	22200011010100112200111101101011111031001
ZMB 18643*	*L. siebenrocki*	222000110101001122
ZMB 18644*	*L. siebenrocki*	122100210101001122
ZMB 18645*	*L. siebenrocki*	12210011010100112200121110101111011031001
ZMB 18200*	*Ph. hardeggeri*	12210101000101111011121012111120011011102
ZMB 19817	*Ph. hardeggeri*	12210111000101111001121012111121011011102
ZMB 79709	*Ph. hardeggeri*	22210101000101111010121012111120011011102
ZMB 19791*	*Ph. spinalis*	10200001000101111011111011111120011031102
ZMB 10270	*Ph. spinalis*	21200001100101111001111111111120011011112
ZMB 19752	*Ph. spinalis*	11200001000101111011111012111110011001112
ZMB 6443*	*Ps. brenneri*	01201111100100021211120101101001110100010
ZMB 76539	*Ps. brenneri*	02221111100100021211120101100001110100110
ZMB 76540	*Ps. brenneri*	02201111100100021211120101001001110110010
ZMB 19803	*Ps. mucronata*	10100111100100121211120101101000110110000
ZMB 19803a	*Ps. mucronata*	102001111001001212
ZMB 19803b	*Ps. mucronata*	002001111001001212
ZMB 19804*	*Ps. mucronata*	10200111100100121201110101101001110130001
ZMB 19804a	*Ps. mucronata*	102001011001001212
ZMB 79701	*Ps. mucronata*	10200111100100121211120111101000110130010
ZMB 29823*	*N. boulengeri kilosae*	10200001000000110101021010101021001121002
ZMB 76685*	*A. andreanskyi*	00100001100100110000021100101011001011102

Identification of characters and character states suitable for phylogenetic analysis was primarily based on personal observations, as well as studies performed by Arnold (1898), Müller (2002), Evans (2008), and Gauthier *et al.* (2012).

Phylogenetic reconstruction

For phylogenetic analyses a character matrix was generated using Mesquite (Maddison & Maddison 2016, Version: 3.03), based on a total of 18 external and 23 osteological non-additive/unordered characters. We performed a parsimony analysis with TNT (Tree analysis using New Technology; Version: Jun. 2015) using the settings traditional search, Wagner tree, 1 random seed, 10 replicates, and tree bisection reconnection, but applied an artificial topological backbone for the generic relationships based on previous results from molecular phylogenies (Fu 1998; Mayer & Pavlicev 2007; Kapli *et al.* 2011; Hipsley *et al*. 2014). We constructed the topological backbone using one specimen from each genus (*Atlantolacerta andreansky* ZMB 76685, *Nucras boulengeri kiliosae* ZMB 29823, *Heliobolus lugubris* ZMB 7774, *Latastia longicaudata* ZMB 22443, *Philochortus hardeggeri* ZMB 18200, *Pseuderemias brenneri* ZMB 6443), whereas the remaining taxa were not included in the backbone and allowed to "float". The genus *Atlantolacerta* was chosen as outgroup due its sister position to all other African lacertids (e.g. Engleder *et al.* 2013). We also performed a standard bootstrap analysis (10 000 replicates), and graphically modified the final tree using FigTree (Version: 1.4.2.; Rambaut 2008). In addition, we conducted a Bayesian analysis in MrBayes 3.2.6 (Ronquist *et al.* 2012; see SOM for settings).

Results

External morphological characterisation of Heliobolus

Below we provide a short external morphological characterisation of the different species of *Heliobolus,* with focus on head scalation. Terminology is derived from Arnold (1986). A comparative plate of specimens investigated in this study is given in Fig. 3.

H. lugubris *and* H. spekii

Scalation of *H. lugubris* and *H. spekii* are extremely similar. The caudal scales of the both species are consistently keeled, the lateral scales are largely smooth and the development of keels on the dorsal scales is variable. The number of dorsal scales around the middle section varies between 61–75 in *H. lugubris* and from 59–67 in *H. spekii*, although there is a lower number in the subspecies *H. spekii spekii* (59–61) compared to *H. spekii sextaeniata* (Stejneger, 1894) (66–67). The ventral scales between the neckband and the base of the hind limb are arranged in six longitudinal rows of 25–30 scales in *H. lugubris* and 20–29 in *H. spekii*. The number of femoral pores varies between 13–16 in *H. lugubris* and 9–16 in *H. spekii*. Lamellae under the toes bear two keels. In both species the nostrils are surrounded by three shields/scales: a small upper postnasal, a larger lower nasal, and a large supranasal scale/shield (Fig. 4). The lower nasal shield forms a relatively broad interface with the rostral and the supranasals meet dorsally. Posterior to the supranasals there is a roughly trapezoid frontonasal shield. The two prefrontal

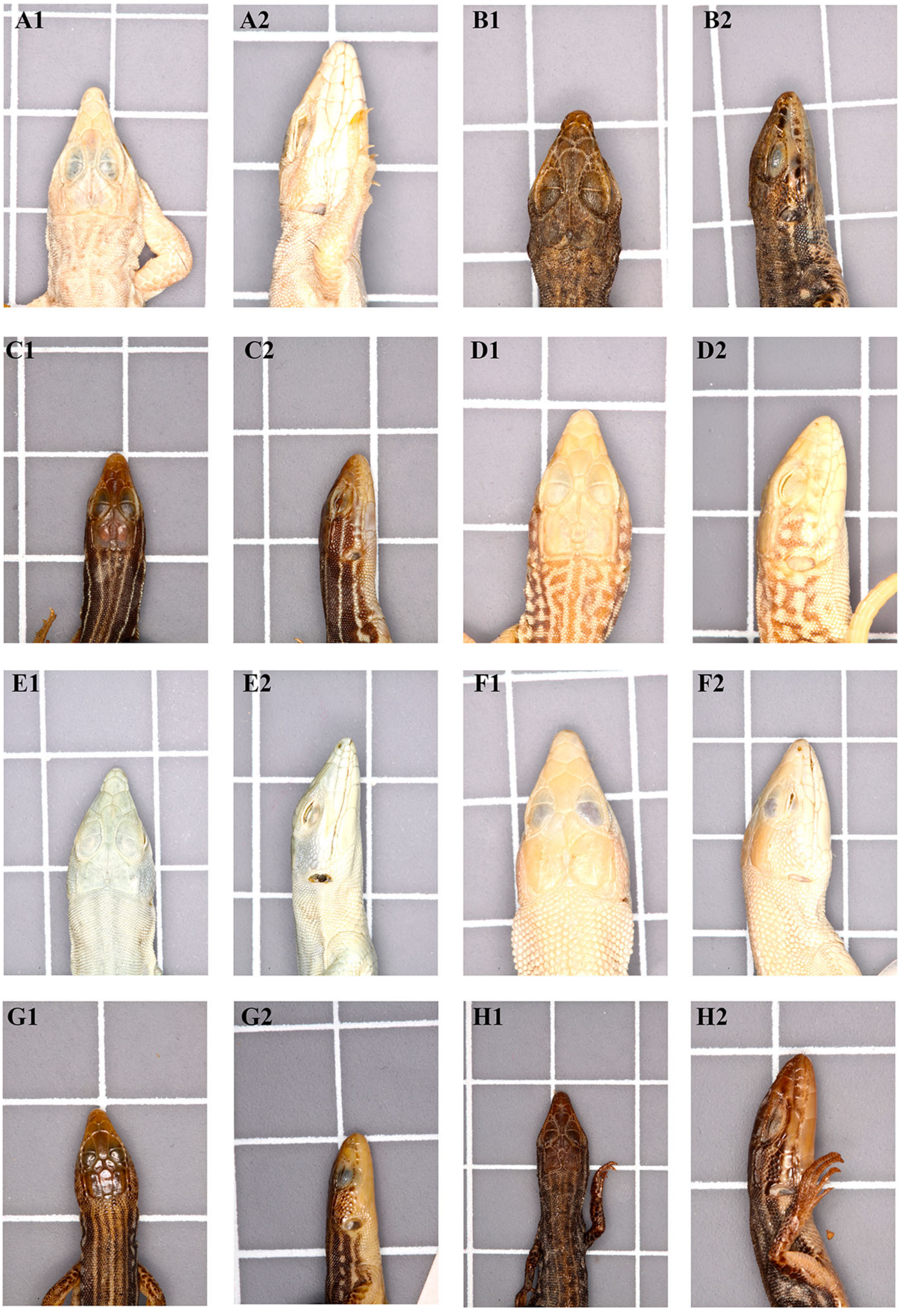

Figure 3. Photographs of the head and anterior body region of specimens investigated in (1) dorsal and (2) lateral view taken against a 1 cm monitoring grid. A – *Heliobolus lugubris* (ZMB 18328); B – *Heliobolus spekii* (ZMB 48324); C – *"Heliobolus nitidus"* (BMNH 1946.8.6.51); D – *Latastia longicaudata* (ZMB 19784); E – *Pseuderemias brenneri* (ZMB 6443); F – *Philochortus hardeggeri* (ZMB 79709); G – *"Heliobolus neumanni"* (CAS 245014); H – *"Heliobolus neumanni"* (MCZ 40203).

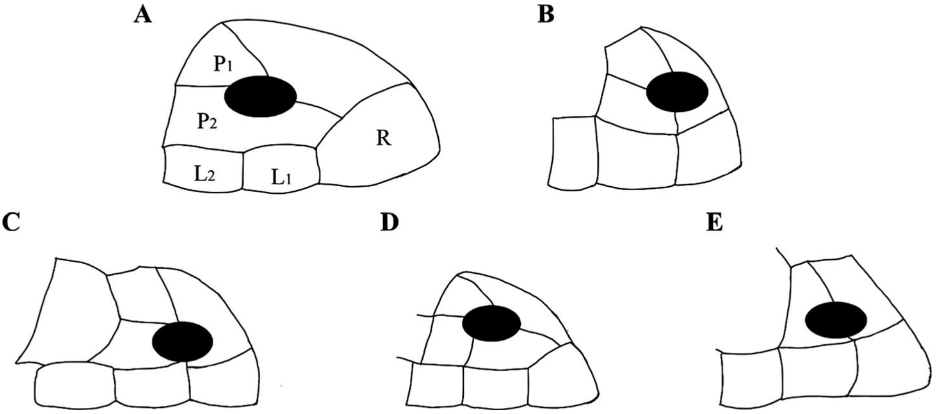

Figure 4. Scheme of scutes surrounding the nostril. A – *Heliobolus lugubris/spekii*; B – "*Heliobolus*" *nitidus*; C – *Latastia*; D – *Pseuderemias*; E – *Philochortus*. L1 = labial No. one, L2 = labial No. two, P1 = upper postnasal, P2 = lower postnasal, R = rostral. Not to scale.

shields are posterior to the frontonasal and meet along the midline. The frontal has a conical shape. The paired frontoparietal shields are almost triangular in shape. At their posterior ends the parietals form a straight line. Between the parietal shields is a small interparietal. Contrary to the original description by Duméril and Bibron (1839), a minute occipital shield is present in most (eight out of twelve; see Table 3) specimens. The two large supraocular shields are completely encompassed by small granular scales, and the subocular reaches the oral fissure.

