

**Review article**

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## Rediscovery of the enigmatic Madagascan endemic *Belohina inexpectata* Paulian, 1958, with notes on its morphology and phylogenetic position (Coleoptera, Scarabaeoidea: Belohinidae)

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**Abstract**

*Belohina inexpectata* Paulian, 1958, the only known representative of Belohinidae (Coleoptera: Scarabaeoidea) and a Madagascan endemic, is redescribed based on recently collected material. Some remarks are provided on its unusual morphology and in particular its mouthparts, with recessed mandibles and membranous epipharynx, its antennae with a V-shaped sensory area and its capsule-like aedeagus, with a regular, unrotated position at rest and the presence of “parameroids”. Data on its life history are also provided, including evidence of stridulation. Finally, its phylogenetic position is briefly discussed based on a molecular analysis, which points towards a sister-group relationship with the genus *Orubesa* (Dynamopodidae), with both taxa together being sister to Hybosoridae.

**Key words:** Madagascar, systematics, mouthparts, flightlessness, stridulation, spiny forest.

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**Introduction**

The Scarabaeoidea are one of the megadiverse taxonomic groups within Coleoptera, with some 35.000 species recognized thus far (Scholtz & Grebennikov 2005). The classification of the superfamily has seen many changes in recent years. Many major taxonomic groups at family or subfamily level have been the subject of various phylogenetic reconstructions, so that we now have a good set of hypotheses about their evolution (e.g., Ahrens et al. 2011; Ballerio & Grebennikov 2016; Boucher 2005; Kim & Farrel 2015; Ocampo 2006; Struempfer et al. 2014; Tarasov & Génier 2015). Among the lesser known taxa stands the family Belohinidae, possibly one of the most enigmatic families of Scarabaeoidea. The main problem with this family is that up to a few years ago it was known by the type series only

of the single known species (*Belohina inexpectata* Paulian, 1958, Fig. 1), six specimens in all, collected in 1957 during a mission of IRSM/ORSTOM in Southern Madagascar. They deposited in the Muséum National d'Histoire Naturelle in Paris (holotype, Fig. 2, and one paratype) and in the collection of the Institut de Recherche Scientifique de Madagascar (now Institut de Recherche pour le Développement) in Antananarivo (four paratypes). This shortage of material has hampered detailed morphological studies and has not allowed for DNA analysis. A recent effort to rediscover the species has yielded additional specimens, including well-preserved material suitable for molecular analysis, thereby allowing a better understanding of this unusual beetle. This paper provides a detailed morphological description, data on life history and a first phylogenetic analysis based on molecular data.

## Materials and Methods

**Materials.** Specimens studied are deposited in the following collections:

ABCB: private collection of Alberto Ballerio, Brescia, Italy

BMNH : The Natural History Museum, London, UK

DMNS: Denver Museum of Nature & Science, Denver, Colorado, U.S.A.

MNHM: Muséum National d'Histoire Naturelle, Paris, France

PBZT: Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar

UCRC: Entomology Research Museum, University of California, Riverside, California, USA

UFMT: Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brasil

UNSM: University of Nebraska State Museum, Lincoln, Nebraska, USA

UPSA: Department of Zoology & Entomology, University of Pretoria, South Africa

ZIN: Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia

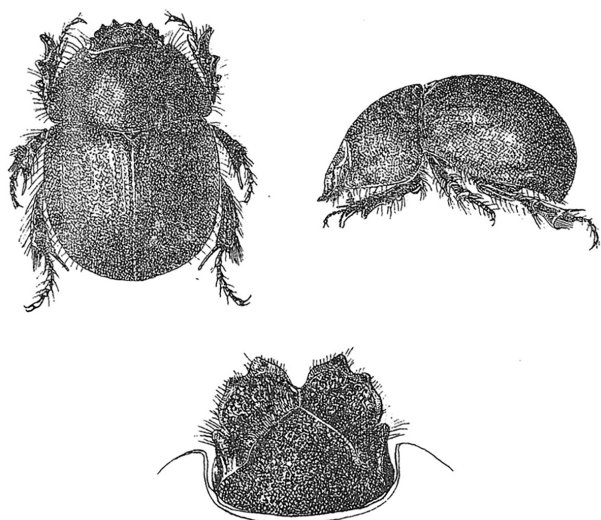
**Morphology.** Morphological terminology follows Ritcher (1969), Edmonds (1972), Nel & De Villiers (1988),

Holter & Scholtz (2011) and Krell (1996), the latter being the most comprehensive genital anatomy and myology in Scarabaeoidea. Thus, *Melolontha* serves as the baseline for comparative myology in this group of beetles. The anatomy of the aedeagus of the studied species was analyzed by dissection of one specimen in 75% ethanol under an Olympus SZX16 dissection microscope. Occasional staining with methylene blue in distilled water helped to determine the muscular connections, but a comprehensive myological description was prevented by the specimen having originally been preserved in high percentage alcohol, causing muscles and membranes to become brittle.

Micrographs were obtained with a Zeiss EVO 40 XVP Scanning Electron Microscope at the MUSE (Trento, Italy), after gold coating. Habitus photographs were taken with a Canon EOS D5 MII with a macro lens MP 65 mm, mouthparts photos with a Mitutoyo M Plan APO 10× microscope objective on bellows and the dissections of the male genitalia were documented with a Passport II system from Visionary Digital. Serial photos were then combined with the Zerene Stacker or Helicon Focus software and cleaned using photo processing software.

**Stridulation.** Jasmin E. Randrianirina recorded the stridulation in his laboratory in Antananarivo, later analysed by J. Sueur. The sound was spontaneously produced by a single individual. Sound files were digitized with a 22.05 kHz / 16 bits sampling rate. A total of 115 stridulation echemes were analysed. A 200 Hz high-pass filter was applied to remove low-frequency background noise. Temporal parameters were estimated on amplitude envelopes with a  $10^{-4}$  s precision. Parameters regarding fine time structure were assessed on a selection of four successive pulses chosen in the middle of the 115 stridulation echemes for a total of 460 pulses. Frequency parameters were derived from a frequency spectrum computed with a 512 samples (= 0.023 s) Hanning window in the middle of each echeme. The peak of highest energy or dominant frequency and the bandwidth covering 50% of energy were measured on these spectra with a 43.1 Hz precision. All parameters were measured using *seewave* (Sueur et al., 2008), a package of the R environment (R Core Team 2012), and were summarised as mean ± standard-deviation (minimum–maximum, n = sample size). The sound records are kept in the sound library of MNHN with the following accession numbers: MNHN-SO-2015-16 and MNHN-SO-2015-17.

**Molecular analysis.** *Specimen inclusion for phylogenetic analysis.* The molecular matrix consists of 1006 individuals, collected over many years and prepared by various researchers. The phylogenetic work presented here focuses on the taxa nearest to *Belohina*, with the full matrix to be published elsewhere (Hawks et al. in prep). The extended sampling regime is used because using subsets of the matrix can result in instability in topology and branch



**Fig. 1** – Drawings by Germaine Boca (MNHN) published in the original paper by Paulian (1958) showing *Belohina inexpectata*.



**Fig. 2** – *Belohina inexpectata*, holotype (MNHN) and its labels. Far right: labels of the paratype in MNHN.

support across Scarabaeoidea, and it is most justified to accept the topology built under the densest taxon sampling and most data-rich matrix. Superfamilies represented in the full matrix include Dascilloidea, Nosodendroidea, Hydrophiloidea, and Scarabaeoidea. The taxon of inter-

est, *Belohina inexpectata*, is represented in the matrix by one individual with full data. The sequences for *Belohina* and its closest relatives (28 samples total) can be accessed through GenBank (18S accession numbers: OR754010-24, 28S accession numbers: OR736260-85, Tab. 1).

**Table 1** – Species of Belohinidae (*Belohina*, 1 species), Dynamopodidae (*Orubesa*, 2 species), and Hybosoridae (17 genera, 25 species) included in the Figure 15 phylogeny. Locality information and repository of the voucher specimens are listed. The rightmost columns show GenBank (“GB”) accession numbers for 18S and 28S ribosomal sequences. In the fourth column an “N/A” indicates that there was no sequence available, and three sequences were previously published. A total of 15 new 18S sequences and 26 new 28S sequences were generated.

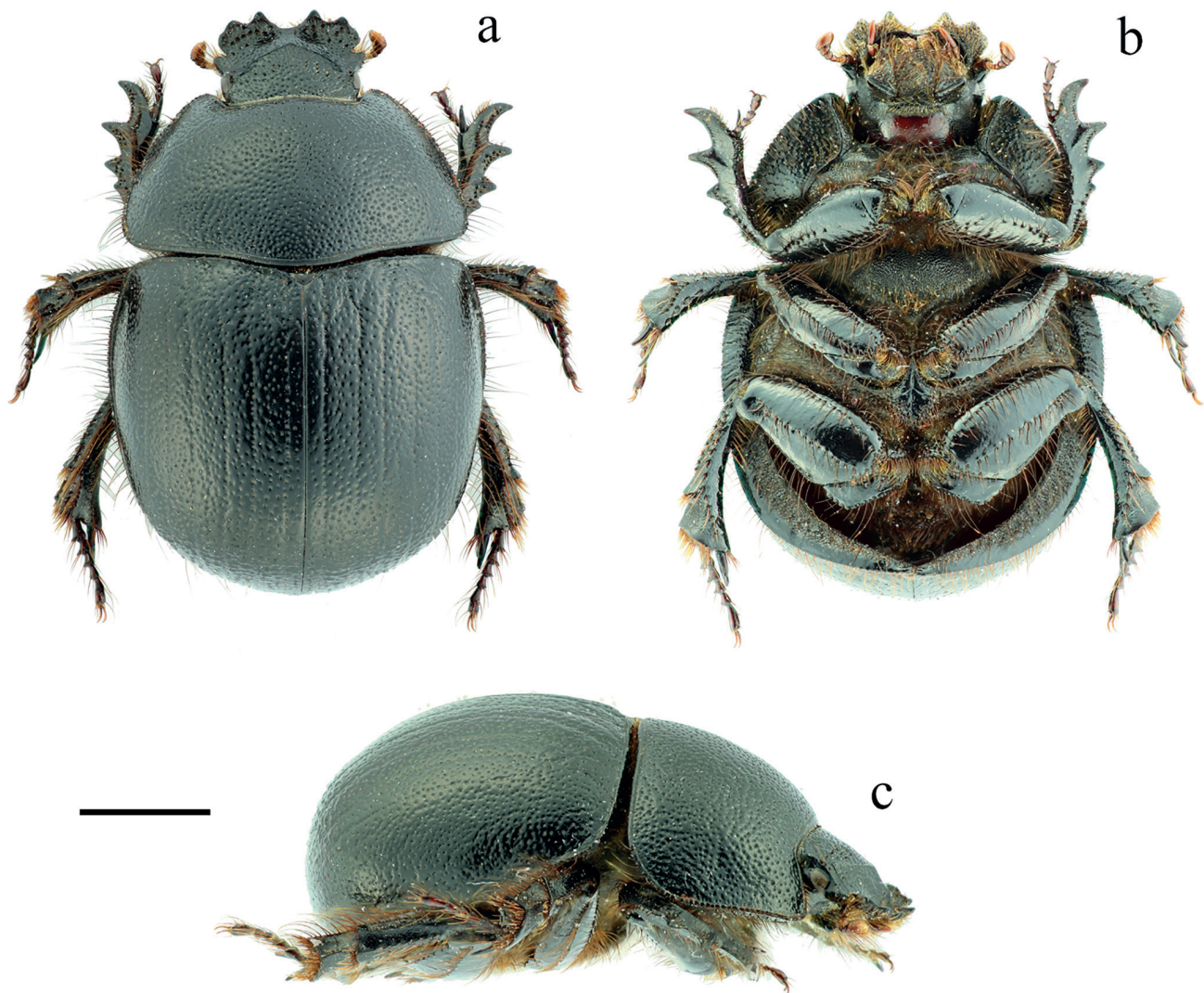
Species	Locality	Repository	GB 18S Accession #	GB 28S Accession #
<i>Belohina inexpectata</i> Paulian	Madagascar, Beloha Androy District: Antreaky	UCRC (leg/extract) ABCB (specimen)	OR754010	OR736260
<i>Orubesa plicifrons</i> (Fairmaire)	Senegal, Saint-Louis: Richard Toll	UNSM	OR754012	OR736262
<i>Orubesa ata</i> (Semenov-Tian-Shanskij & Medvedev)	Iran, Khuzestan Province: 5 km W of Sheikh-Tomeh sands	UNSM	OR754011	OR736261
<i>Brenskea coronata</i> Reitter	Iran, Khorasan Province: 30 km N Gonabad	UNSM	OR754013	OR736263
<i>Phaeochrous emarginatus</i> Laporte de Castelnau	Thailand, Mae Hong Song Province: Pha Sua Waterfall	UCRC	OR754014	OR736264
<i>Phaeochroops rattus</i> Arrow	Malaysia, UM Forest Centre	UCRC	OR754015	OR736266
<i>Coilodes castaneus</i> Westwood	Nicaragua, Matagalpa Department: Selva Negra, 1300 m	UCRC	N/A	OR736265
<i>Metachaetodus brunneicollis</i> de Borre	N/A	N/A	OR754016	OR736267
<i>Hybosorus ruficornis</i> Boheman	South Africa, Limpopo Province: Blouberg	UNSM	N/A	OR736268
<i>Hybosorus illigeri</i> Reiche	USA, California: Riverside Co., Blythe	UCRC	KP419125	KP419480
<i>Pachyplectrus laevis</i> LeConte	USA, California: Imperial Co., Algodones Dunes	UCRC	OR754017	KJ845150
<i>Anaides laticollis</i> Harold	Nicaragua, Matagalpa Department: Selva Negra, 1300 m	UCRC	OR754018	OR736269
<i>Cryptogenius westwoodi</i> Costa-Silva & Vaz-de-Mello	Bolivia, Santa Cruz: Refugio Los Volcanes, 1080 m	UNSM	OR754019	OR736270
<i>Chaetodus piceus</i> Westwood	Brazil, Minas Gerais: Lavras	UNSM	N/A	OR736272
<i>Chaetodus teamscaraborum</i> Ocampo	Nicaragua, Matagalpa Department: Selva Negra, 1300 m	UNSM	N/A	OR736271
<i>Liparochnrus infantus</i> Petrovitz	Australia, Queensland: Yarramulla, HS Unchera National Park	UNSM	N/A	OR736273
<i>Liparochnrus matthewsi</i> Paulian	New Caledonia, Mt Koghis, 500 m	UNSM	OR754020	OR736273
<i>Antiochnrus aberrans</i> (Fairmaire)	Australia, Queensland: Yarramulla	UNSM	N/A	OR736276
<i>Liparochnrus silphoides</i> Harold	Australia, Queensland: Yarramulla	UNSM	N/A	OR736275
<i>Ceratocanthus relucens</i> Bates	Nicaragua, Matagalpa Department: Selva Negra, 1300 m	UNSM	N/A	OR736283
<i>Pterorthochaetes insularis</i> Gestro	Thailand, Sri Sawat Distr.: Dong Yai subdistrict, 350 m	UNSM	N/A	OR736277
<i>Ivieolus inflaticollis</i> Howden & Gill	Ecuador, Napo: Yasuni Reserve	CMNC	OR754022	OR736279
<i>Ivieolus brooksi</i> Howden & Gill	French Guiana, 4 km SSE Roura, 200 m	CMNC	OR754021	OR736278
<i>Martinezostes fortecosatus</i> (Gutiérrez)	Argentina	UCRC (extract)	N/A	OR736285
<i>Martinezostes posticus</i> (Germar)	Chile, Chachapoal Province: La Miranda, El Rulo	UNSM	OR754024	OR736284
<i>Germarostes</i> sp. 2	El Salvador	UNSM	OR754023	OR736282
<i>Germarostes</i> sp. 1	El Salvador	UNSM	N/A	OR736281
<i>Germarostes globosus</i> (Say)	USA, South Carolina: Greenville Co., Simpsonville	UCRC	N/A	OR736280

