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Explosive radiation versus old relicts: The complex history of Ethiopian Trechina, with description of a new genus and a new subgenus (Coleoptera, Carabidae, Trechini)

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Abstract

The trechine beetle fauna (Coleoptera, Carabidae) of the Ethiopian Highlands is known to be highly diverse in species, and many species groups were recognized to be characterized by unusual character states of external and genital morphology. Earlier authors described several genera and subgenera of Ethiopian Trechina endemic to certain high mountains of the country. However, the relationships of these species groups and their evolutionary history are unknown so far. Here, we present the first molecular phylogenetic analysis of Ethiopian Trechina, detect several synonymic names under *Trechus* sensu lato, and introduce two new species groups to the country's fauna: the monotypic genus *Baehria* Schmidt & Faille, **gen. nov.**, with the type species *B. separata* **sp. nov.** from Mt. Choke in northern Ethiopia, and the *Trechus* subgenus *Abunetrechus* Schmidt & Faille, **subgen. nov.**, with the type species *T. bipartitus* Raffray, 1885; this subgenus includes three species of northern Ethiopia. We show that the composition of the Ethiopian fauna is based on multiple events of immigration, which started simultaneously with or some million years after the Oligocene-Early Miocene orogenic events north and south of the Rift Valley. Our results support the habitat island hypothesis for the evolution of the Ethiopian highland fauna. We found no evidence for an alternative hypothesis assuming a close connection of the Trechina immigration to Ethiopia and Pleistocene cooling. We, thus, conclude that the geomorphological development rather than the climatic changes are the main drivers of the diversification of the high-altitude Trechina fauna in Ethiopia.

Key Words

Abunetrechus, *Baehria*, biogeography, checklist, mountains of East Africa, new species, new synonymy, phylogeny, *Trechus*

Introduction

The biogeographic and evolutionary history of the Trechini fauna of Ethiopia is complex and poorly understood. Members of two trechine subtribes are known to occur in the country. Within the subtribe Trechodina, the genus *Pachydesus* Motschulsky is a typical element of the southern African fauna, and two species were found in Ethiopia so far (Basilewsky 1974; Merene et al. 2023). Similarly, only two species of *Trechodes* Blackburn occur in Ethiopia; the genus belongs to Trechodina and is widely distributed in tropical-subtropical regions of Africa, Madagascar, Indochina, the Philippines and Australia (Casale and Laneyrie 1982; Magrini et al. 2005; Faille et al. 2021). Another Trechodina genus, *Perileptus* Schaum, has a distribution similar to *Trechodes* but also occurs in the warm temperate zone of the Palearctic region. Four species of *Perileptus* are noted for the Ethiopian fauna (Casale and Laneyrie 1982; Deuve 2004; Merene et al. 2023). Based on our field investigations in Ethiopia, species of *Pachydesus*, *Perileptus*, and *Trechodes* have their habitats along brooks and rivers at lower and medium elevations, with the highest occurrences of *Pachydesus* at altitudes up to 3200 m.

Most of the Trechini species of the Ethiopian fauna belong to the megadiverse Holarctic genus *Trechus* Clairville (in the widest sense) of the subtribe Trechina and have their occurrences restricted to afromontane and afroalpine environments (Fig. 1). Molecular phylogenetic analyses have shown that the taxon *Trechus* (sensu lato) is polyphyletic (Faille et al. 2010, 2013). However, so far, the systematic position of the Ethiopian and East African representatives has not been addressed.

In the mountains of East Africa, several *Trechus* (sensu lato) lineages occur in widely separated high-altitude habitats ("mountains islands"): 21 species are placed in the subgenera *Elgonophyes* Jeannel, *Elgonotrechus* Jeannel, and *Trechus* s. str. on Mt. Elgon, two species of the subgenus *Meruitrechus* Jeannel on Mt. Meru, and 64 species are placed in the subgenera *Abyssinotus* Quéinnec & Ollivier, *Archeotrechus* Magrini, Quéinnec & Vigna Taglianti, *Minitrechus* Vigna Taglianti & Magrini, and *Trechus* s. str.) in the Ethiopian Highlands (Jeannel 1954a; Casale and Laneyrie 1982; Geginat 1995, 2008; Pawłowski 2003; Vigna Taglianti and Magrini 2010; Ortuño and Novoa 2011; Magrini et al. 2012; Schmidt and Faille 2018; Quéinnec et al. 2021).

The eyeless Trechini species *Nunbergites aethiopicus* Pawłowski & Stachowiak, 1991, is special to the country's fauna. This species was found in the Simien Mountains (Fig. 1) and is considered closely related to *Neotrechus* J. Müller of the subtribe Trechina from the eastern Mediterranean region (Pawłowski and Stachowiak 1991).

Four additional Trechini genera and a total of 13 species were described from the mountains of northern Ethiopia just recently (Quéinnec et al. 2021): *Aethiopsis* Quéinnec & Ollivier, from Mt. Abune Yosef, and *Afrotrechus* Quéinnec & Ollivier, *Deuveopsis* Quéinnec & Ollivier, and *Nilotrechus* Quéinnec & Ollivier from Mt. Choke (Fig. 1). Based on morphological character analyses, the authors conclude that the hypothesis of phylogenetic relationships between these genera and Trechodina is debatable.

Overall, these data indicate that the Ethiopian Highlands might be considered a hotspot of Trechini diversity,

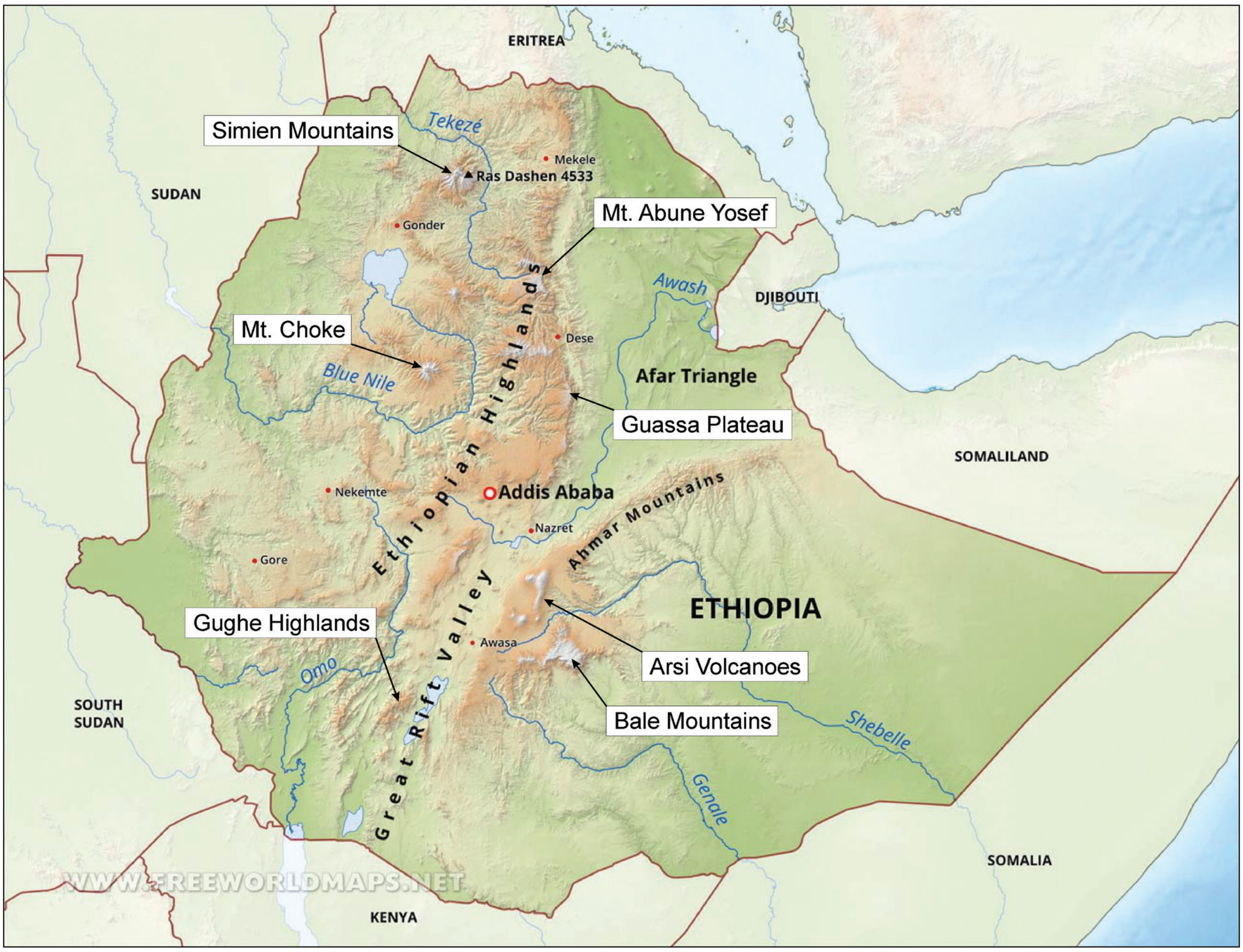


Figure 1. Map of Ethiopia showing the main topographic features of the country. Seven prominent volcanic massifs which are discussed in the text are highlighted. The base map was downloaded from www.freeworldmaps.net (01-07-2023).

not only in terms of species numbers but also lineage diversity. Remarkably, in some Trechini genera, several species seem to be highly endemic to single Ethiopian volcanos (Quéinnec et al. 2021). However, phylogenetic relationships among Ethiopian Trechini species and species groups are largely unknown, and taxonomic concepts are in flux (Ortuño and Novoa 2011; Schmidt and Faille 2018). Also, the biogeographical history and evolution of the East African high-altitude Trechini fauna are rarely known. Related questions are part of a persisting controversial debate (Jeannel 1954b; Mani 1968; Ortuño and Novoa 2011; Schmidt and Faille 2018; Quéinnec et al. 2021).

In recent years, a more intensive field investigation of the diversity, ecology and distribution of the high-altitude ground beetle fauna of Ethiopia was performed by authors of the present study. As a result, several new synonymies could be detected, and two additional, previously unrecognized trechine species groups were identified and are described in this paper. Most importantly, representatives of all Ethiopian *Trechus* (s. l.) species groups and the genera recently described by Quéinnec et al. (2021) became available for molecular analysis. Based on this material, we present the first dated phylogeny of the Ethiopian species. Using sequence fragments of two mitochondrial and two nuclear ribosomal genes, we aimed at answering the following questions: Are species groups recently described by Quéinnec et al. (2021) representatives of Trechina or Trechini? How many independent immigration events caused the Ethiopian high-altitude trechine fauna to emerge? When did immigration of Palearctic trechine taxa occur – in the course of the Late Cenozoic cooling or, alternatively, in response to the major orogenic events in East Africa, starting in the Oligocene?

Materials and methods

Materials

Specimens used for the morphological studies are listed in the respective Material sections of the relevant taxa, below. Specimens included in the molecular phylogenetic analyses are listed in Suppl. material 1. Taxonomy and identification of Ethiopian *Trechus* species and species groups follow Jeannel (1927), Pawłowski (2001, 2003), Ortuño and Novoa (2011), Schmidt and Faille (2018) and Quéinnec et al. (2021). Institutional codes used in the taxonomic treatment are as follows:

CAF	Arnaud Faille working collection, Stuttgart, Germany;
CSCHM	Joachim Schmidt working collection, later to be deposited in the Zoologische Staatssammlung, Munich;
MNHN	Muséum National d'Histoire Naturelle, Paris;
UARK	University of Arkansas Arthropod Collection;
NHMAA	Natural History Museum, Addis Ababa University.

Morphological studies

Specimens were examined by stereomicroscope Leica M205-C. The photographs were taken with a Leica DFC450 digital camera using a motorised focussing drive, light base Leica TL5000 Ergo, diffused light with Leica hood LED5000 HDI, subsequently processed with Leica LAS application software, and enhanced with CorelDRAW Graphics Suite X5.

Body size was measured from the tip of mandibles in opened position to the apex of the longer elytron. The width of the head was measured across the widest portion including compound eyes. The width of pronotum and the width of elytra were measured at their widest points. The length of pronotum was measured along the median line. The widths of pronotal, apical and basal margins were measured between the tips of the apical and basal angles, respectively. The length of elytra was measured from the tip of the scutellum to the apex of the longer elytron. The length of the hind tibia was measured along its maximum length including its basal joint. The length of aedeagal median lobe was measured across the longest distance without consideration of the sagittal aileron. The following abbreviations were used in the species descriptions:

AL	Length of aedeagal median lobe;
EL	Length of elytra;
EW	Width of elytra;
HW	Width of head;
PL	Length of pronotum;
PAW	Width of pronotal apical margin;
PBW	Width of pronotal basal margin;
PW	Width of pronotum;
TL	Length of hind tibia.

Molecular data acquisition

Specimens used for the molecular study were collected alive by hand in the field and preserved in absolute ethanol. Genomic DNA was isolated from whole specimens using a non-destructive extraction protocol (Rowley et al. 2007) and the DNeasy Tissue Kit (Qiagen GmbH, Hilden, Germany). The specimens were then dry mounted on a card, male genitalia extracted and included in a drop of water-soluble dimethyl hydantoin formaldehyde resin (DMHF) on a transparent card beneath the specimen. Vouchers and DNA samples are deposited in the collections of the State Museum of Natural History, Stuttgart (CAF, SMNS). In the phylogenetic analyses, we included 55 specimens belonging to 49 species of Ethiopian Trechini, including representatives of all genera and subgenera described so far (Suppl. material 1). We complemented this data set with representatives of Trechodina and *Trechus* subgenera from Tanzania (*Meruitrechus* Jeannel) and Yemen (*Arabotrechus* Mateu), as well as representatives of all the lineages and clades of *Trechus* Clairville and allied genera identified in Faille et al. (2013).

Table 1. Node ages (My) and 95% HPD (height posterior density) of high-altitude trechine groups endemic to Ethiopia obtained from BEAST2 based on the concatenated data set. For calibration, two age constraints (ac) were implemented or combined with available substitution rates (sr) (see text, for details).

	***Baehria* gen. nov.**		***Trechus* (s. l.) *Abunetrechus* subg. nov.**		***Trechus* (s. l.) subgen. *Abyssinotus***		***Trechus* (s. l.) subgen. *Minitrechus***	
	Stem	**Crown**	**Stem**	**Crown**	**Stem**	**Crown**	**Stem**	**Crown**
Ac	15.19 (9.86–21.13)	2.13 (1.03–3.27)	10.67 (6.83–14.62)	3.62 (1.52–5.96)	n.a.	17.5 (13.01–22.23)	n.a.	16.57 (12.44–21.04)
ac+sr	22.87 (15.9–30.08)	4.19 (2.12–6.85)	17.74 (12.93–22.96)	6.01 (3.02–9.36)	n.a.	26.22 (21.51–30.96)	n.a.	22.87 (20.89–24.00)

The sampling includes most of the type species of the genera treated in this paper, including *Trechus*. Other genera of uncertain affinities were also included: *Anchotrechus* Jeannel from the Canary Islands, *Paratrechus* Jeannel and *Oxytrechus* Jeannel from Ecuador, *Duvaliomimus* Jeannel from New Zealand, *Tasmanorites* Jeannel from Tasmania, *Bhutanotrechus* Uéno from Bhutan, *Agonotrechus* Jeannel from Nepal, *Trechisibus* Motschulsky from Chile. We used Anillini and Bembidiini as outgroups. Two species of Patrobini were selected to root the tree since they are known to belong to the subfamily Trechinae but are outside the group revised in the present study (Maddison et al. 2019).

