

A taxonomic reorganization of European *Trechus* CLAIRVILLE, 1806 (Coleoptera: Carabidae: Trechinae)

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Abstract

The European species of the poly- and paraphyletic genus *Trechus* CLAIRVILLE, 1806 are reorganized in monophyletic genera, subgenera and species groups, according to published molecular phylogenies: Three genera are introduced to resolve the polyphyly: *Epaphius* LEACH, 1819 stat.rev., *Mediterranoblemus* gen.n., and *Trechus* in a new scope. The genus *Epaphius* LEACH, 1819 stat.rev. is divided into three subgenera: *Epaphius* s.str., *Trechoepaphius* subgen.n. and *Alpinoepaphius* subgen.n. The genus *Trechus* is divided into a total of 18 subgenera; 13 of these are new: *Austriatrechus* subgen.n., *Balcanotrechus* subgen.n., *Dinarotrechus* subgen.n., *Eurotrechus* subgen.n., *Italotrechus* subgen.n., *Latotrechus* subgen.n., *Lepontinotrechus* subgen.n., *Mediterranotrechus* subgen.n., *Montanotrechus* subgen.n., *Nigrinotrechus* subgen.n., *Orinotrechus* subgen.n., *Oropatrechus* subgen.n., and *Penninotrechus* subgen.n. Two genera are downgraded to subgenera of *Trechus*: *Apoduvalius* JEANNEL, 1953 stat.n. from the Iberian Peninsula and *Irinea* MATEAU & COMAS, 2006 stat.rev. from Morocco. Two former taxa – previously synonymized with *Trechus* s.str. – are re-established in the rank of subgenera: *Antoinella* JEANNEL, 1937 stat.n. and *Calotrechus* WOLLASTON, 1854 subgen.rev. A new synonym among subgenera is established: *Atlantotrechus* LOMPE, 1999 syn.n. = *Calotrechus* WOLLASTON, 1854 subgen.rev.

A total of 342 species are assigned within this new generic and subgeneric arrangement, based on molecular data of 187 species. All remaining former species of *Trechus* s.str. (several hundred species) are treated as *Trechus* incertae sedis.

Thirty-six new combinations are established: Seventeen species are transferred from *Trechus* to *Epaphius*: *E. amplicolis* (FAIRMAIRE, 1859) comb.n., *E. apicalis* (MOTSCHULSKY, 1865) comb.n., *E. chalybaeus* (DEJEAN, 1831) comb.n., *E. coloradensis* (SCHAEFFER, 1915) comb.n., *E. crassiscapus* (LINDROTH, 1955) comb.n., *E. oregonensis* (HATCH, 1951) comb.n., *E. rubens* (FABRICIUS, 1792) comb.n., *E. tenuiscapus* (LINDROTH, 1961) comb.n., *E. yvesbousqueti* (DONABAUER, 2010) comb.n., *E. alpicola* (STURM, 1825) comb.n., *E. latibuli* (JEANNEL, 1948) comb.n., *E. limacodes* (DEJEAN, 1831) comb.n., *E. ochreateus* (DEJEAN, 1927) comb.n., *E. ovatus* (PUTZEYS, 1845) comb.n., *E. pinkeri* (GANGLBAUER, 1892) comb.n., *E. rudolphi* (GANGLBAUER, 1891) comb.n., and *E. wagneri* (GANGLBAUER, 1906) comb.n. Four species are transferred from *Trechus* to *Mediterranoblemus* subgen.n.: *M. barratxinai* (ESPAÑOL, 1971) comb.n.; *M. cruciatus* (PIOCHARD DE LA BRULERIE, 1876) comb.n., *M. diecki* (PUTZEYS, 1870) comb.n., and *M. schaufussi* (PUTZEYS, 1870) comb.n. One species is transferred from *Irinea* to *Trechus*: *T. (Irinea) aurouxi* (MATEU & COMAS, 2006) comb.n. Fourteen species are transferred from *Apoduvalius* to *Trechus* (*Apoduvalius*): *T. alberichae* (ESPAÑOL, 1971) comb.n., *T. aphaenopsianus* (ESPAÑOL & VIVES, 1983) comb.n., *T. asturiensis* (SALGADO, 1991) comb.n., *T. champagnati* (SALGADO, 1991) comb.n., *T. drescoi* (JEANNEL, 1953) comb.n., *T. espanoli* (SALGADO, 1996) comb.n., *T. franzi* (JEANNEL,

1958) comb.n., *T. lecoqi* (DEUVE, 1991) comb.n., *T. leonensis* (SALGADO & ORTUÑO, 1998) comb.n., *T. nalonii* (SALGADO, 1993) comb.n., *T. negrei* (JEANNEL, 1953) comb.n., *T. purroyi* (SALGADO, 1987) comb.n., *T. salgadoi* (CARABAJAL, GARCÍA & RODRÍGUEZ, 2002) comb.n., and *T. serrae* (VIVES, 1976) comb.n.

Key words: Carabidae, Trechinae, *Trechus*, *Epaphius*, new genus, new subgenera, new combinations, new synonym, Europe, taxonomy.

Zusammenfassung

Die europäischen Arten der poly- und paraphyletischen Gattung *Trechus* CLAIRVILLE, 1806 werden in monophyletische Gattungen, Untergattungen und Artengruppen reorganisiert, gemäß publizierten molekularen Phylogenien: Drei Gattungen werden eingeführt, um die Polyphylie aufzulösen: *Epaphius* LEACH, 1819 stat.rev., *Mediterranoblemus* gen.n. und *Trechus* in einem völlig neuen Umfang. Die Gattung *Epaphius* LEACH, 1819 stat.rev. wird in drei Untergattungen eingeteilt: *Epaphius* s.str., *Trechoepaphius* subgen.n. und *Alpinoepaphius* subgen.n. Die Gattung *Trechus* wird in 18 Untergattungen eingeteilt, 13 davon sind neu: *Austriatrechus* subgen.n., *Balkanotrechus* subgen.n., *Dinarotrechus* subgen.n., *Eurotrechus* subgen.n., *Italotrechus* subgen.n., *Latotrechus* subgen.n., *Lepontinotrechus* subgen.n., *Mediterranotrechus* subgen.n., *Montanotrechus* subgen.n., *Nigrinotrechus* subgen.n., *Orinotrechus* subgen.n., *Oropatrechus* subgen.n. und *Penninotrechus* subgen.n. Zwei Gattungen werden zu Untergattungen von *Trechus* herabgestuft: *Apoduvalius* JEANNEL, 1953 stat.n. von der Iberischen Halbinsel und *Irinea* MATEAU & COMAS, 2006 stat.n. von Marokko. Zwei Taxa, die vorher mit *Trechus* s.str. synonymisiert waren, werden im Rang von Untergattungen wiederhergestellt: *Antoinella* JEANNEL, 1937 stat.n. und *Calotrechus* WOLLASTON, 1854 subgen.rev. Ein neues Synonym wird erstellt: *Atlantotrechus* LOMPE, 1999 syn.n. = *Calotrechus* WOLLASTON, 1854 subgen.rev.

Insgesamt 342 Arten werden in diese neue Gattungs- und Untergattungseinteilung eingeordnet, basierend auf molekularen Daten von 187 Arten. Alle verbleibenden bisherigen *Trechus* s.str. (mehrere hundert Arten) werden als *Trechus incertae sedis* behandelt.

36 neue Kombinationen werden eingeführt: Siebzehn Arten werden von *Trechus* zu *Epaphius* überführt: *E. amplicolis* (FAIRMAIRE, 1859) comb.n., *E. apicalis* (MOTSCHULSKY, 1865) comb.n., *E. chalybaeus* (DEJEAN, 1831) comb.n., *E. coloradensis* (SCHAEFFER, 1915) comb.n., *E. crassiscapus* (LINDROTH, 1955) comb.n., *E. oregonensis* (HATCH, 1951) comb.n., *E. rubens* (FABRICIUS, 1792) comb.n., *E. tenuiscapus* (LINDROTH, 1961) comb.n., *E. yvesbousqueti* (DONABAUER, 2010) comb.n., *E. alpicola* (STURM, 1825) comb.n., *E. latibuli* (JEANNEL, 1948) comb.n., *E. limacodes* (DEJEAN, 1831) comb.n., *E. ochreateus* (DEJEAN, 1927) comb.n., *E. ovatus* (PUTZEYS, 1845) comb.n., *E. pinkeri* (GANGLBAUER, 1892) comb.n., *E. rudolphi* (GANGLBAUER, 1891) comb.n. und *E. wagneri* (GANGLBAUER, 1906) comb.n. Vier Arten werden von *Trechus* zu *Mediterranoblemus* subgen.n. überstellt: *M. barratxinai* (ESPAÑOL, 1971) comb.n.; *M. cruciatus* (PIOCHARD DE LA BRULERIE, 1876) comb.n., *M. diecki* (PUTZEYS, 1870) comb.n. und *M. schaufussi* (PUTZEYS, 1870) comb.n. Eine Art wird von *Irinea* zu *Trechus* überführt: *T. (Irinea) aurouxii* (MATEU & COMAS, 2006) comb.n. Vierzehn Arten werden von *Apoduvalius* zu *Trechus* (*Apoduvalius*) gestellt: *T. alberichae* (ESPAÑOL, 1971) comb.n., *T. aphaenopsianus* (ESPAÑOL & VIVES, 1983) comb.n., *T. asturiensis* (SALGADO, 1991) comb.n., *T. champagnati* (SALGADO, 1991) comb.n., *T. drescoi* (JEANNEL, 1953) comb.n., *T. espanoli* (SALGADO, 1996) comb.n., *T. franzi* (JEANNEL, 1958) comb.n., *T. lecoqi* (DEUVE, 1991) comb.n., *T. leonensis* (SALGADO & ORTUÑO, 1998) comb.n., *T. nalonii* (SALGADO, 1993) comb.n., *T. negrei* (JEANNEL, 1953) comb.n., *T. purroyi* (SALGADO, 1987) comb.n., *T. salgadoi* (CARABAJAL, GARCÍA & RODRÍGUEZ, 2002) comb.n. und *T. serrae* (VIVES, 1976) comb.n.