*DNA extraction and amplification.* Samples have been extracted and prepared by several workers; all followed the same general protocols. Both alcohol and dried specimens were used for DNA extraction. Specimen DNA was non-destructively extracted using a standard Chelex and Proteinase K protocol or the DNeasy Blood and Tissue Kit (Qiagen, Germantown, MD, U.S.A.). Three nuclear ribosomal regions were amplified via PCR: 18S, 28S-D2 and 28S-D3-D5. Amplified DNA was purified using GeneClean (MP Biomedicals, Salon, OH, U.S.A.) and sequenced at the IIGB Genomics Core Facility at UC Riverside. Sequencher 4.8 (Gene Codes Corp) was used to verify and edit chromatograms. Individual regions were manually aligned in MacClade 4.0 (Maddison & Maddison 2005), due to the nature of the ribosomal stem and loop regions, which could not be adequately addressed by general alignment programs. Of a total matrix length of 3682 characters, 18S had 441

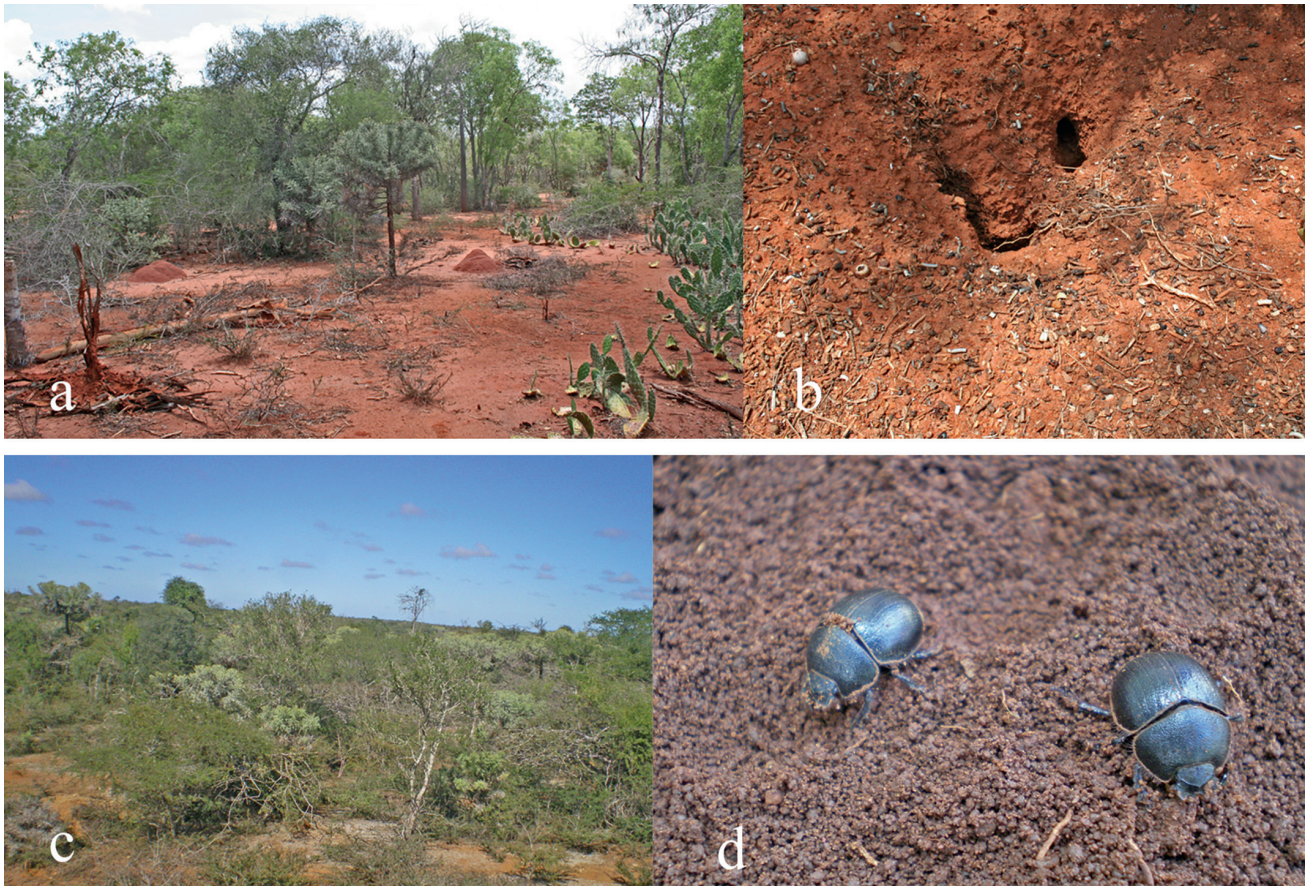
parsimony-informative sites (21.9% of the total 2011 sites) and 28S had 898 (53.7% of 1671 sites).

*Phylogenetic analysis.* The 1006-taxon matrix was partitioned into 18S and 28S D2-D5 for a maximum likelihood phylogenetic analysis. The analysis was run using IQ-Tree multicore v2.2.0 (Minh et al. 2020) with free rate heterogeneity. Substitution model selection (Kalyaanamoorthy et al. 2017) was implemented with a model merging option (meaning the two data subsets would be combined under one model if most appropriate), but the best scheme resulted in 28S and 18S treated as separate partitions. Ultrafast bootstrap values were calculated for branch support (Hoang et al. 2017).

*Distribution map.* The distribution map was created with SimpleMappr (Shorthouse 2010) and contains all published and unpublished records known to us.



**Fig. 3** – *Belohina inexpectata* (Atreaky forest), habitus of adult **a**, dorsal; **b**, ventral; **c**, lateral. Scale bar: 3 mm.



**Fig. 4** – *Belohina inexpectata* **a**, type locality (December 2007); **b**, entrance of a nest of the ant *Aphaenogaster swammerdami* at type locality, many fragments of various beetles are visible around the entrance holes (December 2007); **c**, Antreaky forest landscape (February 2008); **d**, two specimens from Antreaky forest, freshly dug out (February 2008).

## Systematics

### Belohinidae Paulian, 1958

Type genus: *Belohina* Paulian, 1958

#### *Belohina* Paulian, 1958

Type species: *Belohina inexpectata* Paulian, 1858 (by monotypy)

Etymology: not provided by the author, but clearly related to the type locality (Beloha). Gender feminine.

#### *Belohina inexpectata* Paulian, 1958

(Fig. 3)

Etymology: not provided by the author, but clearly from Latin *inexpectatus*, *a*, *um* (unexpected), due to the unexpected discovery of this strange beetle.