We amplified three DNA fragments, two mitochondrial (the 5' end of cytochrome c oxidase subunit 1, cox1 and a fragment containing the 5' end of large ribosomal unit plus the Leucine transfer plus the 3' end of NADH dehydrogenase subunit 1, rrnL+trnL+nad1; ca 740 bp) and two nuclear (large and small ribosomal unit, LSU and SSU rRNA). For the primers used, see Suppl. material 2, and for the general PCR conditions, see Faille et al. (2010). Sequences were assembled and edited with Bioedit v. 7.0 (Hall 1999) and Geneious Prime 2019.2.3 (Kearse et al. 2012). New sequences have been deposited in GenBank database, with accession numbers indicated in Suppl. material 1. A few sequences were taken from Faille et al. (2010, 2011, 2013, 2014) and Fresneda et al. (2019) (Suppl. material 1).

We aligned the sequences using the online version of MAFFT v.7 (Katoh et al, 2019) using the L-INS-i algorithm and default parameters. Maximum likelihood analyses were conducted on the concatenated alignment using RAxML v.7.2 (Stamatakis 2006), with thorough bootstraps, 20 runs, 500 reps, and a GTR+I+G evolutionary model (Stamatakis 2006, 2014). We used the default values for other parameters of the search (Stamatakis 2014).

Divergence time estimations were performed based on the concatenated data set, partitioned by genes and codons using BEAST2 v.2.6.7 (Bouckaert et al. 2019). We specified HKY substitution models, a birth-death prior, and a relaxed log-normal clock. To calibrate the tree, we implemented two age constraints: c1, upper age range of 24 Mya for the *Trechus* clade of southern Ethiopia based on the maximum age of the Bale Mountains (Abbate and Bruni 2015) (uniform distribution); c2, a minimum age of 98 Mya for the Trechini stem group based on the earliest fossil of that group (log-normal distribution M=2, S=1.105, offset=99). The oldest trechini fossils are known from Burmese amber (coll. D.R. Maddison and coll. A. Faille; data will be published by A. Faille and co-workers elsewhere). The amber is dated as about 98.79 ± 0.62 Ma (earliest Cenomanian; Shi et al. 2012). We also used the rates estimated for the same gene fragments in a previous work on Carabidae, all with a normal distribution and a standard deviation of 0.3 (i.e. 0.0016 changes/branch/Ma for 16S; 0.0013 for 28S; and 0.0145 for COI; Andújar et al. 2012). Two dating approaches were performed: i) using the age constraints only, and ii) including age constraints and available rates. Six (i) and three (ii) runs were performed, each with 100 million generations, and a thinning range of 10,000. Replicate runs were then combined with BEAST2 LogCombiner v.2.6.7 by re-sampling logs and trees from the posterior distributions at a lower frequency (ii) and using a burn-in of 10% for each data-set, resulting in a final set of ~18,000 (i) and ~27,000 trees (ii). Convergence and stationary levels were verified with Tracer v1.7.1 (Rambaut et al. 2018). We annotated the tree information with TreeAnnotator v.2.6.7 and visualized it with FigTree v.1.4.2.

Results

In accordance with previous molecular phylogenetic studies on Trechinae (Faille et al. 2013, 2021; Maddison et al. 2019), we recovered a monophyletic Trechini clade with Trechodina forming the sister clade of Trechina. The genus *Oxytrechus* is sister to the remaining Trechina, and the Tasmanian *Tasmanorites* together with the Chilean representative of *Trechisibus* form a well-supported clade. These two taxa are sister clade to the remaining Trechina. Inside this large clade of Trechina, the main clades found in Faille et al. (2013) are largely recovered: the Isotopic clade (Clade 2 in Faille et al. 2013), the Pyrenean hypogean clade (Clade 1.1 in Faille et al. 2013), the *Epaphius* clade, the Dinaro-Alpine clade (Clade 1.3.2.1 in Faille et al. 2013) and the *Trechus* clade (Clade 1.3.2.2 in Faille et al. 2013).

Phylogeny of Ethiopian Trechina

The Ethiopian high-altitude trechine fauna consists of at least three isolated clades, all of which cluster within Trechina (Figs 2, 3). Because *Nungbergites* was not available to our study, the systematic position of this taxon remains to be tested.

The monotypic genus *Baehria* gen. nov. from Mt. Choke in northern Ethiopia (see below, for description) forms a well-supported clade together with the Trechina

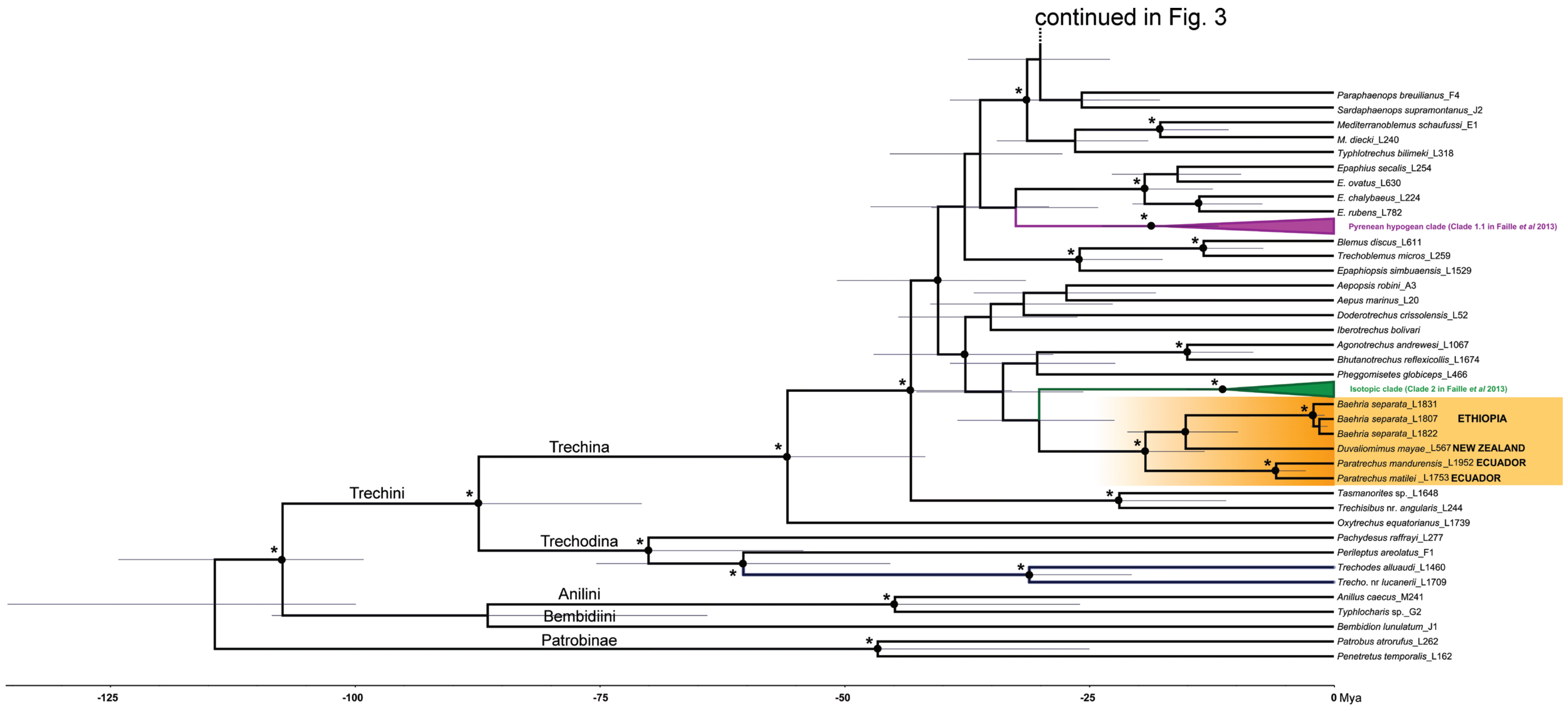


Figure 2. Ultrametric time-calibrated phylogeny of Trechini beetles and outgroups (basal part of the tree, continues in Fig. 3). The tree was obtained from BEAST2 based on the concatenated sequence data and using two age constraints (for details see text). Black circles and stars at branch nodes refer to posterior probabilities ≥0.98 and bootstrap values >75, respectively. Grey bars specify the 95% HPD of the respective node age. Collapsed, colored trechine clades refer to previous results of Faille et al. (2013). The southern hemisphere *Duvaliomimus*-*Paratrechus* clade with the Ethiopian endemic *Baehria* gen. nov. is highlighted ochre.

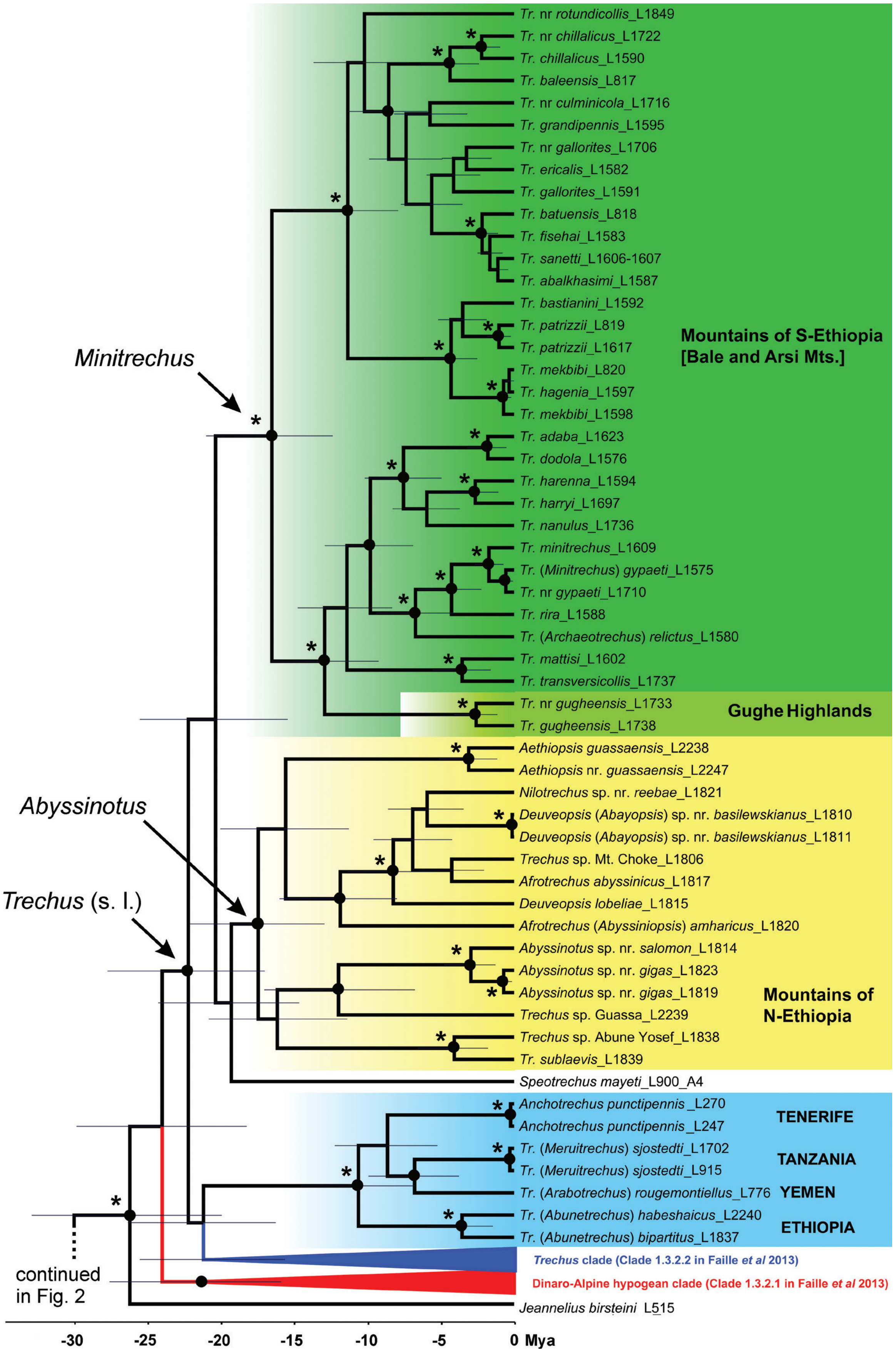


Figure 3. Subtree of the ultrametric time-calibrated phylogeny of Trechini beetles as shown in Fig. 2 (see there for details). Collapsed, colored clades refer to previous results of Faille et al. (2013). Clades which include Ethiopian *Trechus* (sensu lato) species are highlighted by different colors (see text for details).

genera *Duvaliomimus* from New Zealand and *Paratrechus* from South and Central America (in the following the BDP clade). Based on our dataset, the sister group of this clade is formed by the Palearctic "isotopic clade" of Trechina (Faille et al. 2013), although with low support (Fig. 2).

All other Ethiopian high-altitude trechine species cluster within the megadiverse genus *Trechus* (sensu lato). Within the genus *Trechus*, *Abunetrechus* subgen. nov. (see below, for description) is a member of a well-supported clade which includes the monotypic *Anchotrechus* Jeannel from Tenerife, the monotypic *Arabotrechus* Mateu from Yemen, as well as the subgenus *Meruitrechus* Jeannel with two species from Mt. Meru, Tanzania (in the following the "AAMA clade"). The tree shows low supported basal branching of *Abunetrechus* subgen. nov. within the AAMA clade (Fig. 3).

The remaining Ethiopian *Trechus* (s. l.) form two clades that strictly separate the northern and southern Ethiopian faunas (Fig. 3). A sister relationship of the northern and southern Ethiopian clades is not supported by our tree. Moreover, the results do not support a close relationship of these two clades with any of the Holarctic *Trechus* (s. l.) lineages.

The southern Ethiopian *Trechus* clade includes all species known to occur in the Bale and Arsi Mountains and the Gughe Highlands, south and west of the Rift Valley. The two species from the Gughe Highlands form a separate lineage within one of the two main clades of South Ethiopian *Trechus* (Fig. 3). This clade comprises only species with markedly small body size (Schmidt and Faille 2018). The taxa *Archeotrechus* and *Minitrechus* are closely related and representatives of a terminal clade within southern Ethiopian *Trechus* (s. l.) (Fig. 3).

Our phylogenetic analyses show a similar picture for the trechine fauna of the highlands in northern Ethiopia. Samples of this clade originated from the Abune Yosef Massif, Guassa Plateau, and Mt. Choke. Based on the dated tree, all of the Trechini genera and subgenera recently described by Quéinnec et al. (2021) cluster within the northern Ethiopian *Trechus* (s. l.) clade (Fig. 3); these are *Abyssinotus*, *Abayopsis*, *Abyssiniopsis*, *Aethiopsis*, *Afrotrechus*, *Deuveopsis*, and *Nilotrechus*.

The systematic positions of the *Trechus* (s. l.) species from the Simien Mountains in northern Ethiopia and of *T. aethiopicus* Alluaud, 1918 from the mountains near Addis Abeba remain unknown due to the lack of molecular material.

Noteworthy, among the Palearctic species groups, both the monotypic genera *Anchotrechus* Jeannel from Tenerife, and *Speotrechus* Jeannel from France, are nested within *Trechus* (s. l.) in our phylogeny.

Molecular dating of the Trechina species groups endemic to Ethiopia

Stem and crown group ages of the trechines endemic to Ethiopia, as calculated with BEAST2 using two different dating approaches, are summarized in Table 1.

Taxonomic results

Baehria **Schmidt & Faille, gen. nov.**

https://zoobank.org/71FD62CE-3922-4927-9A70-E94D7DD7A7A0

Figs 4–15

Type species. *Baehria separata* sp. nov., herewith designated.