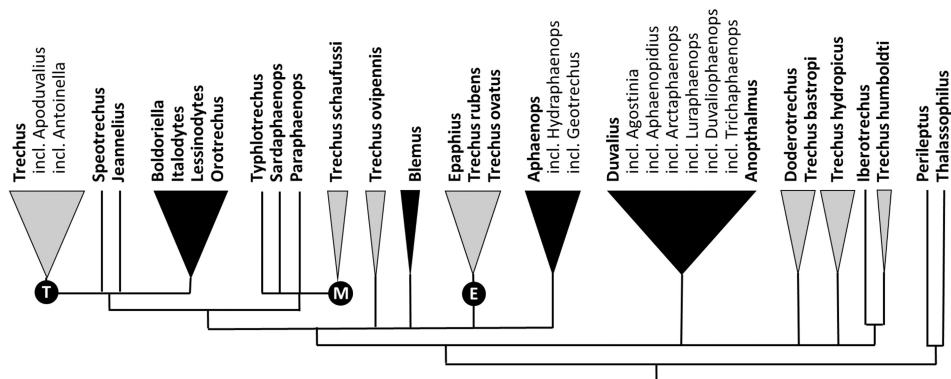


Fig. 1: Phylogeny of Trechini (redrawn from FAILLE et al. 2013, combined with results of MADDISON et al. 2019), demonstrating multiple polyphyly and paraphyly of former *Trechus* and other genera of Trechini. Clades including taxa of former *Trechus* in grey. T = *Trechus* clade; M = *Mediterranoblemus* gen.n.; E = *Epaphius* clade.

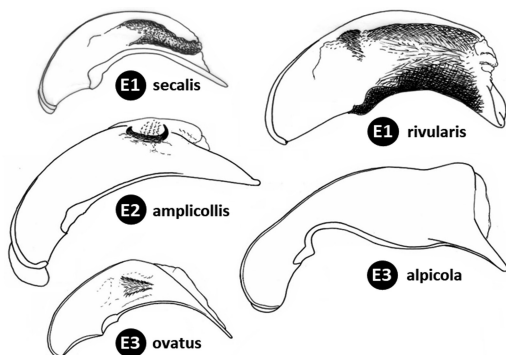
Introduction

The tribe Trechini is a group of small ground beetles with a worldwide distribution, extraordinarily diverse in species (MADDISON et al. 2019). Some winged species excepted, the majority are incapable of flight and adapted to a hidden life on or in the ground, preferring moist and cool microclimates. This mode of life led to hundreds of species with restricted distribution and with some highly derived body shapes, especially in the subterranean environment. This tribe was monographed by JEANNEL (1926, 1927, 1928) and his arrangement into genera, subgenera and species groups was kept until today (CASALE & LANEYRIE 1982, MORAVEC et al. 2003, LÖBL & LÖBL 2017), although dozens of new genera and hundreds of new species have been described since then. Interestingly, Jeannel followed two very distinct taxonomic strategies within Trechini: Most of the epigeal “primitive” species of the northern hemisphere were “lumped” together in the huge genus *Trechus*, avoiding the usage of subgenera. Informal species groups were used instead, partly defined primarily on geographical considerations. On the other hand, the endogean “derived” taxa were “split” into many genera.

The megadiverse carabid genus *Trechus* (ca. 1,300 taxa) is the nominate genus of the tribe Trechini, mainly consisting of epigeal and Holarctic species. Most taxa are aggregated in the subgenus *Trechus* s.str. Neither the genus nor the subgenus can be defined by any set of characteristics and the genus in the present sense may be understood as all “normally shaped” Trechini of the northern hemisphere lacking special characteristics. The phylogeny of *Trechus* was never elaborated due to two main reasons: First, it is almost impossible to have an overview of that many species, which are often incompletely sampled in collections due to rarity and extremely restricted distribution. Second, the widespread convergence in external features of distinct species inhabiting similar ecological niches makes a morphology-based phylogenetic placement extremely difficult.

Expressed in numbers: The latest catalogue of palaearctic Carabidae (LÖBL & LÖBL 2017) lists 178 genera of Trechini and a total of 2,933 valid taxa of the species group including 1,027 taxa of *Trechus*. Thus, the genus *Trechus* represents just 0.56% of the genera but 35% of the species taxa.

Genus *Epaphius*



Genus *Trechus*

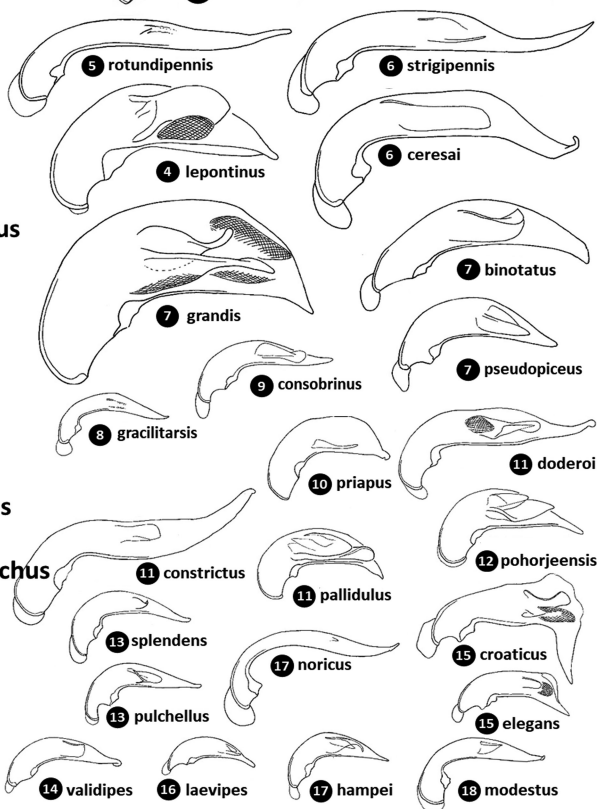
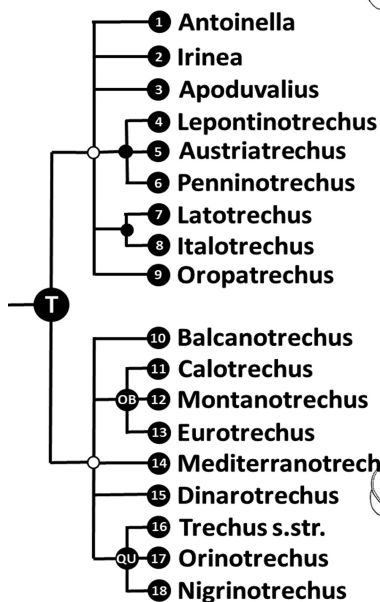


Fig. 2: Schematic phylogeny of subgenera of *Epaphius* and *Trechus*. Male aedeagi of representative species from Europe. The black nodes are numbered according to the sequence of subgenera in the catalogue section.

In recent years, MADDISON et al. (2019) and FAILLE et al. (2010, 2011, 2012, 2013, 2014) sequenced mitochondrial and nuclear genes of many Trechini and achieved highly interesting results about the phylogeny of global Trechini and several European derived subterranean clades. A fundamental reorganization of Trechini was indicated, but not implemented.

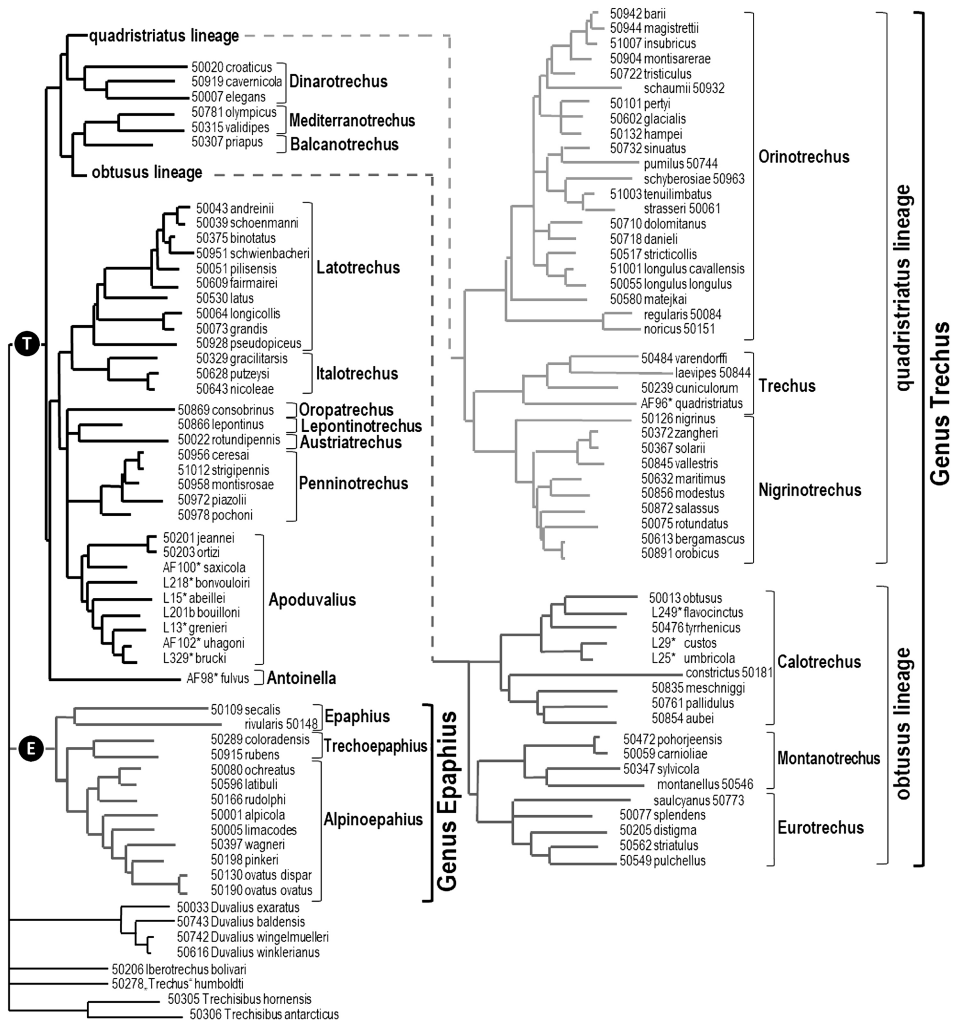


Fig. 3: Phylogeny of *Epaphius* and *Trechus* calculated on a combined dataset (partial 28S rRNA gene and mitochondrial partial COI gene concatenated) of sequences from FAILLE et al. (2012, marked with an asterisk “*”) and material of the author (voucher IDs starting with 50 or 51). Selected records can be downloaded from GENBANK and are identifiable by species name and voucher code. Phylogeny is inferred using the Maximum Likelihood method on the General Time Reversible Model, conducted in MEGA7.

As a side effect, the genus *Trechus* was demonstrated to be both polyphyletic and paraphyletic (Fig. 1). Additional molecular phylogenies have been published of *Trechus* from the Canary Islands (CONTRERAS-DÍAZ et al. 2007), of an alpine group of closely related *Trechus* from the southern Alps (LOHSE et al. 2010) and of *Trechus* from the Cantabrian mountains (FRESNEDA et al. 2019).