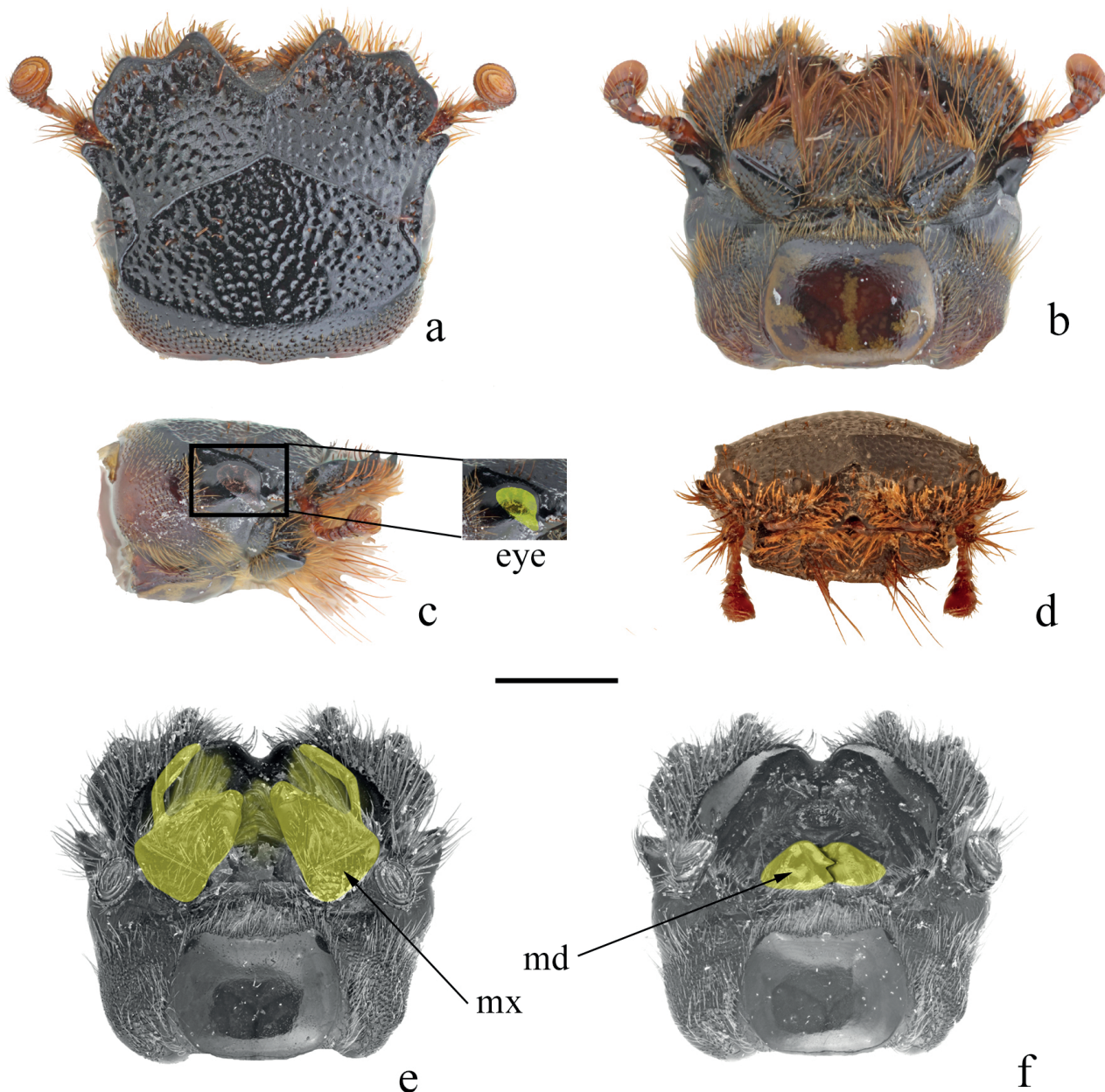
Type locality: road between Beloha and Tsihombe, 25 km from Beloha (Paulian only mentions “road between Beloha and Tsihombe”, which is the only locality reported on the labels of the holotype, but the paratype in MNHB bears a label indicating the exact distance from Beloha, a detail that has greatly facilitated the first author’s field research).

**Material examined:** Holotype (female): Madagascar Sud, entre Beloha et Tsihombe, III.57, R. J. E. [probably Jean Elie Randiamasy] / *Belohina inexpectata* n. g. n. sp. R Paulian det., 1957 / Holotype [pinned, in good condition]; one paratype (male): 25 km de Beloha Rte de Tsihombe III.57 Jean Elie / *Belohina inexpectata* n. g. n. sp. / Institut Scientifique Madagascar / Paratype [pinned, in good condition] (both holotype and paratype in MNHN).

Further material examined: Madagascar, forêt sèche d’Antreaky (Beloha Androy district), 25° 08’ 09” S; 45° 09’ 58” E, 150 m a.s.l., 1.III.2008, J. E. Randrianirina leg. (6 specimens: 3 males and 1 female dissected) (ABCB, DMNS, UPSA, PBZT). Madagascar, road Tsiombe-Beloha (Beloha Androy district), 25 km from Beloha, 25° 08’ 11” S; 45° 13’ 16” E, 96 m a.s.l., 10.XII.2007 A. Ballerio & J. E. Randrianirina leg. (one almost complete dead specimen and many fragments) (ABCB, BMNH, UFMT, UNSM, ZIN).

## Redescription

*Size.* Maximum body length: 14 mm. Maximum body width: 10 mm.



**Fig. 5** – *Belohina inexpectata* **a**, dorsal view of head; **b**, ventral view of head; **c**, lateral view of head, with a squared box highlighting the eye surface (in yellow); **d**, frontal view of head; **e**, black and white ventral view of head showing the maxillae (mx, in yellow) covering the mandibles; **f**, black and white ventral view of head with maxillae removed, showing the recessed mandibles (md, in yellow). Scale bar: 1 mm.

Medium sized scarab. Body convex and compact. Flightless. Entirely black, antennae, palpi, tarsi and setation reddish-brown. Shiny (fresh specimens) subject to wear.

Head (Figs 5 a-f). prognathous, slightly inclined in resting position, subsquared (W/L ratio = 1.0) (dorsal view), dorsal surface slightly convex, clypeus large with four frontal teeth, gently protruding upwards, two at each side, with a wide deep V-shaped emargination between inner teeth, emargination between inner and outer teeth much less deep, widely U-shaped, outer margin of outer teeth broadly rounded, genal suture present, lateral lobes narrow and longitudinally oriented, distinctly acutely protruding

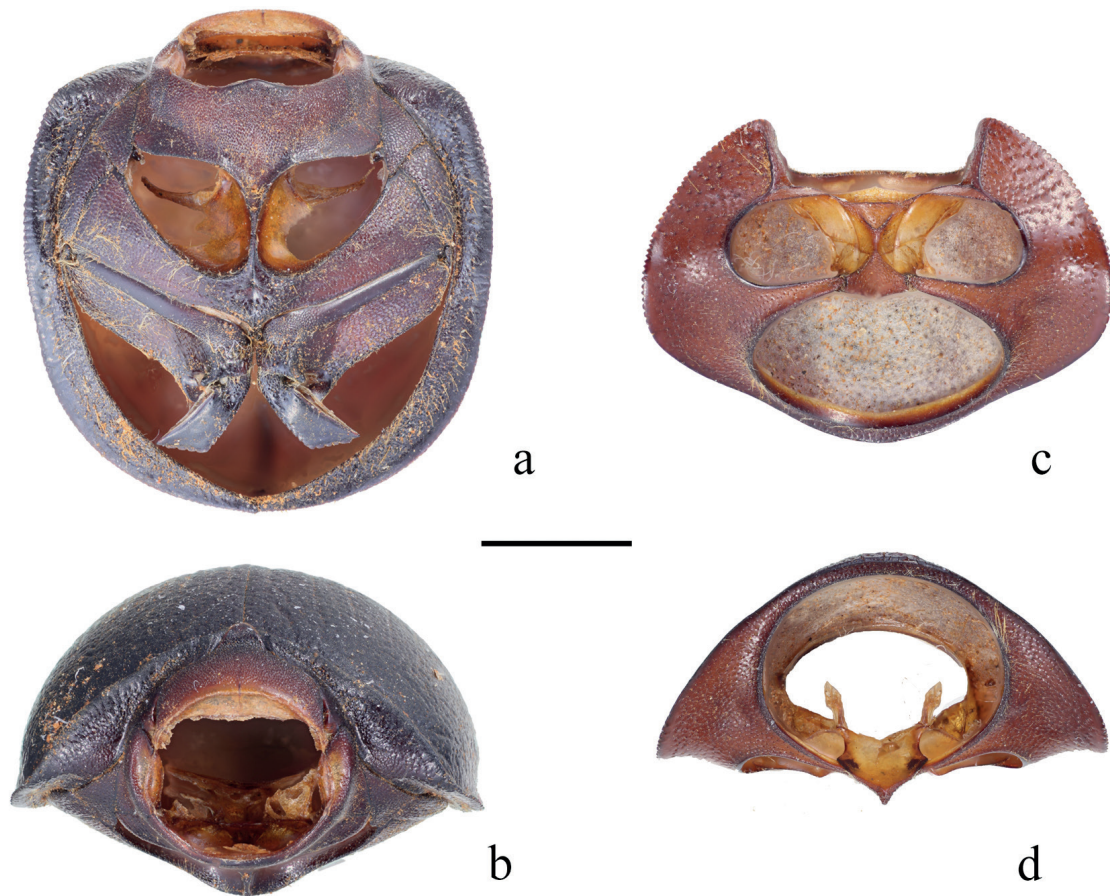
forwards, ocular canthus absent; frontoclypeal suture present and complete, inverted-V-shaped. One further suture dividing the clypeus longitudinally. Head surface completely covered by irregular deep punctation. Punctures medium sized, their distance being about the same as their diameter. Occiput gently declivous, densely punctate, punctures small and deep, often bearing short fine recumbent setae. Eyes small, visible from above, transversely oriented and narrowed ventrally. Head dorsally almost glabrous apart from some very short thick erect setae on frons, two fine long erect setae at the proximal extremity of genae, some fine long erect setae in the distal part of clypeus and some

short thick lanceolate erect setae on the clypeal teeth. Underside of head with a large subrectangular glabrous gula, labio-gular fimbria fringed with long fine recumbent setae directed forwards, oculo-gular space wide, smooth and glabrous, occipital area of parietals finely punctate, covered by long fine recumbent setae. Underside of clypeus covered by long fine semi-erect setae.

Mouthparts: Figs 5 e, f, 7 a-d, 8 a-g, 9 a-e. Exposed labrum absent. Distal epipharynx (Figs 9 a, b, e) membranous, subtrapezoidal, with a deep narrow excavation in the middle of anterior margin, which is narrow and has few short thick setae, without any median process or mesal brush, sides covered by relatively dense irregularly spaced medium-sized thick pointed setae. Proximal epipharynx strongly extended and larger than distal epipharynx. Mentum (Figs 9 c-d) ventrally flat, with surface irregularly broadly wrinkled and with long setae, narrow, with a very weak short emargination in the middle of rounded fore margin; labial palpi (including palpiger) four jointed; first palpomere relatively long, about as long as second one, with a few long fine setae; second palpomere wider than first one, distally slightly protruding forwards, covered by dense long fine setae fringed distally with four to five long thick setae; third palpomere slightly

shorter than second one, subconical, with an apical sensory area. Maxillae (Figs 8 a-g) with cardo and stipital sclerite I visible covered by semi-erect sparse long fine setae; lacinia narrow and long, not protruding over the galea, strongly sclerotized, ventrally fringed along its whole length by a comb-like row of short dense thick setae, apically ending with a tuft of about five very thick setae; monolobed galea sclerotized, tooth-like, protruding outwards with a galeal hook (sensu Holter & Scholtz 2011), dorsally glabrous, apart from seven curved very thick setae with blunt apex, possibly replacing the galeal distal pad, maxillary palpi (including palpiger) four jointed, palpiger very small, palpomere two smooth, wide and relatively short; palpomere three smooth, relatively short, about as long as joint two; palpomere four about as long as palpomeres two and three together, smooth, fusiform, apically bearing some short sensilla. Mandibles (Figs 7 a-d) small and short, distal lobe poorly sclerotized, regularly curved, ventrally fringed by very dense short fine setation, apicalis with pointed apical tooth very short and blunt, basalis with molar lobe wide and relatively strong.