Diagnosis. Representative of subtribe Trechina due to presence of bidentate mandibles (absence of retinacle) and dorsally closed aedeagal median lobe (Jeannel 1926). Comparatively large trechines characterized by robust head, large mandibles, small but markedly protruded eyes, smooth, markedly convex tempora, cordiform pronotum, straight pronotal basal margin with large, rectangular to acute laterobasal angles, slender elytra, short metepisternum, reduced hindwings, moderately slender antenna and legs, protibia with a complete longitudinal groove on external surface, presence of a row of long adhesive hairs on apical margins of 4th tarsomeres which are as long as the 5th tarsomeres, and by a markedly slender median lobe of aedeagus, which possesses a small, slightly sclerotized endophallic copulatory piece. The new genus is particularly distinguished from other representatives of Trechina by unusual chaetotaxy of head capsule and elytra as follows: clypeus plurisetose, each side with 3–5 setae; submentum with three setae each side; anterior elytral discal seta located in the 4th interval, adjoined to the 4th stria.

Etymology. The new genus name is given *in memoriam* of our dear friend and colleague, the distinguished entomologist Martin Baehr, Munich (10.03.1943–17.04.2019).

Description. ***Head***: Large and robust, without pilosity. Mandibles large, moderately slender, with bidentate dentition pattern as shown in Fig. 8. Labrum with apical margin moderately emarginated, with six setae near apical margin. Clypeus each side with three or four setae (Figs 5, 7; seldom only two setae at one of the sides). Eyes moderately small, as long as or slightly shorter than tempora, markedly convexly protruded (Figs 5, 7). Two supraorbital setae each side in normal position for Trechina. Supraorbital furrows unevenly bent in posterior half, markedly deep in front and middle portions, slightly flatter near insertion of posterior supraorbital seta. Tempora markedly convex, markedly wrinkled to the neck, smooth. Mid of head convexly elevated, with a distinct transverse depression between supraorbital area and neck (Figs 5, 7). Antennae slender, with third antennomere longest, 1/9–1/10 longer than first respectively fourth antennomere, and with second antennomere about 2/3 of length of third. Suborbital seta present. Apical tooth of mentum bifid, sensory pits of mentum present; submentum with three setae each side (Fig. 9).

Prothorax: Pronotum rather small, without pilosity, moderately transverse, cordate, broadest distinctly before middle, with lateral margin markedly concave before base, and with basal margin slightly smaller than apical margin (Figs 4, 6). Disc moderately convex. Anterior margin straight or slightly concave in middle with anterior angles small but distinct, rounded, moderately protruded. Basal margin straight along internal 3/4, with laterobasal angles slightly shifted posteriad. Lateral margin convexly rounded in anterior 2/3 and concave towards laterobasal angles, latter large, rectangular or sharp at tip, sometimes slightly protruded laterally. Marginal gutter moderately broad throughout. Median longitudinal impression sharply incised, disappearing near apex, somewhat deepened before base. Anterior and posterior transverse impressions shallow and smooth. Laterobasal foveae large, internally and externally (towards lateral gutter) distinctly sloped, without punctures but with fine transversal wrinkles. Lateral and laterobasal setae present, with the former situated at or slightly anterad of maximum width of pronotum. Proepisternum glabrous and smooth.

Pterothorax**:** Elytra without pilosity, long and very slender ovate, very slightly convex or flattened in middle of disc, in dorsal view broadest distinctly posterad middle, shoulders flatly rounded (Fig. 13), apical sinuation distinct, apex rounded with the indication of a very obtuse apical angle. Striae 1–8 complete, moderately deep impressed, impunctate, intervals moderately convex, parascutellar stria free, 1/6–1/9 of length of elytra. Recurrent preapical stria deep, long, in most specimens reaching the apex of the fifth stria. Parascutellar seta present. Anterior discal seta located in the 4th interval, adjoined to the 4th stria, located near the end of the anterior elytral 5th (Fig. 13); second discal seta located at the 3rd stria about at elytral middle (in most specimens, the posterior setiferous pore together with the 3rd stria is switched into the 4th interval); posterior discal seta (= subapical seta near the end of 3rd stria) present, located about 1/9 of elytral length from elytral apex; subapical seta of the recurrent stria isolated, distinctly removed from this stria by distance of 2–3 diameters of the setiferous pore. Number and positions of the setae of the marginal umbilicate series as in *Trechus* s. str. Metepisternum very short, glabrous and smooth, with outer margin about as long as anterior margin.

Legs**:** Moderately long and robust. Protibia distinctly dilated towards apex, straight, with longitudinal groove on dorsal surface complete, and with several fine setae on anterior surface near apex (Fig. 12). Two basal protarsomeres of males dilated and dentoid at the inner apical border (Fig. 10). Fourth pro-, meso- and metatarsomeres each with a row of long adhesive hairs on apical margins which are as long as the 5th tarsomeres (Figs 10, 11).

Male genitalia (Figs 14, 15): Aedeagal median lobe markedly elongated, slender tube-like, in lateral view slightly sinusoidal, with apex distinctly bent upwardly, simple, with apical lamella insignificant; basal bulb rather small with large sagittal aileron. Endophallus with a small, very slightly sclerotized copulatory piece. Parameres with 3–4 apical setae.

Distribution. So far only known from Mt. Choke in northern Ethiopia (Fig. 1).

Relationships and identification. Based on the molecular data, *Baehria* gen. nov. is representative of a well-supported clade comprising *Duvaliomimus* Jeannel from New Zealand and *Paratrechus* Jeannel from South and Central America (Fig. 2). Apart from a general "*Duvalius*-like" appearance, the three genera share some common features like the large size, cordate pronotum, rounded head with salient temples, and pubescent protibiae. *Baehria* gen. nov. differs from both these genera by the presence of three or four setae instead of two on each side of the clypeus, and by the position of the anterior discal seta on elytra: in *Baehria* gen. nov., this seta inserts in the 4th interval instead on the 3rd stria in *Duvaliomimus* and on the 5th stria in *Paratrechus*. *Baehria* gen. nov. differs additionally from *Paratrechus* by the simple apex of the aedeagal median lobe, which is button-like shaped in *Paratrechus* (Jeannel 1928; Barr 1982; Townsend 2010).

Baehria separata **Schmidt & Faille, sp. nov.**

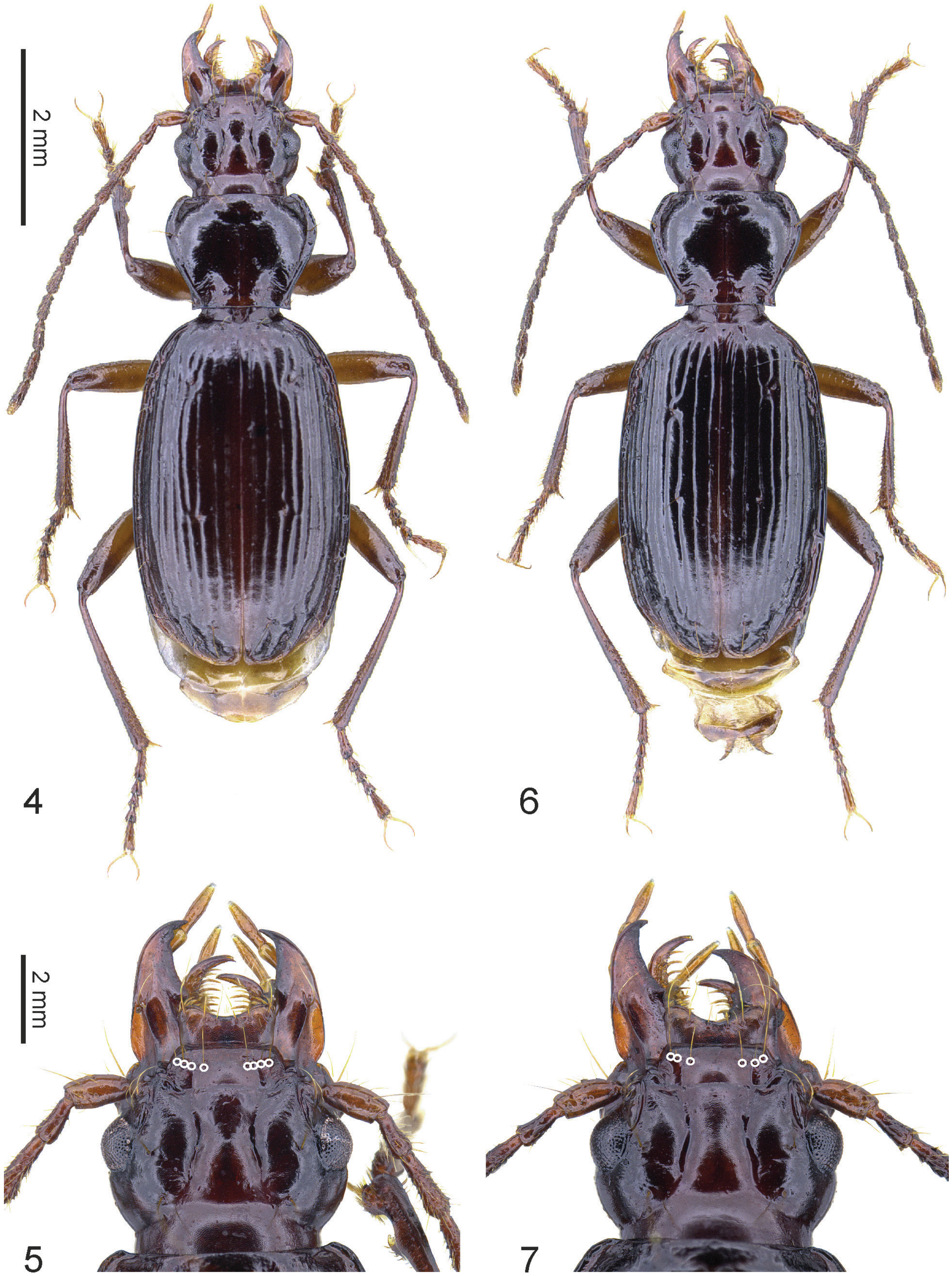
https://zoobank.org/430BB485-1056-462B-8088-FF992DE5F947

Figs 4–15

Type material. ***Holotype*** male, with label data: Ethiopia, Amhara, Mt. Choke, crater valley, alt. 3780–3900 m, 10°42'12"N, 37°50'58"E, 27.II.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CSCHM).

Paratypes**:** 39 males, 54 females, same data as holotype (CAF, CSCHM, NHMAA); 2 males, Mt. Choke, crater valley, alt. 3700–3800 m, 10°41'14"N, 37°50'07"E, 24.II.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CSCHM); 6 males, 7 females, Mt. Choke, western crater valley, alt. 3500–3600 m, 10°41'00"N, 37°50'35"E, 01.V.2022, leg. J. Schmidt, Yeshitla M., (CSCHM).

Additional material. 3 males, 3 females, W-slope Mt. Choke, alt. 3370 m, 10°38'07"N, 37°45'51"E, 23.II.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CAF, CSCHM); 6 males, 7 females, W-slope Mt. Choke, alt. 3700–3900 m, 10°42'17"N, 37°50'29"E, 25.II.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CAF, CSCHM); 43 males, 31 females, W-slope Mt. Choke, "Shoa Kidaneberet" valley, alt. 3700–3800 m, 10°39'08"N, 37°49'45"E, 8.V.2022, leg. J. Schmidt, Yeshitla M. (CSCHM); 10 males, 10 females, N-slope Mt. Choke, alt. 3800–3950 m, 10°43'16"N, 37°51'15"E, 26.II.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CSCHM); 18 males, 20 females, N-slope Mt. Choke, alt. 3750–3850 m, 10°43'51"N, 37°52'15"E, 09.V.2022, leg. J. Schmidt, Yeshitla M. (CSCHM); 3 males, 2 females, N-slope Mt. Choke, above Gumadur, alt. 3750–3850 m, 10°44'10"N, 37°53'48"E, 05.V.2022, leg. J. Schmidt, Yeshitla M. (CSCHM); 1 male, N-slope Mt. Choke, N of Waber, alt. 3450–3600 m, 10°44'48"N, 37°46'22"E, 07.V.2022, leg. J. Schmidt, Yeshitla M. (CSCHM); 13 males, 5 females, Mt. Choke, eastern crater valley, alt. 3700–3800 m, 10°42'59"N, 37°54'13"E, 06.V.2022, leg. J. Schmidt, Yeshitla M. (CSCHM).



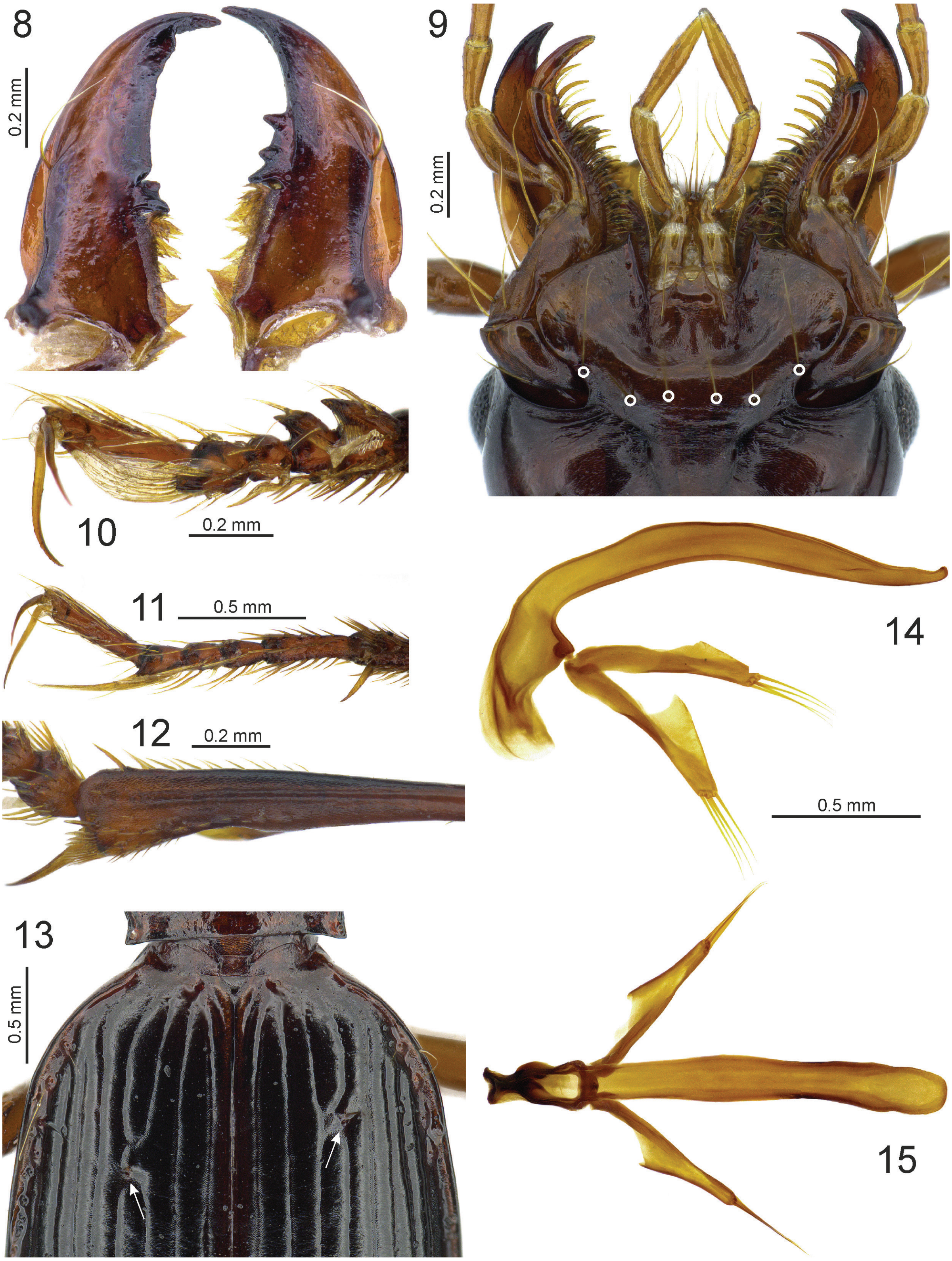
Figures 4–7. *Baehria separata* Schmidt & Faille, gen. nov., sp. nov., dorsal aspect of body (**4, 6**) and head (**5, 7**) of paratypes; **4, 5.** Male; **6, 7.** Female. The small white circles in Figs 5 and 7 mark the insertion points of the clypeal setae.