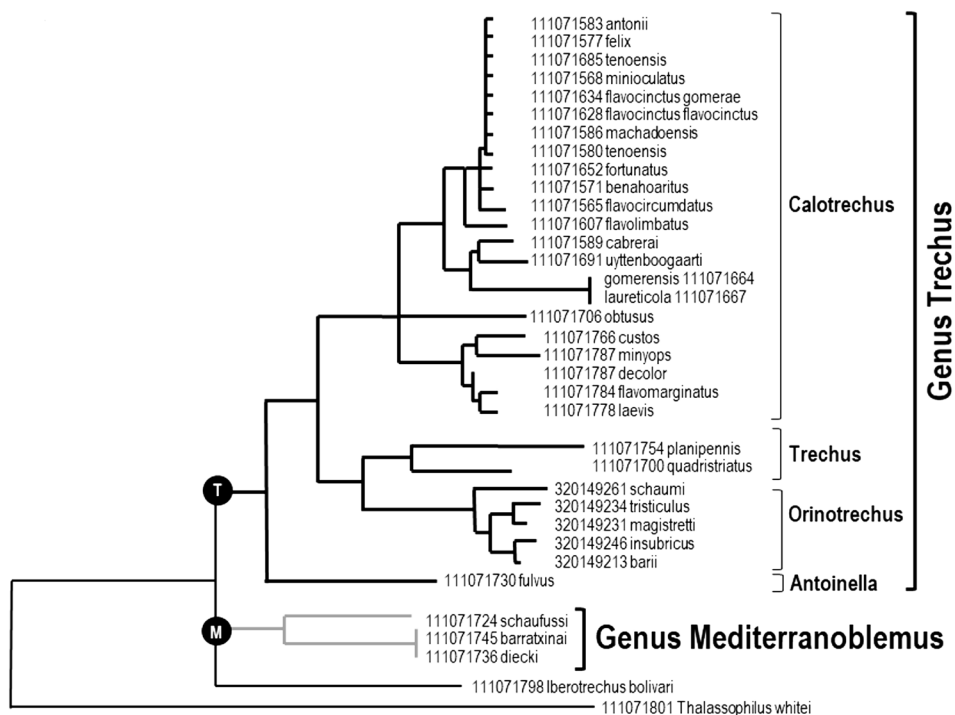


Fig. 4: Phylogeny of *Mediterranoblemus* and *Trechus* calculated on a dataset (mitochondrial partial COI/II gene and tRNA-Leu gene) of comparable sequences from CONTRERAS-DÍAZ et al. (2007) and LOHSE et al. (2010). Selected records downloaded from GENBANK (2019) and identifiable by species name and GI-Code. Phylogeny is inferred using the Maximum Likelihood method on the General Time Reversible Model, conducted in MEGA7.

Encouraged by Faille's work, the author collected approximately one thousand specimens of one hundred taxa of *Trechus* in pure alcohol. This material was partly sequenced by the University of Innsbruck (ARTHOFFER et al., submitted) and the sequences are published on GENBANK. The combination of these new and previously published data of in total 187 *Trechus* species combined with morphological comparison paints a clear picture of the phylogeny of European *Trechus* for the first time (Fig. 3). The main purpose of this paper is the rearrangement of European *Trechus* into monophyletic genera, subgenera and species groups according to the results of published molecular phylogenies.

Material and methods

All hitherto published molecular phylogenies of *Trechus* have been studied (CONTRERAS-DÍAZ et al. 2007, LOHSE et al. 2010, FAILLE et al. 2010, 2011, 2012, 2013, 2014, FRESNEDA et al. 2019, MADDISON et al. 2019, ARTHOFFER et al., submitted). Additionally, comparable molecular sequences of different studies were downloaded from GENBANK (1,773 sequences) and BARCODING OF LIFE DATABASE (BOLD; 529 sequences), aligned with Clustal X and

analysed with Mega 7, using the GTR+G+I as the evolutionary model on combined datasets. Two examples of such an analysis are given in Figures 3 and 4: For the construction of the phylogenetic trees presented herein, a total of 259 molecular sequences were used (112 COI, 35 mitochondrial partial COX1 gene, partial COX2 gene and tRNA-Leu gene, 112 28S rRNA). The main purpose of these calculations was the assignment of taxa into major hierarchies, and not sophisticated statistical analysis.

In total, genetic sequences of 187 species of *Trechus* were analysed; these taxa are marked with an asterisk (*) in the catalogue section. Based on these published or calculated phylogenies, 342 species of *Trechus* were arranged within a new taxonomic framework, covering most of the European and North African taxa of former *Trechus*. In addition, morphological characteristics (especially habitus and aedeagal characteristics), distributional patterns and mode of life were taken into account. For example, five out of eleven species from the *Trechus strigipennis* group could be included in a molecular phylogeny (Fig. 3). All remaining species share an almost identical habitus, are alpine endemics of a compact area within the southern Alps and can be distinguished by aedeagal differences only. Thus, it was concluded that these eleven taxa belong to a monophyletic clade as already suggested by previous authors (JEANNEL 1927, MONGUZZI 2002).

Due to the vast number of taxa treated herein, the text needs to be restricted to an absolute minimum. Descriptions and figures are replaced by references to books and publications (especially JEANNEL 1927). Synonyms and subspecies are not listed here; the reader is advised to refer to catalogues (MORAVEC et al. 2003, LÖBL & LÖBL 2017). Molecular phylogenies are not discussed in detail, just summarized in phylogenetic trees (Figs. 1–4) to support taxonomic decisions.

All remaining *Trechus* s.str. – still several hundred species – should be treated as *Trechus incertae sedis* and not as *Trechus* s.str., as previously done.

Results

Generic rearrangement of the former genus *Trechus*

The former genus *Trechus* in Europe and North America is polyphyletic according to published molecular phylogenies (Fig. 3; FAILLE et al. 2010, 2013, MADDISON et al. 2019), consisting of seven clades scattered across a northern radiation (“the *Trechus* assemblage” sensu MADDISON et al. 2019), including three clades in Europe, recognized as genera herein (Fig. 1). In addition, four species groups from North America and Central Asia need to be removed from *Trechus*, which is postponed until more molecular data from these regions are available. This generic treatment is chosen in a way to (1) establish monophyletic genera for the European fauna and (2) to minimize the impact on the actual generic system of Trechini (Fig. 1).

***Epaphius* stat.rev.:** Ten European species of former *Trechus* and two species of *Epaphius* belong to a strongly supported clade (Fig. 3). Some taxa from the Nearctic region belong here as well (MADDISON et al. 2019, Fig. 3, COI sequences from BOLD). The major evolutionary centre is the Eastern Palearctic region, the distribution is holarctic. The clade is morphologically supported by a common configuration of the internal sack of the male aedeagus lacking the complicated, two parted armatures characteristic for (typical) *Trechus*. *Epaphius* in the present sense does not include the *Trechus*-like genus *Epaphiopsis* UENO, 1953 (MADDISON et al. 2019) as suggested several times.

***Mediterranoblemus* gen.n.:** The Iberian *T. schaufussi* represents an isolated clade (FAILLE et al. 2010). Additional molecular data provided by CONTRERAS-DÍAZ et al. (2007) confirm that two Spanish species of the former *T. austriacus* group closely related to the winged, eastern Mediterranean *T. crucifer* belong here as well. My material includes *T. olympiae* and *T. saulcyanus* from Cyprus of the former *T. austriacus* group, but these two species are members of two unrelated groups within the *Trechus*-clade (Fig. 3) and do not belong to *Mediterranoblemus* gen.n. *Mediterranoblemus* gen.n. is confined to areas with Mediterranean climate, reaching countries like Egypt and Jordan. Its species share a highly simplified aedeagal configuration with a single, scale shaped copulatory piece.

***Trechus*:** The majority (ca. 90%) of *Trechus* sequenced from Europe represent a monophyletic lineage including the type species, *Trechus quadristriatus* (FAILLE et al. 2010, 2013). Additionally, the former (sub)genera *Antoinella*, *Irinea* and *Apoduvalius* belong herein, making former *Trechus* paraphyletic (FAILLE et al. 2013). The distribution of the clade is not confirmed yet, as none of the North American taxa sequenced can be placed herein (MADDISON et al. 2019, Fig. 3). A further fragmentation of this clade into genera is neither indicated by molecular phylogenies nor by morphology.

Unnamed Nearctic genus 1: *Trechus humboldti* VANDYKE, 1945 from coastal California (DONABAUER 2014; MADDISON et al. 2019; Fig. 3) does not belong to any of the previous clades and should be removed from *Trechus*. It has a basal position within Trechini close to *Iberotrechus* (Fig. 3).

Unnamed Nearctic genus 2: *Trechus hydropicus* HORN, 1883 belongs to a highly characteristic group from the Appalachians (Nearctic region), an isolated clade (MADDISON et al. 2019).

Unnamed Nearctic genus 3: Several individuals of four species of the Nearctic *Trechus ovipennis* group (DONABAUER 2014) were sequenced (MADDISON et al. 2019, ARTHOFER et al., submitted). The 28S rRNA sequence is consistently aberrant and there is no evidence for a close relationship to any of the above-mentioned clades. This was confirmed recently by MADDISON et al. (2019), with sequences of *Trechus arizonae*, another member of the *T. ovipennis* group.

***Doderotrechus*:** The *Trechus dacatraianus* group sensu SCHMIDT (2009) includes five species from Tibet and is very close to *Doderotrechus* VIGNA TAGLIANTI, 1968 from the Alps (indicated by molecular data and aedeagal morphology), but distantly related to *Trechus* (FAILLE et al. 2013). These species should be removed from *Trechus*.

The subgeneric structure of the genus *Epaphius* LEACH, 1819 stat.rev.

Epaphius in the new sense is strongly supported in all molecular phylogenies (Figs. 1, 3) as well as by similarities in male aedeagi and distributional patterns (mainly northern distribution, cool temperate climate). However, appearance of species is extraordinary differentiated from very large (*E. rubens*) to very small (*E. limacodes*), fully winged to wingless, variable chaetotaxy of elytra (position of subapical setae in third stria) and degree of pigmentation. This group is Holarctic, moderately diversified in Europe with a dozen species, widespread in the Nearctic region and certainly more diversified in East Asia (*Epaphius* s.str. with ca. 50 species). Several or many other *Trechus* from East Asia (see MORAVEC et al. 1995, 1997, 1998) may belong to *Epaphius*, which needs further exploration.

The internal structure of the genus in Europe is best represented by a division into three subgenera (Figs. 2, 3):

***Epaphius* (s.str.):** Supported by the shifted preapical pore, aedeagal configuration and molecular phylogeny (Fig. 3). Two widespread species from northern Europe (*E. secalis* and *E. rivularis*) and several more from Eastern Asia, including winged taxa. Unknown from Nearctic region.