Antennae (Figs 10 a-d) 10-segmented, scapus short (shorter than the remaining antennomers of funicle), gently clavate, pedicellus plump and irregularly rounded, flagellum



**Fig. 6** – *Belohina inexpectata* **a**, ventral areas of meso- and metathorax (legs removed); **b**, mesothorax and elytra in sagittal view; **c**, ventral area of prothorax (legs removed); **d**, sagittal view of prothorax. Scale bar: 3 mm.

short; antennomere three and four short, shorter than wide; antennomere five about as long as the preceding two, with two long thick setae distally; antennomere six shorter than five but much wider, fringed distally by several long thick pointed setae directed forwards; antennomere seven about as

long as six but much wider, fringed distally by several long thick pointed setae directed forwards; antennal club made of three articles, first antennomere of club convex and glabrous externally, enclosing the remaining two antennomeres, densely and finely setose inside, with a fringe of short thick

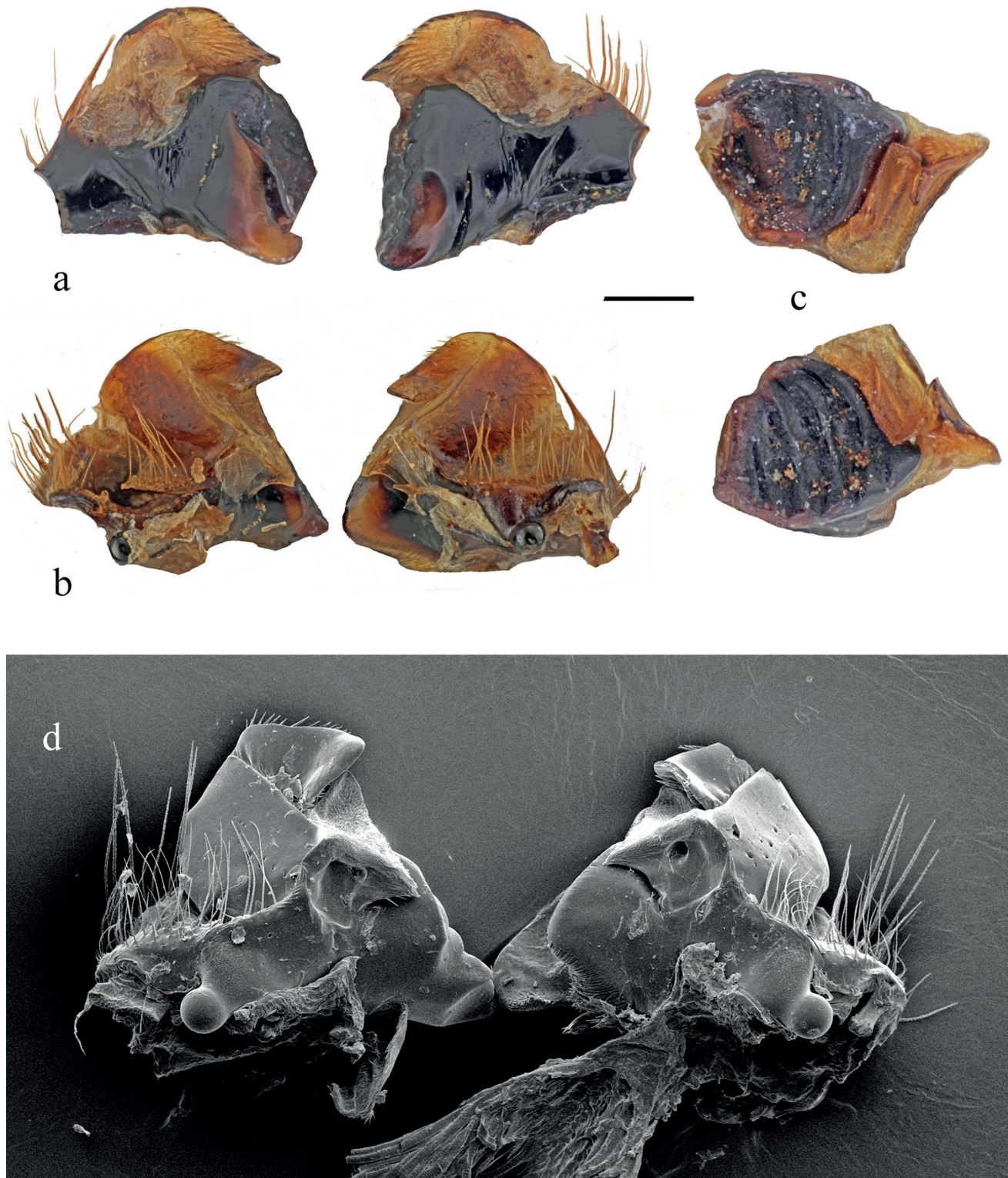
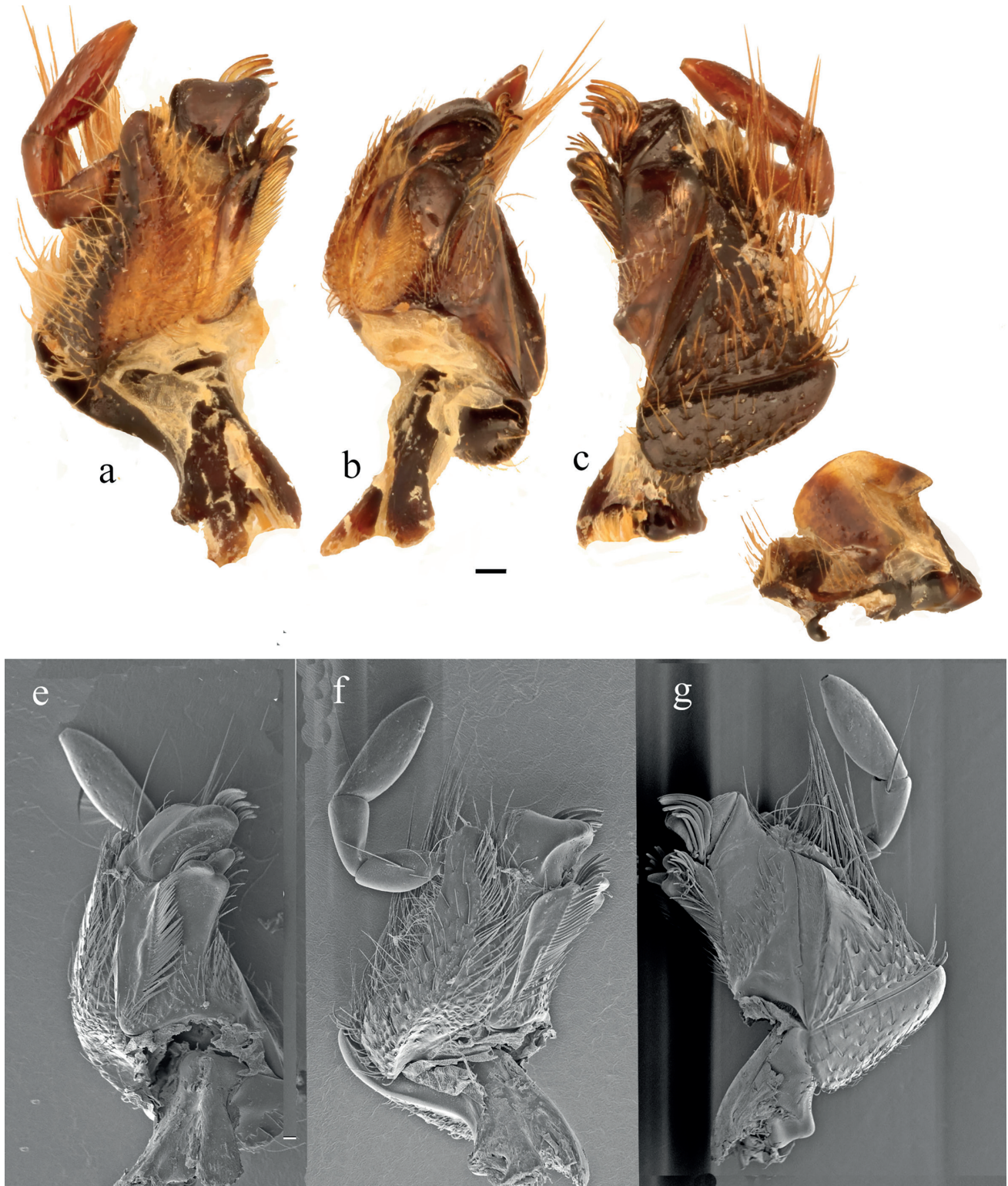


Fig. 7 – *Belohina inexpectata*, mandibles a, ventral view; b, dorsal view; c, molar lobe; d, SEM of dorsal view. Scale bar for a, b, c: 0.3 mm.

pointed setae only apically. Antennomere nine completely enclosed by antennomere eight, densely and finely setate inside, with a fringe of short, pointed setae apically, antennomere ten with a V-shaped sensory area covered by dense and fine setae, remaining surface fringed by short, pointed setae.

Pronotum. Convex, subtrapezoidal, wider than long (W/L ratio = 1.7-1.8), basally almost as wide as elytra, insertion of head marked by a short membrane, fore margin feebly bisinuate; fore angles slightly but distinctly protruding forward, triangular; fore edge continuously finely mar-



**Fig. 8** – *Belohina inexpectata* a, b, c, three views of maxilla and a mandible to scale; e, f, g SEM for maxilla. Scale bar for a, b, c: 0.1 mm.

gined, edges of sides and base distinctly margined (dorsal view); lateral margins finely serrated, fringed with long fine setae, base at middle slightly protruding backwards; pronotal surface regularly convex, covered by uniform dense punctation. Punctures deep and irregularly circular; distance between punctures equal to up to twice their diameter.

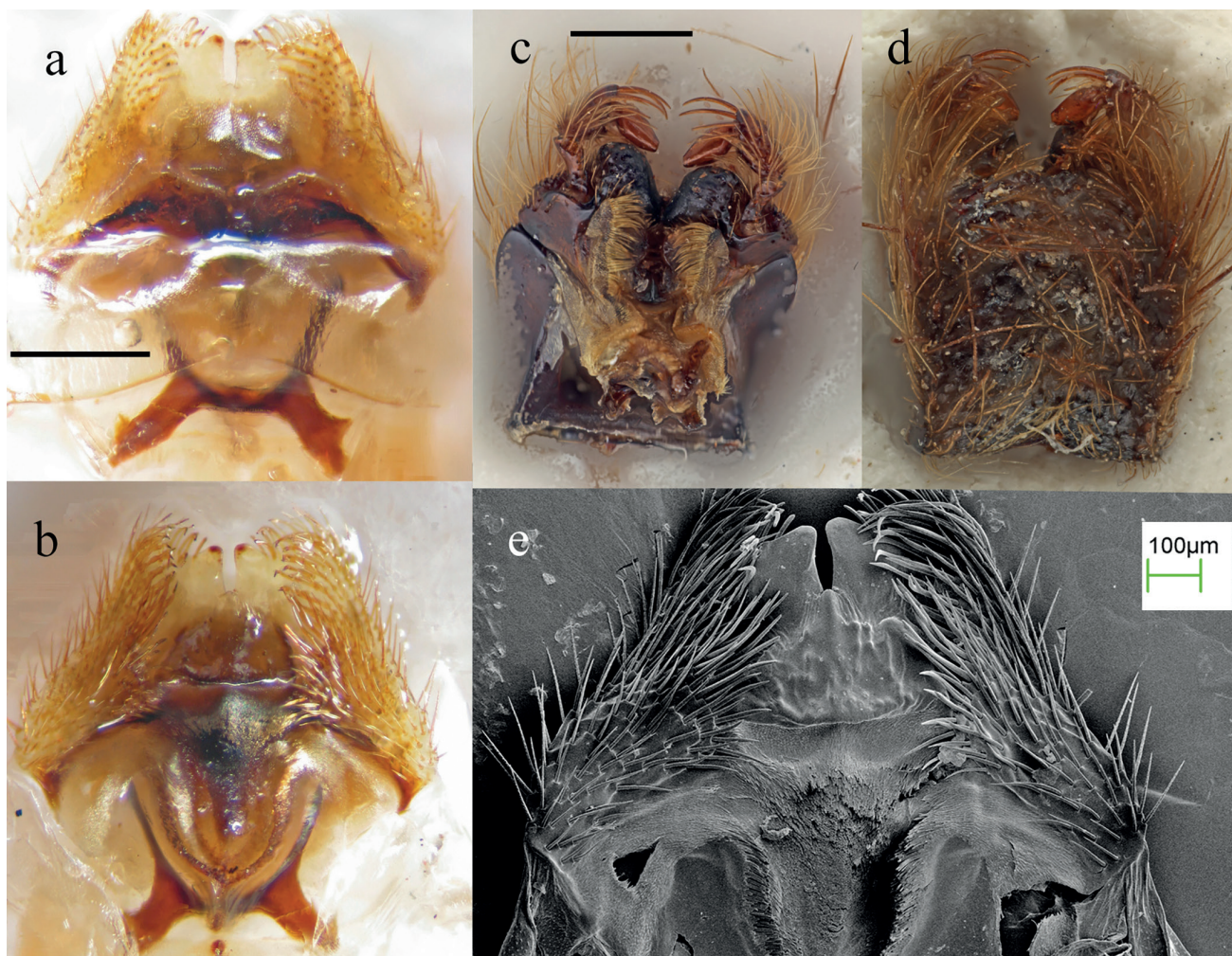
Scutellum. Small and very short, distinctly wider than long (W/L ratio = 3), sides regularly curved outwards. Surface smooth.

Elytra. Slightly wider than long (W/L ratio = 1.1), regularly convex, apical fourth regularly rounded (dorsal view); elytral suture not raised; humeral callus absent; elytral margins finely serrate and fringed with long fine setae directed outwards. Elytral surface glabrous, apart from few sparse short fine setae on apical third, densely punctured, six longitudinal shallow striae of punctures hardly visible, interstriae with punctures deep and irregularly circular, their bottom finely reticulated, rasplike only on apical third, surface between punctures smooth, punctures spaced out about their diameter to up to three times their

diameter. Epipleura downflexed at a right angle, wide, smooth along outer margin, densely punctured/wrinkled and with setae along inner margin.