Etymology. The specific epithet refers to the markedly separated distributional area of the taxon, which is, based on current knowledge, far away from its next relatives. It is built by the past participle of the Latin verb *separare*.

Description. See description of genus.

***Body length*:** 6.9–7.5 mm (Ø = 7.19 mm, n = 20).

Proportions (n = 20): PW/HW = 1.18–1.25 (Ø = 1.21); PW/PL = 1.30–1.38 (Ø = 1.34); PW/PBW = 1.48–1.54 (Ø =



Figures 8–15. *Baehria separata* Schmidt & Faille, gen. nov., sp. nov. **8.** Left and right mandible, dorsal aspect; **9.** Ventral aspect of head; the small white circles mark the insertion points of the setae on submentum; **10.** Right male protarsomeres, left latero-ventral aspect; **11.** Left male metatarsomeres, right lateral aspect; **12.** Right male protibia, dorsal aspect; **13.** Anterior part of elytra and pronotal base; the arrows point to the insertions of the anterior elytral discal setae; **14.** Aedeagus, left lateral aspect; **15.** Aedeagus, dorsal aspect.

1.50); PBW/PAW = 0.92–1.00 (Ø = 0.96); EW/PW = 1.42–1.48 (Ø = 1.45); EL/EW = 1.46–1.56 (Ø = 1.51).

Colour**:** Dark brown to blackish, moderately shiny in both sexes; palpi light brown, labrum and scapus reddish brown, basal 3/4 of femora light brown; antennal base in some specimens more widely brightened.

Microsculpture**:** Same in males and females. Head with deeply engraved, rather large, almost isodiametric sculpticells on disc and supraorbital area, slightly smaller sculpticells on clypeus. Pronotum with moderately deep engraved, slightly transverse sculpticells on disc and markedly deep engraved sculpticells near base; the sculpticells are somewhat smaller than on head disc. Elytral intervals with more finely engraved sculpticells which are more transverse than on pronotum.

Aedeagus. Proportion EL/AL (n = 10): 2.40–2.64 (Ø = 2.52). Median lobe in lateral view unevenly bent, dorsally with a distinct concavity before middle (Fig. 14), in dorsal view not or very slightly broadened before apex (Fig. 15).

Differential diagnosis. See Diagnosis and Identification sections of the genus, above.

Distribution and geographical variability. The type series was collected on the western side of the crater valley of Mt. Choke. Additional populations were collected on the north eastern side of the crater valley and on northern and western slopes of Mt. Choke. Specimens of these populations differ +/- distinctly from those of the type series and from each other by the curvature of the aedeagal median lobe, the number of lightened basal antennomeres, and the depth of the engraving of the elytral microsculpture. Slight differences were also found in the DNA sequence segments of the three investigated specimens representing three different populations (Fig. 2; Suppl. material 1). Further morphological and molecular genetic studies are needed to answer the question of whether certain populations represent separate species or subspecies.

Habitat. Specimens of *Baehria separata* gen. nov., sp. nov. have been found in stone packs traversed by running water in small steep streams in the afroalpine zone, together with Dytiscidae beetles (Fig. 16). Based on this finding, *Baehria separata* gen. nov., sp. nov. seems to be adapted to a rheophilic way of life.

Trechus Clairville, 1806

Abunetrechus Schmidt & Faille, subgen. nov.

https://zoobank.org/608E14D6-39EC-4CEC-97C9-68870B659966

Type species. *Trechus bipartitus* Raffray, 1885, herewith designated.

Diagnosis. Representative of Trechina and *Trechus* s. l. sensu Jeannel (1926, 1927, 1928) due to presence of bidentate mandibles (absence of retinacle), dorsally closed aedeagal median lobe, well-developed compound eyes, protibia glabrous on anterior surface, presence of two elytral dorsal setae situated in third interval, elytral intervals glabrous, 4+2+2 pattern of umbilicate setae, and two basal tarsomeres of male dilated. Externally, *Abunetrechus* subgen. nov. reminders a non-specialised high-altitude *Trechus* of moderate body size, short mandibles, antenna and legs, moderately large eyes, rounded humeri, short metepisternae and hindwings reduced to short stubs. *Trechus* sensu lato, *Abunetrechus* subgen. nov. is characterized by the combination of following character states: bisetose clypeus (Figs 18, 20, 22), smooth tempora, pronotum with fully rounded laterobasal angles and with laterobasal setae markedly protruded anteriorly (Figs 18, 20, 21), elytral striae 3 and 4 merging at level of the anterior discal seta (Fig. 23), elytral preapical seta of the third interval present and situated about at level of the elytral apical tenth, protibia with longitudinal groove on external surface; aedeagus with two moderately sclerotized portions of the endophallus arranged one behind the other in apical half of the median lobe (Figs 24–29).

Etymology. The subgenus name combines the name of the Abune Yosef Massif in northern Ethiopia, where the species of this subgenus occur, with the name of the genus *Trechus*.

Description. *Head*: Size averaged for *Trechus* sensu lato, without pilosity. Mandibles short, with dentition pattern as in *Trechus* sensu stricto. Labrum with apical margin moderately emarginated, with six setae near apical margin. Clypeus each side with one long seta (Figs 18, 20, 22; very seldom with an additional very fine seta situated interior of one of the primary setae). Eyes moderately large, convexly protruded, more than two times as long as tempora, latter moderately convex (Figs 18, 20, 22). Two supraorbital setae each side in normal position for *Trechus*. Supraorbital furrows moderately deep and almost evenly bent throughout. Tempora moderately convex, markedly wrinkled to the neck, smooth. Mid of head convexly elevated. Antennae short, with third antennomere slightly longer than pedicellus. Suborbital seta present. Apical tooth of mentum truncate or slightly bifid, sensory pits of mentum present but very small; submentum with 4–7 setae.

***Prothorax*:** Pronotum with size averaged for *Trechus* sensu lato, without pilosity, slightly transverse, broadest distinctly before middle, with lateral margin completely rounded towards base, and with laterobasal angles indistinct. Basal margin (between insertion points of laterobasal setae) distinctly broader than apical margin. Disc markedly convex. Anterior margin slightly or moderately concave with anterior angles shortly rounded, moderately protruded. Basal margin straight or slightly convex in middle and with outer quarters markedly shifted anteriorly towards lateral margin (Figs 18, 20, 21). Lateral margin convexly rounded throughout; laterobasal angle fully rounded or marked as a very small blunt tooth. Marginal gutter very narrow throughout. Median longitudinal impression slightly incised, disappearing near apex and base, not deepened within area of posterior transverse impression. Anterior and posterior transverse impressions very shallow, smooth or (posterior transverse impression) sometimes finely wrinkled. Laterobasal foveae rather small, moderately impressed, smooth. Lateral and laterobasal setae present, with the former situated near maximum width of pronotum. Proepisternum glabrous and smooth.

***Pterothorax*:** Elytra without pilosity, slender ovate, markedly domed towards disc, not flattened in middle of disc, in dorsal view broadest slightly posterad middle, shoulders flatly rounded, apical sinuation very slightly developed or indistinct, apex rounded or marked as an obtuse apical angle. Parascutellary stria short to moderately

Figure 16. North-exposed slope on Mt. Choke with *Erica* forest and a steep small brook at an altitude of 3600 m during dry season (May, 2022). The stone pack in the brook is habitat of *Baehria separata* Schmidt & Faille, gen. nov., sp. nov.: the beetles were collected between the stones along which the water flows (in order to find the beetles, the creek bed was partially dug up).

long, free; striae 1–8 almost complete, moderately deep impressed in middle of disc, less deeply towards sides, disappearing near base, crenulated, striae 3 and 4 merging at level of the anterior discal seta; intervals slightly convex. Recurrent preapical stria deep, long, connected with the apex of the fifth stria. Parascutellar seta present. Anterior discal seta situated at merging point of the 3rd and 4th stria, near the end of the anterior elytral 5th (Fig. 23); second discal seta located at the 3rd stria somewhat behind elytral middle; posterior discal seta (= subapical seta near end of 3rd stria) present, located about 1/10 of elytral length from elytral apex; subapical seta of the recurrent stria isolated, removed from this stria by distance of 1–2 diameters of the setiferous pore. Number and positions of the setae of the marginal umbilicate series as in *Trechus* s. str. Metepisternum very short, glabrous and smooth, with outer margin about as long as anterior margin.

***Legs*:** Short and moderately robust. Protibia distinctly dilated towards apex, straight, glabrous, with longitudinal groove on dorsal surface complete. Two basal protarsomeres of males dilated and dentoid at the inner apical border. Chaetotaxy as in *Trechus* sensu stricto.

Male genitalia (Figs 24–29): Aedeagal median lobe moderately large, in lateral view markedly curved, with apical lamella short, latter with distinct terminal capitulum; basal bulb and saggital aileron averaged. Endophallus with a moderately large, moderately sclerotized folding structure (copulatory piece) in the shape of a half-open cylinder or cone which is located in apical half of the median lobe and directed to its longitudinal axis, and with the open part of the copulatory piece facing ventrad. Apicad of this piece, an additional slightly more strongly sclerotized folding structure is developed which is shaped as a small plate (best visible in lateral view); the basal part of this piece overlaps with the apex of the more dorsal copulatory piece. Parameres with 2–4 apical setae.

Remarks. In his redescription of *Trechus bipartitus*, Jeannel (1927) noted the presence of a single copulatory piece which is characterized by a long sinusoidal appendix. However, in his figure of the left lateral view of the copulatory piece (Jeannel 1927: 195) he merged the more strongly sclerotized folding structure near median lobe apex with the more basad located larger copulatory piece which leads to the impression of a single, very long piece.

Distribution. Northern Ethiopia Plateau (Fig. 1): Three species are known so far, two from Mt. Abune Yosef (*T. bipartitus* Raffray, *T. lalibelae* Quéinnec & Ollivier) and one from the Guassa Plateau (*T. habeshaicus* Quéinnec & Ollivier).

Relationships and identification. Based on the molecular data, *Abunetrechus* subgen. nov. is representative of a clade comprising *Anchotrechus* Jeannel from Tenerife, the *Trechus* subgenus *Arabotrechus* Mateu from Yemen, and the *Trechus* subgenus *Meruitrechus* Jeannel from Mt. Meru, Tanzania (Fig. 3; in the following called the AAMA clade). *Abunetrechus* subgen. nov. differs from all species groups of the AAMA clade by bisetose clypeus. A quadrisetose clypeus was hypothesized plesiomorphic character state in Trechini (Schmidt et al. 2021). Within this tribe, a bisetose clypeus is also developed in the genus *Omalodera* Blanchard from Chili, the Caucasian genus *Alanorites* Belousov of the *Neotrechus* Phyletic Series, and two *Epaphiopsis* Uéno species occurring in the central Himalaya (Belousov 1998; Naito 2023). However, this character state has to be considered homoplasic because none of these taxa cluster within *Trechus* sensu lato (Faille et al. 2013, 2021; Maddison et al. 2019, see Fig. 2 in this paper). *Abunetrechus* subgen. nov. additionally differs from all other species of the AAMA clade by rounded pronotal laterobasal angles, from *Meruitrechus* by presence of the elytral preapical seta of the third interval, the isodiametric sculticells on elytra less deeply engraved, and eight striae well marked, from *Anchotrechus* by smaller and stouter body, glabrous elytra and much shorter aedeagal median lobe, and from *Arabotrechus* by the smaller body size, presence of a second discal setae (missing in *Arabotrechus*, as well as in *T. aethiopicus* and some species of *Elgonotrechus* Jeannel. *Abunetrechus* subgen. nov. shares the elytral striae 3 and 4 merging at level of the anterior discal seta with *Arabotrechus* (based on a single investigated specimen; larger series would be necessary to confirm the stability of this character).

Trechus (*Abunetrechus*) *bipartitus* Raffray, 1885

Figs 17, 18, 23–25

Trechus bipartitus Raffray, 1885: 318; locus typicus: "col du mont Abouna-Yousef (4024 m)".

Trechus bipartitus: Jeannel 1927: 194.

Trechus bipartitus: Pawłowski 2003: 157.

Trechus bipartitus: Ortuño and Novoa 2011: 137.

Trechus (s. str.) *bipartitus*: Quéinnec et al. 2021: 20.

Type material. Not studied. The lectotype was designated by Quéinnec et al. (2021). Identification is based on the redescriptions of the species, including habitus and male genital figures of the type specimens, presented by Jeannel (1927) and Quéinnec et al. (2021), as well as on comprehensive material collected at the type locality (see below).

Additional material. 6 males, 9 females, Ethiopia, Amhara, Mt. Abuna Yosef, N-slope, 3800–3950 m, 12°07'52"N, 39°11'39"E, 4.III.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CAF, CSCHM); 6 males, 12 females, ditto, S-slope, 3850–3900 m, 12°07'29"N, 39°11'21"E, 5.III.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CSCHM, NHMAA); 5 males, 2 females, ditto, S-slope, 3700–3850 m, 12°09'10"N, 39°09'35"E, 5.III.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CSCHM).

Additions to the species description. Mature species with elytra including suture blackish brown (Quéinnec et al. 2021: "suture distinctly brown shiny"; this information is probably based on confusion with *T. habeshanicus*). Body length 4.1–4.7 mm (Quéinnec et al. 2021: "> 4.5 mm"). Length of aedeagus 0.98–1.05 mm. PW/PL = 1.29–1.37; n = 20 (Quéinnec et al. 2021: PW/PL = 1.6; this value is very probably based on a measurement error). PW/TL = 1.06–1.15; n = 20. EL/AL = 2.15–2.46; n = 10.

Differential diagnosis. See Key to species of the subgenus *Abunetrechus*, below.

Distribution. Endemic to the Abune Yosef Mountains of the northern Ethiopian Highlands.

Habitat. As in *T.* (*Abunetrechus*) *lalibelae* Quéinnec & Ollivier (see below).

Trechus (*Abunetrechus*) *lalibelae* Quéinnec & Ollivier

Figs 19, 20, 26, 27

Trechus (*Abunetrechus*) *lalibelae*: Quéinnec et al. 2021: 21; locus typicus: Mt. Abuna Yosef, 12°08'32"N, 39°10'59"E.

Type material. Not studied. Identification is based on the original description, including habitus and male genital figures of the type specimens (Quéinnec et al. 2021), as well as on comprehensive material collected at the type locality (see below).