***Trechoepaphius* subgen.n.:** The former *T. rubens* group and *T. amplicollis-micans* group. Large and robust, several taxa fully winged. Holarctic distribution including widespread species from North America.

***Alpinoepaphius* subgen.n.:** Strongly supported by a common aedeagal configuration (lack of sagittal lamella, hyaline internal sack lacking chitinized copulatory pieces). Narrowly distributed in the eastern Alps (Austria and Slovenia) with eight endemic, wingless species; extraordinarily similar in habitus to some *Trechus* species by convergence (comp., e.g., *Trechus elegans* and *Epaphius pinkeri*).

The subgeneric structure of the genus *Trechus* CLAIRVILLE, 1806

The *Trechus* clade sensu FAILLE et al. (2013) is strongly supported in all published genetic phylogenies and consists of the clear majority (> 90%) of European *Trechus*, including the type species, *Trechus quadristriatus*, and the endogean genera *Antoinella*, *Irinea* and *Apoduvalius* (FAILLE et al. 2010, 2011, 2013, 2014, ARTHOFER et al. submitted; Figs. 1–4). This clade is understood as the genus *Trechus* from here on. The genus cannot be defined by morphological characteristics yet. Basically, most of the lineages herein have epigeal members with modified apices of aedeagi and two differentiated copulatory pieces of unequal and complex shape and size in a lateral position. Unfortunately, some *Trechus* show a secondary reduction of the copulatory pieces to a single rudimentary plate, although being very close in molecular phylogeny to taxa with complicated and large copulatory pieces, thereby obscuring their relationship (e.g., the closely related species *Trechus grandis* and *T. binotatus*; Figs. 2 and 3).

The phylogeny in deeper nodes needs to be elaborated on more genes and longer sequences. However, most analyses published cluster the larger, hygrophilous (living beside water bodies, reflecting the original mode of life within Trechitae; see MADDISON et al. 2019) species together, albeit with low support (Fig. 2; subgenera 1 to 9). Some of these species should reflect the basal group of the genus. Secondarily, the smaller, less hygrophilous species (forest floor, alpine grassland, lowland) clustered in a second large clade, also with low support (Fig. 2, subgenera 10 to 18). These species – in case monophyly can be demonstrated – form the crown group including the nominate *T. quadristriatus*.

However, molecular data provided excellent support for the next level of nodes, which have been translated to subgenera herein. These subgenera are fully compliant with distributional patterns and morphological characteristics, partly reflecting the traditional species groups established by JEANNEL (1927), partly not (ARTHOFER et al., submitted). Three subgenera (*Trechus* s.str., *Orinotrechus* and *Nigrinotrechus*) belong to a strongly supported clade, the “*T. quadristriatus* lineage”. Most of the alpine and some subalpine species (*T. pyrenaeus* group, *T. pertyi* group, *T. obtusiusculus* group) and three eurytopic and winged lowland species tolerating drought (*T. nigrinus*, *T. quadristriatus* and *T. cuniculorum*) belong herein (Fig. 3). Another three subgenera (*Eurotrechus*, *Calotrechus* and *Montanotrechus*) belong to a second strongly supported clade, the “*T. obtusus*-lineage”.

Many of the forest dwelling (living in leaf litter, moderately hygrophilous) *Trechus* species belong herein, including the winged and widespread *T. obtusus*.

Thus, the most eurytopic and widespread (winged!) species of the genus in Europe, *T. obtusus* and *T. quadristriatus*, previously suggested to be closely related by striking morphological similarity (JEANNEL 1927), are in fact distantly related and should reflect the unspecialized, winged ancestral type of the speciose crown group of *Trechus*.

Taxonomic actions and catalogue section

Genus *Epaphius* LEACH, 1819 stat.rev.

Subgenus *Epaphius* (s.str.)

= *Trechus* (*Epaphius*) sensu JEANNEL (1927: 130).

Type species: *Carabus secalis* PAYKULL, 1790.

Distribution: Palearctic.

Description: Preapical elytral pore in stria 3 strongly shifted forward. Aedeagus without copulatory pieces. For detailed descriptions and figures please refer to JEANNEL (1927).

Taxonomic changes: The following European species are transferred from *Trechus* subgen. *Epaphius* to *Epaphius* (s.str.):

Epaphius (s.str.) *secalis* (PAYKULL, 1790)*

Epaphius (s.str.) *rivularis* (GYLLENHAL, 1810)*

Subgenus *Trechoepaphius* subgen.n.

= *Trechus* (s.str.) *rubens* group sensu JEANNEL (1927: 179); *Trechus* (s.str.) *amplicollis* group sensu JEANNEL (1927: 166).

Type species: *Carabus rubens* FABRICIUS, 1792.

Distribution: Holarctic.

Description: Large or very large. Habitus robust, with prominent shoulders; partly winged. Elytral striae strongly impressed and punctured; preapical pore in stria 3 in normal position, not shifted forward. Aedeagus characterized by a single, small and simple copulatory piece; apical opening is strongly prolonged towards basal part; sagittal lamella present. For detailed descriptions and figures please refer to JEANNEL (1927).

Comments: A relationship of *E. rubens*, *E. amplicollis* and *Epaphius* s.str. was already suggested by JEANNEL (1927) as indicated by similarities in aedeagal configuration, distribution, and mode of life. Although habitus and chetotaxy strongly resembles a normal *Trechus*, genetic data unambiguously demonstrate a very close relationship to *Epaphius* s.str. (FAILLE et al. 2013; Fig. 3).

Taxonomic changes: The following species are transferred from *Trechus* s.str. to *Epaphius* subgen. *Trechoepaphius* subgen.n.:

Epaphius (*Trechoepaphius*) *amplicollis* (FAIRMAIRE, 1859) comb.n.

Epaphius (*Trechoepaphius*) *apicalis* (MOTSCHULSKY, 1865) comb.n.*

Epaphius (*Trechoepaphius*) *chalybaeus* (DEJEAN, 1831) comb.n.*

Epaphius (*Trechoepaphius*) *coloradensis* (SCHAEFFER, 1915) comb.n.*

Epaphius (Trechoepaphius) crassiscapus (LINDROTH, 1955) comb.n.
Epaphius (Trechoepaphius) oregonensis (HATCH, 1951) comb.n.*
Epaphius (Trechoepaphius) rubens (FABRICIUS, 1792) comb.n.*
Epaphius (Trechoepaphius) tenuiscapus (LINDROTH, 1961) comb.n.*
Epaphius (Trechoepaphius) yvesbousqueti (DONABAUER, 2010) comb.n.

Subgenus *Alpinoepaphius* subgen.n.

= *Trechus* (s.str.) *ochreateus* group sensu JEANNEL (1927: 369); *Trechus* (s.str.) *limacodes* group sensu JEANNEL (1927: 512); *Trechus* (s.str.) *alpicola* group sensu JEANNEL (1927: 406); *Trechus* (s.str.) *pinker* sensu JEANNEL (1927: 432).

Type species: *Trechus alpicola* STURM, 1825.

Distribution: eastern Alps and isolated adjacent areas.

Description: Small to large; habitus very variable, especially elytra either elongated and parallel sided with strongly flattened disc or strongly convex. Hindwings reduced; shoulders completely rounded. Elytral stria weakly impressed and not punctured, preapical pore in stria 3 in normal position, not shifted forward. Pigmentation and eyes reduced. Aedeagus characterized by lack of well chitinized copulatory pieces; strongly evolved scales in most species; sagittal lamella and basal bulbus reduced.

Comment: Although the highly characteristic aedeagi of this group strongly resemble that of *E. secalis*, a relationship of the following eight “*Trechus*” species neither to this nor to any other species now placed in *Epaphius* or *Trechoepaphius* was suggested until the molecular phylogeny was provided by FAILLE et al. (2013).

Taxonomic changes: The following species are transferred from *Trechus* s.str. to *Epaphius* subgen. *Alpinoepaphius* subgen.n.:

Epaphius (Alpinoepaphius) alpicola (STURM, 1825) comb.n.*
Epaphius (Alpinoepaphius) latibuli (JEANNEL, 1948) comb.n.*
Epaphius (Alpinoepaphius) limacodes (DEJEAN, 1831) comb.n.*
Epaphius (Alpinoepaphius) ochreateus (DEJEAN, 1927) comb.n.*
Epaphius (Alpinoepaphius) ovatus (PUTZEYS, 1845) comb.n.*
Epaphius (Alpinoepaphius) pinkeri (GANGLBAUER, 1892) comb.n.*
Epaphius (Alpinoepaphius) rudolphi (GANGLBAUER, 1891) comb.n.*
Epaphius (Alpinoepaphius) wagneri (GANGLBAUER, 1906) comb.n.*

Genus *Mediterranoblemus* gen.n.

= *Trechus* (s.str.) *pandellei* group sensu JEANNEL (1927: 251); *Trechus* (s.str.) *austriacus* group sensu JEANNEL partim (1927: 417).

Type species: *Trechus schaufussi* PUTZEYS, 1870.

Distribution: Mediterranean, Iberian.

Description: External habitus and chetotaxy identical to typical *Trechus*, but already separated by the shape of the single aedeagal copulatory piece, which is simple triangular (as seen in several endogean genera) and by the southern, Mediterranean distribution. The first group consists of the Iberian, depigmented *T. schaufussi*, described in detail by JEANNEL (1927: 251). The second group includes at least three similar, Mediterranean

species including *M. crucifer* with simple aedeagus, functional wings and spotted elytra, described in detail by JEANNEL (1927: 419).

Comment: A relationship of three of these taxa is shown by molecular phylogeny by CONTREAS-DIAZ et al. (2007). FAILLE et al. (2010) demonstrated, that *M. schaufussi* does neither belong to the “*Trechus*-clade” in a strict sense nor is closely related to any other sequenced Trechini.

Taxonomic changes: The following species are transferred from *Trechus* s.str. to *Mediterranoblemus* gen.n.:

1. *Mediterranoblemus schaufussi* group
Mediterranoblemus schaufussi (PUTZEYS, 1870) comb.n.*
2. *Mediterranoblemus cruciatus* group
Mediterranoblemus barratxinai (ESPANOL, 1971) comb.n.*
Mediterranoblemus cruciatus (PIOCHARD DE LA BRULERIE, 1876) comb.n.
Mediterranoblemus diecki (PUTZEYS, 1870) comb.n.*

Genus *Trechus* CLAIRVILLE, 1806

Subgenus *Antoinella* JEANNEL, 1937 stat.n.

= *Trechus* (s.str.) *fulvus* group sensu JEANNEL (1927: 198).