The most obvious difference between *H. lugubris* and *H. spekii* is the ornamentation of cranial shields and a keeled temporal shield in *H. spekii*. Unfortunately, the original description of *H. spekii* (Günther, 1872) lacks a detailed description of the colouration and because of preservational issues the colouration is neglected in our study. However, the three either continuous or interrupted dorsal stripes are purported to be golden yellow on a black or brownish background in *H. lugubris* (Smith, 1838), and white on a brownish background in *H. spekii* (Günther, 1872).

In *"H." nitidus*, the caudal and dorsal scales are consistently keeled. The lateral scales are smooth. The dorsal scales are arranged in 38–61 rows around the mid-body, with the lowest number found in a small specimen of *"H." nitidus nitidus* (BMNH 1946.8.6.51) and the highest in a large specimen of *"H." nitidus quadrinasalis* (Chabanaud, 1918) (MNHN 1904161). The ventral scales are arranged in six longitudinal rows of 25–29 scales. The number of femoral pores varies from 11 to 15. The lamellae under the toes bear two keels.

In various respects the cranial shield arrangement of *"H." nitidus* is very similar to *H. lugubris* and *H. spekii*. However, they differ distinctly in two aspects: in *"H." nitidus* the granular scales between the supraocular and frontal shields are absent, and the lower postnasal is distinctly smaller so that it only reaches the very posteroventral corner of the rostral shield (Fig. 12).

Regarding colouration, Günther (1872) mentioned in his original description the presence of a brown longitudinal band on the back, which is separated from black lateral bands by a brownish red line. Tail and limbs are of a uniform brownish colour.

Heliobolus: skull osteology and comparison to other North/East African Taxa

Terminology of the following osteological characterisations and comparisons is based on Müller (2002) and Evans (2008). Images of three-dimensional CT reconstructions of the skulls of selected specimens from each species of *Heliobolus* and one species of the other genera of interest are provided in Figs 5 to 12.

Skull osteology of **H. lugubris** *and* **H. spekii**

In general, the skull of *Heliobolus* is of a relatively stout appearance. It is comparatively broad compared to other genera of the North/East African group, and the snout is not appreciably elongated. The bones are relatively thin and dermal rugosities are rare. A low level of ossification is evident.

Premaxilla

In dorsal view, the premaxilla has a nasal process that is fairly elongate, of a slight fusiform shape and distinctly projecting between the nasals to a variable extent. Posterior to the nasal insertion the bone becomes narrower, and at its most posterior end it forms a relatively sharp tip. The ventral part of the premaxilla is divided into two short and broadened branches pointing posteriorly. Within the external nares the two projections of the maxilla encompass the posterior branches dorsally in a U-shape.

Ventrally the posterior branches bear triangular processes that articulate with the maxilla. A small gap between premaxilla and maxilla remains posterolaterally. The premaxilla bears eight to nine teeth of unicuspid morphology, which are bent lingually to a variable degree. Tooth number varies irrespective of the species, i.e. all species that we analysed can have either 8 or 9 teeth.

Nasal

The nasal bones are separated from each other and relatively long, but vary in length. However, they do not extend far anteriorly and the nares are relatively large. Anteromedially, the nasals bear processes that embrace the dorsal process of the premaxilla. Their lateral edges articulate with the maxilla. In *H. lugubris* and one specimen of *H. spekii sextaeniata*, a long and slender process of the frontal protrudes approximately halfway from posterior. Posteriorly the bone forms a convexity at its lateral edge, and in a few cases the convexity projects more medially, which overlies the frontal bone. There is a slight tendency towards longer nasals and a more distinct convexity in *H. lugubris* compared with *H. spekii*.

Frontal

The frontal bones are generally fused, although in some individuals a short suture is still recognizable in the posterior part. Anteriorly the frontal bone forms five processes: a short and broad medial tip that protrudes between the posterior convexities of the nasal bones, two long and elongate processes that project between the nasal bones and the maxilla, and two anterolateral short and slender processes that project between the maxilla and prefrontal. Between the latter projections, a process of the maxilla overlies the frontal bone anterolaterally. In *H. spekii* the process between nasals and maxilla is distinctly shortened. Along almost the entire anterior half, the lateral edges meet the prefrontal.

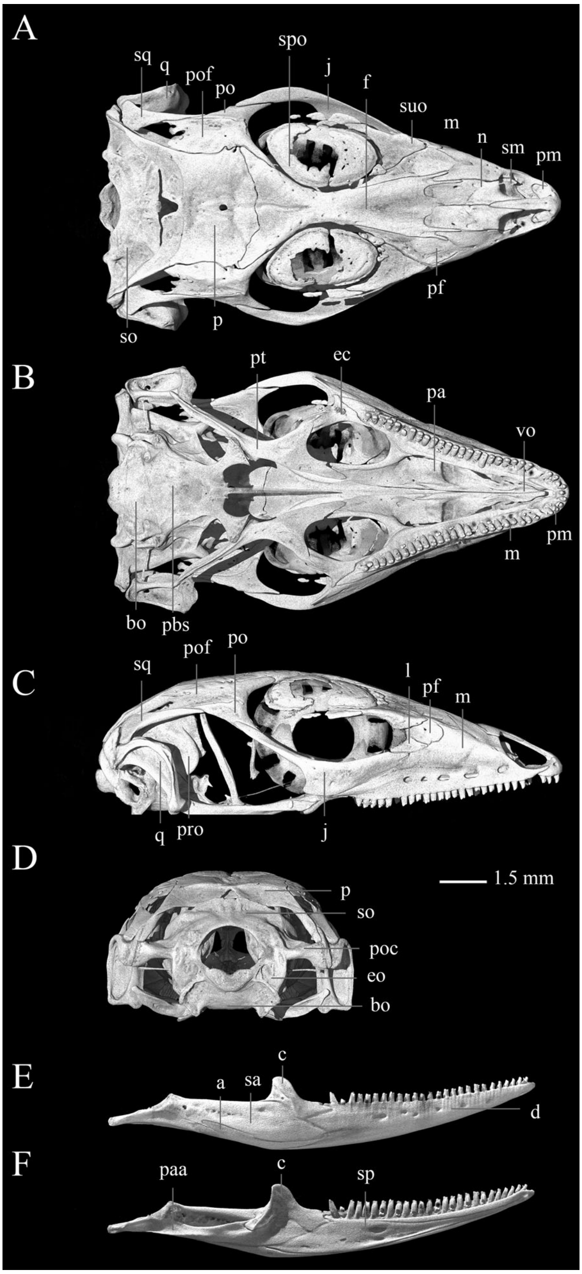

Figure 5. Skull of *Heliobolus lugubris* (ZMB 18328). A – dorsal view; B – palatal view; C – lateral view; D – lateral view of mandible; E – medial view of mandible; F – posterior view. a = angular, bo = basioccipital, c = coronoid, d = dentary, ec = ectopterygoid, eo = exoccipital, f = frontal, j = jugal, l = lacrimal, m = maxilla, n = nasal, p = parietal, pa = palatine, paa = fused prearticular and articular, pbs = fused para- and basisphenoid, pm = premaxilla, po = postorbital, pof = postfrontal, poc = paraoccipital, pf = prefrontal, pt = pterygoid, q = quadrate, sa = surangular, sp = splenial, so = supraoccipital, spo = supraocular ossifications, sq = squamosal, suo = supraorbital, v = vomer.

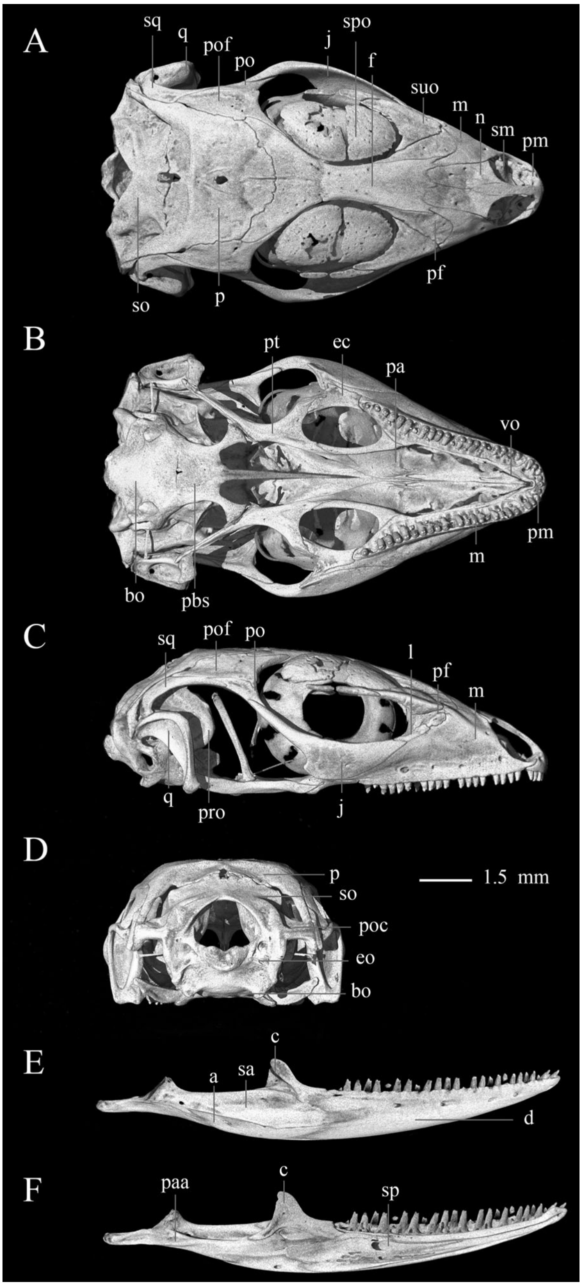

Figure 6. Skull of *Heliobolus spekii spekii* (ZMB 48324). A – dorsal view; B – palatal view; C – lateral view; D – lateral view of mandible; E – medial view of mandible; F – posterior view.

Shortly posterior to the end of the posterior prefrontal process, the frontal reaches its narrowest point. A distinct process of the postfrontal embraces the frontal bone posterolaterally.