Additional material. 13 males, 11 females, Ethiopia, Amhara, Mt. Abuna Yosef, N-slope, 3800–3950 m, 12°07'52"N, 39°11'39"E, 4.III.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (SCHM, NHMAA); 1 male, 1 female, ditto, S-slope, 3850–3900 m, 12°07'29"N, 39°11'21"E, 5.III.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CSCHM); 1 male, ditto, S-slope, 3700–3850 m, 12°09'10"N, 39°09'35"E, 5.III.2019, leg. D. Hauth, J. Schmidt, Yeshitla M., Yitbarek W. (CSCHM).

Additions to the species description. Body length 4.2–5.1 mm (Quéinnec et al. 2021: 4.8–5.1 mm). Length of aedeagus 0.98–1.02 mm. PW/PL = 1.24–1.30; n = 20. PW/TL = 0.99–1.04; n = 20. EL/AL = 2.39–2.65; n = 10.

Differential diagnosis. See Key to species of the subgenus *Abunetrechus*, below.

Distribution. Endemic to the Abune Yosef mountains of the northern Ethiopian Highlands.

Habitat. Specimens of *T. lalibelae* were found syntopic with *T. bipartitus* and *T. sublaevis* Raffray under stones and in humus and rotten plant material near brooks in the afroalpine zone.

Trechus (*Abunetrechus*) *habeshanicus* Quéinnec & Ollivier

Figs 21, 22, 28, 29

Trechus (*Abunetrechus*) *habeshanicus*: Quéinnec et al. 2021: 23; locus typicus: Guassa Plateau 10°17'19"N, 39°48'13"E.

Type material. Not studied. Identification is based on the original description, including habitus and male genital figures of the type specimens (Quéinnec et al. 2021), as well as on comprehensive material collected at the type locality (see below).

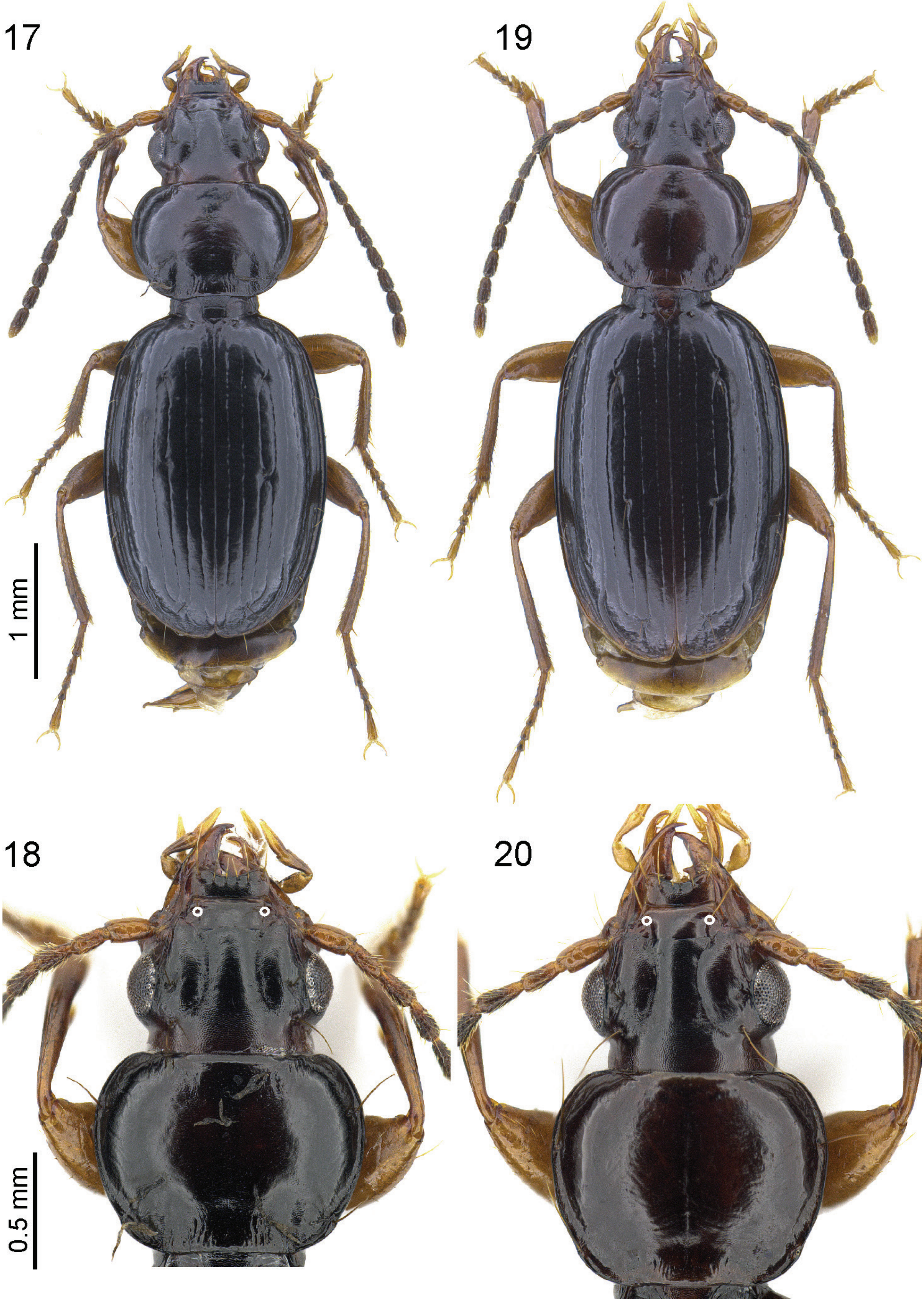
Additional material. 98 exx. (males, females), Ethiopia, Amhara, northern Guassa Plateau, near Guassa Comm. Lodge 3330 m, 10°17'17"N, 39°47'54"E, 18.V.2022, leg. J. Schmidt, Yeshitla M. (CAF, CSCHM, NHMAA); 360 exx. (males, females), ditto, "Aste wuha" 3400 m, 10°24'N, 39°48'E, 19.V.2022, leg. J. Schmidt, Yeshitla M. (CAF, CSCHM, NHMAA); 11 exx. (males, females), ditto, "Yegana Natural Forest", river valley, 3125 m, 10°26'03"N, 39°47'16"E, 20.V.2022, leg. J. Schmidt, Yeshitla M. (CSCHM).

Additions to the species description. Mature species with elytra blackish brown, and with suture and first interval reddish brown lightened in most specimens (Quéinnec et al. 2021: "suture distinctly darkened"; this information is probably based on confusion with *T. bipartitus*). Body length 4.1–5.0 mm (Quéinnec et al. 2021: 4.1–4.3 mm). Length of aedeagus 0.70–0.80 mm. PW/PL = 1.28–1.38; n = 20. PW/TL = 1.08–1.13; n = 20. EL/AL = 3.00–3.33; n = 10.

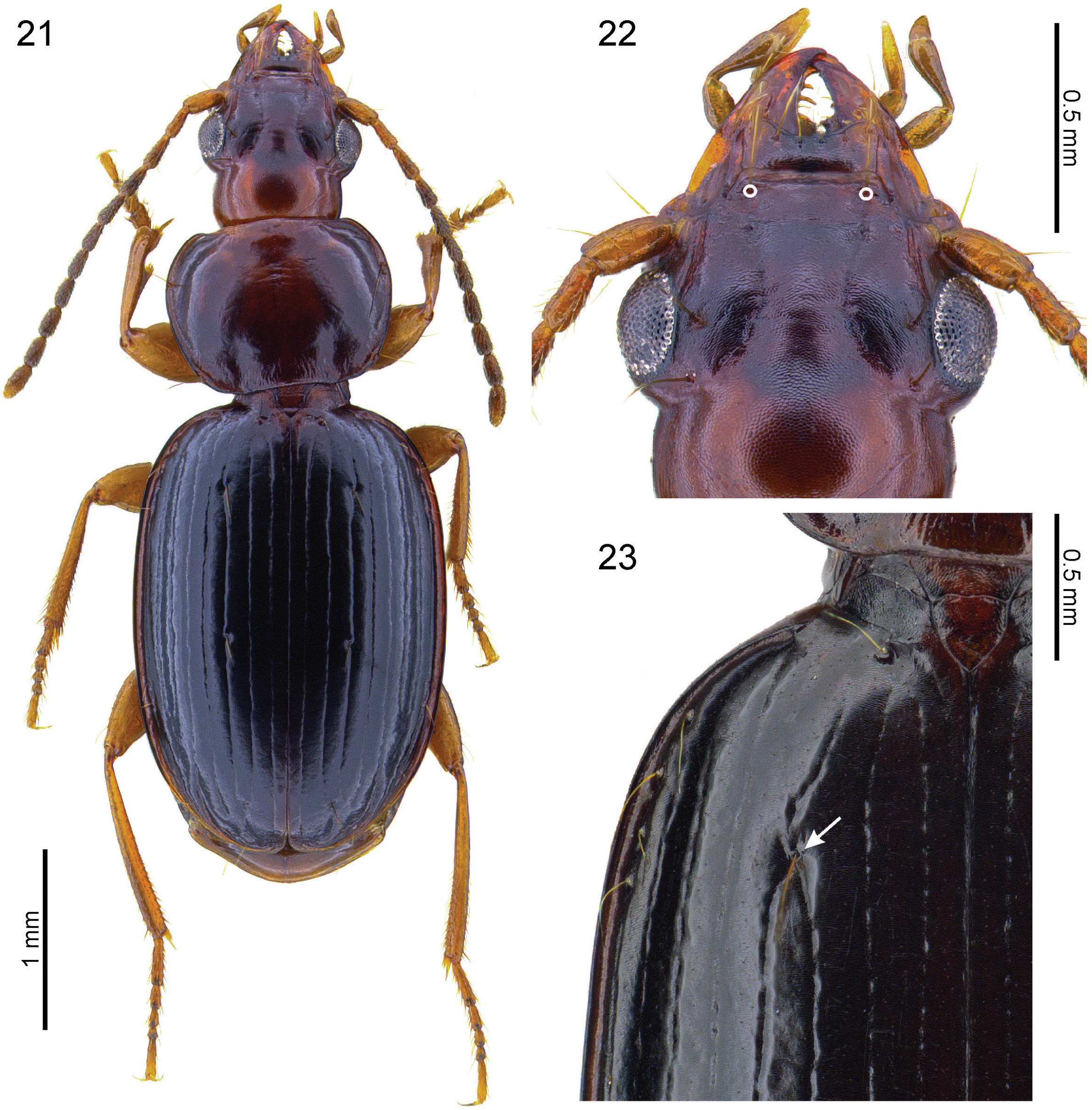
Differential diagnosis. See Key to species of the subgenus *Abunetrechus*, below.

Distribution. Endemic to the Guassa Plateau of the northern Ethiopian Highlands.

Habitat. Specimens of *T. habeshanicus* were found syntopic with *T. guassaensis* (Quéinnec & Ollivier) and two hitherto undescribed *Trechus* species in humus and rotten plant material along brooks in the afromontane zone.



Figures 17–20. *Trechus* subgenus *Abunetrechus* nov., dorsal aspect of body (**17, 19**), head and pronotum (**18, 20**). **17, 18.** *T. bipartitus* Raffray; **19, 20.** *T. lalibelae* Quéinnec & Ollivier. The small white circles in Figs 18 and 20 mark the insertion points of the clypeal setae.



Figures 21–23. *Trechus* subgenus *Abunetrechus* nov., dorsal aspect of body (**21**) and head (**22**), and anterior part of left elytron (**23**). **21, 22.** *T. habeshaicus* Quéinnec & Ollivier; **23.** *T. bipartitus* Raffray. The small white circles in Fig. 22 mark the insertion points of the clypeal setae; the arrow in Fig. 23 points to the insertion of the anterior elytral discal seta.

Revised key to species of *Abunetrechus* subgen. nov.

Remarks. Quéinnec et al. (2021) proposed a key to the species of their *Trechus* (s. str.) *bipartitus* group, which includes the three species we here assigned to the subgenus *Abunetrechus* nov. For species' differentiation, the authors used total body length, proportions of the pronotum and coloration patterns of the elytra. However, we found that these character states are unsuitable due to high intraspecific variability. In addition, the pronotal proportion value was probably erroneously presented by Quéinnec et al. (2021; see Additions to the species descriptions, above).

1 Body more slender, with shoulders more gently rounded (Fig. 19) and with appendages slightly longer: tibiae about as long as width of pronotum (PW/TL < 1.05). Endemic to Mt. Abune Yosef .... ***Trechus*** (***Abunetrechus***) ***lalibelae*** Quéinnec & Ollivier
– Body more robust, with shoulders broader (Figs 17, 21) and with appendages shorter: tibiae distinctly shorter than width of pronotum (PW/TL > 1.05 2
2 Aedeagal median lobe much smaller (length: 0.70–0.80 mm; EL/AL > 2.9), its ventral margin almost evenly curved from base to apex (lateral view, Fig. 28). Endemic to the Guassa Plateau .... ***Trechus*** (***Abunetrechus***) ***habeshaicus*** Quéinnec & Ollivier
– Aedeagal median lobe larger (length: 0.98–1.05 mm; EL/AL < 2.5), its ventral margin almost straight near apex (lateral view, Fig. 24). Endemic to Mt. Abune Yosef .... ***Trechus*** (***Abunetrechus***) ***bipartitus*** Jeannel

Figures 24–29. *Trechus* subgenus *Abunetrechus* nov., aedeagus in left lateral aspect (**24, 26, 28**) and dorsal aspect (**25, 27, 29**). **24, 25.** *T. bipartitus* Raffray; **26, 27.** *T. lalibelae* Quéinnec & Ollivier; **28, 29.** *T. habeshaicus* Quéinnec & Ollivier.

Subgenus *Minitrechus* Vigna Taglianti & Magrini, 2010

Type species. *T. gypaeti* Vigna Taglianti & Magrini, 2010.

New synonymy. *Archeotrechus* Magrini, Quéinnec & Vigna Taglianti, 2012 (type species: *T. relictus* Magrini, Quéinnec & Vigna Taglianti, 2012), syn. nov.

Remarks. Based on the molecular data, all *Trechus* species known to occur in the mountains of southern Ethiopia (Bale and Arsi Mountains, Gughe Highlands), form a monophyletic clade (Fig. 3). This clade includes species characterized by widely differing body sizes, shapes, and proportions, and by many other morphological characters, including elytral chaetotaxy, the number of dilated male protarsomeres, and the extent of the dorsal opening of the aedeagal median lobe. Similar character states can likewise be found in *Trechus* sensu lato species occurring in northern Ethiopia which, however, do not cluster within the south Ethiopian clade. At the current state of knowledge, a morphological definition of this clade together with a differential diagnosis with respect to other species groups of *Trechus* sensu lato cannot be presented here and require more comprehensive morphological investigations.

For the monophyletic southern Ethiopian *Trechus* clade, the oldest valid species group name is *Minitrechus* Vigna Taglianti & Magrini, which was given for a very tiny, depigmented species from Mt. Enkuolo (Vigna Taglianti and Magrini 2010). The subgenus *Archeotrechus* Magrini, Quéinnec & Vigna Taglianti was described two years later for a likewise tiny and depigmented species from the Bale Mountains, which is additionally characterized by a very wide dorsal opening of aedeagus (Magrini et al. 2012). In our phylogeny, the type species of both of these subgenera cluster together within one of the two main clades of South Ethiopian *Trechus*, both of which are highly supported by the molecular data (Fig. 3). Consequently, the status of *Archeotrechus* as a separate subgenus within *Trechus* sensu lato can no longer be maintained.

A complete list of species we propose to summarize within the subgenus *Minitrechus*, is shown in the checklist of the Ethiopian Trechini species, see Discussion, below.

Trechus (*Minitrechus*) *patrizii* Jeannel

Figs 30–35

Trechus Patrizzi [sic!] Jeannel, 1960: 265; locus typicus: "mont Chillálo".