Type species: *Duvalius groubei* ANTOINE, 1936.

Distribution: northwestern Africa, western Europe.

Comment: *Antoinella* was correctly synonymized with the *Trechus fulvus* group by CASALE (2011). However, this group is established as a subgenus of *Trechus* herein. The phylogeny of the *Trechus fulvus* group/*Antoinella* was worked out in detail by FAILLE et al. (2014).

Taxonomic changes: The following species are transferred from *Trechus* (s.str.) to *Trechus* subgen. *Antoinella*:

- Trechus (Antoinella) alicantinus* ESPAÑOL, 1971*
- Trechus (Antoinella) atlasicus* MORAVEC & LOMPE, 2003
- Trechus (Antoinella) bedeli* JEANNEL, 1922
- Trechus (Antoinella) beltrani* TORIBIO, 1990
- Trechus (Antoinella) breuili* JEANNEL, 1913
- Trechus (Antoinella) delhermi* SAULCY, 1880*
- Trechus (Antoinella) djbelgloubensis* QUEINNEC & OLLIVIER, 2013
- Trechus (Antoinella) djebalicus* COMAS & MATEU, 2008*
- Trechus (Antoinella) espanyoli* MATEU & ESCOLÀ, 2006*
- Trechus (Antoinella) fadriquei* MATEU & ESCOLÀ, 2006
- Trechus (Antoinella) fulvus* DEJEAN, 1831*
- Trechus (Antoinella) gamae* REBOLEIRA & SERRANO, 2009
- Trechus (Antoinella) gigoni* CASALE, 1982*
- Trechus (Antoinella) groubei* ANTOINE, 1935*
- Trechus (Antoinella) iblanensis* MATEU & ESCOLÀ, 2006*

Trechus (Antoinella) idriss PEYERIMHOFF, 1924
Trechus (Antoinella) incola PEYERIMHOFF, 1909
Trechus (Antoinella) kabylicus CASALE, 1983
Trechus (Antoinella) lallemantii (JEANNEL, 1927)*
Trechus (Antoinella) lencinai MATEU & ORTUÑO, 2006*
Trechus (Antoinella) lunai REBOLEIRA & SERRANO, 2009
Trechus (Antoinella) machadoi JEANNEL, 1941
Trechus (Antoinella) martinezi JEANNEL, 1927*
Trechus (Antoinella) messoulia CASALE, 2011
Trechus (Antoinella) oligops BEDEL, 1895
Trechus (Antoinella) parapandus ORTUÑO & BARRANCO, 2015
Trechus (Antoinella) rottroui ANTOINE, 1934
Trechus (Antoinella) sendrai COMAS & MATEU, 2008*
Trechus (Antoinella) tatai REBOLEIRA & ORTUÑO, 2010
Trechus (Antoinella) torressalae ORTUÑO & ARRILLO, 2005
Trechus (Antoinella) zaerensis ANTOINE, 1928*
Trechus (Antoinella) zorgatii QUEINNEC & OLLIVIER, 2013

Subgenus *Irinea* MATEU & COMAS, 2006 stat.rev.

Type species: *Antoinella aurouxi* MATEU & COMAS, 2006.

Distribution: Morocco.

Comment: *Irinea* was described as a monotypic subgenus of *Antoinella* for a single, aberrant and endogean species with pubescent elytra and just the basal segment of protarsi enlarged in males. In the latest Palearctic catalogue it is listed as a valid genus (LÖBL & LÖBL 2019). However, *Irinea* is not part of *Antoinella* but closer to *Apoduvalius* according to molecular phylogeny (FAILLE et al. 2014) and is best treated as a monotypic subgenus of its own.

Taxonomic changes: The following species is transferred from *Irinea* to *Trechus* subgen. *Irinea*:

Trechus (Irinea) aurouxi (MATEU & COMAS, 2006) comb.n.*

Subgenus *Apoduvalius* JEANNEL, 1953 stat.n.

= *Trechus* (s.str.) *uhagoni* group sensu JEANNEL (1927: 222); *Trechus* (s.str.) *angusticollis* group sensu JEANNEL (1927: 236); *Trichapoduvalius* VIVES, 1976; *Hydrotrechus* CARABAJAL, GARCIA & RODRIGUEZ, 1999.

Type species: *Apoduvalius negrei* JEANNEL, 1953.

Distribution: Pyrenean-Cantabrian area.

Comments: Molecular phylogenies strongly support a “large Pyrenean-Cantabrian clade” of approximately 60 species, some epigeal and many highly specialized endogean species including *Apoduvalius* (FAILLE et al. 2012, 2013, FRESNEDA et al. 2019). Within this clade, three (sub)generic names are available (LÖBL & LÖBL, 2019): (1) *Apoduvalius* as a valid genus, (2) *Trichapoduvalius* as a synonym of *Apoduvalius* and finally (3) *Hydrotrechus* as a synonym of *Trechus* s.str. Unfortunately, none of the type species are

included in the latest phylogeny of FRESNEDA et al. (2019), and *Apoduvalius* turned out to be polyphyletic. To be on the safe side, the entire clade is combined into one large subgenus, named *Apoduvalius*. Two species groups were worked out in detail: the *T. brucki* group by FAILLE et al. (2012) and the *T. saxicola* group by FRESNEDA et al. (2019). Both studies provide excellent descriptions, photographs of habitus and aedeagi, distributional information, and further grouping of this clade.

Taxonomic changes: the following species are transferred from *Trechus* (s.str.) and *Apoduvalius* to *Trechus* subgen. *Apoduvalius*:

- Trechus (Apoduvalius) abeillei* PANDELLÉ, 1872*
 - Trechus (Apoduvalius) alberichae* (ESPAÑOL, 1971) comb.n.*
 - Trechus (Apoduvalius) aphaenopsianus* (ESPAÑOL & VIVES, 1983) comb.n.
 - Trechus (Apoduvalius) angusticollis* KIESENWETTER, 1850
 - Trechus (Apoduvalius) anseriformis* SALGADO & PELÁEZ, 2004
 - Trechus (Apoduvalius) arrechaei* ORTUNO, GUESTA, GILGADO & LEDESMA, 2014
 - Trechus (Apoduvalius) arribasi* JEANNE, 1988
 - Trechus (Apoduvalius) asturiensis* (SALGADO, 1991) comb.n.
 - Trechus (Apoduvalius) aubryi* COIFFAIT, 1953*
 - Trechus (Apoduvalius) bonvouloiri* PANDELLÉ, 1867*
 - Trechus (Apoduvalius) bordei* PEYERIMHOFF, 1909*
 - Trechus (Apoduvalius) champagnati* (SALGADO, 1991) comb.n.
 - Trechus (Apoduvalius) distinctus* FAIRMAIRE & LABOULBÈNE, 1854*
 - Trechus (Apoduvalius) drescoi* (JEANNEL, 1953) comb.n.
 - Trechus (Apoduvalius) enigmaticus* COIFFAIT, 1971
 - Trechus (Apoduvalius) espanoli* (SALGADO, 1996) comb.n.
 - Trechus (Apoduvalius) franzi* (JEANNEL, 1958) comb.n.
 - Trechus (Apoduvalius) latebricola* KIESENWETTER, 1850
 - Trechus (Apoduvalius) lecoqi* (DEUVE, 1991) comb.n.
 - Trechus (Apoduvalius) leonensis* (SALGADO & ORTUÑO, 1998) comb.n.
 - Trechus (Apoduvalius) meregallii* CASALE, 1981
 - Trechus (Apoduvalius) nalonii* (SALGADO, 1993) comb.n.
 - Trechus (Apoduvalius) navaricus* (VUILLEFROY, 1869)*
 - Trechus (Apoduvalius) negrei* (JEANNEL, 1953) comb.n.
 - Trechus (Apoduvalius) pecoudii* COLAS & GAUDIN, 1935
 - Trechus (Apoduvalius) purroyi* (SALGADO, 1987) comb.n.
 - Trechus (Apoduvalius) salgadoi* (CARABAJAL, GARCÍA & RODRÍGUEZ, 2002) comb.n.
 - Trechus (Apoduvalius) serrae* (VIVES, 1976) comb.n.
1. *Trechus (Apoduvalius) brucki* group sensu FAILLE et al. (2012)
 - Trechus (Apoduvalius) beusti* (SCHAUFUSS, 1862)*
 - Trechus (Apoduvalius) bouilloni* FAILLE, BOURDEAU & FRESNEDA, 2012*
 - Trechus (Apoduvalius) brucki* FAIRMAIRE, 1862*
 - Trechus (Apoduvalius) bruckoides* FAILLE, BOURDEAU & FRESNEDA, 2012*
 - Trechus (Apoduvalius) grenieri* PANDELLÉ, 1867*

- Trechus (Apoduvalius) pieltaini* JEANNEL, 1920*
- Trechus (Apoduvalius) uhagoni* CROTCH, 1869*
2. *Trechus (Apoduvalius) saxicola* group sensu FRESNEDA et al. (2019)
- Trechus (Apoduvalius) apoduvalipenis* SALGADO & ORTUÑO, 1998*
- Trechus (Apoduvalius) baztanensis* DUPRE, 1991
- Trechus (Apoduvalius) bourdeau* FRESNEDA, VALENZUELA & FAILLE, 2015*
- Trechus (Apoduvalius) carrilloi* TORIBIO & RODRÍGUEZ, 1997
- Trechus (Apoduvalius) cifrianae* ORTUNO & JIMÉNEZ-VALVERDE, 2011
- Trechus (Apoduvalius) croceus* FRESNEDA & BOURDEAU, 2019*
- Trechus (Apoduvalius) enedaphos* FRESNEDA & VALENZUELA, 2019*
- Trechus (Apoduvalius) escalerae* ABEILLE, 1903*
- Trechus (Apoduvalius) gloriensis* JEANNE, 1970
- Trechus (Apoduvalius) hyperythros* FAILLE & FRESNEDA, 2019*
- Trechus (Apoduvalius) jeannei* SCIAKY, 1998*
- Trechus (Apoduvalius) kricheldorffi* WAGNER, 1913
- Trechus (Apoduvalius) marcilhaci* PHAM, 1987*
- Trechus (Apoduvalius) odontopeos* FRESNEDA & FAILLE, 2019*
- Trechus (Apoduvalius) ortizi* ESPAÑOL, 1970*
- Trechus (Apoduvalius) pecignai* TORIBIO, 1992
- Trechus (Apoduvalius) pilonensis* TORIBIO, 2014
- Trechus (Apoduvalius) pisuensis* ORTUNO & TORRIBIO, 2005
- Trechus (Apoduvalius) pongensis* FAILLE & BOURDEAU, 2019*
- Trechus (Apoduvalius) riberae* FAILLE & VALENZUELA, 2019*
- Trechus (Apoduvalius) saxicola* PUTZEYS, 1870*
- Trechus (Apoduvalius) sharpi* JEANNEL, 1921
- Trechus (Apoduvalius) teverneganus* TORRIBIO, 2015
- Trechus (Apoduvalius) triamicorum* ORTUNO & JIMÉNEZ-VALVERDE, 2011
- Trechus (Apoduvalius) udiensis* ORTUNO, GUTIÉRREZ, PASCUAL & RUIZ, 2017
- Trechus (Apoduvalius) valenzuelai* FRESNEDA, BOURDEAU & FAILLE, 2015*

Subgenus *Lepontinotrechus* subgen.n.