The posterior margin of the frontal contacts the parietal along its complete extension. The suture between frontal and parietal is only slightly interdigitating. A medial depression

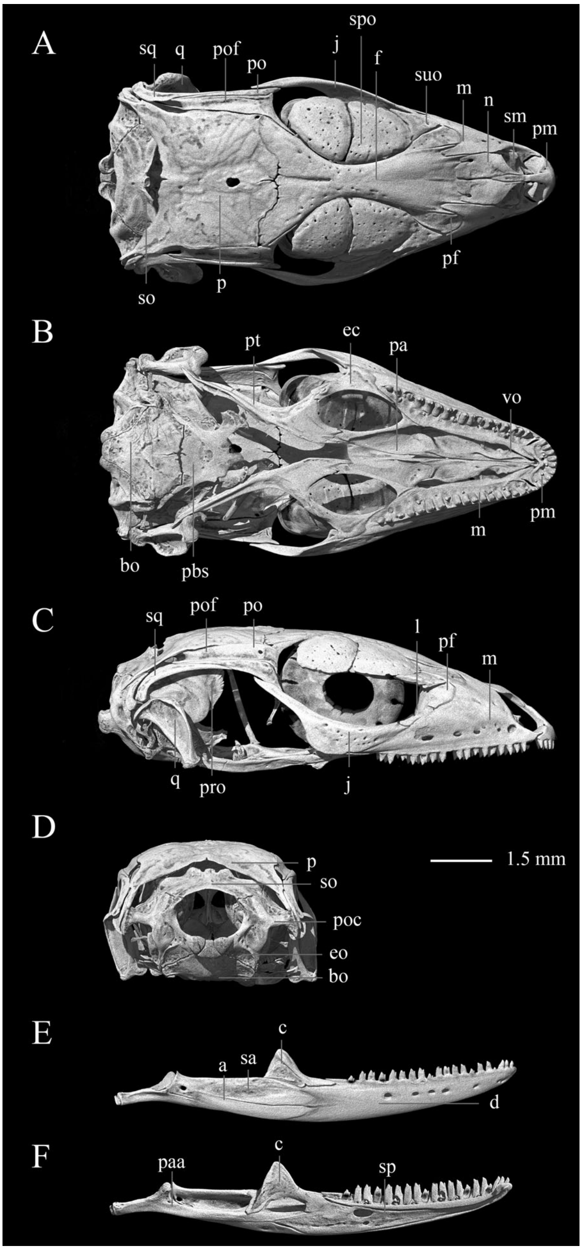

Figure 7. Skull of **"***Heliobolus*" *nitidus nitidus* (BMNH 1946.8.6.51). A – dorsal view; B – palatal view; C – lateral view; D – lateral view of mandible; E – medial view of mandible; F – posterior view.

is situated on the posterior part of the bone, but varies in its extent between individuals. On its ventral side, the lateral edges are thickened from the posterior to anterior corner of the orbit and project ventrally. However, compared to other lacertid species, the ventral extension is clearly reduced (Fig. 13). The anterior section of the frontal shows a prominent ventral ridge along the midline.

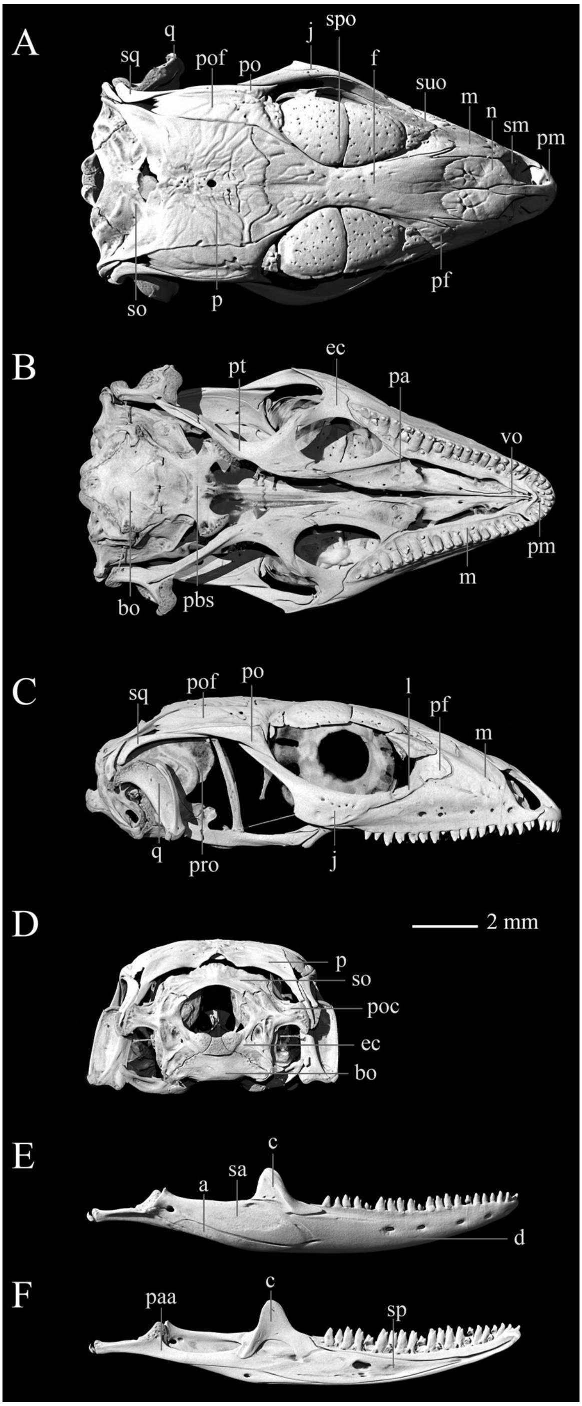

Figure 8. Skull of *Latastia longicaudata* (ZMB 19784). A – dorsal view; B – palatal view; C – lateral view; D – lateral view of mandible; E – medial view of mandible; F – posterior view.

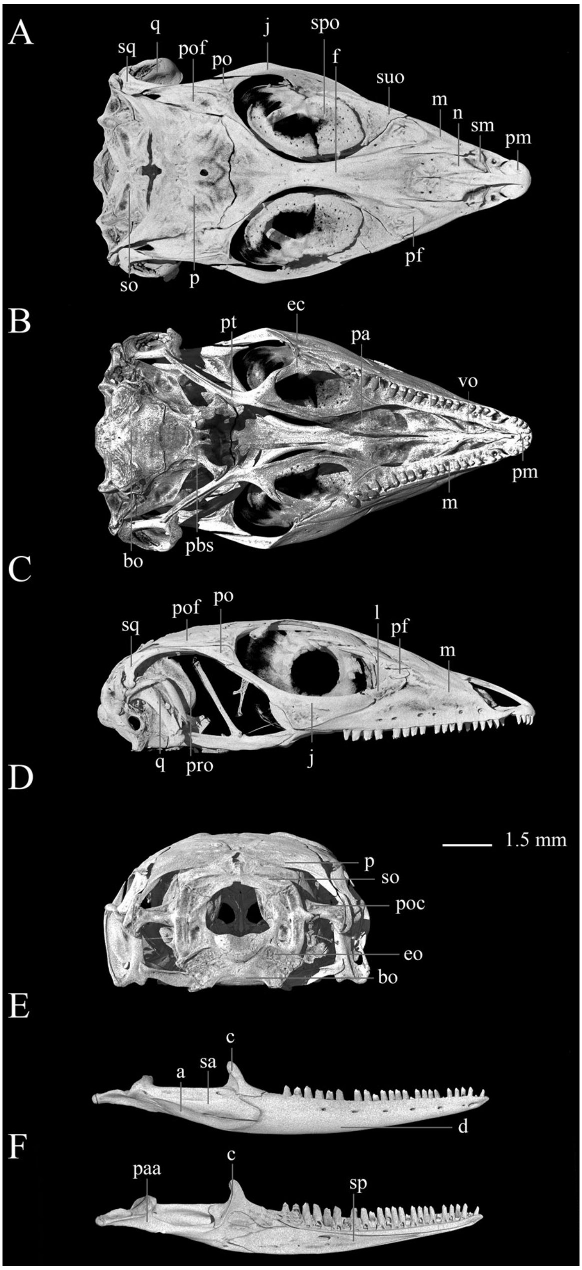

Figure 9. Skull of *Pseuderemias brenneri* (ZMB 6443). A – dorsal view; B – palatal view; C – lateral view; D – lateral view of mandible; E – medial view of mandible; F – posterior view.

Parietal

The parietal bone is relatively short and of a rectangular shape compared to other African lacertid genera, such as *Nucras*, *Pedioplanis*, *Tropidosaura* and *Holaspis* (pers. obs., M.D.). Ossifications do not extend far posteriorly, so the posterodorsal part of the braincase is not roofed over by the parietal. Dermal ossifications are rarely present, although imprints

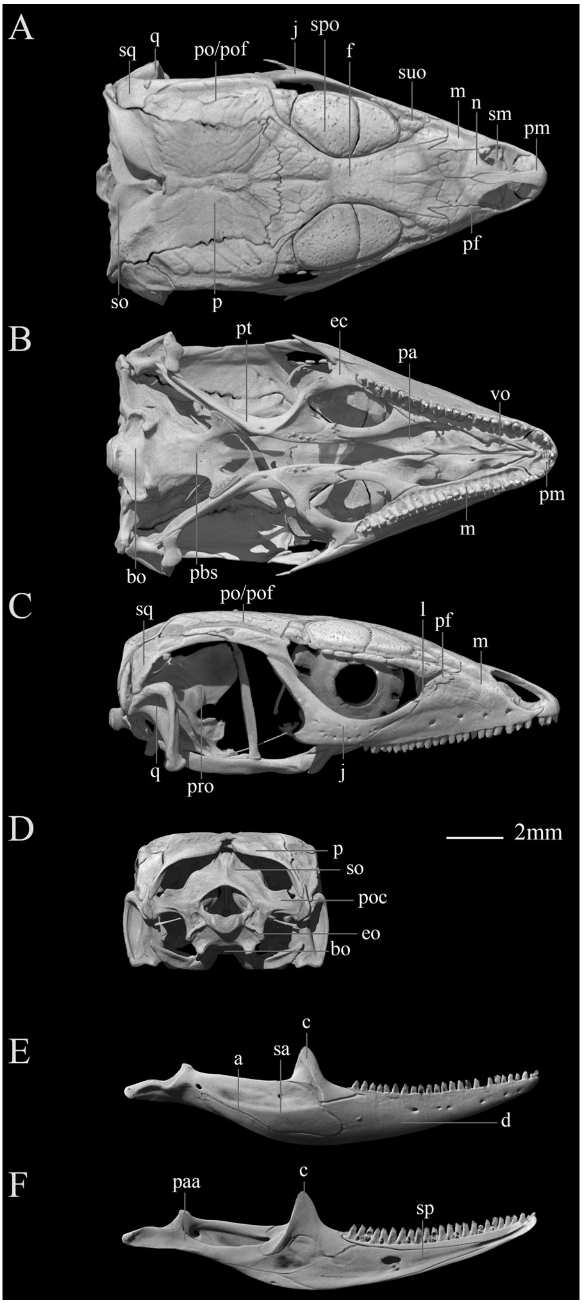

Figure 10. Skull of *Philochortus hardeggeri* (ZMB 79709). A – dorsal view; B – palatal view; C – lateral view; D – lateral view of mandible; E – medial view of mandible; F – posterior view.

of the interparietal shield are apparent in all individuals to a variable extent. A parietal foramen is always present, situated at or slightly anterior to the centre of the bone. Anteriorly the typical triangular tabs, which extend below the frontal bones, are poorly developed and rounded. Alongside its lateral edge, the parietal is either overlain by or vertically