Trechus Patrizii Jeannel (1960): 266.

Trechus patrizii Jeannel: Casale and Laneyrie (1982): 125.

Trechus (s. str.) *patrizzii* [sic!] Jeannel: Lorenz (2005): 186.

Trechus patrizii Jeannel: Ortuño and Novoa (2011): 135.

Trechus (s. str.) *oromiensis* Magrini, Quéinnec & Vigna Taglianti, 2012: 26; locus typicus: Oromia Province, Bale massif, South of Goba, alt. about 3200 m.

Trechus patrizii Jeannel: Schmidt and Faille (2018): 37.

Trechus oromiensis Magrini et al.: Schmidt and Faille (2018): 37.

Trechus (s. str.) *patrizii* Jeannel: Quéinnec et al. 2021: 65.

Trechus (s. str.) *oromiensis* Magrini et al.: Quéinnec et al. 2021: 65.

New synonymy. *Trechus patrizii* Jeannel, 1960 = *Trechus oromiensis* Magrini, Quéinnec & Vigna Taglianti, 2012, syn. nov.

Type material examined. *Trechus patrizii* Jeannel: ***Holotype*** female, with label data "TYPE" (printed on red card), "A.O.I. Arussi occ. / Reg. Aselle m. 2600 ca / pend. M.te Cillalo / S. Patrizi 20:27.4.38", "Trechus / patrizii nov. / R. Jeannel det., 19" in UARK (Fig. 30).

Paratype male, with label data "A.O.I. Arussi occ. / Torr. Asciabacá / S. Patrizi 28.IV.38 / m 2500", "Trechus / patrizii n.", "Lectotype / E. Quéinnec dés. 1994" (printed on red card), "Trechus / patrizii / MNHN Paris" (printed and handwritten on red card) in MNHN (Fig. 32).

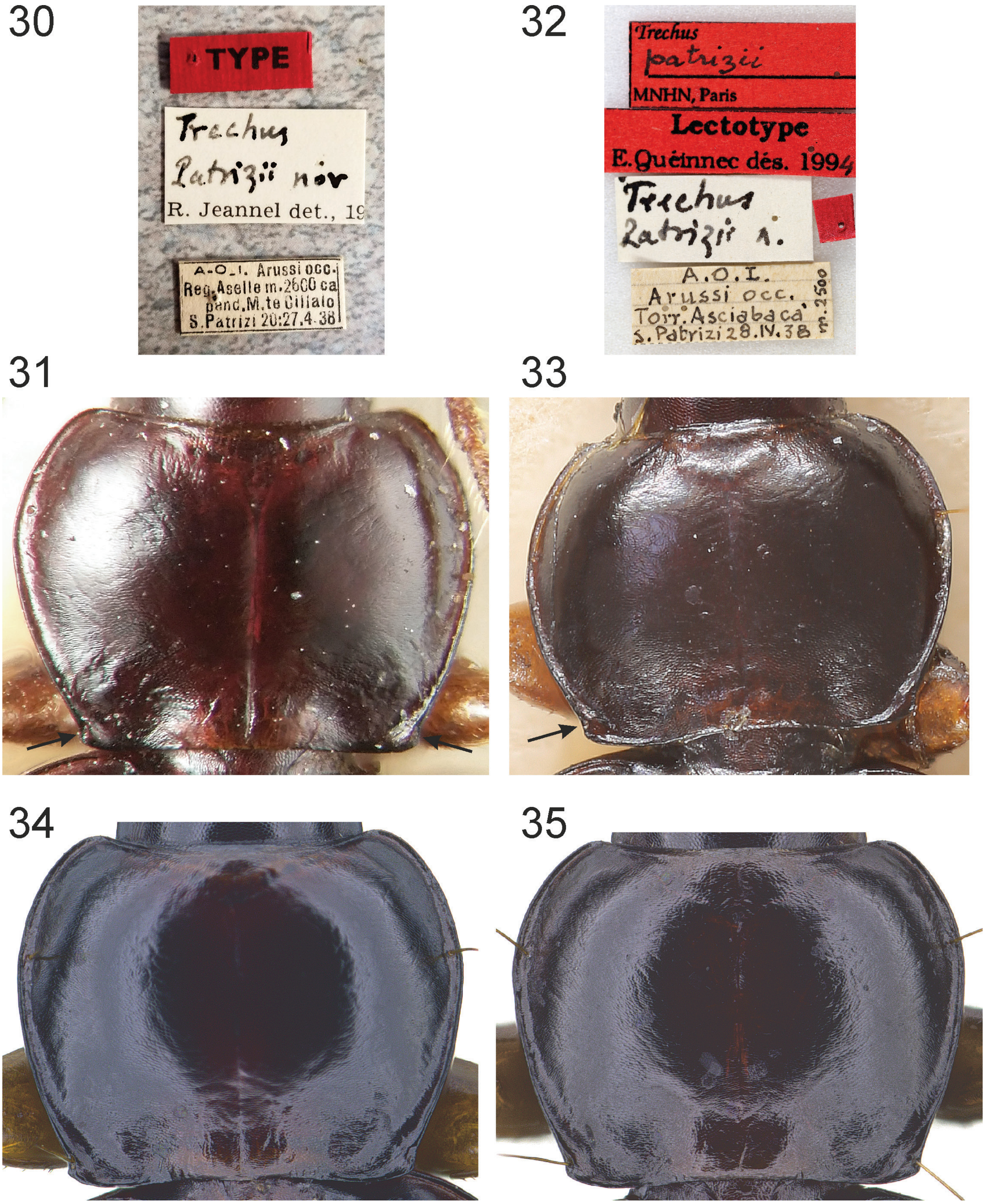
Remarks. Jeannel (1960: 266) stated that the type specimen is deposited in the S.L. Straneo collection. Significant parts of the Straneo collection together with the *T. patrizii* specimen cited by Jeannel (1960) are now preserved in the UARK (M. Pavesi, pers. comm. 2018). The above cited *T. patrizii* specimen from the UARK collection has thus to be considered the holotype of *T. patrizii*, while the (unpublished) lectotype designation made by E. Quéinnec for the specimen preserved in the MNHN has to be considered unjustified.

Trechus oromiensis Magrini et al.: Type material not studied. Identification is based on the detailed description of this distinctive taxon and comprehensive material from the type locality (see Schmidt and Faille 2018).

Additional material. For comprehensive material studied see our previous paper (Schmidt and Faille 2018). Note that in this study, *T. oromiensis* Magrini, Quéinnec & Vigna Taglianti was erroneously treated as a distinct species. In the meantime, the following additional material was available for us: Ethiopia, Oromia, SE-slope of Mt. Chillalo, Dhaba village, alt. 3200 m, 19.II.2020, 7.861644°N, 39.27711°E, leg. J. Schmidt, C. Wirkner, Yeshitla M. (1 female: CSCHM); ditto, Bale Mts., Web river N Dinsho, alt. 3000 m, 5.II.2019, 07°07'18"N, 39°46'03"E, leg. R. Emmerich, J. Schmidt, Yeshitla M. (12 specimens: CSCHM); ditto, Bale Mts., forest remain W Dinsho, alt. 3100 m, 8.II.2019, 07°06'16"N, 39°44'46"E, leg. R. Emmerich, J. Schmidt, Yeshitla M. (12 specimens: CSCHM); ditto, Bale Mts., Sebsebe Washia Forest, Salgen Valley, alt. 2720–2800 m, 3.II.2019, 07°02'08"N, 39°36'06"E, leg. R. Emmerich, J. Schmidt, Yeshitla M. (7 specimens: CSCHM); ditto, Bale Mts., Sebsebe Washia Forest, Salgen Valley, alt. 3130 m, 4.II.2019, 07°02'08"N, 39°36'06"E, leg. R. Emmerich, J. Schmidt, Yeshitla M. (30 specimens: CSCHM); ditto, Bale Mts., Angeso Valley S Goba, alt. 3050 m, 5.II.2020, 6.932923°N, 39.951341°E, leg. J. Schmidt, C. Wirkner, Yeshitla M., Yitbarek W. (53 specimens: CSCHM); ditto, Bale Mts., Shaya Valley SW Goba, alt. 3100–3150 m, 6.II.2020, 6.991843°N, 39.884397°E, leg. J. Schmidt, C. Wirkner, Yeshitla M., Yitbarek W. (15 specimens: CSCHM).

Justification of the new synonymy. Jeannel (1960) noted for his *T. patrizii* the absence of pronotal basolateral setae as diagnostic character. Up to today, *T. patrizii* is considered the only Ethiopian species bearing this particular character (for development of this character state in *T. amharicus* Ortuño & Novoa, for which absence of pronotal basolateral setae was likewise determined, see Quéinnec et al. 2021). However, based on re-investigation of the type material of *T. patrizii*, we found that a pore is present in the normal position for the basolateral seta both sides of the pronotum (Figs 30, 31). Very probably, absence of these setae is based on preservation artefacts. The *T. patrizii* type specimens correspond in all external and genital diagnostic characters with the many specimens we previously identified as *T. oromiensis* Magrini et al. from the Bale Mts, Mt. Enkuolo and from the type locality of *T. patrizii*, Mt. Chillalo (Schmidt and Faille 2018). In far most of these specimens, the pronotal basolateral seta is present but lost on one or both sides in very few cases (Figs 32, 33; Schmidt and Faille 2018: 38, figs 58–60). Consequently, we conclude junior synonymy for the taxon *T. oromiensis* Magrini, Quéinnec & Vigna Taglianti under *T. patrizii* Jeannel.

Diagnosis. Within the *Trechus* fauna of the Bale and Arsi Mountains, *T. patrizii* is easily recognized by absence of the posterior elytral discal seta (Schmidt and Faille 2018). Beside *T. patrizii*, absence of the posterior elytral discal seta is also characteristic for *T. amharicus* Ortuño & Novoa and *T. aethiopicus* Alluaud. *Trechus patrizii* differs from *T. amharicus* by two male protarsomeres dilated, by presence of an apical disc on aedeagal median lobe, and by very differently sclerotized endophallus (for comparison see Ortuño and Novoa 2011: 134, fig. 3b, d, and Schmidt and Faille 2018: 37, figs 64–66). *Trechus patrizii* differs from *T. aethiopicus* by the pronotum with



Figures 30–35. *Trechus* (*Minitrechus*) *patrizii* Jeannel, type labels (**29, 31**) and pronotum (**31, 33–35**). **30, 31.** Holotype, female (UARK); **32, 33.** Paratype, female (MNHN); **34.** Specimen from Mt.Chillalo, locus typicus of *T. patrizii*; **35.** Specimen from Goba, Bale Mts, locus typicus of *T. oromiensis* Magrini, Quéinnec & Vigna Taglianti. The arrows in Figs 32, 33 point to the insertion pores of the seta on laterobasal angles of pronotum (setae are lacking).

smaller laterobasal angles, and by the copulatory piece of the endophallus, which is long and spine-like (short and tube-like in *T. aethiopicus*, see Jeannel 1927: 197, figs 598, 599).

Relationships. Based on the molecular data, *T. patrizii* is representative of a well-supported clade comprising also *T. hagenia* Schmidt & Faille, *T. mekbibi* Schmidt & Faille, and *T. bastianinii* Magrini & Sciaky, all endemic to the Bale Mountains (Fig. 3). Within this clade, *T. patrizii* is identified sister species of *T. bastianinii*.

Distribution. Occurrences of *T. patrizii* are known from the northern slope of the Bale Mountains as well as from the northerly adjacent Arsi volcanos Chillalo, Enculo, and Kaka (Schmidt and Faille 2018; Fig. 1).

Habitat. Based on our field work data, *T. patrizii* is an epedaphic-hemiedaphic species adapted to shadowed and moderately humid soil conditions at altitudes of about 2500–3300 m (Schmidt and Faille 2018). It was found under large stones and by sifting leaf litter in mesophilic *Hagenia* forests and layers of humus shadowed by shrubs and rock faces. It was also found in large numbers in humid soils on shadowed places along mountain streams.

Discussion

Diversity, distribution, and taxonomic reorganization of the Ethiopian Trechina

Our phylogenetic tree shows that all high-altitude trechine species of Ethiopia belong to the subtribe Trechina, contradicting a recent hypothesis that suggests relationships of some afroalpine species with Trechodina (Quéinnec et al. 2021). Consequently, particular morphological character states of the mandibles which are Trechodina-like developed, e.g., in *Aethiopsis*, *Afrotrechus*, *Deuveopsis*, *Nilotrechus*, have to be considered homoplasic. Trechodina representatives occurring in Ethiopia (*Pachydesus*, *Perileptus* and *Trechodes*) are restricted to areas below the high montane zone.

Based on the molecular phylogenetic analyses, the species group diversity of the Ethiopian high-altitude trechines is lower than the taxonomic and morphological data suggest. Within Trechina, we identified only four isolated species groups. Because *Nunbergites* and several *Trechus* (s. l.) species from the Simien Mountains are not included in the analyses, the actual Trechina species group diversity might be slightly higher. However, seven species groups were recently described by Quéinnec et al. (2021) from Mt. Abune Yosef, Mt. Choke and the Guassa Plateau (*Abayopsis*, *Abyssiniopsis*, *Abyssinotus*, *Aethiopsis*, *Afrotrechus*, *Deuveopsis*, *Nilotrechus*). All of them form a single terminal clade within *Trechus* (s. l.). For this clade, we propose the name *Abyssinotus* Quéinnec & Ollivier because it is the first of the species group names introduced in the paper of Quéinnec et al. (2021). The resulting synonymy is summarized in the revised checklist of the Ethiopian Trechini species (below).

Distribution of *Abyssinotus*, in the new sense, is restricted to the mountains north of the Rift Valley. Unfortunately, we could not include species known to occur in the Simien Mountains in our molecular phylogenetic analyses. These mountains are the highest in Ethiopia and situated north of Mt. Abune Yosef and Mt. Choke where *Abyssinotus* is distributed. Pawłowski (2003) suggested close relationships of species occurring in the latter mountains with those from the Simien. In our opinion, there is a high probability that most, if not all, of the *Trechus* (s. l.) species described from the Simien Mountains belong to *Abyssinotus*. However, at the current state of knowledge and with the lack of a phylogenetic analysis, we decided to list these species under *Trechus* subgenus *incertae sedis* (see checklist of the Ethiopian Trechini species, below).

Two of the species groups described from the Bale and Arsi mountains, namely *Archaeotrechus* and *Minitrechus* (Vigna Taglianti and Magrini 2010; Magrini et al. 2012), also form a single terminal clade within *Trechus* (s. l.) in our phylogeny. This highly species-rich clade is endemic to the southern Ethiopian highlands, and we proposed the subgeneric name *Minitrechus* Vigna Taglianti & Magrini for it, due to priority (see checklist of the Ethiopian Trechini species, below). Morphologically, this subgeneric name might be misleading, because *Minitrechus*, in the new sense, besides many tiny species, also includes particularly large ones, such as *T. rotundicollis* (Basilewsky), which is characterized by a body length of up to 7 mm (Basilewsky 1974).

Because the branching pattern of *Abyssinotus* and *Minitrechus* with other lineages of *Trechus* (s. l.) remains unresolved in our phylogeny, the relationships of these subgenera remain unknown. The monotypic *Speotrechus* Jeannel, from the mountains of central France, clusters with *Abyssinotus*, however, with low support. Based on the current data a sister relationship of *Abyssinotus* and *Minitrechus* cannot be excluded.