= *Trechus* (s.str.) *lepontinus* group sensu JEANNEL (1927: 433), partim.

Type species: *Trechus lepontinus* GANGLBAUER, 1891.

Distribution: Endemic in a small area west of Lago Maggiore (Italy), strongly hygrophilous, along small water bodies and in wet leaf litter, montane to subalpine.

Description: This monotypic subgenus contains a single, medium sized, pale red-dish species. Eyes reduced. Elytra strongly convex, shoulders rounded. Aedeagus highly characteristic (Fig. 2), robust and large, without sagittal lamella; copulatory piece strongly chitinized and large. This species is described in detail by JEANNEL (1927: 434) including figures of habitus and aedeagus.

Comment: A genetically and morphologically isolated species, distantly related to the syntopic *T. consobrinus*, thus not combined in a group as suggested by JEANNEL (1927).

Taxonomic changes: The following species is transferred from *Trechus* (s.str.) to *Trechus* subgen. *Lepontinotrechus*:

Trechus (Lepontinotrechus) lepontinus GANGLBAUER, 1891*

Subgenus *Austriatrechus* subgen.n.

= *Trechus* (s.str.) *elegans* group sensu JEANNEL (1927: 430), partim.

Type species: *Carabus rotundipennis* DUFTSCHMID, 1812.

Distribution: Eastern Alps (Austria, adjacent Slovenia and Hungary). Foothills to subalpine, always in forests close to water, strongly hygrophilous.

Description: This monotypic subgenus contains a single species, characterized by medium body size, slender pronotum with pronounced and sharp basal angles. Elytra oval and convex, with weakly impressed striae. Legs and antenna slender and elongated. The aedeagus is unique by extremely elongated shape, strongly reduced copulatory pieces, and a very large sagittal lamella (Fig. 2). This species is described and imaged by JEANNEL (1927: 152).

Comment: JEANNEL (1927) suggested a relationship with some other species from the Eastern Alps (the *T. elegans* group: *T. elegans*, *T. gracilitarsis*, *T. regularis* and *Epaphius pinkeri* comb.n.), which is an artificial assemblage of unrelated Trechini (Fig. 3) as already indicated by the highly different aedeagal morphologies. In fact, it is closest to *Trechus lepontinus*.

Taxonomic changes: The following species is transferred from *Trechus* (s.str.) to *Trechus* subgen. *Austriatrechus* subgen.n.:

Trechus (Austriatrechus) rotundipennis DUFTSCHMID, 1812*

Subgenus *Penninotrechus* subgen.n.

= *Trechus* (s.str.) *strigipennis* group sensu JEANNEL (1927: 398).

Type species: *Trechus strigipennis* KIESENWETTER, 1861.

Distribution: Western Alps: Alpi Pennine, Alpi Lepontine, Alpi Graie. High subalpine and alpine zone, strongly hygrophilous.

Description: Highly characteristic group by several adaptations to alpine, wet soil habitats and subterranean life: body pale yellowish; elytra strongly flattened and elongated, with well impressed and punctuate striae; eyes strongly reduced in size. Aedeagus elongated with modified apex; copulatory pieces simple and weakly sclerotized (Fig. 2). Please refer to JEANNEL (1927) and MONGUZZI (1998, 2002) for detailed descriptions, habitus and genital figures, and maps of distribution.

Comments: This group of extraordinarily derived species was recognized as a natural group by all authors, which is confirmed by molecular data (FAILLE et al. 2013, Fig. 3). Distribution, ecology, configuration of aedeagus and genetic data support a relationship to *Lepontinotrechus* and *Austriatrechus*.

Taxonomic changes: The following species are transferred from *Trechus* (s.str.) to *Trechus* subgen. *Penninotrechus* subgen.n.:

Trechus (Penninotrechus) artemisiae PUTZEYS, 1872

Trechus (Penninotrechus) caprai JEANNEL, 1927

Trechus (Penninotrechus) cerasai BINAGHI, 1938*
Trechus (Penninotrechus) focarilei MONGUZZI, 1998
Trechus (Penninotrechus) goidanichi FOCARILE & CASALE, 1978
Trechus (Penninotrechus) montisrosae JEANNEL, 1921*
Trechus (Penninotrechus) piazzolii FOCARILE, 1950*
Trechus (Penninotrechus) pochoni JEANNEL, 1939*
Trechus (Penninotrechus) sajuncaicus MONGUZZI, 2002
Trechus (Penninotrechus) sivellae MONGUZZI, 2003
Trechus (Penninotrechus) strigipennis KIESENWETTER, 1861*

Subgenus *Latotrechus* subgen.n.

= *Trechus* (s.str.) *latus* group sensu JEANNEL (1927: 361); *Trechus* (s.str.) *banaticus* group sensu JEANNEL (1927: 354); *Trechus* (s.str.) *subnotatus* group sensu JEANNEL (1927: 437).

Type species: *Trechus latus* PUTZEYS, 1847.

Distribution: Widespread between Italy and the Caucasus. Hygrophilous, from foothill to alpine zone. At least one species is capable of flight.

Description: Medium to large *Trechus* of robust and broad habitus, often dark with bluish lustre, sometimes depigmented, some species with maculate elytra. Elytra with deeply impressed striae, slightly punctured in most species. Pronotum with distinct and deeply impressed basal fovea. Aedeagus of variable size, but apex always short and unmodified. Copulatory pieces highly variable, ranging from a simple, highly characteristic saddle-shaped copulatory piece in the *T. subnotatus* group to extraordinary complicated copulatory pieces like in *T. latus* and *T. grandis* (Fig. 2).

Comments: This clade is supported by molecular phylogenies, similarities in habitus, mode of life (confined to margins of water bodies), and a compact distribution (absent from Western Europe). *Trechus pseudopiceus* belongs here, a rare high alpine species of the southeastern Alps (Austria and Slovenia, described and figured in JEANNEL 1927: 500). It lives and looks exactly like representatives of the *Trechus (Orinotrechus) pertyi* group, where it was placed by JEANNEL (1927). However, different configuration of copulatory pieces of the male aedeagus and molecular data indicate that this species was misplaced in the *T. pertyi* group. *Trechus pseudopiceus* is another interesting case of convergence.

Taxonomic changes: The following species are transferred from *Trechus* (s.str.) to *Trechus (Latotrechus)* subgen.n.):

Trechus (Latotrechus) banaticus DEJEAN, 1831
Trechus (Latotrechus) fontinalis RYBINSKI, 1901
Trechus (Latotrechus) grandis GANGLBAUER, 1891*
Trechus (Latotrechus) latus PUTZEYS, 1847*
Trechus (Latotrechus) longicollis MEIXNER, 1912*
Trechus (Latotrechus) plicatulus MILLER, 1868
Trechus (Latotrechus) pseudolatus LOMPE, 2011
Trechus (Latotrechus) pseudomontanellus RIZUN, 1994

1. *Trechus (Latotrechus) pseudopiceus* group
Trechus (Latotrechus) pseudopiceus DANIEL & DANIEL, 1898*

2. *Trechus (Latotrechus) subnotatus* group
 - Trechus (Latotrechus) andreinii* JEANNEL, 1921*
 - Trechus (Latotrechus) asiaticus* JEANNEL, 1927
 - Trechus (Latotrechus) binotatus* PUTZEYS, 1870*
 - Trechus (Latotrechus) byzantinus* APFELBECK, 1902
 - Trechus (Latotrechus) cardioderus* PUTZEYS, 1870*
 - Trechus (Latotrechus) controversus* BINAGHI, 1959*
 - Trechus (Latotrechus) fairmairei* PANDELLE, 1867*
 - Trechus (Latotrechus) genevanorum* PAWLOWSKI, 1977
 - Trechus (Latotrechus) italicus* DANIEL, 1898*
 - Trechus (Latotrechus) pilisensis* CSIKI, 1917*
 - Trechus (Latotrechus) quadrimaculatus* MOTSCHULSKY, 1850
 - Trechus (Latotrechus) schoenmanni* DONABAUER & LEBENBAUER, 2005*
 - Trechus (Latotrechus) schwienbacheri* DONABAUER & LEBENBAUER, 2003*
 - Trechus (Latotrechus) subnotatus* DEJEAN, 1831
 - Trechus (Latotrechus) arthuri* MORAVEC & LOMPE, 2003

Subgenus *Italotrechus* subgen.n.

= *Trechus* (s.str.) *putzeysi* group sensu JEANNEL (1927: 390).

Type species: *Trechus putzeysi* PANDELLE, 1867.

Distribution: Italian and French Alps, northern parts of Apennine, montane to sub-alpine forests, strongly hygrophilous, common.

Description: Smaller than the previous, body length ca. 3.5 mm; hindwings reduced; body pigmented. This group strongly resembles the previous, but aedeagus is simple, slender and curved, with unmodified apex and with small, simple, weakly sclerotized copulatory pieces (Fig. 2).

Comments: This new subgenus consists of two separated groups (Fig. 3), both geographically and in aedeagal morphology. The first consists of three taxa in the western Alps and has been described by JEANNEL (1927: 390) as the *T. putzeysi* group including habitus and aedeagus figures. The second group consists of *T. gracilitarsis* described and imaged by JEANNEL (1927: 429). The close relationship of these two groups and a sister group relationship to *Latotrechus* was first demonstrated by FAILLE et al. (2013).

Taxonomic changes: The following species are transferred from *Trechus* (s.str.) to *Trechus* subgen. *Italotrechus* subgen.n.:

1. *Trechus (Italotrechus) gracilitarsis* group
 - Trechus (Italotrechus) gracilitarsis* DANIEL & DANIEL, 1898*
2. *Trechus (Italotrechus) putzeysi* group
 - Trechus (Italotrechus) liguricus* JEANNEL, 1921*
 - Trechus (Italotrechus) nicoleae* MONCOUTIER, 1986*
 - Trechus (Italotrechus) putzeysi* PANDELLE, 1867*

Subgenus *Oropatrechus* subgen.n.