Hind Wings. Flightless (apterous).

Sternum fringed with sparse setation, setae long and fine, surface with sparse raspose punctures and irregular short wrinkles. Prosternum (Figs 6 c-d) with propleura wide, covered by raspose punctures. Procoxal cavities transverse, closed by narrow postcoxal bridges, postcoxal bridges joined to sternellum, proepimeron narrowly joined to sternellum. Sternellum triangular, protruding downwards. Prosternal apophyses short, vertically oriented, not reaching the dorsal wall of prothorax (Fig. 6 d). Procoxae transversely oriented, apices nearly touching each other, fore trochanters relatively wide, with fore tips bearing a tuft of long setae; profemora slender, fore margin rectilinear, surface almost smooth with two longitudinal rows of erect long fine setae, surface of the profemora opposing the procoxae with an extensive patch of dense setae; protibiae slightly curved inwards (Fig. 11 d), with



**Fig. 9** – *Belohina inexpectata* a, b, epipharynx (dorsal and ventral), c, d, labium (ventral and dorsal); e, again ventral view of epipharynx. Scale bar for a, b: 0.5 mm, for c, d: 0.5 mm.

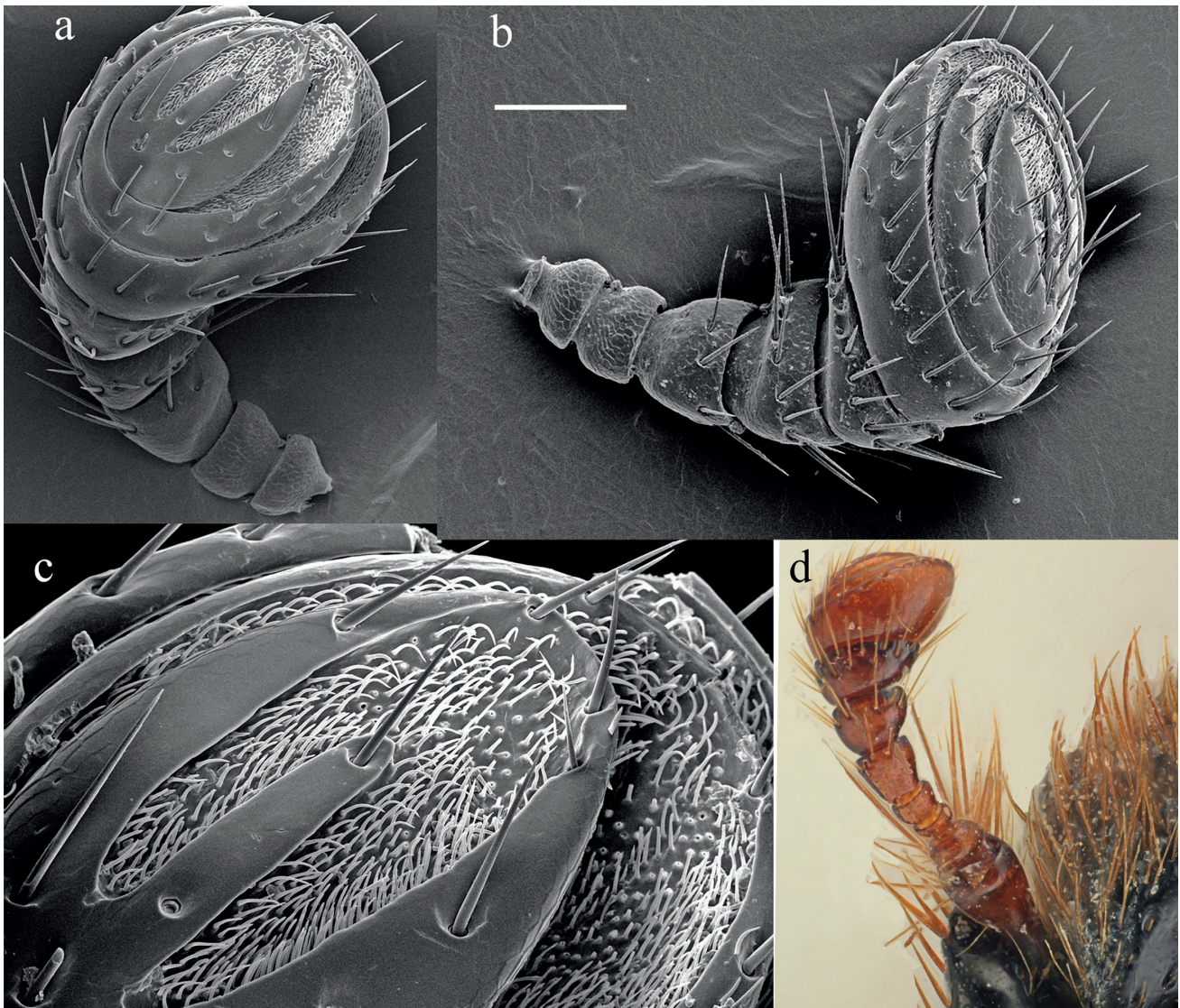


Fig. 10 – *Belohina inexpectata* a, b, c SEM of last antennomere showing the V-shaped sensory area (scale bar for b and c: 0.1 mm); d, antenna.

four outer teeth, the first one short and small, the remaining three large and long, ventral side smooth, with a short longitudinal row of erect setae basally and a transverse carina on the ventral side of the third outer tooth; apical spur sharp, distally curved downward, about as long as the first three tarsomeres together; protarsi with first article shorter than the second, tarsomeres 2, 3 and 4 short, slightly longer than wide, each one bearing two setae, tarsomere 5 ending with two sharp and curved claws.

Mesosternum wide (Figs 6 a-b), short and plump, deeply and densely punctate, mesocoxae large, almost adjacent to each other, transversely oriented; trochanters narrow, with hind tip acute, mesofemora slender, surface smooth and shiny, with hind edge slightly emarginated at distal third, ventral side with two transversal rows of long recumbent fine setae; mesotibiae short, with one transversal outer carina, apically bearing two spurs, the inner one being about one third longer than the outer one, apex of tibia

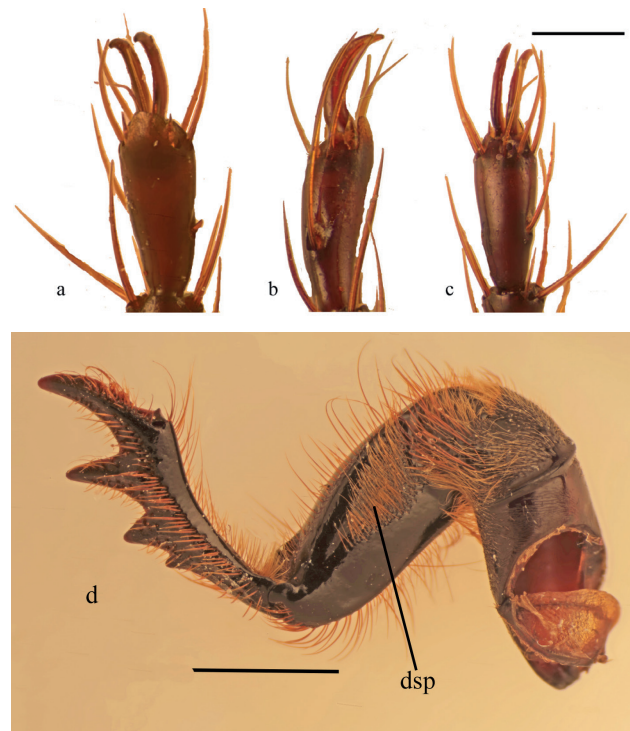
fringed by a row of dense short setae; mesotarsi slightly longer than apical edge of tibia, with first article about as long as articles two, three and four together, which are plump and subequal in length, fifth slightly longer than the preceding one, bearing two small curved claws (Fig. 11 a-c); each tarsomere, except the last one, bearing some long thick setae directed forwards.

Metasternum (Fig. 6 a) short with sparser punctation compared to mesosternum and almost smooth in the middle; trochanters of metafemora narrow (but larger than mesotrochanters), with outer edge strongly serrate and hind tip acute; metafemora plumper than mesofemora, surface smooth and shiny with hind edge slightly emarginated at distal third, ventral side with two transversal rows of long recumbent fine setae, metatibiae short, with one transversal outer carina, apically bearing two spurs, the inner one being about one third longer than the outer one, apex of tibia fringed by a row of dense short setae,

metatarsi slightly longer than apical edge of tibia, with first article about as long as articles two, three and four together, which are plump and subequal in length, fifth slightly longer than the preceding one, bearing two small curved claws; each tarsomere, except the last one, bearing some long thick setae directed forwards.

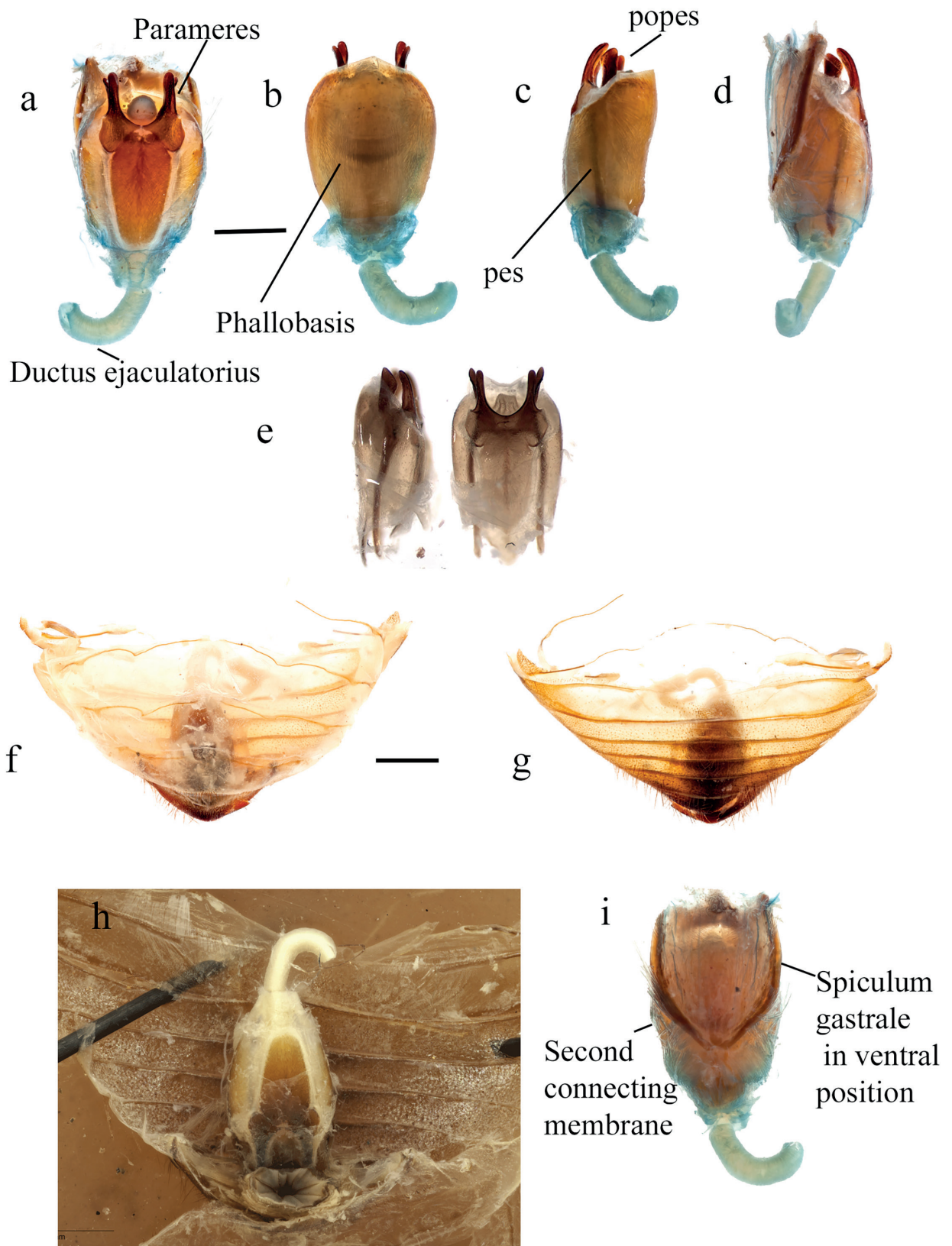
Abdomen (Figs 12 f-g, 13 a-d). with five complete, visible sternites covered by short fine semi-erect setae, pygidium slightly wrinkled, covered by dense long fine semi-erect setae, apically mixed with a few thicker long semi-erect setae. Abdominal spiracle elliptical, with strong, smooth peritreme without extension; filter apparatus consisting of two lips, probably fused in the middle, with clear suture but without visible slit (possible preparation artefact). Lips of the operculum consisting of dense arrangement of dendritic subunits, with spikes on the surface; these subunits leave spaces between them, although the large slits visible might be a preparation artefact. Sexual dimorphism: not recognizable.