We could further identify two additional, hitherto unknown Trechina species groups within the Ethiopian fauna which are both endemic to the northern part of the country. One of these, *Abunetrechus* subgen. nov., clusters within *Trechus* (s. l.) and includes three species from Mt. Abune Yosef and the Guassa Plateau. For the type species of *Abunetrechus* subgen. nov., *T. bipartitus*, Jeannel (1927) proposed the group of *T. bipartitus* which, however, is polyphyletic in our analyses because *T. sublaevis* Raffray is placed within the subgenus *Abyssinotus*. *Abunetrechus* subgen. nov. is not related to any of the other Ethiopian *Trechus* clades but represents an isolated lineage within the AAMA clade of *Trechus* (s. l.). Members of this clade (*Abunetrechus*, *Anchotrechus*, *Meruitrechus*, resp. *Arabotrechus*) are characterized by disjunct distributions across widely separated mountains of North and East Africa (Ethiopia, Tenerife, Tanzania, resp. Yemen). Further studies are necessary to elucidate the affinities with the rich trechine fauna of the Elgon Massif.

One of the most surprising results of our study is the finding of *Baehria* gen. nov. in the Choke Mountain of northern Ethiopia. Besides *Nunbergites* (a genus with uncertain taxonomic position), *Baehria* gen. nov., is the only known Trechina taxon that clusters outside the megadiverse *Trechus* (s. l.). The New Zealand endemic *Duvaliomimus* is placed as sister group to *Baehria* gen. nov., and both these groups together are next related to *Paratrechus* from the mountains of northern South America. Given these findings, we assume *Baehria* gen. nov. to be a relic of a species group which was widely distributed on Earth during deep times. However, it is possible that further, so far unidentified members of that clade exist, e.g., in East and Southeast Asia, where the Trechina fauna is particularly rich in lineages but phylogenetically poorly known. Therefore, the sister group relationship of *Baehria* gen. nov. and *Duvaliomimus*, as shown by our molecular data, should be considered as a preliminary hypothesis. Interestingly, both genera, *Duvaliomimus* and *Paratrechus*, were regarded as completely isolated among the respective regional Trechine faunas (Jeannel 1930, 1931; Barr 1982; Townsend 2010). Jeannel (1928) even erected a new "série phylétique" for each of the two genera. Future analyses including Trechina taxa from the whole distribution area of the subtribe may solve the question of whether lineages exist which are likewise members of the BDP clade and closer related to the Ethiopian *Baehria* gen. nov. We consider our results as preliminary with respect to the distribution and species diversity of *Baehria* gen. nov. in Ethiopia. Currently, the genus includes a single species which is distributed on Mt. Choke. Due to the very particular habitat of this species (see section Habitat in species description), and its rheophilic way of life, additional species of the genus could have been overseen by earlier explorers but may occur, e.g., along streams in the afroalpine zone of the Simien Mountains.

Revised checklist of the Ethiopian Trechini species

Our phylogenetic findings and the identification of new taxa result in comprehensive taxonomic changes in the recently published checklist of Ethiopian Trechini species (Quéinnec et al. 2021). The revised checklist is shown below. For references of original descriptions and details of the species' distribution in Ethiopia see Merene et al. (2023).

SUBTRIBE TRECHINA S. STR.

Genus *Baehria* Schmidt & Faille, gen. nov.
  B. separata Schmidt & Faille, sp. nov.

Genus *Nunbergites* Pawłowski & Stachowiak, 1991
  N. aethiopicus Pawłowski & Stachowiak, 1991

Genus *Trechus* Clairville, 1806

Subgenus *Abunetrechus* Schmidt & Faille, subgen. nov.
  A. bipartitus Raffray, 1885
  A. habeshaicus Quéinnec & Ollivier, 2021
  A. lalibelae Quéinnec & Ollivier, 2021

Subgenus *Abyssinotus* Quéinnec & Ollivier, 2021
  = *Abayopsis* Quéinnec & Ollivier, 2021, syn. nov.
  = *Abyssiniopsis* Quéinnec & Ollivier, 2021, syn. nov.
  = *Aethiopsis* Quéinnec & Ollivier, 2021, syn. nov.
  = *Afrotrechus* Quéinnec & Ollivier, 2021, syn. nov.
  = *Deuveopsis* Quéinnec & Ollivier, 2021, syn. nov.
  = *Nilotrechus* Quéinnec & Ollivier, 2021, syn. nov.
  A. abunaensis (Quéinnec & Ollivier, 2021), comb. nov.
  A. abyssinicus (Quéinnec & Ollivier, 2021), comb. nov.
  A. afroalpinus (Quéinnec & Ollivier, 2021), comb. nov.
  A. amharicus Ortuño & Novoa, 2011
  A. basilewskianus (Geginat, 2008): 124
  = *A. minutus* (Basilewsky, 1974)
  A. bunae (Quéinnec & Ollivier, 2021), comb. nov.
  A. chioriae (Quéinnec & Ollivier, 2021), comb. nov.
  A. chokensis Pawłowski, 2001
  A. delantae (Quéinnec & Ollivier, 2021), comb. nov.
  A. dimorphicus Pawłowski, 2001
  A. gigas Pawłowski, 2001
  A. guassaensis (Quéinnec & Ollivier, 2021), comb. nov.
  A. lastaensis (Quéinnec & Ollivier, 2021), comb. nov.
  A. lobeliae (Quéinnec & Ollivier, 2021), comb. nov.
  A. meneliki (Quéinnec & Ollivier, 2021), comb. nov.
  A. niloticus (Quéinnec & Ollivier, 2021), comb. nov.
  A. reebae (Quéinnec & Ollivier, 2021), comb. nov.
  A. sabae Quéinnec & Ollivier, 2021
  A. salomon Quéinnec & Ollivier, 2021
  A. sublaevis Raffray, 1885
  A. wolloi (Quéinnec & Ollivier, 2021), comb. nov.

Subgenus *Minitrechus* Vigna Taglianti & Magrini, 2010
  = *Archeotrechus* Magrini, Quéinnec & Vigna Taglianti, 2012, syn. nov.
  M. abalkhasimi Schmidt & Faille, 2018
  M. adaba Schmidt & Faille, 2018
  M. angavoensis Schmidt & Faille, 2018
  M. baleensis (Basilewsky, 1974)
  M. balesilvestris Schmidt & Faille, 2018
  M. bastianinii Magrini & Sciaky, 2006
  M. batuensis Magrini & Sciaky, 2006
  M. bombi Schmidt & Faille, 2018
  M. chillalicus Jeannel, 1936
  = *M. robini* (Basilewski, 1974)
  M. clarkeianus (Basilewsky, 1974)
  M. colobus Schmidt & Faille, 2018
  M. culminicola Jeannel, 1936
  M. depressipennis Schmidt & Faille, 2018
  M. dodola Schmidt & Faille, 2018
  M. ericalis Magrini, Quéinnec & Vigna Taglianti, 2013
  M. fisehai Schmidt & Faille, 2018
  M. gallorites Jeannel, 1936
  M. grandipennis Schmidt & Faille, 2018
  M. gugheensis Jeannel, 1950
  M. gypaeti Vigna Taglianti & Magrini, 2010
  M. hagenia Schmidt & Faille, 2018
  M. haggei Schmidt & Faille, 2018
  M. harenna Schmidt & Faille, 2018
  M. harryi Schmidt & Faille, 2018
  M. iridescens Schmidt & Faille, 2018
  M. kosso Quéinnec & Ollivier, 2021
  M. mattisi Schmidt & Faille, 2018
  M. mekbibi Schmidt & Faille, 2018
  M. minitrechus Schmidt & Faille, 2018
  M. nanulus Schmidt & Faille, 2018
  M. nigrifemoralis Schmidt & Faille, 2018
  M. oppositus Schmidt & Faille, 2018
  M. patrizzii Jeannel, 1960
  = *M. oromiensis* Magrini, Quéinnec & Vigna Taglianti, 2012, syn. nov.
  M. relictus Magrini, Quéinnec & Vigna Taglianti, 2012
  M. rira Schmidt & Faille, 2018
  M. rotundicollis (Basilewsky, 1974)

M. sanettii Schmidt & Faille, 2018
M. scotti Jeannel, 1936
M. tragelaphus Schmidt & Faille, 2018
M. transversicollis Schmidt & Faille, 2018
M. wiersbowskyi Schmidt & Faille, 2018

Trechus subgenus *incertae sedis*
T. aethiopicus Alluaud, 1918
T. ambarasensis Jeannel, 1954
T. buahitensis Jeannel, 1954
T. degienensis Jeannel, 1954
T. loeffleri Magrini & Sciaky, 2006
T. martelluccii Magrini & Sciaky, 2006
T. peynei Magrini & Sciaky, 2006
T. pilosipennis Jeannel, 1954
T. raffrayanus Jeannel, 1954
T. rougemonti (Basilewsky)
= *T. derougemonti* Geginat, 2017
T. schimperanus Jeannel, 1954
T. simienensis Jeannel, 1954

SUBTRIBE TRECHODINA JEANNEL

Genus *Pachydesus* Motschulsky, 1864
= *Plocamotrechus* Jeannel, 1926
P. aethiopicus Basilewsky, 1974
P. rufipes clarkei Basilewsky, 1972

Genus *Perileptus* Schaum, 1860
= *Ochthephilus* Nietner, 1857 [preocc.]

Subgenus *Parablemus* G. Müller, 1939
P. latimargo G. Müller, 1939

Subgenus *Perileptus* s. str.
P. africanus aethiopicus Jeannel, 1935
P. ledouxi Deuve, 2004

Subgenus *Pyrrotachys* Sloane, 1896
= *Pyrrhotachys* Jeannel, 1926 [unav.]
P. testaceus Putzeys, 1870

Genus *Trechodes* Blackburn, 1901
T. lebioderus (Chaudoir, 1876)
T. lucanerii Magrini, Sciaky & Bastianini, 2005

Historical biogeography

Based on the dated phylogenetic tree, the evolution of the Ethiopian high-altitude fauna started during the Oligocene or Early Miocene, simultaneous with or some million years after the onset of large-scale mountain building in the area which was caused by extensive volcanism about 30 Mya (Hofmann et al. 1997; Table 1). The oldest Trechina lineages endemic to Ethiopia are the *Trechus* subgenera *Abyssinotus* and *Minitrechus*. The trechine phylogeny supports the geological data which show somewhat younger ages for the volcanism on the Somali Plateau in southern Ethiopia (ca. 24 Mya for the Bale Basalts; Abbate and Bruni 2015). Crown ages of southern Ethiopian *Minitrechus* are about 1–3.5 My younger than those of *Abyssinotus*, depending on the dating approach (Table 1). Altogether, these data support the hypothesis of the immigration of ancestral *Trechus* originating from the Cenozoic Boreal. Subsequent diversification takes place as a result of the geomorphological development of the Ethiopian Highlands and the related large-scale development of habitats characterized by extratropical climates (Schmidt and Faille 2018).

Crown ages of the endemic *Trechus* subgenus *Abunetrechus* subgen. nov. and *Baehria* gen. nov. from northern Ethiopian are much younger than *Minitrechus* and *Abyssinotus*, and estimated to a period between the Miocene-Pliocene and the Pliocene-Quaternary boundaries, depending on the dating approach (Table 1). However, the evolution of these groups started much earlier. *Abunetrechus* subgen. nov. separated from the AAMA clade about 10.7 or 17.7 Mya, and *Baehria* gen. nov. from the BDP clade about 15.2 or 22.9 Mya. However, these stem group data have to be treated with caution because we have no information on the stem group evolution, which might have taken place exclusively in the Ethiopian Highlands. Alternatively, additional lineages might exist or might have existed which are stem group members of *Abunetrechus* subgen. nov. or *Baehria* gen. nov., and which are or were distributed outside Ethiopia. Consequently, our dating in both these groups does not provide certain evidence for the respective onset of species group evolution within the Ethiopian Highlands.

Taxonomic remarks on Trechina species groups occurring outside Ethiopia

Earlier studies have proven that *Trechus* (s. l.) *sensu auctorum* represents a polyphyletic assemblage of Trechina (Faille et al. 2013; Maddison et al. 2019). However, a highly species-diverse, monophyletic terminal clade was identified by these studies and by our present phylogenetic analyses, including *Trechus* (s. str.) (= clade 1.3.2.2 in Faille et al. 2013) as well as several additional *Trechus* lineages containing the Ethiopian *Abunetrechus* subgen. nov., *Abyssinotus* sensu novo, and *Minitrechus* sensu novo (Figs 2, 3). Our results also show that two species groups which, based on the currently accepted taxonomy, are considered independent genera outside of *Trechus* (s. l.), are, in fact, ingroup members of this megadiverse genus. One of these groups is the monotypic taxon *Anchotrechus* Jeannel from Tenerife, a member of the AAMA clade of *Trechus* (s. l.). The other one is the monotypic *Speotrechus* Jeannel from central France, with unknown relationships within *Trechus* (s. l.) (Fig. 3). Based on these results, we propose the following taxonomic changes:

Genus *Trechus* Clairville, 1806:
Subgenus *Anchotrechus* Jeannel, 1927, stat. nov.
Subgenus *Speotrechus* Jeannel, 1922, stat. nov.

Conclusions

Our phylogeny of the Ethiopian Trechini beetles shows that the composition of the high-altitude fauna is based on multiple events of immigration which started during the Oligocene or Early Miocene. These results support the habitat island hypothesis proposed by Schmidt and Faille (2018) for the evolution of the Ethiopian highland Trechina fauna. Based on this hypothesis, immigration by flight-active ancestors and subsequent diversification of the trechines occurred almost immediately after the development of extratropical habitats in the course of the Oligocene-Early Miocene volcanism and the resulting uplift of high mountains in the area. In contrast, we found no evidence supporting the alternative hypothesis of a Trechina evolution in Ethiopia aided by Pleistocene cooling (Jeannel 1954b; Mani 1968; Ortuño and Novoa 2011). In the two most species-diverse clades, *Abyssinotus* and *Minitrechus*, diversification started long before the Pliocene and Quaternary periods and continued since then. We, thus, assume that the geomorphological formation of the highlands and the associated development of the local climates were the main drivers of the diversification of the high-altitude Trechina fauna in Ethiopia, rather than the late Cenozoic changes of the global climates.

Up to today, 79 species of Trechina beetles have been described from the Ethiopian Highlands (see species' checklist above). However, this number represents probably only a part of the actual number of species occurring in the country. From our fieldwork, we are aware of several undescribed species (descriptions will be presented elsewhere), and large parts of the Highlands are greatly understudied by carabidologists. All but one of the Ethiopian Trechina species are endemic to single volcanic mountains or valley systems along high mountain slopes, and those mountains with altitudes ≥4000 m a.s.l. are particularly species-rich areas (see summary in Quéinnec et al. 2021). *Trechus patrizii* is the only species known to occur on the Arsi Volcanoes as well as in the Bale Mts. We, therefore, assume that the Cenozoic uplift of the volcanic massifs on both sides of the Rift Valley led to massive, if not explosive, radiation of the regional carabid beetle fauna as it was likewise described from other volcanic mountains of lower latitudes, e.g. the Canary Islands (Contreras-Díaz et al. 2007) and Hawaii (Liebherr 2015). It remains unknown whether the phylogenetic position of the enigmatic new genus *Baehria* contrasts with this scenario. Future studies using a larger taxon sampling are required to show whether *Baehria* gen. nov. is a relic of a moderately old Trechina lineage with its ancestor having immigrated to the Ethiopian Highlands at about the same time as the ancestors of the highly species diverse *Abyssinotus* and *Minitrechus*.