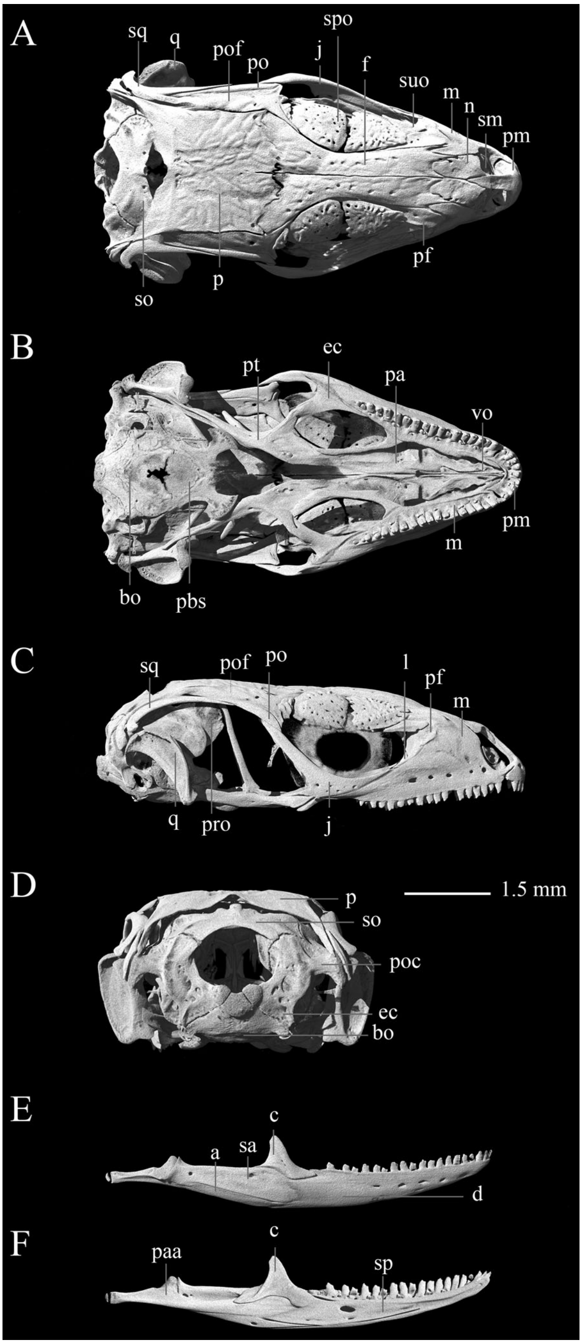

Figure 11. Skull of "*Heliobolus neumanni*" (CAS 245014). A – dorsal view; B – palatal view; C – lateral view; D – lateral view of mandible; E – medial view of mandible; F – posterior view.

interlocked with the postfrontal. The posterior margin of the parietal is broadened, tilted ventrally, very distinct, and concave. The parietal meets the supraoccipital almost along its entire length. The elliptical, almost vertical, post-temporal openings face ventrolaterally.

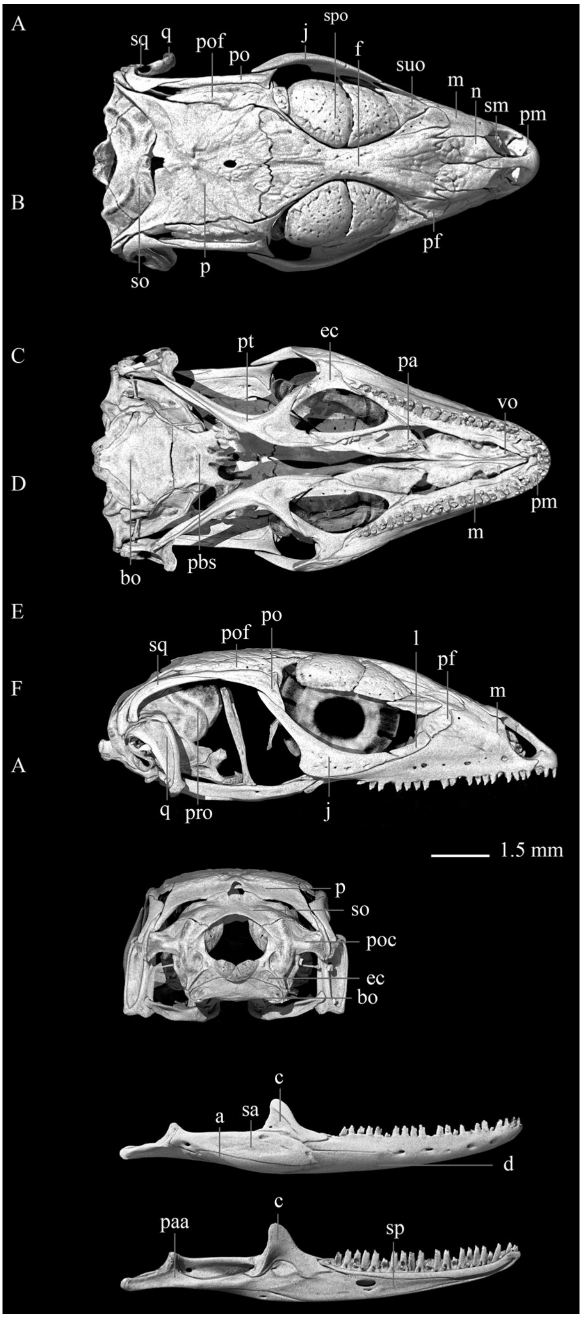

Figure 12. Skull of "*Heliobolus neumanni*" (MCZ 40203). A – dorsal view; B – palatal view; C – lateral view; D – lateral view of mandible; E – medial view of mandible; F – posterior view.

The posterolateral processes of the parietal are long and bent ventrally, reaching up to the paraoccipital processes. Within *H. spekii*, especially the subspecies *H. spekii spekii*, these processes seem to be shortened and slightly thickened, compared with *H. lugubris*. In palatal view, no distinct ventral crests are apparent.

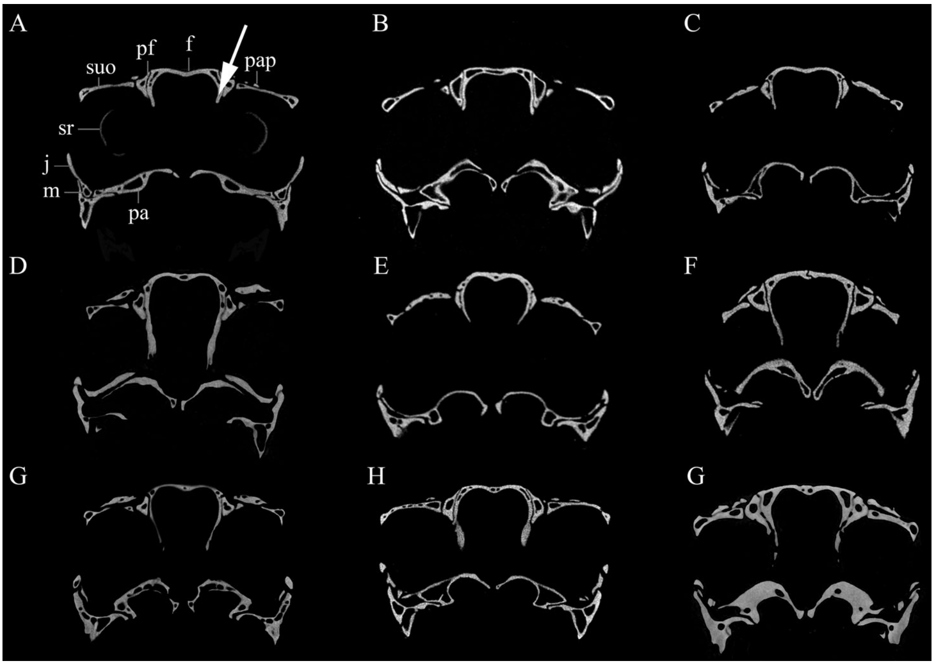

Figure 13. Ventral extension of the frontal bone in A – *Heliobolus lugubris* (ZMB 18328); B – *Heliobolus spekii* (ZMB 48324); C – *"Heliobolus" nitidus* (BMNH 1946.8.6.51); D – *"Heliobolus" nitidus* (ZMB 78926); E – *"Heliobolus neumanni"* (MCZ 40203); F – *"Heliobolus neumanni"* (CAS 245014); G – *Latastia longicaudata* (ZMB 19784); H – *Pseuderemias brenneri* (ZMB 6443); G – *Philochortus hardeggeri* (ZMB 79709). Not to scale.

Postfrontal

The postfrontal is well ossified and not fused with the postorbital. The medial process is very well developed and rather long. The lateral process, on the other hand, is either lacking, as in the subspecies *H. spekii sextaeniata*, or reduced to a thickened bulge overlying the postorbital. Alongside the orbital rim the postfrontal is undergrown by a slender process of the postorbital. Its posterior extent is variable. In *H. lugubris* the postfrontal does not extend far posteriorly and leaves a large temporal opening. In *H. spekii* the temporal opening is either closed completely or reduced to a narrow gap, with the exception of one of the specimens of *H. spekii sextaeniata* (ZMB 19807a), which also reveals a large opening.

Postorbital

The postorbital is short and broad compared to other lacertid lizards. Anteriorly two projections are well developed; the first anterior projection proceeds medioventrally far beneath the postfrontal, whereas the second lateral projection extends along the ascending posterodorsal process of the jugal. The posterior extension is underestimated when examining the skull from external view only, because it extends deeply to reach the suture between the postfrontal and squamosal. However, especially in *H. spekii*, the postorbital does not reach as far posteriorly as in other lacertid lizards, such as *Latastia* or *Pedioplanis*.

Squamosal

Unlike many Palearctic lacertid species (Lacertini), the squamosal is not of a hockey-stick shape. The bone is relatively short, not extending anterior to the level of the epipterygoid, and is dorsoventrally expanded at its rear part. The overall shape of the bone varies between individuals; commonly it bends posterolaterally and widens at the summit of the curvature, almost forming a hump. If a temporal opening is present, the squamosal margins the fenestra laterally.

Supratemporal

The supratemporal is a slender, slightly fusiform bone wedged between squamosal, parietal and paraoccipital process. Together with the squamosal and the paraoccipital process, the bone forms the articulation surface for the quadrate.

Quadrate

The shape of the quadrate is of typical lacertid morphology. It has a broad conch, therefore the bone almost forms a triangle with a curved basis, and bears a prominent curvature for the tympanum. Foramina are absent.

Jugal

The jugal is a prominent triradiate bone. Posteriorly a zygomatic process is developed, but its dimension varies individually. The posterodorsal process is long and slender and externally overlies the lateral projection of the postorbital. Below the orbital cavity the jugal is dorsoventrally expanded. Medially the jugal proceeds deeply alongside the maxilla. Anterodorsally a small depression is present, into which the lacrimal bone is inserted. On its lateral side the jugal shows four to five foramina of variable arrangement.

Lacrimal

The lacrimal is of moderate size and well visible in lateral view. It is situated between the jugal and prefrontal and separates them along the orbital rim. In the articulated skull the lacrimal appears as a slender elongate bone facing the orbital cavity anteroventrally. Externally the interface between lacrimal and maxilla appears smooth, because the latter overlies the former, but medially a relatively broad projection proceeds ventrally to the maxilla, between the jugal and prefrontal. In one specimen of *H. spekii sextaeniata* (ZMB 19807a), the lacrimal emerges as a small triangular bone externally.

Prefrontal

Because cranial osteoderms are developed only to a small extent, the large prefrontals are clearly visible, forming the anterolateral corner of the orbit. The posterodorsal process is elongated and extends to about a quarter of the orbital cavity length. Internally the bone proceeds deeply ventrally and forms a broad suture with the palatine; thus the prefrontal forms the anterior margin of the orbit. Anteriorly a triangular process of the maxilla overlies the prefrontal, resulting in a larger anterodorsal and a smaller anterolateral section. The lacrimal extends posteroventrally to the prefrontal at the anterior edge of the orbital cavity.