= *Trechus* (s.str.) *consobrinus* in JEANNEL (1927: 436).

Type species: *Trechus consobrinus* DANIEL & DANIEL, 1898.

Distribution: Western Alps, currently known from a unique location, the beech forests around the sanctuary Oropa on Monte Mucrone in the Alpi Pennine (Italy).

Description: Medium sized (ca. 3.5 mm), depigmented, eyes reduced. Aedeagus as in Figure 2. *Oropatrechus* subgen.n. is monotypic containing *T. consobrinus*, described and imaged by JEANNEL (1927: 436).

Comment: This is a relict species, isolated within *Trechus* (Fig. 3).

Taxonomic changes: The following species is transferred from *Trechus* (s.str.) to *Trechus* (*Oropatrechus* subgen.n.):

Trechus (*Oropatrechus*) *consobrinus* DANIEL & DANIEL, 1898*

Subgenus *Balcanotrechus* subgen.n.

= *Trechus* (s.str.) *pulchellus* group sensu JEANNEL (1927: 534), partim.

Type species: *Trechus priapus* K. DANIEL, 1902.

Distribution: Dinaric karst, Balkan, forests.

Description: Medium sized, body length ca. 3.5 mm. Hindwings reduced: Elytra with slightly impressed striae and rounded shoulders. Pronotum with slightly impressed basal fovea. Aedeagus highly characteristic, short and very broad; apex short; a single copulatory piece of simple, elongate shape in unusual ventral position (Fig. 2).

Comments: An isolated group (Fig. 3) immediately recognized by the distinct aedeagal configuration, not closely related to *T. pulchellus* or *T. croaticus* as suggested by JEANNEL (1927).

Taxonomic changes: The following species are transferred from *Trechus* (s.str.) to *Trechus* subgen. *Balcanotrechus* subgen.n.:

Trechus (*Balcanotrechus*) *priapus* K. DANIEL, 1902*

Trechus (*Balcanotrechus*) *rhodopeius* JEANNEL, 1921

Subgenus *Calotrechus* WOLLASTON, 1854 subgen.rev.

= *Trechus* (s.str.) *tingitanus* group sensu JEANNEL (1927: 268); = *Trechus* (s.str.) *quadristriatus* group sensu JEANNEL (1927: 291), partim; *Trechus* (*Atlantotrechus* LOMPE, 1999) syn.n.

Type species: *Trechus nigrocruciatus* WOLLASTON, 1854.

Distribution: Strong radiations on Madeira, the Canary Islands and the Azores (43 species!); North Africa, Europe. Centre of diversification in the western Mediterranean. Mainly forest dwelling species, in leaf litter. Three species in the Alps restricted to the alpine zone. Endogean species with strongly reduced eyes on some of the Atlantic islands.

Description: Medium to large *Trechus* of rather variable habitus and coloration; fully winged or wings not functional. Most species can be characterized by the combination of a large pronotum with shallow basal fovea and a large aedeagus with two well-developed, complicated and strongly chitinated copulatory pieces of different size, length and shape, partly covered by dense fields of scales; apex short or elongated and sometimes modified (hooked, reflexed). The aedeagus is hyperevolved in many cases.

Comments: Most species are described and imaged in JEANNEL (1927), MACHADO (1992), and LOMPE (1999). CONTRERAS-DÍAZ et al. (2007) provided a very detailed molecular phylogeny of many taxa from the Canary Islands, Madeira and the Azores, showing that each archipelago hosts a monophyletic clade. Five species from the Alps belong here as well (Fig. 3). The subgenus *Atlantotrechus* (LOMPE 1999, DONABAUER 2003) was erected for *Trechus cautus* WOLLASTON, 1854 from the Island Porto Santo (Madeira) based on the reduction of the dilatation of the male protarsus (seen in many other lineages of Trechini) and a distinct microsculpture on elytra (likely not relevant in terms of phylogeny). However, consistent distribution pattern, mode of life in dry leaf litter, the broad pronotum with shallow basal impressions and the configuration of the copulatory pieces strongly indicate, that *Atlantotrechus* rather belongs here than in a subgenus of its own (see JEANNEL 1927).

Taxonomic changes: The following species are transferred from *Trechus* (s.str.) or *Trechus* (*Atlantotrechus*) to *Trechus* subgen. *Calotrechus*:

- Trechus* (*Calotrechus*) *algericus* JEANNEL, 1922
 - Trechus* (*Calotrechus*) *barnevillei* PANDELLÉ, 1867*
 - Trechus* (*Calotrechus*) *doderói* JEANNEL, 1927*
 - Trechus* (*Calotrechus*) *echarouxi* OLLIVIER & QUÉINNEC, 2011
 - Trechus* (*Calotrechus*) *obtusius* ERICHSON, 1837*
 - Trechus* (*Calotrechus*) *rufulus* DEJEAN, 1831
 - Trechus* (*Calotrechus*) *tingitanus* PUTZEYS, 1870
 - Trechus* (*Calotrechus*) *tyrrhenicus* JEANNEL, 1927*
1. *Trechus* (*Calotrechus*) *flavocinctus* group (Canarian radiation)
 - Trechus* (*Calotrechus*) *antonii* JEANNEL, 1927*
 - Trechus* (*Calotrechus*) *benahoaritus* MACHADO, 1990*
 - Trechus* (*Calotrechus*) *cabrerai* (JEANNEL, 1936)*
 - Trechus* (*Calotrechus*) *detersus* WOLLASTON, 1864*
 - Trechus* (*Calotrechus*) *felix* WOLLASTON, 1864*
 - Trechus* (*Calotrechus*) *flavocinctus* JEANNEL, 1922*
 - Trechus* (*Calotrechus*) *flavocircumdatus* JEANNEL, 1922*
 - Trechus* (*Calotrechus*) *flavolimbatus* WOLLASTON, 1863*
 - Trechus* (*Calotrechus*) *fortunatus* JEANNEL, 1927*
 - Trechus* (*Calotrechus*) *gomerensis* FRANZ, 1986*
 - Trechus* (*Calotrechus*) *laureticola* JEANNEL, 1936*
 - Trechus* (*Calotrechus*) *machadoensis* FRANZ, 1984*
 - Trechus* (*Calotrechus*) *minioculatus* MACHADO, 1987*
 - Trechus* (*Calotrechus*) *sylviae* LOMPE, 2000
 - Trechus* (*Calotrechus*) *tenoensis* ISRAELSON & PALM, 1979*
 - Trechus* (*Calotrechus*) *uyttenboogaarti* JEANNEL, 1936*
 2. *Trechus* (*Calotrechus*) *torretassoi* group (Azorean radiation)
 - Trechus* (*Calotrechus*) *isabelae* BORGES et al., 2007*
 - Trechus* (*Calotrechus*) *jorgensis* OROMI & BORGES, 1991*
 - Trechus* (*Calotrechus*) *montanheirorum* OROMI & BORGES, 1991*

- Trechus (Calotrechus) oromii* BORGES et al., 2004*
- Trechus (Calotrechus) peireirai* BORGES et al., 2004*
- Trechus (Calotrechus) picoensis* MACHADO, 1988*
- Trechus (Calotrechus) terceiranus* MACHADO, 1988*
- Trechus (Calotrechus) terrabravensis* BORGES et al., 2004*
- Trechus (Calotrechus) torretassoi* JEANNEL, 1937
3. *Trechus (Calotrechus) cautus* group (Porto Santo)
Trechus (Calotrechus) cautus WOLLASTON, 1854
4. *Trechus (Calotrechus) flavomarginatus* group (Madeira radiation)
Trechus (Calotrechus) assingi LOMPE, 1999
Trechus (Calotrechus) alticola WOLLASTON, 1854
Trechus (Calotrechus) bibulus LOMPE, 1999
Trechus (Calotrechus) custos WOLLASTON, 1854*
Trechus (Calotrechus) debilis WOLLASTON, 1871
Trechus (Calotrechus) decolor JEANNEL, 1938*
Trechus (Calotrechus) dilutus WOLLASTON, 1854
Trechus (Calotrechus) flavomarginatus WOLLASTON, 1854*
Trechus (Calotrechus) laevis WOLLASTON, 1857*
Trechus (Calotrechus) laranensis LOMPE, 1999
Trechus (Calotrechus) lundbladi JEANNEL, 1938
Trechus (Calotrechus) minyops WOLLASTON, 1862*
Trechus (Calotrechus) nigrocruciatus WOLLASTON, 1854
Trechus (Calotrechus) nugax LOMPE, 1997
Trechus (Calotrechus) signatus WOLLASTON, 1857
Trechus (Calotrechus) silveiranus LOMPE, 1997
Trechus (Calotrechus) tetracoderus GEMMINGER & HAROLD, 1868
Trechus (Calotrechus) umbricola WOLLASTON, 1854*
5. *Trechus (Calotrechus) constrictus* group
Trechus (Calotrechus) constrictus SCHAUM, 1860*
6. *Trechus (Calotrechus) pallidulus* group
Trechus (Calotrechus) aubei PANDELLE, 1867*
Trechus (Calotrechus) meschniggi JEANNEL, 1928*
Trechus (Calotrechus) morandinii LEBENBAUER, 2003
Trechus (Calotrechus) pallidulus GANGLBAUER, 1891*

Subgenus *Montanotrechus* subgen.n.

= *Trechus* (s.str.) *montanellus* group sensu JEANNEL (1927: 377).

Type species: *Trechus montanellus* GEMMINGER & HAROLD, 1868.

Distribution: Central Europe, southeastern Alps.

Description: This subgenus is identical to the *Trechus montanellus* group sensu JEANNEL (1927: 377). Please refer to the descriptions and figures therein. Additional descriptions

and figures are provided by DONABAUER (2006). Aedeagus (Fig. 2) large and short; apex rounded and short; copulatory pieces very large like those seen in *Calotrechus*.

Comments: Four relict species, distributed in the south-eastern Alps and Central Europe, localized and rare, similar in both genital morphology and body shape (DONABAUER 2006, JEANNEL 1927). *Montanotrechus* is the sister group to the more western clade of *Calotrechus* and the more eastern clade of *Eurotrechus* (FAILLE et al. 2013; Fig. 3).

Taxonomic changes: The following species are transferred from *Trechus* (s.str.) to *Trechus* subgen. *Montanotrechus* subgen.n.:

Trechus (*Montanotrechus*) *carnioliae* MÜLLER, 1921*

Trechus (*Montanotrechus*) *montanellus* GEMMINGER & HAROLD, 1868*

Trechus (*Montanotrechus*) *pohorjeensis* DONABAUER, 2006*

Trechus (*Montanotrechus*) *silvicola* DANIEL & DANIEL, 1898*

Subgenus *Eurotrechus* subgen.n.