Male genitalia: Figs 12 a-i. Aedeagus (Figs 12 a-e) short and compact, sitting longitudinally in midline of abdomen in a regular dorsoventral position (Figs 12 f-h). Urite IX largely membranous (second connecting membrane, Fig. 12 i) with sclerites reduced to a paired spiculum gastrale in ventral position (Fig. 12 i), unfused at the tip. It is the only sclerotization of the pouch in which the aedeagus sits. Third connecting membrane laterally connected to spiculum gastrale. No muscles connect pouch to membranous tergites or rectum. At apical tip of spiculum gastrale *Musculus urosternoantecosta-spicularis* [M(G)] and a single *M. urotergoapodemo-spicularis* [M(C) or M(D)] insert, and *M. spiculo-rectalis* [M(H)] originates. At the cranial tip of the spiculum gastrale sits a muscle which was torn on the other end, but it was probably connected to the last sternum, possibly representing a second M(G), whereas *Melolontha* has two urotergoapodemo-spicularis muscles and only one muscle connecting sternum and spiculum (Krell 1996). Also, at this cranial tip of the spiculum, but inside, below the second connecting membrane, we find a *M. spiculo-phallicus* [M (B) or M(C)]. Dorsal part of aedeagus covered by membrane (third and second connecting membranes), which is very thin at the basal half and getting thicker towards the apical/caudal end, particularly where it is folded in the cavity between the parameres. No connection of thin median part of this membrane to aedeagus detectable, but membrane was fragile and ruptured in this area. Phallobasis broad and almost as long as whole aedeagus, with second connecting membrane inserting close to cranial basis, forming a very short phallobasal apodeme, if at all. Phallobasis forming ventral and lateral part of tegmen, leaving a dorsal gap. Since the phallobasis is not fused anywhere dorsally, it does not form a tube as in many other groups within the Scarabaeoidea but only a shell surrounding the ventral three quarters of the aedeagus. Parameres dorsoventrally flattened and positioned on dorsal side of aedeagus,

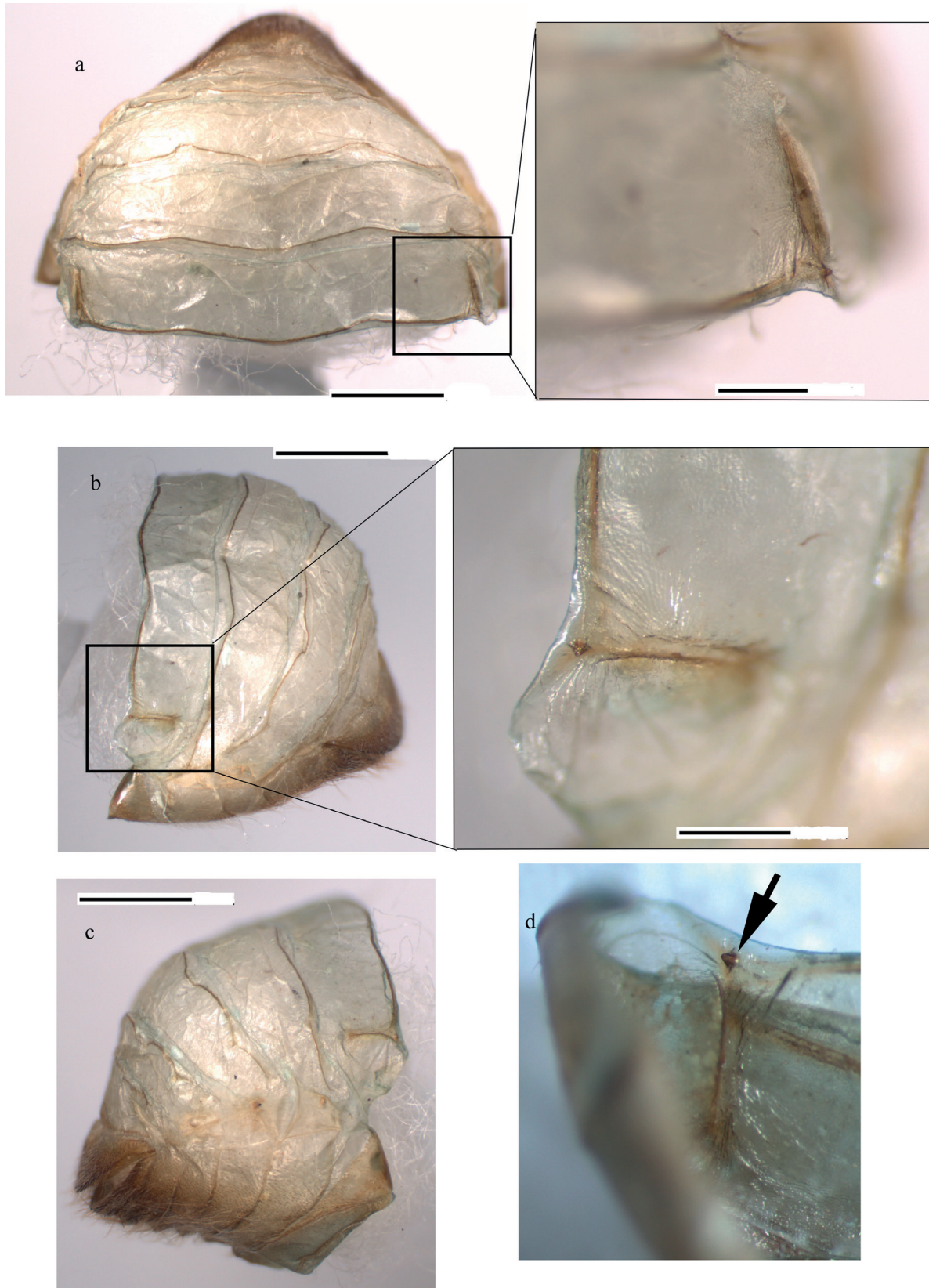


**Fig. 11** – *Belohina inexpectata* **a, b, c**, last tarsomere of mesotarsi; **d**, patch of dense setae (dsp) on the surface of the profemora opposing the procoxae. Scale bar for a, b, c: 0.05 mm. Scale bar for d: 2 mm.

originating from and fused to a median, longitudinal, flat sclerite that covers the dorsal opening of the phallobasis (Fig. 12 a). This sclerite has a longitudinal furrow. Ventral to this flat sclerite and parameres, a paired proximal endophallic sclerite (Fig. 12 c) extending from basis of aedeagus almost as far as parameres, parallel to the latter, forming parameroids (paramere-like structures that are not homologous with parameres) (Fig. 12 c). The parameres seem to articulate with the parameroids, each extending a lobe ventrally towards the respective parameroid. A broad paired muscle extends from the flat sclerite to the endophallic sclerite which has no equivalent in *Melolontha*. A strong paired *M. phallobasodpodemo-endophallicus* (M(P) or M(Q)) extending from cranial border and another one (*M. phallobaso-endophallicus*) from caudal border of phallobasis to ventrolateral area of endophallus. Endophallus slightly protruding between parameres and parameroids. Sclerotized median lobe absent. First connecting membrane originating at apical margin of phallobasis, wrapping around endophallus and inserting at proximal part of parameroids. From proximal end of parameroid, a muscle runs apically to insert in medioventral area of first connecting membrane. It could be homologous to the ring muscle, *M. endophalloapodemalis*, in *Melolontha*, but a proper ring muscle is lacking in *Belohina*. From the insertion of this muscle, a strong muscle runs to the proximal margin of the phallobasis (*M. phallobasoapodemo-endophallicus ventralis* [M(P)]). From the proximal tip of the



**Fig. 12** – *Belohina inexpectata* male genitalia, **a, b, c, d**, aedeagus (pes = proximal endophallic sclerite; popes = parameroid of proximal endophallic sclerite); **e**, aedeagus of paratype after clearing; **f**, abdomen dorsal; **g**, abdomen ventral; aedeagus in resting position; **i**, spiculum gastrale. Scale bar for **a, b, c, d, i**: 0.7 Scale bar for **f, g**: 2 mm.



**Fig. 13** – *Belohina inexpectata* **a**, abdomen, with insert showing the small, sclerotized tubercle of abdominal tergite 3; **b**, abdomen with detail showing the small, sclerotized tubercle of abdominal tergite 3; **c**, abdomen, lateral view; **d**, detail of the small, sclerotized tubercle of abdominal tergite 3. Scale bar for a, b, c: 2 mm. Scale bar for inserts of a and b: 0.5 mm.

parameroids, a strong muscle runs to the caudolateral part of the endophallus (M. endophalloapodemo-endophalliscus [M(T)]). Ventral preapical side of retracted endophallus (between basal thin part and apex, in resting position) slightly sclerotized and yellow. This could be homologous with the apical endophallic sclerite. Further sclerotized structures lacking in endophallus.

Female genitalia. Bursal sclerites absent; spermatheca small, poorly sclerotized, short-narrow-U-shaped; ovary large, fusiform; vaginal palpi small, elongate and narrow, distally setose, styli absent.

Variability. The whole series from Antreaky forest (i.e., the complete specimens) showed almost no variability, being very homogeneous in size, colour, shape, sculpturing, and setation. Fragments found near the ant nests at the type locality showed strong wear (dulling, loss of setae, de-colouration), although very probably these changes occurred after death.

### Remarks on morphology

Overall, the morphology of *Belohina* is typical of beetles living in arid environments: a compact body with hard exoskeleton providing protection from desiccation, apterous with fused elytra and expanded epipleura, hairy sternum, head and tibiae shaped for burrowing. Fused elytra can be seen as an adaptation to arid conditions, since the spiracles open beneath the sealed elytra into the subelytral cavity, which becomes saturated with exhaled air, therefore respiration occurs in a chamber of high humidity (as observed in Trogidae by Struempfer & Scholtz 2011; however, see also Draney 1993 and Roig-Juñent et al. 2020, for other hypotheses on the function of the subelytral cavity in other Coleoptera). The setation of the ventral body and legs could play a role in minimizing the friction with the ground while digging as hypothesized in burrowing Carabidae by Roig-Juñent et al. (2020; but see also Medvedev 1965). The extensive patch of dense setae on the surface of the profemora opposing the procoxae (Fig. 11 d) could play a role in keeping the surfaces clean during burrowing activities, as Houston (1986) hypothesized while studying Scarabaeinae. There are also tufts of setae on the proximal portion of trochanters, which could be associated with glands for producing pheromones, as hypothesized by Houston (1986) in the genus *Onitis* (Scarabaeidae). Further modifications are related to flightlessness: fused elytra, lack of humeral callus and short mesosternum (Scholtz 2000). The unusual shape of the clypeus is also related to digging capabilities (similar to Scarabaeini), and one individual was observed by JER digging in loose ground using its head. The most unusual morphological traits of *Belohina* are however its mouthparts, antennae and male genitalia.