Maxilla

The maxilla has a tall facial process. The premaxillary process is short, slender and acute, bending approximately halfway alongside the ventral rim of the nasal openings. Posterodorsally two projections are present: a slender elongated process overlying the frontal, almost reaching the maximum posterior extension of the nasal bones and, more laterally, a triangular process overlying the prefrontal. On the ventral side the maxilla expands posteriorly approximately to the thickest area of the jugal bone, while the suborbital margin slopes smoothly into a tip. Four to six maxillary foramina are present, varying in size. The horizontal lamina is broad and contains 21 to 24 pleurodont teeth in *H. lugubris* and 17 to 21 teeth in *H. spekii*. The lamina bears a medial flange and widens posteriorly up to the insertion of the palatine. The section posterior to the insertion is rather short and narrows rapidly. Overall the teeth are slightly broader than those on the premaxilla. Whereas the bases of the teeth are rounded, the tooth tips taper quickly, being slightly convexly curved. Anteriorly the teeth are unicuspid, but transform rapidly into a bicuspid conformation, the distal tip being slightly higher than the mesial. On the medial side there is no evidence of a carina maxillaris. The opening of the alveolar foramen is quite large, especially in one specimen of *H. spekii sextaeniata* (ZMB 19807a). In *H. lugubris* it is situated above the 18th/19th tooth of the maxilla, and in *H. spekii* above the 16th/17th. In dorsal view the anterior end of the maxilla in distinctly concavely indented. In palatal view a semi-circular gap is created between premaxilla and maxilla. Medial to the gap an almost triangular process of the premaxilla proceeds onto the innermost section of the maxilla.

Supraorbital and supraocular ossifications

The supraorbital is clearly visible, because it is not overlain by any supraocular ossifications. Its shape resembles an arch with tapered endings, the lateral process more elongated than the medial one. Posterior to the supraorbital two supraocular ossifications are present, which are analogous in shape to the large external supraorbital shields. The anterior supraocular is more strongly ossified than the posterior one. Lateral to these prominent ossifications one or two rows of two to three small and slender shields may be present. A sclerotic ring consisting of 14 elements is present within the orbit.

Pterygoid

The pterygoid exhibits the typical lacertid morphology, with its quadrate processes bent posterolaterally. It widens at the intersection of the anteromedial, anterolateral, and quadrate processes. At the insertion of the fused para-basisphenoid the quadrate process is directed posterolaterally. Posteromedially to the slender quadrate process an elongated recess for muscle insertion is situated. The relatively short pterygoid flange is embraced by the bifurcated medial end of the ectopterygoid. The anterior process is longer than the pterygoid flange and, in palatal view, forms an oblique ventral structure with the palatine, where the bones are horizontally articulated. Its anterior end is dorsoventrally embraced by the bifurcated end of the palatine. There is no pterygoid dentition.

Ectopterygoid

Although it seems that the ectopterygoid is restricted to the posterolateral corner of the suborbital fenestra in palatal view, the bone is more strongly developed than it superficially appears. Dorsally it runs alongside the maxilla in a broad projection and nearly reaches the palatine. In one specimen of *H. lugubris* (ZMB 17951), palatine and ectopterygoid meet at their distal tips. A small and slender projection proceeds posteriorly. At the end of this projection, the ectopterygoid meets the posterior process of the maxilla at the broadest section of the jugal. The medial slender process runs ventrally well below the pterygoid flange.

Palatine

The palatines are long and narrow and do not meet along the midline. Posteriorly they show a more or less dorsoventrally bifurcated termination; the dorsal branch is more elongated than the ventral one. At its anterior edge a gap arises between the palatine and vomer. This gap is bridged by a long and slender process of the vomer alongside the midline. A triangular elevation surrounds this vertically articulated projection. The posterior parts of the palatines approach one another dorsally, forming a ventral convexity. The middle section, i.e. where the palatine contacts the maxilla, is distinctly dorsally curved and forms a broad suture with the lateral edge of the prefrontal. Anteriorly the palatines approach one another ventrally in a U-shape. Only in one specimen of *H. spekii sextaeniata* (ZMB 19807a) the bone is pierced by a small foramen, forming the ventral part of the posterior wall of the nasal capsule. The palatines in *H. spekii* tend to be farther apart posteriorly, and the palatines of large specimens of *H. lugubris* are broadened anteriorly.

Vomer

because of limited ossification at its posterior end, a broader gap between the palatine and vomer, and sometimes even a cavity, is formed. This gap is bridged by a slender triangular projection that is slightly broader and shorter in *H. spekii* than in *H. lugubris* . The position where the paired bones meet is variable; they tend to meet farther towards their posterior end in *H. spekii*. The slender vomers are waisted anteriorly, forming the fenestra exochoanalis. This opening is medially subdivided by a small, posterolaterally directed peak of the vomer. Anterior to this peak a smaller triangular process is present. The anterior section between the vomeronasal openings bears a median recess flanked by prominent ventral ridges. The broad posterior part of the vomer forms a ventrally recurved plate, whereas the narrow anterior part cants dorsolaterally. Anterolaterally the bone neither contacts the maxilla, nor does its anterior process meet the premaxilla.

Epipterygoid

The long and slender epipterygoid is attached to the quadrate process of the pterygoid. At its ventral end it is slightly thickened. It does not meet the alar process of the prootic, nor does it reach the same dorsal height.

Septomaxilla

The septomaxilla is visible in the external naris and forms a strongly dorsally concave plate. The anterior part of the arc abuts the maxilla, whereas the posterior portion leans towards the vomers. A dorsomedial flange varies individually in extent, as does the degree of the anterolateral process. Posterior to the apex, small lateral alae are developed on the lateral and medial side, pointing posteriorly, and are most apparent in lateral view.

Orbitosphenoid

Ossification of the orbitosphenoid varies individually. In cases where it is highly developed its shape resembles an “S” when viewed from posterior, whereupon the lower curvature is more distinct and bears a triangular projection. In most cases only the ventral bracket is ossified; parts of the dorsal arc are, however, recognizable.

Braincase

The bones of the braincase tend to be fused, with sutures only superficially recognizable. The supraoccipital is very wide and does not possess an ascending process. It expands underneath the broadened posterior margin of the parietal. Together they form a large and slightly ventrally bent even surface, presumably for muscle insertion. Strong paraoccipital processes are developed by the opisthotic. These processes expand laterally and create, together with the supratemporal, a socket for the quadrate joint. In some cases the supratemporal and the paraoccipital process are fused. In younger specimens (i.e. those with a shorter snout-vent length) the suture between the opisthotic and the small exoccipital is visible. In most individuals the basioccipital is well differentiated from the remaining occipital complex. It is of moderate size and possesses prominent, low basal tubera with posteroventrally concave ends. In palatal view, the braincase is ventrally completed by a fused para-basisphenoid. Similar to the edges of the occipital complex, a suture between the occipital complex and the sphenoids is only recognizable in one specimen of *H. spekii spekii* (ZMB 48525). The para-basisphenoid forms a slightly ventrally emarginated plate, bearing a more or less hook-shaped dorsal process facing anteriorly, which extends into the lower temporal opening. The basipterygoid processes emerge anterolaterally towards the basis of the quadrate processes of the pterygoid. Their distal areas are distinctly wider than their proximal bases and bear a sharp triangular dorsal process. Medially the parasphenoid rostrum projects anteriorly, varying individually in its extent of ossification and length. The shape of the prootic differs between the two examined species. In both species, the prominent alar process projects anteriorly and bears a pointed crest dorsally, but there is variation in the shape of the alar process and the magnitude of the deep crista. In *H. lugubris* the vertical, anteriorly curved crista is more strongly developed and appears even deeper as it subdivides the process into a lateral semi-circular and a medial bell-shaped section. In *H. spekii*, on the other hand, the crista is shallower and the medial section is represented by a small spike. The stapes is a thin rod that forms an expanded internal end. It nearly fills the distance between the occipital complex and the quadrate horizontally.

Mandible

Like in all lacertid lizards, the mandible of *H. lugubris* and *H. spekii* comprises 6 bones. The dentary is modestly curved and bears 25 to 27 teeth in *H. lugubris* and 23 to 26 in *H. spekii*. All teeth are slender and distinctly bicuspid distally, with the distal tip higher than the mesial one. They slightly lean labially and are somewhat bulbous at their bases. The foramen for the passage of the alveolar nerve is broad and situated between the 18th to 22nd teeth. On its lateral side the dentary shows a row of five to seven mental foramina. Posteriorly two projections are developed. In most cases the posteroventral process is only slightly longer than the posterodorsal one. The coronoid has a prominent, yet not deep, anteriorly directed labial process. Together with the anteromedial process it embraces the rear section of the dentary. The apex of the coronoid is rounded, knob-like and expanded. The anteromedial and posteromedial processes are of approximately equal length, the latter being indented laterally and bearing a lateral bulge that dorsally overlies the surangular. Medially, the large splenial occupies most of the surface. At its anterior end it is bifurcated and shows one major anterior inferior alveolar foramen and one to three smaller mylohyoid foramina. The angular is slender, yet clearly visible in both lateral and medial views. Posteriorly, the angular is bifurcated and the superior branch overlaps the surangular. This bifurcation, though lacking in one specimen of *H. spekii sextaeniata* (ZMB 19807a), is situated directly upon a suture, which indicates the intersection between the surangular and the fused prearticular and articular. The large surangular is pierced by two foramina; the anterior surangular foramen posterior to the coronoid, and the posterior surangular foramen at the end of the poorly developed mandibular crest anterior to the pronounced articular surface. Articular and prearticular are fused and bear a distinct medial projection in their anterior part reaching the anterior portion of the coronoid. The mandibular fossa is conspicuous, but not extraordinarily expanded, compared with other lacertids. The retroarticular process is relatively long and tapers posteriorly, showing a dorsomedial concavity and bearing a ventromedial flange, which is less distinct in *H. spekii spekii*.

Although the skulls of *H. lugubris* and *H. spekii* differ in a few details, the basic bauplan with its low degree of ossification is shared. Compared to *H. lugubris* , *H. spekii* possesses relatively shorter nasals, thicker posterolateral processes of the parietal, a reduced medial part of the prootic, a lower number of teeth and, subsequently, a relatively anteriorly shifted alveolar foramen. There is also a tendency towards a complete obliteration of the upper temporal opening, as well as a reduced frontal projection between the nasals and the maxilla.

Comparison with **"H." nitidus**

With the exception of the single examined specimen of "*H.*" *nitidus garambensis* (AMNH R-10686), the skull of "*H.*" *nitidus* is generally more gracile than that of *H. lugubris* and *H. spekii*. The occiput posterior to the orbits is more elongated and the degree of ossification appears greater. Particularly in larger specimens, dermal rugosities and grooves are notable. The premaxilla bears seven to eleven teeth of similar shape. Whereas in palatal view *H. lugubris* and *H. spekii* share a ventral flange medially, a more distinct triangular ventral projection is developed in "*H.*" *nitidus*. In smaller specimens of "*H.*" *nitidus*, the nasal process is more slender and elongated.

The nasals also differ among the specimens of "*H.*" *nitidus*. In some specimens (ZMB 78926–28978 from Togo) they are very similar to those of *H. lugubris* and *H. spekii*, whereas in the remaining cases, the bones are broader and shorter than the projection of the maxilla, which proceeds dorsally onto the frontal. The nasals of BMNH 1946_8_6_51–52 (syntypes of "*H.*" *nitidus nitidus* from West Africa), MNHN 1904 161 (holotype of "*H.*" *nitidus quadrinasalis* from Chad) and AMNH R-10686 (holotype of "*H.*" *nitidus garambensis* from Congo) do not form a convexity posteriorly, so that no triangular process of the frontal separates their rear part. The posterior part of the nasal of BMNH 1946_8_6_51 is remarkable, because it forms a deep indention up to the foramen (Fig. 7).