Given the limited taxon and gene sampling our evolutionary scenarios have to be considered preliminary. Also, the results of our study do not allow for conclusions concerning the relationship between the species diverse North Ethiopian *Trechus* clade (*Abyssinotus*) and the likewise diverse South Ethiopian clade (*Minitrechus*). It remains open whether the evolution of these groups results from a single Oligocene-Early Miocene immigration event from the Cenozoic Boreal. Alternatively, independent immigrations of two ancestral trechines into two separated volcanic areas of the country, which were uplifted at different times, are possible. Especially species of the Simien Mountains in Ethiopia, including the enigmatic genus *Nunbergites*, representatives of the diverse Trechina fauna from the Elgon Massif, and additional Holarctic Trechina lineages need to be included in future molecular analyses to better understand the relationships of the Ethiopian lineages. Moreover, using a larger number of molecular markers may improve the resolution of the more basal branches in the phylogenetic tree.

Evidence emerged from our study regarding the taxonomic positions of most of the trechine groups known to occur in Ethiopia. We could reject an earlier hypothesis of potential relationships of some of the highland trechines with Trechodina (Quéinnec et al. 2021). Further, we could show that the species group diversity is much lower than suspected by earlier authors. Consequently, morphological character states which were used to define species groups on subtribal, genus or subgenus levels, for the Ethiopian high-altitude fauna are often unsuitable to define natural groups, e.g. bidentate or tridentate mandibles, patterns of chaetotaxy and pilosity, the number of dilated male protarsomeres and the extent of the dorsal closure of the aedeagal median lobe (e.g., Pawłowski 2003; Vigna Taglianti and Magrini 2010; Magrini et al. 2012; Quéinnec et al. 2021). In fact, the molecular data demonstrate that the high morphological diversity in both, the northern and the southern Ethiopian *Trechus* clades, *Abyssinotus* and *Minitrechus*, are the result of independent morphological radiations within these clades. These radiations might have been fostered by i) the absence or very limited presence of additional hygrophilic ground beetles in the high-altitude forests of Ethiopia, such as Nebriini, Patrobini, Platynini and Pterostichini, and ii) interspecific concurrence. The latter argument is supported by the fact that up to eight *Abyssinotus* species can be found syntopically, e.g., along slopes of Mt. Choke (own unpubl. data). Within trechine beetles, this is a unique ecologic-faunistic phenomenon, supporting Jeannel's observation on the abundance of *Trechus* on Mount Elgon (Jeannel 1950). Detailed morphological studies, intensive fieldwork and a significant extension of the molecular databases are required to test these hypotheses and to understand the evolution of the high diversity of Trechina species and their morpho-types in the Ethiopian Highlands.

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References

Abbate E, Bruni P (2015) Geology of Ethiopia: A review and geomorphological perspectives. In: Billi P (Ed.) Landscapes and Landforms of Ethiopia. Springer International Publishing, 33–63. https://doi.org/10.1007/978-94-017-8026-1_2

Andújar C, Serrano J, Gómez-Zurita J (2012) Winding up the molecular clock in the genus *Carabus* (Coleoptera: Carabidae): Assessment of methodological decisions on rate and node age estimation. BMC Evolutionary Biology 12(1): 1–16. https://doi.org/10.1186/1471-2148-12-40

Barr Jr TC (1982) The trechine beetles of the *Paratrechus* series in México and Central America, with special reference to the cave species (Coleoptera: Carabidae: Trechinae). Association for Mexican Cave Studies Bulletin 8: 193–236.

Basilewsky P (1974) Les Placomotrechina d'Ethiopie (Col. Carabidae Trechinae). Revue de Zoologie Africaine 88(1): 148–158.

Belousov IA (1998) Le Complexe Générique de *Nannotrechus* Winkler du Caucase et de la Crimée (Coleoptera, Carabidae, Trechini). Pensoft, Sofia, 256 pp.

Bouckaert R, Vaughan TG, Barido-Sottani J, Duchêne S, Fourment M, Gavryushkina A, Heled J, Jones G, Kühnert D, De Maio N, Matschiner M, Mendes FK, Müller NF, Ogilvie HA, du Plessis L, Popinga A, Rambaut A, Rasmussen D, Siveroni I, Suchard MA, Wu C-H, Xie D, Zhang C, Stadler T, Drummond AJ (2019) BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. PLoS Computational Biology 15(4): e1006650. https://doi.org/10.1371/journal.pcbi.1006650

Casale A, Laneyrie R (1982) Trechodinae et Trechinae du monde. Tableau des sous-familles, tribus, séries phylétiques, genres, et catalogue général des espèces. Memoires de Biospeologie 9: 1–226.

Contreras-Díaz HG, Moya O, Oromí P, Juan C (2007) Evolution and diversification of the forest and hypogean ground-beetle genus *Trechus* in the Canary Islands. Molecular Phylogenetics and Evolution 42(3): 687–699. https://doi.org/10.1016/j.ympev.2006.10.007

Deuve T (2004) Nouveaux Trechidae d'Afrique et d'Asie. Coléoptères 10(19): 215–234.

Geginat G (1995) Die Verbreitung der Gattungen *Trechus* und *Pachydesus* in den Gebirgen Zentral- und Ostafrikas (Coleoptera, Carabidae, Trechinae). Verhandlungen Westdeutscher Entomologentag 1994, Löbbecke-Museum, Düsseldorf: 89–96.

Geginat G (2008) Revision of the genus *Cothresia* Jeannel, 1964 (Coleoptera: Carabidae: Trechinae: Trechodina). Annals of the Transvaal Museum 45: 115–126.

Faille A, Ribera I, Deharveng L, Bourdeau C, Garnery L, Quéinnec E, Deuve T (2010) A molecular phylogeny shows the single origin of the Pyrenean subterranean Trechini ground beetles (Coleoptera: Carabidae). Molecular Phylogenetics and Evolution 54(1): 97–106. https://doi.org/10.1016/j.ympev.2009.10.008

Faille A, Casale A, Ribera I (2011) Phylogenetic relationships of Western Mediterranean subterranean Trechini ground beetles (Coleoptera: Carabidae). Zoologica Scripta 40(3): 282–295. https://doi.org/10.1111/j.1463-6409.2010.00467.x

Faille A, Casale A, Balke M, Ribera I (2013) A molecular phylogeny of alpine subterranean Trechini (Coleoptera: Carabidae). BMC Evolutionary Biology 13(1): e248. https://doi.org/10.1186/1471-2148-13-248

Faille A, Andújar C, Fadrique F, Ribera I (2014) Late Miocene origin of a Ibero-Maghrebian clade of ground beetles with multiple colonisations of the subterranean environment. Journal of Biogeography 41(10): 1979–1990. https://doi.org/10.1111/jbi.12349

Faille A, Balart-García P, Fresneda J, Bourdeau C, Ribera I (2021) A remarkable new genus of Iberian troglobitic Trechodina (Coleoptera: Carabidae: Trechinae: Trechini), with a revisited molecular phylogeny of the subtribe. Annales de la Société entomologique de France (N.S.) 57(2): 85–106. https://doi.org/10.1080/00379271.2021.1880339

Fresneda J, Valenzuela E, Bourdeau C, Faille A (2019) Nouvelles espèces de *Trechus* Clairville, 1806 du clade de *T. saxicola* des monts Cantabriques, Asturies, Espagne –biogéographie et spéciation (Coleoptera: Carabidae: Trechinae). Annales de la Société entomologique de France (N.S.) 55(1): 17–47. https://doi.org/10.1080/00379271.2018.1546553

Hall TA (1999) BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.

Hofmann C, Courtillot V, Féraud G, Rochette P, Yirgu G, Ketefo E, Pik R (1997) Timing of the Ethiopian flood basalt event and implications for plume birth and global change. Nature 389(6653): 838–841. https://doi.org/10.1038/39853

Jeannel R (1926) Monographie des Trechinae. Morphologie comparée et distribution géographique d'un groupe de Coléoptères (Première livraison). L'Abeille. Journal d'Entomologie 32: 221–550.

Jeannel R (1927) Monographie des Trechinae. Morphologie comparée et distribution géographique d'un groupe de Coléoptères (Deuxième livraison). L'Abeille. Journal d'Entomologie 33: 1–592.

Jeannel R (1928) Monographie des Trechinae. Morphologie comparée et distribution géographique d'un groupe de Coléoptères (Troisième livraison). L'Abeille. Journal d'Entomologie 35: 1–808.

Jeannel R (1930) Monographie des Trechinae. Morphologie comparée et distribution géographique d'un groupe de coléoptères. Supplément. (Quatrième livraison). L'Abeille. Journal d'Entomologie 34(2): 59–122.

Jeannel R (1931) Révision des Trechinae de l'Amérique du Nord. Archives de Zoologie Expérimentale et Générale 71: 403–499.

Jeannel R (1950) Hautes montagnes d'Afrique. Vers les neiges éternelles sous l'Équateur. Avec un appendice sur les montagnes du Choa et du Chillalo par Hugh Scott, ScD, FRS, FLS. Publications des Éditions du Muséum, Paris, suppl. n°1, 252 pp.

Jeannel R (1954a) Les *Trechus* du Mont Elgon (Coleoptera Trechidae). Mémoires du Muséum national d'Histoire naturelle, n.s., série A. Zoologie 7(2): 147–177.

Jeannel R (1954b) Les *Trechus* du Simiène récoltés par le Dr H. Scott en 1952, (Coleoptera Trechidae) avec les planches I et II. Revue française d'Entomologie 21(3): 171–183. [+ 2 plates]

Jeannel R (1960) Un nouveau *Trechus* de l'Abyssinie. Revue Française d'Entomologie 27(4): 265–266.

Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics 20(4): 1160–1166. https://doi.org/10.1093/bib/bbx108

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A (2012) Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28(12): 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Liebherr JK (2015) The *Mecyclothorax* beetles (Coleoptera, Carabidae, Moriomorphini) of Haleakalā, Maui: Keystone of a hyperdiverse Hawaiian radiation. ZooKeys 544: 1–407. https://doi.org/10.3897/zookeys.544.6074

Lorenz W (2005) Systematic List of Extant Ground Beetles of the World (Insecta Coleoptera "Geadephaga": Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodinae) (2nd edn.). Published by the author, Tutzing, 530 pp.

Maddison DR, Kanda K, Boyd OF, Faille A, Porch N, Erwin TL, Roig-Juñent S (2019) Phylogeny of the beetle supertribe Trechitae (Coleoptera: Carabidae): unexpected clades, isolated lineages, and morphological convergence. Molecular Phylogenetics and Evolution 132: 151–176. https://doi.org/10.1016/j.ympev.2018.11.006

Magrini P, Quéinnec E, Vigna Taglianti A (2012) A new subgenus and two new species of *Trechus* from Ethiopia (Coleoptera, Carabidae). Fragmenta entomologica, Roma 44(1): 19–32. https://doi.org/10.4081/fe.2012.30

Magrini P, Sciaky R, Bastianini M (2005) A new *Trechodes* species from Ethiopia (Coleoptera Carabidae). In: Cavanna C (Ed.) Wolayta: una Regione d'Etiopia, Studi e richerche (1995–2004). Atti del Museo di Storia Naturale della Maremma 21(suppl.): 167–173.

Mani MS (1968) Ecology and Biogeography of High Altitude Insects. Junk Publishers, The Hague, 527 pp. https://doi.org/10.1007/978-94-017-1339-9

Merene Y, Lorenz W, Opgenoorth L, Woldehawariat Y, Schmidt J (2023) Ground and tiger beetles (Coleoptera: Carabidae, Cicindelidae) of the Federal Democratic Republic of Ethiopia: a provisional faunistic checklist based on literature data. Zootaxa 5247(1): 1–345. https://doi.org/10.11646/zootaxa.5247.1.1

Naito T (2023) A new subgenus of *Epaphiopsis* Uéno, 1953 (Coleoptera, Carabidae, Trechini) discovered in the mountains of South-East Asia and a new species of subgenus *Allepaphiama* with atypical characteristics. Annales de la Société Entomologique de France 59(4): 285–311. https://doi.org/10.1080/00379271.2023.2218335

Ortuño VM, Novoa F (2011) A new species of *Trechus* from the Ethiopian Highlands (Coleoptera: Carabidae: Trechinae) and key to the *Trechus* species of Ethiopia. Annals of the Entomological Society of America 104(2): 132–140. https://doi.org/10.1603/AN10122

Pawłowski J (2001) Le genre *Trechus* Clairville, 1806 (Coleoptera: Carabidae: Trechini) dans la collection Èthiopienne du Musée Royal de l'Afrique Centrale. I. Groupe du *T. chokiensis*. Elytron 15: 97–108.

Pawłowski J (2003) Preliminary report on Ethiopian species of the genus *Trechus* Clairville, 1806 (Coleoptera: Carabidae). Baltic Journal of Coleopterology 3(2): 157–160.

Pawłowski J, Stachowiak M (1991) *Nunbergites aethiopicus* gen. et sp. n. – an anophthalmic beetle (Coleoptera, Carabidae) from northern Ethiopia. Polskie Pismo Entomologiczne 61: 39–45.

Quéinnec E, Ollivier E, Reeb C (2021) Insights on Ethiopian montane ground beetle biodiversity: Taxonomic study of afro-alpine and sub-alpine Trechini (Coleoptera: Carabidae: Trechinae). Journal of Insect Biodiversity 27(1): 1–70. https://doi.org/10.12976/jib/2021.27.1.1

Raffray A (1885) Note sur la dispersion géographique des coléoptères en Abyssinie et descriptions d'espèces nouvelles. Annales de la Société Entomologique de France 6(5): 293–326. [+ 1 plate]

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarization in bayesian phylogenetics using Tracer 1.7. Systematic Biology 67(5): 901–904. https://doi.org/10.1093/sysbio/syy032

Rowley DL, Coddington JA, Gates MW, Norrbom AL, Ochoa RA, Vandenberg NJ, Greenstone MH (2007) Vouchering DNA-barcoded specimens: Test of a nondestructive extraction protocol for terrestrial arthropods. Molecular Ecology Notes 7(6): 915–925. https://doi.org/10.1111/j.1471-8286.2007.01905.x

Schmidt J, Faille A (2018) Revision of *Trechus* Clairville, 1806 of the Bale Mountains and adjacent volcanos, Ethiopia (Coleoptera, Carabidae, Trechini). European Journal of Taxonomy 446(446): 1–82. https://doi.org/10.5852/ejt.2018.446

Schmidt J, Scholz S, Maddison DR (2021) *Balticeler kerneggeri* gen. nov., sp. nov., an enigmatic Baltic amber fossil of the ground beetle subfamily Trechinae (Coleoptera, Carabidae). Deutsche Entomologische Zeitschrift 68(1): 207–224. https://doi.org/10.3897/dez.68.66181

Shi G, Grimaldi DA, Harlow GE, Wang J, Wang J, Yang M, Lei W, Li Q, Li X (2012) Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research 37: 155–163. https://doi.org/10.1016/j.cretres.2012.03.014

Stamatakis A (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22(21): 2688–2690. https://doi.org/10.1093/bioinformatics/btl446

Stamatakis A (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30(9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Townsend JI (2010) Trechini (Insecta: Coleoptera: Carabidae: Trechinae). Fauna of New Zealand 62. Manaaki Whenua Press, Lincoln, 101 pp.

Vigna Taglianti A, Magrini P (2010) A new subgenus and a new species of *Trechus* from Ethiopia (Coleoptera, Carabidae). Fragmenta entomologica, Roma 41(1): 69–76. https://doi.org/10.4081/fe.2009.82

Supplementary material 1

Material used in the study with voucher IDs, locality data, and accession numbers of the sequences

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Data type: docx

Link: https://doi.org/10.3897/dez.70.107425.suppl1

Supplementary material 2

Primers used for DNA amplification and sequencing

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