Adults feed as shown by the gut of all four dissected specimens having been full of a brownish/blackish sub-

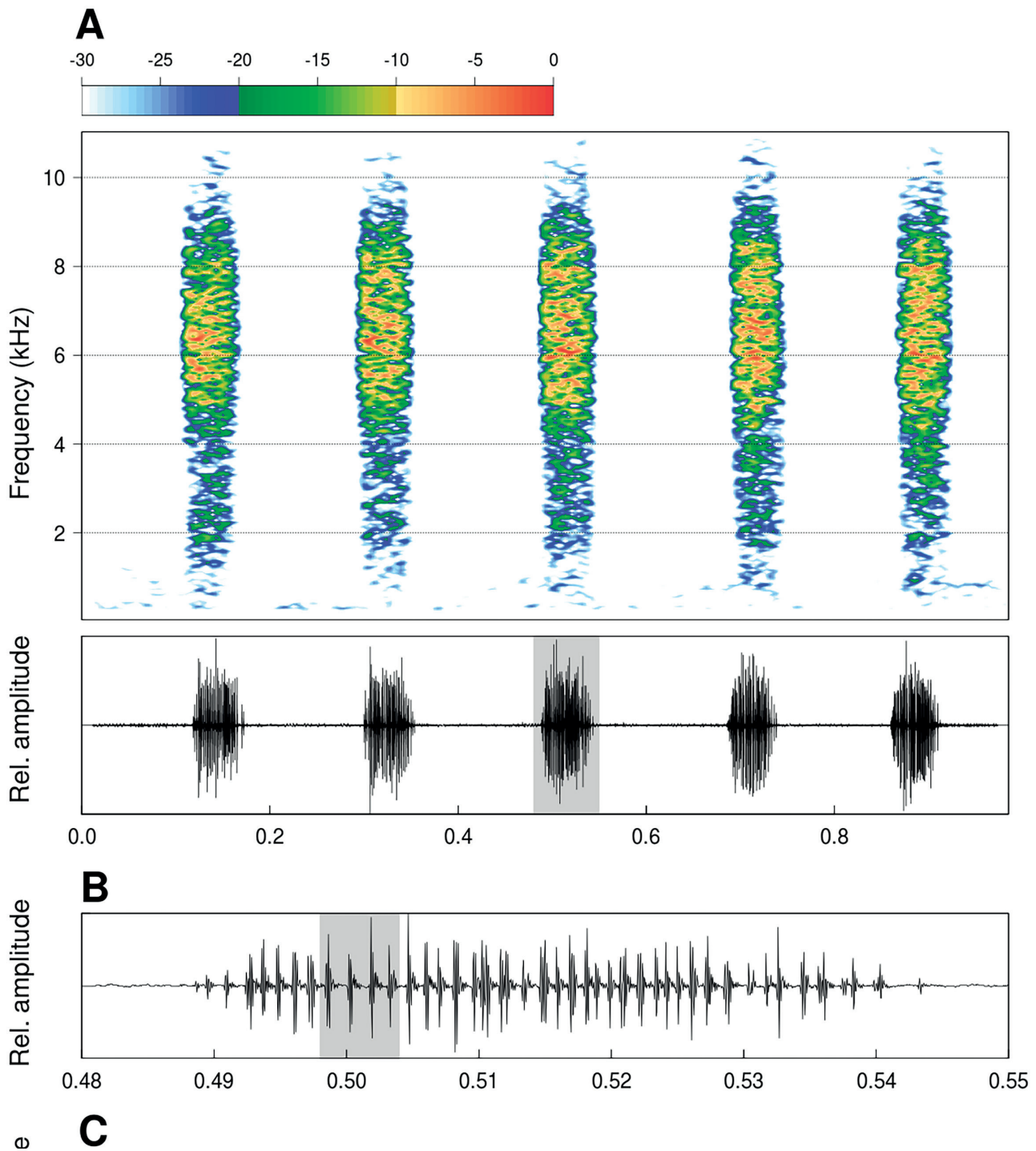
stance. It is therefore hypothesized that *Belohina* has functional mouthparts, although shaped in a unique way with mandibles being small (less than half the size of maxillae), less sclerotized than maxillae and recessed, so that only the maxillae are visible externally. Perhaps the mandibles are not functional, although their inner surface covered by hairs suggests that they could still play some role in the sensing process. Maxillae in turn are large, their galea is tooth-like (galeal hook). It could be hypothesized that the maxillae of *Belohina* replace the mandibles in their biting function. Holter & Scholtz (2011) suggested that the galeal hook found in some species of *Pachysoma* (Scarabaeidae Scarabaeinae) could play a role in the process of cutting large food items into smaller pieces, an indispensable process for detritus feeders. Because of the similar structure in *Belohina*, it could be hypothesized that it, too, is a detritus feeder, a common trait among many beetles living in nutrient-poor environments. Recessed mandibles not visible externally are found also in *Orubesa*, while all other plesiomorphic families of Scarabaeoidea phylogenetically close to *Belohina* have exposed mandibles. The membranous epipharynx, situated on the inner surface of clypeus, is the most remarkable character of mouthparts, since all other taxa closely related to *Belohina* (*Orubesa*, Hybosoridae, Ochodaecidae, Glaphyridae) and, more generally, all other Scarabaeoidea, except for Scarabaeidae, have a exposed sclerotized labrum. To our knowledge this is the only case within the “less derived” clades of Scarabaeoidea where there is a membranous epipharynx but no labrum. Antennae have the first article of club enclosing the remaining two, a character otherwise found in Hybosorinae (Hybosoridae) and few other scarabs (such as *Parascatonomus* in Scarabaeidae: Onthophagini). The outer surface of the last article of club is covered by an extensive, V-shaped, sensory area, unique within Scarabaeoidea, although recently an elliptical groove on the last antennal lamella, similar but not identical to the one here discussed, has been reported in *Ceratotrupes bolivari* Halfpter & Martínez, 1962 (Geotrupidae) by Arriaga-Jiménez et al. (2023). Sensilla are trichoid (Pacheco et al. 2022) as in the majority of other Laparosticti.

Male genitalia recall the unusual morphology found in the genus *Pleocomia* (Pleocomidae) with a capsule-like aedeagus. The short and compact shape of the aedeagus allows a regular, unrotated position at rest, whereas longer and curved aedeagi often are turned on their side at rest, the so-called *déverisement* (Jeannel 1955), which we find in *Melolontha* and other scarab taxa, namely Geotrupidae, Ochodaecidae, Scarabaeinae, Rutelinae and Dynastinae (Krell 1996).

The most conspicuous characteristic of the *Belohina* aedeagus is a second pair of sclerites ventral of the parameres. We call these structures parameroids, but they are extensions of a paired endophallic sclerite. This is the only case of endophallic sclerites extruding out of the phallobasis and protruding parallel and ventral to the parameres,

with which they articulate at their basis. Because of its topographical position within the phallobasis, this protruding paired endophallic sclerite is likely to be homologous with the proximal endophallic sclerite in *Melolontha* (Krell 1996) and with at least the majority of sclerites called “te-

mones” by d’Hotman & Scholtz (1990, 1991). Since the latter authors examined only sclerites, but not their position and integration within the soft parts of the genitalia, it is difficult to interpret the homology of those “temones” (Krell 1996) and the similarly shaped sclerites that they



**Fig. 14** – Sound production by *Belohina inexpectata*. **A**, Oscillogram (relative amplitude vs time) and spectrogram (time vs frequency vs relative amplitude) of five echemes. The spectrogram was based on a short-time Fourier transform with a sliding Hanning window (512 samples, 85% of overlap) and 30 dB dynamic range. A 200 Hz high-pass filter was applied before analysis. **B**, Detail (grey region of **A**) of a single echeme showing successive pulses. **C**, Detail (grey region of **B**) of four successive pulses showing elementary oscillations.

call “ventral and dorsal phallobasis apophyses” and “dorsal and ventral paramere extensions” in various groups of Scarabaeoidea.

Another unique character is the flat sclerite that covers the dorsal opening of the phallobasis. It could be homologous to the paired dorsal paramere extensions of d’Hotman & Scholtz (1991) as found in, e.g., Aulonocnemidae where they also are fused and cover a part of the opening of the phallobasis (d’Hotman & Scholtz 1991: 14). Being dorsally open, the phallobasis of *Belohina* appears to be upside down whereas in most Scarabaeoidea the phallobasis is open ventrally. In *Melolontha* where the phallobasis is open ventrally, indications for a *retournement* (sensu Jeannel 1955), i.e., a 180° longitudinal rotation of the aedeagus, were found (Krell 1996). This rotation is common in many other taxa of Scarabaeoidea (d’Hotman & Scholtz 1990). The aedeagus of *Belohina* might not have undergone such rotation, presenting this opening on the dorsal side. With neither *déversement* nor *retournement* realized in the aedeagus of *Belohina*, we expect a simpler muscular system. A regularly resting aedeagus without structural rotation needs only to move in one direction to function: outwards. Indeed, we found a less complex muscular system in *Belohina* compared to *Melolontha*, but much more comprehensive knowledge about the myology of scarabaeoid genitalia is necessary to draw robust conclusions.

## Distribution and Habitat

*Belohina inexpectata* occurs in the extreme south of Madagascar (Fig. 16), being known from only two localities, both in the Beloha Androy District: the type locality (road Tsiombe-Beloha, about 25 km from Beloha) (Fig. 4 a, b) and the dry forest of Antreaky (Fig. 4 c), just a few kilometres from the type locality. Both localities fall within the “Southwestern dry spiny forest-thicket” vegetation type (sensu Moat & Smith 2007), an arid environment dominated by xeric vegetation (characterized by the dominance of Euphorbiaceae, Didieraceae, the baobab *Adansonia za* and other xerophytes). Soil is limestone-derived and sandstone-derived, leading to a continuous succession of stretches of white and red soil along the road between Beloha and Tsihombe. The type locality had red soil.

## Life history

Very little is known about the life history of *Belohina inexpectata*. The type series has been found in March (which corresponds to the rainy season in the area) after strong rains. When Alberto Ballerio and Jasmin E. Randrianirina visited the type locality on 10 December 2007, the day was sunny, although some days before a little rain had fallen.

The environment was very dry and hot, the soil very hard, probably impossible to be penetrated by a small beetle. While they inspected various microhabitats (under stones, under dead logs, under dead leaves and other debris, cow dung, a termite nest of an unidentified species), no live specimens of *Belohina* were detected, although one dead complete specimen was found under a dead log of a tree. Because of its near perfect condition, the beetle probably had died shortly before. Several fragments of *Belohina* (mostly elytra and prothorax) were found around the entrance hole of nests (Fig. 4 b) of the ant *Aphaenogaster swammerdami* Forel, 1886 (Formicidae Myrmicinae), a large and common ant, which feeds on arthropods and seeds and lives in large underground nests that have one large entrance hole (Böhning-Gaese et al. 1999). Fragments of many other beetles were found around the nests (mainly Tenebrionidae, Carabidae and Scarabaeidae). It is therefore