The anterior section of the frontal bone is variable in "*H.*" *nitidus*, because is the ventral elongation of the frontal. In the type series of "*H.*" *nitidus nitidus* (BMNH 1946_8_6_51-52) the frontal bone is bent ventrally and reaches slightly deeper than in *H. lugubris* and *H. spekii* (Fig. 13). In the remaining specimens the frontal extends farther, almost reaching the palatine (Fig. 13). The posterolateral part of the frontal overlies the parietal. Compared to *H. lugubris* and *H. spekii*, the parietal of *"H." nitidus* forms less of a rectangular shape, because of the elongated occiput. The foramen is also situated slightly more anteriorly, triangular tabs are more distinctly developed, the posterior margin is less broad, and the parietal and supraoccipital do not meet along their entire length. The posterior margin of the parietal in *"H." nitidus* is also broadened but not to the same extent as in *H. lugubris* and *H. spekii*. Moreover it is less recurved ventrally, less inclined, and narrows towards the parietal fossa. In smaller specimens (*"H." nitidus nitidus*) the distance between parietal and supraoccipital is greater than in *H. spekii* and *lugubris*, and the posterior processes are rather short. The larger *"H." nitidus garambensis* and *"H." nitidus quadrinasalis* have longer posterior processes, as the distance between the parietal and supraoccipital is relatively larger.

The postfrontal of *"H." nitidus* is narrower and more elongated. A short lateral projection is present (except in *"H." nitidus garambensis* (AMNH R-10686)), which overlies the postorbital and processes anterior to it along the orbital rim. The postfrontal leaves a moderate temporal opening, again except in the case of *"H." nitidus garambensis*, where it is almost closed completely. Compared to *H. lugubris* and *H. spekii*, the postorbital of *"H." nitidus* is more elongated, reaching approximately the same length as the postfrontal, and its complete extension is visible in lateral view. The anteroventral process is shorter and, compared to the total skull length, the broadening alongside the orbital rim is less extensive. The latter issue is most obvious in smaller specimens. The squamosal of *"H." nitidus* is comparatively narrower and curved. Overall it is more similar to the "hockey stick" shape of Palearctic lacertid species.

As in *H. lugubris* and *H. spekii*, the supratemporal is wedged between the squamosal, quadrate, and paraoccipital process, although it is more of an anteriorly recurved hook-shape. In smaller, and presumably less mature specimens of *"H." nitidus*, the conch of the quadrate is less broad, therefore it lacks the triangular shape. However, the quadrates of the larger *"H." nitidus garambensis* and *"H." nitidus quadrinasalis* resemble those of *H. lugubris* and *H. spekii*.

The jugal is quite similar to those of *H. lugubris* and *H. spekii,* although its posterodorsal process is somewhat stouter. The extent of the zygomatic process varies individually. The prefrontal and lacrimal are very similar to those of *H. lugubris* and *H. spekii*.

In general, the maxilla and tooth shape of *"H." nitidus* are similar to those of *H. lugubris* and *H. spekii*. The number of teeth is more variable (15–23), as is the position of the opening of the alveolar nerve (between 11th/12th up to 17th/18th tooth). The mental foramina are comparatively larger in the types of *"H." nitidus nitidus*, *"H." nitidus garambensis* and *"H." nitidus quadrinasalis*.

The main difference between *"H." nitidus* and *H. lugubris* and *H. spekii* in the supraorbital and supraocular ossifications is their respective degrees. Both ossifications, analogous to the external supraocular shields, are completely ossified and smaller lateral ossifications are lacking. However, in some specimens of *"H." nitidus nitidus* (ZMB 78926–78928), as well as *"H." nitidus quadrinasalis* and *"H." nitidus garambensis*, two smaller additional supraocular ossifications are present, one anterior and one posterior to the larger shields. The sclerotic ring is similar to *H. lugubris* and *H. spekii* in the number of elements, the exception being *"H." nitidus garambensis*, in which it consists of 16 elements.

Pterygoid, ectopterygoid, palatine, and vomer are quite similar to those of *H. lugubris* and *H. spekii*. However, they do vary in some details, but these variabilities differ between the different specimens. The long and slender quadrate process of the pterygoid of "*H.*" *nitidus nitidus* (ZMB 78926–78928) resembles those of *H. lugubris* and *H. spekii*, whereas in the remaining specimens *of "H." nitidus nitidus*, as well as "*H.*" *nitidus garambensis* and "*H.*" *nitidus quadrinasalis*, it shows a second distinct recess on the lateral side. The palatine of "*H.*" *nitidus* is not as broad as in *H. lugubris* and *H. spekii* at its most anterior section, and a triangular elevation around the processes of the vomer is only present in larger specimens. Less mature individuals show a medial flange. The triangular processes of the vomer tend to be less elevated and broader, the posterior part of the vomer is more ossified and the small projections subdividing the fenestra exochoanalis are not as distinct and pointed.

The epipterygoid is longer in "*H.*" *nitidus*, except in "*H.*" *nitidus quadrinasalis* (MNHN 1904 1619). This elongation is especially apparent in the non-type specimens of "*H.*" *nitidus nitidus* (ZMB 78926–78928).

Differences regarding the septomaxilla are difficult to identify, as it is variable among specimens of "*H.*" *nitidus*. In general, it appears that the height of the dorsomedial flange varies individually, as well as the development of an anterolateral process, which is rather small. In non-type specimens of "*H.*" *nitidus nitidus* (ZMB 78926–78928) the flange is the largest of all *Heliobolus* specimens examined, although it is of a different shape than in *H. lugubris* and *H. spekii*, i.e. instead of facing anteriorly, the anterolateral process forms a crest that tilts laterally.

The degree of ossification of the orbitosphenoid is relatively consistent among "*H.*" *nitidus*. Viewed posteriorly, it resembles the poorly ossified orbitosphenoids of *H. lugubris* and *H. spekii*, being shaped like a curved funnel.

The braincase of "*H.*" *nitidus* differs in several aspects from *H. lugubris/spekii*. In smaller specimens (BMNH 1946_8_6_51-52) the sutures between the bones of the occipital complex are well developed, and it is apparent that only the opisthotic forms the paraoccipital processes. However, the larger the specimens, the less recognisable are the sutures. The parietal and supraoccipital do not meet along their entire length. The distance between these bones becomes greater in larger specimens, as does the development of a distinct ascending process. The basal tubera are also poorly developed in the types of "*H.*" *nitidus nitidus*. Among the remaining specimens they are very distinct and strongly developed as in *H. lugubris* and *H. spekii*, whereas in BMNH 1946_8_6_51 -52 the tubera are hardly visible in lateral view and point laterally instead of ventrally. The dorsal crest of the prootic is either lacking or very poorly developed and a crista on the alar process is always present. Both parts of the alar process are circular, whereas in "*H.*" *nitidus garambensis* the interior section is dorsally cropped and bears a distinct anteroventral projection. The stapes of "*H.*" *nitidus nitidus* is rather short and stout, but in "*H.*" *nitidus garambensis* and *quadrinasalis* it is of the same shape as in *H. lugubris* and *H. spekii*.

The mandible of "*H.*" *nitidus* appears less curved, because it is narrower at its central part. It differs from the mandible of *H. lugubris* and *H. spekii* in few aspects that are, yet again, variable within the species. The teeth are of a similar shape compared to *H. lugubris/spekii* and vary in number (18–27), as does the position of the large alveolar opening (between 14th/15th tooth up to 18th/19th). The dentary shows five to six relatively large mental foramina, but differences in size do not differ to the same extent as in the maxilla. The mandibular fossa is moderately developed. The retroarticular process of the type specimens of *"H." nitidus nitidus* (BMNH 1946_8_6_51-52) is not posteriorly tapered but ends straight with a semi-circular cartilage in front, and lacks a ventromedial flange. In the other specimens of *"H." nitidus*, the ventromedial flange is hardly ever developed to the same extent as in *H. lugubris* and *H. spekii*.

Comparison with Latastia

The overall appearance of the skull of *Latastia* is quite similar to that of *"H." nitidus*. *Latastia* is more slender compared with *H. lugubris/spekii* and the occiput is more elongated. This difference is most apparent in one specimen of *L. carinata* (ZMB 19793) and *L. johnstonii* (ZMB 27570). Mature specimens show distinct dermal rugosities and ossifications. The major differences between *Latastia* and *H. lugubris/spekii* are a more slender postfrontal, shorter and broader nasals, and a farther ventral extension of the frontal bones. For a more detailed description and comparison see SOM.

Comparison with Pseuderemias

The skull shape of *Pseuderemias* is quite similar to that of *H. lugubris* and *H. spekii*. The occiput is short and the parietal is of a more rectangular shape, yet with a slender posterior margin. The frontal extends far ventrally and the zygomatic process on the jugal is consistently lacking. The frontal is remarkably slender. For a more detailed description and comparison with *H. lugubris/spekii* see SOM.

Comparison with Philochortus

The overall skull shape of *Philochortus* is similar to *Latastia*. The occiput is elongated when compared to *H. lugubris/spekii* and *Pseuderemias*. The snout is relatively narrower and the general appearance more compact. The postfrontal and postorbital appear to be mostly fused under a thick layer of dermal ossifications. For a more detailed description and a comparison with *H. lugubris/spekii* see SOM.

*Morphological and osteological variability of "*H. neumanni*"*

The specimens of "*H. neumanni*" investigated in this survey differ vastly from each other in both their external morphology and their skull osteology, which makes it difficult to describe the species as a single entity.

The specimen from the California Academy of Science (CAS 245014) represents the first morphotype (Fig. 3G, Fig. 11). Only its caudal scales are keeled. Dorsal scales are arranged in 31 rows. Ventrally there are six longitudinal scale rows of 30 scales each. Twelve femoral pores are present on each side and the lamellae underneath the toes bear a single keel. Also the cranial scutes differ clearly from the other specimens of the genus *Heliobolus*. The orientation of the scutes embracing the nostril is similar to *"H." nitidus* (Fig. 7), yet the upper postnasal is much smaller. The frontoparietals are reduced in size. In contrast the interparietal is clearly enlarged and the parietal shields are elongated. Granular scales around the subocular are completely lacking.

Because of the elongated occiput, the overall appearance of the skull of CAS 245014 is more slender than for *H. lugubris* and *H. spekii*. The premaxilla bears nine teeth. The ventral projection is rather poorly developed and there is a broadened, yet acute, nasal process. The nasals are relatively narrow and show a posterior convexity that is shifted towards the skull midline.

Particularly noticeable in CAS 245014 is the separation of the frontal bones. The frontals bear five projections anteriorly and overlie the parietal posterolaterally, and the ventral extension of the frontal is developed to a remarkable extent (Fig. 13).

Because the occiput is elongated, the parietal of CAS 245014 is less of a rectangular shape when compared to *H. lugubris* and *H. spekii*. Triangular tabs are well developed. A parietal foramen is lacking. The postfrontal and postorbital of CAS 245014 are relatively slender. The postfrontal bears two anterior projections and tapers posteriorly, so that the temporal opening is closed. In lateral view the anteroposterior extent of the comparatively long postorbital is completely visible.

The squamosal is comparatively narrow and comes closest in appearance to the typical hockey-stick shape among all the specimens investigated. The supratemporal is of a distinct hook-shape that is well developed in CAS 245014. The quadrate is relatively slender. The jugal bears a distinctive zygomatic process. The lacrimal is explicitly slender in CAS 245014 and only lines the rim of the orbital cavity. The prefrontals are similar to those of *H. lugubris/spekii*.

In general, the maxilla of CAS 245014 is similar to those of *H. lugubris* and *H. spekii*. Laterally it shows five foramina and bears 17 teeth of a similar shape compared to *H. lugubris/spekii*. The opening of the alveolar nerve is situated between the 14th and 15th tooth. In palatal view CAS 245014 resembles "*H.*" *nitidus*, whereas the vomer seems rather narrow and less waisted, so that distinct fenestrae are lacking.

The epipterygoid of CAS 245014 is clearly elongated and nearly reaches the middle section of the alar process of the prootic. An anterolateral process of the septomaxilla is lacking and posterolateral wings are hardly developed. The orbitosphenoid is of a typical funnel shape. Most sutures within the braincase are recognisable and the distance between the parietal and supraoccipital is relatively small, yet the contact surface is not developed to the same extent as in *H. spekii*. The ascending process is poorly developed. The narrow exoccipitals closely approach the relatively small basal tubera. The occipital complex is not as exposed dorsally. The alar process of the prootic is subdivided and the middle section is comparatively large, yet rather poorly ossified. The stapes is comparatively short. The mandible is anteriorly stouter and overall less curved relative to *H. lugubris* and *H. spekii*. The dentary shows 4 mental foramina and two posterior projections, the lower slightly longer than the upper, and bears 19 teeth. The opening for the alveolar nerve is situated between the 16th and 17th tooth. The splenial shows a single mylohyoid foramen. A suture between surangular and the fused articular and prearticular is recognisable. The mandibular fossa is moderately developed. The bifurcation of the angular is minute. A ventromedial flange on the relatively long and slender retroarticular process is lacking. Posteriorly the retroarticular process ends straight and a semi-circular cartilage is attached.

The second morphotype consists of the three specimens from the Museum of Comparative Zoology (MCZ 40203, 40207 and 40216) (Fig. 3H, Fig. 12). Dorsal and caudal scales are keeled, whereas lateral scales are smooth. The number of dorsal scales varies from 40 to 42. Ventrally, scales are arranged in six longitudinal rows of 27 to 29. Ten to twelve femoral pores are present and the lamellae underneath the toes bear two keels.

The cranial shields of this group are very similar to "*H.*" *nitidus*, except for the orientation of the shields embracing the nostrils. Because the lower postnasal is quite small and does not reach the rostral, scale orientation rather resembles the *Latastia*-type (Fig. 4). The occiput is more elongated and the parietal is less rectangular than that of *H. lugubris* and *H. spekii*.

The premaxilla bears nine teeth and a ventral projection is distinctly developed. The nasals are relatively narrow, posteriorly convex and approximately of the same length or slightly shorter than the dorsal projection of the maxilla.

The frontal bones have five projections anteriorly. The middle projection is broadened in specimens MCZ 40203 and 40207, whereas the outermost projections are shortened. Ventrally, the frontal bones are relatively deeper than in *H. lugubris/spekii*. Posterolaterally the frontal bones overlie the parietal. Because of the elongated occiput the parietal is of a less rectangular shape than in *H. lugubris/spekii*. Triangular tabs are well developed and the posterior margin is less offset and tapers towards the skull midline. A relatively large parietal foramen is situated anterior to the parietal centre.

The postfrontal is thin and shows two anterior projections. In MCZ 40303 and 40207 the bone is posteriorly concave and leaves a temporal opening. The postorbital is also comparatively long and narrow, and its complete extension is visible in lateral view. The squamosal is also comparatively narrow, but slightly posteriorly deepened. The supratemporal is of a distinct hook-shape. The quadrate is relatively slender. The jugal bears a small zygomatic process. The lacrimal is elongated, broadly exposed in lateral view and reaches deeply into the orbital rim. The prefrontals are similar to those of *H. lugubris/spekii*.

The maxilla is quite similar to that of *H. lugubris* and *H. spekii.* Laterally it shows 5 foramina and 21 teeth. The opening of the alveolar nerve is situated between the 14th and 15th tooth. In palatal view MCZ 40203 and 40207 are similar to "*H.*" *nitidus*. The anterior projection of the pterygoid is rather short, as are the posterior processes of the vomer. The palatine is anteriorly narrow and lateral projections into the fenestra exochoanalis are hardly developed. The epipterygoid is relatively short in MCZ 40203 and 40207, yet closely approaches the large medial section of the prootic. The septomaxilla is completely ossified, and its lateral wings are well developed and bear an anterolateral process, which is of a plateau shape in 40203 and acute in 40207. The orbitosphenoid is of typical funnel shape.

In MCZ 40203 and 40207 most sutures are still recognisable. The distance between parietal and supraoccipital is relatively small, yet the interface is not as broad as in *H. lugubris/spekii*. The ascending process is poorly developed. The exoccipitals are slender, as is the contact surface between the occipital complex and the fused para-basisphenoid. The alar process of the prootic is clearly subdivided. Only in specimen MCZ 40203 the alar process bears a dorsal crest. The stapes is comparatively short.

Like the mandible of CAS 245014, the mandible of MCZ 40203 and 40207 is anteriorly stouter and overall less curved than in *H. lugubris* and *H. spekii*. The dentary shows 5 mental foramina, two posterior projections, the lower slightly longer than the upper, and bears 24 to 25 teeth (MCZ 40303: 24 teeth, foramen between 18th/19th; MCZ 40207: 25, 19th/20th). A single mylohyoid foramen is situated on the splenial. There is a suture between the surangular and the fused articular and prearticular. The mandibular fossa is moderately developed. The bifurcation of the angular is minute. A ventromedial flange on the retroarticular process is lacking; it therefore appears more slender compared *H. lugubris/spekii*, and bears a dorsomedial concavity and is posteriorly blunt.

Results of the phylogenetic analysis

The parsimony analysis resulted in 20 equally parsimonious trees (202 steps). The consensus tree (Fig. 14) is subdivided into a fairly well resolved section, including the species *H. lugubris* and *H. spekii*, as well as the genera *Philochortus* and *Pseuderemias,* and a rather unresolved section. In the resolved part, all specimens assigned to *Philochortus*, *Pseuderemias*, and *H. lubris/spekii* cluster within their assigned genera, respectively. Within the unresolved part, there is a split between a clade comprising all specimens of *"H." nitidus* and an unresolved clade comprising all specimens of *Latastia* and the specimens of "*H. neumanni*" from the Museum of Comparative Zoology. However, this clade is only poorly supported by the bootstrap analysis. The specimen of "*H. neumanni"* from the California Academy of Science (CAS 245014) is found near the root of the tree as sister taxon of *N. boulengeri*. The latter relationship is highly supported by the bootstrap analysis. The Bayesian analysis, although being less stable in the intrageneric relationships, because of MrBayes not allowing for a topological constraint as detailed as TNT, supports the monophyly of CAS 245014 and *N. boulengeri*, the clustering of the remaining specimens of *H. neumanni* within the genus *Latastia*, and the polyphyly of *H. nitidus* and *H. lugubris/spekii.* All other specimens group with the genera to which they were originally assigned (see SOM for details).

Because parsimony analyses can be sensitive to the ratio of taxa and characters (Wiens and Hillis 1996), a second analysis with identical settings was performed, but with a reduced taxon number (42 taxa, see SOM). Taxa that were fully resolved in the first analysis were now considered with one specimen per monophyletic group only. The second analysis resulted in 30 equally parsimonious trees (162 steps). Bootstrap values for the monophyly of the genera *Heliobolus*, *Pseuderemias*, and *Philochortus* were elevated. However, within the unresolved section the sister group relationship between a monophyletic "*Heliobolus*" *nitidus* and a monophyletic *Latastia* clade collapsed (see SOM for details).

Discussion

Characterisations from external morphology

Based on external morphology, the genera of the North/East African clade can be clearly distinguished from one another. Particularly the arrangement of the shields embracing the nostril is a significant distinguishing character, as are genus-specific features, such as the enlarged dorsal scales in *Philochortus*. However, some characters, such as the number of lamellae under the toes or the presence of granular scales between frontal and supraocular shields, are shared by different genera and species, so that they do not appear useful for drawing conclusions on larger scale phylogenetic relationships. Additionally, there are serious difficulties in distinguishing species within *Latastia*.

Skull osteology of Heliobolus spekii *and* H. lugubris *relative to other taxa*

Similar to external morphological investigations, the genus *Heliobolus* (exclusive of *"H." nitidus* and *"H. neumanni")* can be easily distinguished from the other genera of the "North/East African" group by means of skull osteology. Significant characters typical of *H. lugubris* and *H. spekii* are the strongly reduced ventral extension of the frontal relative

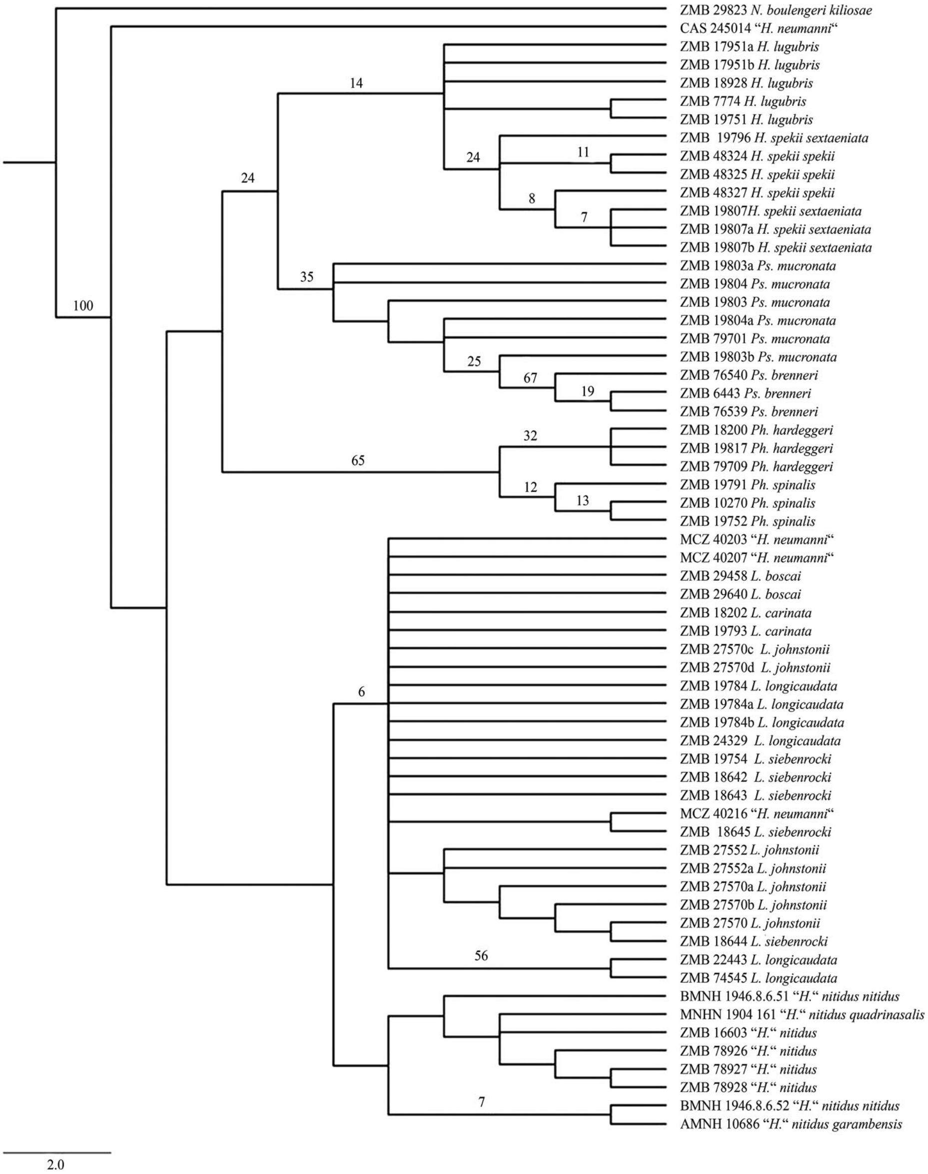

Figure 14. Strict consensus tree of 20 trees, illustrating the relationships of different specimens and taxa investigated in the current study (traditional search, Wagner tree, 10 replicates, and 202 steps). Bootstrap values are given in frequency differences based on 10 000 replicates. Collapsed groups had bootstrap values under five.

to other lacertids (Fig. 13), a comparatively short postorbital, and the large and continuously broad posterior margin of the parietal. Additionally, it is possible to differentiate between the species *H. lugubris* and *H. spekii*, which are also biogeographically clearly separated (Fig. 2, Spawls *et al*. 2004). Especially apparent are the comparatively shorter nasals, an almost consistently closed upper temporal opening, the shallow crista and the reduced medial section of the prootic of *H. spekii* in comparison to *H. lugubris*.