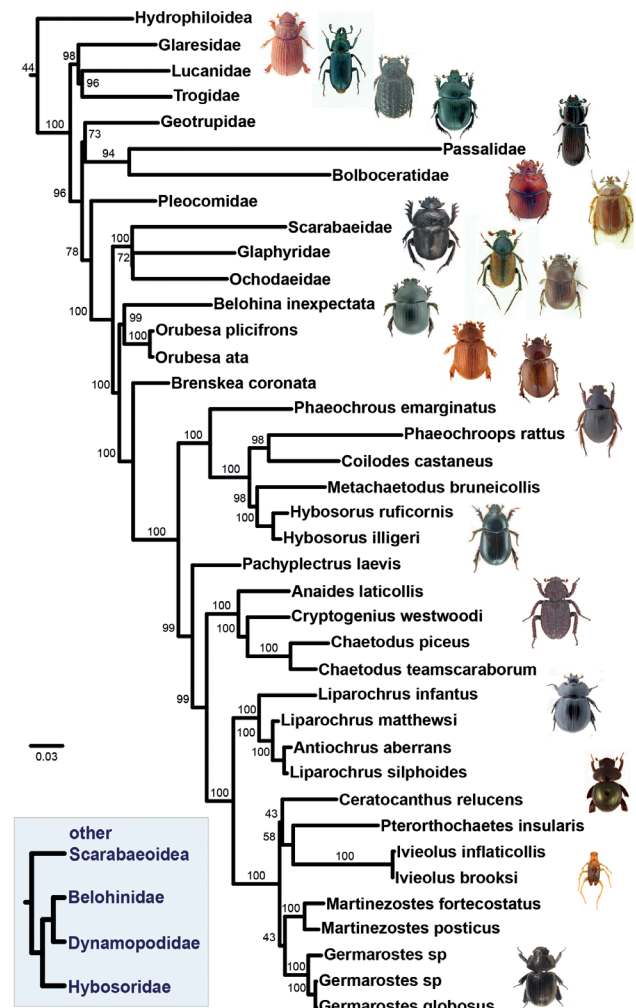
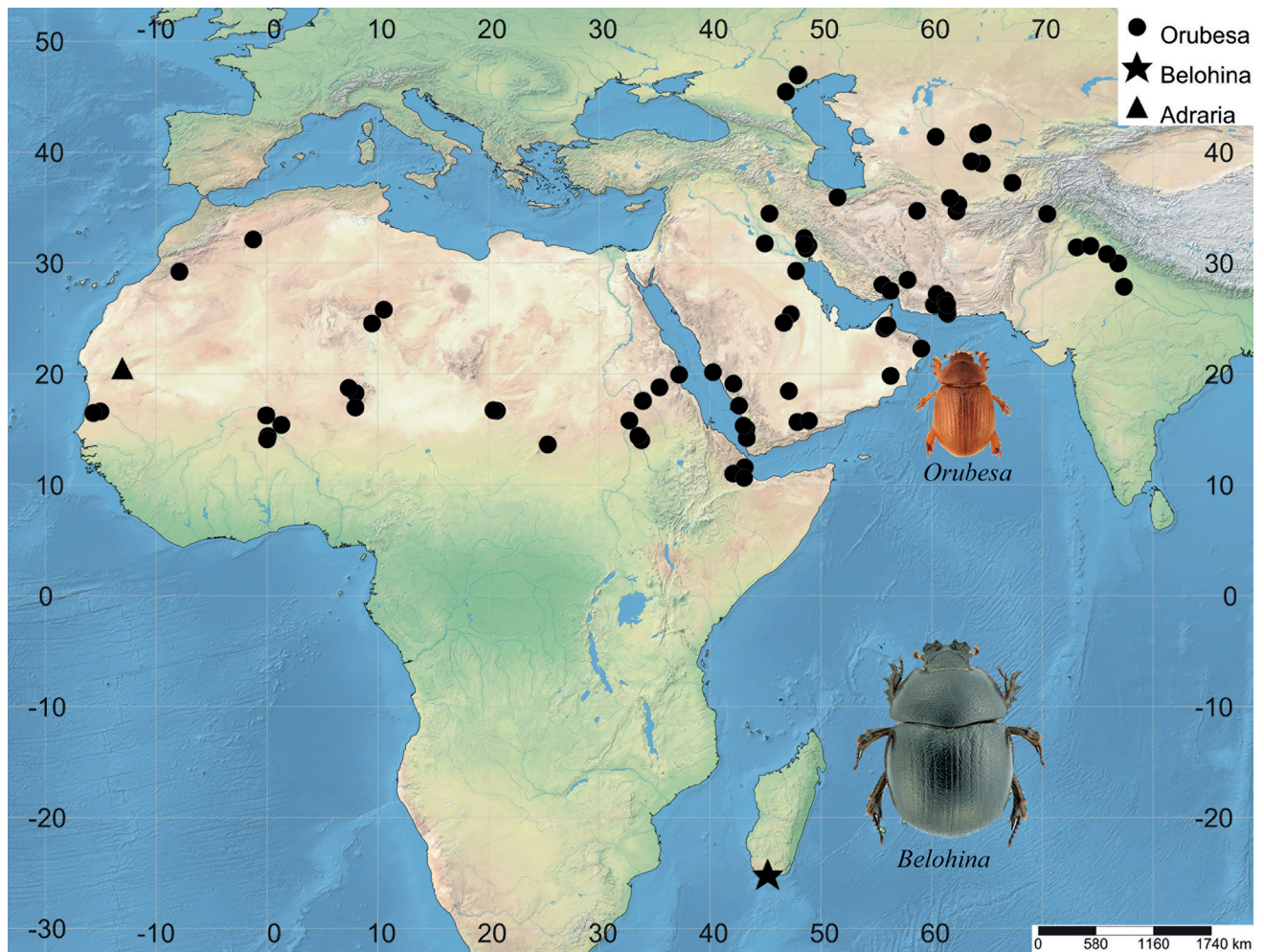


Fig. 15 – Maximum likelihood phylogeny of Scarabaeoidea, with a 39-taxon tree of the clade of Belohinidae, Dynamopodidae, and Hybosoridae, and the related families represented as single tips. Ultrafast bootstrap values show branch support. The inset tree on left displays the summary of the family-level relationships of interest for *Belohina*.



**Fig. 16** – Distribution map of *Belohina*, Belohinidae (star), its sister taxon *Orubesa*, Dynamopodidae (circles), and a potential second Dynamopodidae genus, *Adraria* (triangle). Sources for *Orubesa* occurrences: GBIF (1 record), Balthasar (1968), Barari (2001), Chavanon (2018), Gosh et al. (2020), Kocher (1958), Král et al. (2023), Krell (2021), Paulian (1954), Petrovitz (1958), Reitter (1895), Semenow (1895), Semenov-Tian-Shanskij & Medvedev (1929), Shokhin (2007), Zavattari (1934), A. Ballerio, unpublished, P. Moretto, pers. comm.; M. J. Paulsen, unpublished, D. Potanin, pers. comm., P. Tausin pers. comm. *Adraria* is known only from the *locus typicus* (Villiers 1956).

possible that the ants predate or scavenge on *Belohina*, whose remains are later removed from the nest. Jasmin E. Randrianirina visited the site again in 2008. A first visit during February 2008 did not yield any live specimen. The second visit to the type locality (March 2008, after heavy rain) also was unproductive, but the inspection of a nearby locality (the Antreaky forest) yielded the six live specimens here studied. Pitfall trapping, partly baited with dung, was unsuccessful. All collected specimens (e.g., Fig. 4 d) were found by random digging (about 30–50 cm deep) in areas covered by dense low vegetation. Dissection of those individuals revealed the presence of a blackish substance in their gut, indicating that adult beetles feed. It could be hypothesized that this species needs rain for allowing adults to dig through the soil crust, which otherwise is too hard to be penetrated. This would be like other Scarabaeoidea living in arid environments, such as the Mediterranean *Elaphocera* (Scarabaeidae: Melolonthinae: Tanyproctini)

(Fancelli et al. 2014), or largely subterranean species in a seasonal environment with a dry period, such as the western North American *Pleocomma* (Pleocomidae) (Hovore 2002; Elliott et al. 2017). They would, therefore, be active on the ground only during rainy days when the soil near the surface is softer, and spend the rest of their lives underground, where they find shelter, moisture and possibly also their nourishment (perhaps detritus, see above the discussion on mouthparts morphology).

### Stridulation

Live individuals stridulated (Fig. 14). The stridulation consisted of the regular and fast repetition of a single echeme. This echeme lasted  $0.050 \pm 0.004$  s (0.039–0.059,  $n = 115$ ) and was separated by intervals of  $0.216 \pm 0.091$  s (0.112–0.648,  $n = 113$ ). Each echeme was made

by the succession of pulses. There were 39 pulses  $\pm$  4 (29–46,  $n=115$ ) per echeme. These pulses lasted  $0.73 \pm 0.12$  ms (0.39–1.17,  $n = 451$ ) and were separated by intervals of  $0.63 \pm 0.25$  ms (0.04–1.48,  $n = 340$ ). Among the 460 pulses measured, 9 (1.96%) were groups of 2–3 collapsed pulses. Pulses were made of elementary oscillations with an instantaneous frequency of about 6 kHz. In the frequency spectral domain, the spectra were characterized by a single dominant frequency peak at  $5.896 \pm 0.495$  kHz (4.823–7.149,  $n = 115$ ) and a large bandwidth with 50% of the energy between  $4.559 \pm 0.270$  kHz (3.445–50.820,  $n = 115$ ) and  $7.212 \pm 0.244$  kHz (6.546–8.226,  $n = 115$ ). The spectrum might reach higher frequencies, but this could not be estimated due to low sampling rate. There was no obvious harmonic structure.

Disturbed beetles produced rather loud sounds apparently with a defensive function having a repellent effect on potential predators. Sound production is common in the Scarabaeoidea and a few different types of the stridulation mechanisms evolved, apparently independently, in different scarab beetle lineages. Examination of the adult morphology of *Belohina* did not reveal any stridulatory structures that were known in other scarab groups. Specifically, there were no structures found similar to the coxal pars stridens (stridulatory fields) of Geotrupidae, Orphninae or Allidiostomatinae. Jasmin E. Randrianirina who observed live beetles had impression that the creaks emitted by the beetles were synchronized with the head movements. *Belohina* has large propleural cavities receiving the basal part of the head. The surface of the cavities is granulated. The head has acute, keel shaped margins behind the eyes. It is possible that the creaks are produced by scrapping the keels over the granulate surface of the propleura by moving the head up down or side-to-side. A head-prothoracic stridulation mechanism is not known in scarab beetles (Arrow 1904). It was recorded for Endomychidae and Hispididae although its morphology is different (Arrow 1942; Wessel 2006 and references herein). Other structures with unclear function were found on the abdomen and elytra of *Belohina*. Abdominal tergite 3 (Fig. 13) has a small, sclerotized tubercle on each side near the basal margin and a longitudinal sclerotized ridge originating at this tubercle and extending over 2/3 of the tergite. On the inner side of each elytron, apparently opposite to this abdominal tubercle in situ, there is a round field with the color and sculpture different from the adjacent surface. In this field, the inner layer of the elytron is more strongly sclerotized and has somewhat shagreen sculpture as opposed to being smooth and shiny in the other regions. The position and the shape of these structures resembles stridulatory apparatuses found in some scarab beetle groups (Dynastinae, Ochodaeidae), although these groups have coarser structures located more caudally (the plectrum on pygidium or propygidium and the stridulatory file on the apices of elytra). It seems unlikely that the

structures found in *Belohina* can be used for producing human perceivable sounds, but they may play a role in the communication between undisturbed beetles for example during the courtship. Additional experiments with undisturbed beetles might shed some light on the function of these organs.

## Phylogenetic position

Since the odd morphology of this beetle does not reveal obvious similarities to other extant Scarabaeoidea, its systematic position has remained uncertain. When describing this taxon, Paulian (1958) considered it as a subfamily of Scarabaeidae, close to Aphodiinae and having a strong convergence with Taurocerastinae. It must be considered that at the time most taxa that later were elevated to family level were lumped into an all-embracing family Scarabaeidae. Afterwards, following the trend to elevate all the subfamilies of Scarabaeidae to family level, Paulian (1979) elevated the taxon to family level, while stressing the primitive morphology of it. No changes have been made since (e.g., Lawrence & Newton 1982; 1995; Lawrence et al. 1999; Scholtz & Grebennikov 2005) apart from Nikolajev (2007), who proposed including the taxon within Hybosoridae as a subfamily (Belohininae) on the basis of antennal club morphology (i.e., the first article of antennal club enclosing the remaining two, a typical character of many Hybosoridae). The availability of fresh material suitable for DNA analysis has allowed us to insert the *Belohina* DNA in the framework of the molecular phylogeny of Scarabaeoidea which is being developed by Hawks et al. A phylogeny of 39 tips (Fig. 15) has been pruned from the full 1006-taxon maximum likelihood tree with a higher-level topology of (Dascilloidea, (Nosodendroidea, (Hydrophiloidea, Scarabaeoidea))) (Hawks et al. in prep). Each scarabaeoid family is represented as one terminal branch. *Belohina inexpectata* and its closest relatives are shown in full. *Belohina* is most closely related to *Orubesa* (Dynamopodidae), which is represented by two species (99% branch support for the clade). Since Dynamopodidae are sister to Belohinidae, both should have the same taxonomic rank and be considered families. Dynamopodidae currently contain the genera *Orubesa* (formerly *Dynamopus* Semenow) and the monotypic *Adraria* Villiers from Mauretania. They are distributed in arid regions from Senegal and Morocco to Sudan and Djibouti, the Arab Peninsula, to southern Russia, Uzbekistan, and northern India (Punjab, Uttar Pradesh) (Fig. 16). The systematic position of *Adraria*, which was described after two specimens in bad condition (Villiers 1956) and has never been found again, needs revision. Together, these are sister group to the family Hybosoridae, represented by 25 species in 17 genera. The monophyletic grouping of Belohinidae, Dynamopodidae, and Hybosoridae has 100% branch support in this analysis.

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