Osteologically, *Heliobolus* is most similar to *Pseuderemias*, which is also supported by the phylogeny. A comparatively low degree of ossification, as well as the rectangular shape of the parietal, are common characters of both genera, which can be distinguished from each other by the slender and deeply descending frontal of *Pseuderemias*. Because the rectangular shape of the parietal is exclusive for the terminal sister taxa of the North/East African group, it likely represents a synapomorphy, whereas it should be noted that this character is also shared with other African lacertids, such as *Meroles*, *Ichnotropis*, *Mesalina* and *Ophisops* (pers. obs., M.D.).

Philochortus can be clearly characterised by the broad frontal, and the fused postorbital and postfrontal bones. However, it is difficult to identify unique characteristics for *Latastia*. This and the intricacy of interspecific differentiation by means of highly inconsistent character states stresses the necessity for additional studies on that genus. This problem is also reflected in the large polytomy of *Latastia* specimens in the phylogenetic analysis.

Phylogenetic analysis and the position of "H." nitidus

In the current study the monophyly of the genera *Philochortus*, *Pseuderemias* and *Latastia* was confirmed by external morphology and cranial osteology. However, the genus *Heliobolus* proved to be paraphyletic.

Heliobolus (s. str., *H. lugubris* and *H. spekii*) forms a terminal sister taxon to *Pseuderemias*, whereas "*H.*" *nitidus* is paraphyletic and basal to *Latastia* in the parsimony analysis. Specimens of "*H. neumanni*" are also not arranged monophyletically.

With the exception of *Latastia*, it was possible to clearly differentiate between the different species within the remaining genera of the North/East African group. However, it was not possible to resolve groupings at the subspecies level in *H. spekii* and "*H.*" *nitidus*.

Moreover, it is noteworthy that two specimens of *Latastia longicaudata* (ZMB 2443 and ZMB 74545) are found as sister taxa with high bootstrap support relative to the remaining *Latastia*. The monophyly of the two specimens is also found in the Bayesian analysis. This could be interpreted as an indication of a species complex in *Latastia longicaudata*, because these two specimens, which come from southern Kenya, might also be biogeographically separated from the remaining specimens, which were largely collected in Ethiopia.

Despite low bootstrap support, the placement of "*H.*" *nitidus* in a polytomy basal to the large *Latastia* polytomy is noteworthy and raises the question of the taxonomic status and affiliation of "*H.*" *nitidus*. Already in the original description of "*H.*" *nitidus* (org. *Eremias nitida,* Günther, 1872) it becomes apparent that "*H.*" *nitidus* differs substantially from *H. lugubris* (org. *Lacerta lugubris*, Smith, 1838) and *H. spekii* (*Eremias spekii*, Günther, 1872), although the original description largely focuses on colouration, and the granular scales between frontal and suboculars are not mentioned. The most significant morphological difference, the arrangement of the shields embracing the nostril, was illustrated in more detail in the current study. In the osteological analysis additional differences were also identified, such as the overall higher degree of ossification, the elongated occiput, and the more distinct ventral extension of the frontals in "*H.*" *nitidus*.

The greatest similarities are found between "*H.*" *nitidus* and *Latastia*, because both taxa lack granular scales between frontal and supraocular shields, and the subdigital lamellae are biradiate. However, unique, i.e. apomorphic, osteological features are difficult to identify.

The first official assignment of "*H.*" *nitidus* to *Heliobolus* was by Rödel *et al*. (1997). In their study of the herpetofauna of Comoé (Ivory Coast), the authors refer to Mayer (1989) who states that *Heliobolus* has priority over *Lampreremias*, according to Baletto (1968). Also in 1989, Szczerbak (1989) published a study where he divided the African representatives of *Eremias* into the genera *Lampreremias*, *Pseuderemias*, *Taenieremias*, *Mesalina* and *Meroles*, including a key to the different species and genera. In his identification key he defines nonserrated toes, three or rarely four shields around the nostril, bi- or tricarinate subdigital lamellae and six longitudinal series of ventral scales to be characteristic for the genus *Lampreremias* (Boulenger, 1898). Within the genus *Lampreremias* the absence of granular scales and the punctual contact of the lower postnasal and rostral shields separate "*Lampreremias nitida*" from "*Lampreremias lugubris*" and "*L. spekii*". These differentiations within the genus *Lampreremias* are in accordance with the results from our own study, but prove to be insufficient for *Heliobolus*, because *Heliobolus* (s. str., i.e. *H. lugubris* and *H. spekii*) and "*H.*" *nitidus* do not appear closely related.

The problem regarding "H." neumanni

Morphological investigations of the specimens of "*H. neumanni*", as well as their position in the phylogeny, reveal the necessity of a systematic reconsideration of the species and the taxonomic identity of the different specimens assigned to this taxon.

Specimen CAS 245014 can be likely assigned to *Nucras boulengeri* (Neumann, 1900), because of the specimen's close resemblance with that species regarding skull osteology, external morphology, and collection locality. The most striking feature that distinguishes CAS 245014 from the other specimens analysed in the current study is its separated frontal bones, a character that is only shared by one other genus of the North/East African group, i.e. *Nucras*. Whereas this character is also common in other genera distributed in eastern Africa, such as *Holaspis*, *Congolacerta* and *Adolfus* (pers. obs., M.D.), the specimen also shares other explicit osteological characters with the outgroup genus, such as the lack of a parietal foramen, a slender squamosal, a very narrow lacrimal and postorbital, a distinct zygomatic process on the jugal, a short anterior process of the frontal, as well as its deep ventral extension. Furthermore, *Nucras boulengeri*'s external morphological characters are largely congruent with Neumann's (1900) description, such as two postnasal shields, no granules between supraoculars and supraciliaries, a subocular shield bordering the lip between the fourth and fifth upper labials, two supratemporal shields bordering the parietal shield, small and pointed dorsal scales, six longitudinal ventral scale lines, the absence of keeled lamellae and eleven to twelve femoral pores. In addition, *Nucras boulengeri* is the only species of its genus that is known to occur in the Dar es Salaam region of Tanzania (Spawls *et al*. 2004).

More difficult to assess are the taxonomic identities of specimens MCZ 40203, MCZ 40207 and MCZ 40216. Osteologically these specimens can be clearly discriminated from *H. lugubris* and *H. spekii*, most explicitly via the shape of the parietal and its posterior margin, the ventral extension of the frontal bone, as well as the outline and composition of the postfrontal and postorbital. Among the genera investigated in this survey, these specimens rather resemble *Latastia* with their elongated occiput, slender postorbital, and their tapering posterior margin of the parietal. However, morphologically there are many correspondences between the MCZ specimen and Tornier`s (1905) original description of

"*Eremias neumanni*" (*H. neumanni*; Broadley and Howell, 1991). For instance, the lack of granular scales between the supraorbital and frontal shields, the tendency towards rough cranial shields, the subocular that hardly narrows before it reaches the oral fissure, the insertion of an extra shield between the occipital and interparietal (MCZ 40216 only), and the presence of keeled dorsal scales are in accordance with the original description. Also the number of femoral pores and the number of dorsal scales are similar. The description of the shields embracing the nostril is comprehensible, even though Tornier (1905) states the presence of three shields. Regarding the arrangement and overall shape, the shields conform to those of *Latastia*. Because it is somewhat variable within *Latastia* whether the first labial actually contacts or simply approaches the nostril very closely between the lower postnasal and supranasal shields, this condition was coded with four shields embracing the nostril in our data matrix. The condition of the nasal shield explicitly differs from *H. lugubris* and *H. spekii*, in which an enlarged lower postnasal separates labial and nostril clearly from one another and forms a broad contact with the rostral shield (Fig. 12). Because Tornier's description of *Eremias neumanni* evidently differs from the type species of the genus *Heliobolus* (*H. lugubris* ; Duméril and Bibron 1839) in several attributes, such as the occurrence of an occipital shield and the composition of dorsal and granular scales between supraocular and frontal shields, the question arises why *"H." neumanni* was included in the genus *Heliobolus* in the first place. The first publication assigning *Eremias neumanni* to *Heliobolus* was by Broadley and Howell (1991), but without offering a detailed explanation. This assignment was apparently followed by other authors without checking its validity. An additional problem is that no specimens of *"H. neumanni"* are available from the type locality in Ethiopia. The holotype is lost, and the only other specimens collected from this locality can be clearly assigned to *H. spekii* (pers. obs., H.D.), which impedes the determination of a lectotype.

Conclusions

Our study shows that the genus *Heliobolus* (s. str., *H. lugubris* and *H. spekii*) can be clearly distinguished morphologically from the other genera of the North/East African clade of Lacertidae, and that there is also an interspecific distinction based on osteology. Nevertheless, our results also strongly suggest that the genus *Heliobolus* is polyphyletic. Our study stresses the necessity to remove **"***H." nitidus* from the genus *Heliobolus*. Whether *"H." nitidus* forms a new basal genus within the North/East African group or can be included into the genus *Latastia* to which it is most similar, must await additional investigations, most importantly molecular analyses.

Concerning *"H. neumanni"* the current investigation could not completely resolve issues regarding the validity of the species. However, both osteological and external morphological analyses indicate that all specimens assigned to "*H. neumanni*" do not belong to the genus *Heliobolus* and also are not conspecific, with many of them showing strong affinities to the genus *Latastia*. To finally resolve this matter, genetic analyses and the rediscovery of the holotype are required, but present evidence suggests that "*H. neumanni*" is not a valid species. Furthermore, it could be shown that the genus *Latastia*, as a highly unresolved clade, requires more detailed morphological, osteological and genetic analyses within a comprehensive taxonomic revision.

Supplemental material

Supplemental data for this article can be accessed at https://doi.org.10.1080/21564574.2017.1422153.

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