= *Trechus* (s.str.) *pulchellus* group sensu JEANNEL (1927: 524), partim; *Trechus* (s.str.) *osmanilis* group sensu JEANNEL (1927: 342); *Trechus* (s.str.) *striatulus* group sensu JEANNEL (1927: 346); *Trechus* (s.str.) *splendens* group sensu JEANNEL (1927: 383); *Trechus* (s.str.) *distigma* group sensu JEANNEL (1927: 395).

Type species: *Trechus pulchellus* PUTZEYS, 1846.

Distribution: Europe, Asia Minor, Cyprus, Caucasus, northern Iran. Centres of diversification are in the Carpathians and in northern Turkey. Rather unspecialized inhabitants of forests, in moderately humid leaf litter.

Description: Small to medium sized *Trechus*, on average smaller than species of *Calotrechus* and *Montanotrechus*, otherwise similar. This clade includes at least one winged species and many taxa without functional wings. This group can be distinguished by the aedeagus, which is smaller, more elongated and slenderer than in the previous two subgenera; the larger copulatory piece smaller, much simpler in the European species (both in Turkey and in the Pyrenees, species with extraordinary complicated and hyperevolved copulatory pieces exist); the second piece strongly reduced or absent. In some (e.g., some Carpathian) species, areas of the copulatory pieces are covered by dense scales. Please refer to JEANNEL (1927) for detailed descriptions of the species groups and DONABAUER (2013) for descriptions, figures and photographs of many taxa from Turkey.

Comments: FAILLE et al. (2013) demonstrated the close relationship of *T. distigma* (Pyrenees), *T. pulchellus* (Carpathians) and *T. lazicus* (Turkey), belonging to three different species groups according to JEANNEL (1927). This clade is one of the most unexpected findings in the molecular phylogeny (Fig. 3), although strongly supported by aedeagal configuration. The relationship of the involved species was never suggested before due to the unusual extensive distribution across Europe compared to most other clades. This clade combines species from the Cantabrian chain and the Pyrenees (*T. distigma* group), central France and central Europe (*T. splendens* group), the entire Carpathian chain, and parts of the Balkan Peninsula (*T. pulchellus* and *T. striatulus* group). Further to the east, it radiates along the Black Sea coast in Turkey and stretches to Iran (*T. osmanilis* group). Additionally, the winged *T. saulcyanus* (described and imaged in JEANNEL 1927: 417) from Cyprus and Israel belongs to this subgenus (Fig. 3). Several Caucasian species should belong here as well, including the widespread *T. liopleurus*, but this needs confirmation.

Taxonomic changes: The following species are transferred from *Trechus* (s.str.) to *Trechus* subgen. *Eurotrechus* subgen.n.:

- Trechus* (*Eurotrechus*) *sauleyanus* CSIKI, 1928*
1. *Trechus* (*Eurotrechus*) *splendens* group
Trechus (*Eurotrechus*) *cantalicus* FAUVEL, 1888
Trechus (*Eurotrechus*) *splendens* GEMMINGER & HAROLD, 1868*
 2. *Trechus* (*Eurotrechus*) *distigma* group
Trechus (*Eurotrechus*) *ceballosi* MATEAU, 1953*
Trechus (*Eurotrechus*) *distigma* KIESENWETTER, 1851*
 3. *Trechus* (*Eurotrechus*) *pulchellus* group
Trechus (*Eurotrechus*) *biharicus* MEIXNER, 1912
Trechus (*Eurotrechus*) *carpathicus* RYBINSKI, 1902
Trechus (*Eurotrechus*) *marginalis* SCHAUM, 1862
Trechus (*Eurotrechus*) *pulchellus* PUTZEYS, 1846*
Trechus (*Eurotrechus*) *pulpani* RESKA, 1965
Trechus (*Eurotrechus*) *striatulus* PUTZEYS, 1847*
Trechus (*Eurotrechus*) *szujekii* PAWLOWSKI, 1972
 4. *Trechus* (*Eurotrechus*) *osmanilis* group
Trechus (*Eurotrechus*) *akkusianus* DONABAUER, 2006
Trechus (*Eurotrechus*) *amasraensis* DONABAUER, 2004
Trechus (*Eurotrechus*) *barbaritae* DONABAUER, 2004
Trechus (*Eurotrechus*) *besucheti* PAWLOWSKI, 1977
Trechus (*Eurotrechus*) *boludagensis* DONABAUER, 2006
Trechus (*Eurotrechus*) *catensis* DONABAUER, 2013
Trechus (*Eurotrechus*) *davidwrasei* DONABAUER, 2007
Trechus (*Eurotrechus*) *diagones* PAWLOWSKI, 1979
Trechus (*Eurotrechus*) *dostali* DONABAUER, 2007
Trechus (*Eurotrechus*) *goelkoeyensis* DONABAUER, 2013
Trechus (*Eurotrechus*) *heinzianus* PAWLOWSKI, 1979
Trechus (*Eurotrechus*) *hemsinensis* DONABAUER, 2013
Trechus (*Eurotrechus*) *ilgazicus* PAWLOWSKI, 1979
Trechus (*Eurotrechus*) *kackardagi* PAWLOWSKI, 1978
Trechus (*Eurotrechus*) *karadenizus* PAWLOWSKI, 1976
Trechus (*Eurotrechus*) *lazicus* PAWLOWSKI, 1976*
Trechus (*Eurotrechus*) *lebenbaueri* DONABAUER, 2004
Trechus (*Eurotrechus*) *legorskyi* DONABAUER, 2013
Trechus (*Eurotrechus*) *michaeli* PAWLOWSKI, 1978
Trechus (*Eurotrechus*) *orduensis* DONABAUER, 2007
Trechus (*Eurotrechus*) *osmanilis* DANIEL & DANIEL, 1902
Trechus (*Eurotrechus*) *safranboluensis* DONABAUER, 2004
Trechus (*Eurotrechus*) *schillhammeri* DONABAUER, 2006

Trechus (Eurotrechus) schuhi DONABAUER, 2007
Trechus (Eurotrechus) taghizadehi MORVAN, 1974
Trechus (Eurotrechus) uenyeensis DONABAUER, 2006
Trechus (Eurotrechus) weiserti DONABAUER, 2007
Trechus (Eurotrechus) zetteli DONABAUER, 2007
Trechus (Eurotrechus) ziganensis JEANNE, 1976
Trechus (Eurotrechus) zonguldakensis DONABAUER, 2004

Subgenus *Mediterranotrechus* subgen.n.

= *Trechus* (s.str.) *austriacus* group sensu JEANNEL (1927: 409), partim; *Trechus* (s.str.) *validipes* group sensu JEANNEL (1927: 540).

Type species: *Trechus validipes* K. DANIEL, 1902.

Distribution: Eastern Mediterranean.

Description: The widespread *T. austriacus* (often with winged populations) is described and figured by JEANNEL (1927: 409). It is similar to *T. quadristriatus* and *T. obtusus*, but the elytra possess much deeper and more complete, punctured striae. Aedeagus simple, with simplified copulatory pieces (obscuring relationship). *Trechus olympicus*, endemic on Cyprus, and *T. paphlagonicus* from Ilgaz Dağları (Turkey) strongly resemble *T. austriacus*, but are paler and have the hindwings reduced. *Trechus validipes* from the Dinaric Karst is highly similar in external structures but has a rather distinct aedeagus (Fig. 2; JEANNEL 1927: 540).

Comments: The former *T. austriacus* group sensu JEANNEL, 1927 proved to be highly artificial according to molecular data, consisting of three unrelated groups. *Trechus saulcyanus* belongs to the subgenus *Eurotrechus*, *T. diecki* is a *Mediterranoblemus*, and *T. olympicus* from Cyprus (treated as a synonym of *T. austriacus* by some former authors) clusters together with *T. validipes* from the Dinaric karst, building a group of its own. This finding was unexpected. Further investigations on these groups are necessary as some more species of the eastern Mediterranean region may belong to *Mediterranotrechus* as well.

Taxonomic changes: The following species are transferred from *Trechus* (s.str.) to *Trechus* subgen. *Mediterranotrechus* subgen.n.:

Trechus (Mediterranotrechus) austriacus DEJEAN, 1831
Trechus (Mediterranotrechus) labruleriei JEANNEL, 1921
Trechus (Mediterranotrechus) olympicus PIOCHARD DE LA BRULERIE, 1876*
Trechus (Mediterranotrechus) paphlagonicus MARAN, 1940
Trechus (Mediterranotrechus) validipes K. DANIEL, 1902*

Subgenus *Dinarotrechus* subgen.n.

= *Trechus* (s.str.) *elegans* group sensu JEANNEL (1927: 422), partim; *Trechus* (s.str.) *pulchellus* group sensu JEANNEL (1927: 532), partim.

Type species: *Trechus croaticus* DEJEAN, 1831.

Distribution: Southeastern Alps, Dinaric karst.

Description: Medium sized *Trechus* with reduced wings and rounded shoulders, characterized by a common configuration of the aedeagus (Fig. 2). Aedeagus steeply

truncated towards apex; apex turned down (extreme in *T. croaticus*); copulatory piece shifted towards apex, with a field of strong scales close to apical truncation.

Comments: This isolated clade (Fig. 3) does not include *T. priapus* as suggested by JEANNEL (1927), a species with similar aedeagal shape (but totally different copulatory pieces), habitus, mode of life, and distribution – another example of convergence. Some more, rare and recently described species may belong to *Dinarotrechus* as well, such as *T. keithi* OLLIVIER, PAVICEVIC & QUEINNEC, 2008 and *T. babaensis* LOMPE, 2015. This clade needs further investigation.

Taxonomic changes: The following species are transferred from *Trechus* (s.str.) to *Trechus* subgen. *Dinarotrechus* subgen.n.:

Trechus (*Dinarotrechus*) *cavernicola* J. FRIVALDSZKY, 1881*

Trechus (*Dinarotrechus*) *croaticus* DEJEAN, 1831*

Trechus (*Dinarotrechus*) *elegans* PUTZEYS, 1847*

Trechus (*Dinarotrechus*) *jezerensis* APFELBECK, 1908

Subgenus *Trechus* (s.str.)

= *Trechus* (s.str.) *quadristriatus* group sensu JEANNEL (1927: 291), partim; *Trechus* (s.str.) *pyreaneus* group sensu JEANNEL (1927: 254).

Type species: *Carabus quadristriatus* SCHRANK, 1781.

Distribution: Palearctic.

Description: Small to medium sized *Trechus*, partly winged and capable of flight, partly with hindwings reduced; habitus variable. Pronotum with shallow basal impressions. Elytra with weakly impressed striae. No external characteristic delimits all species of *Trechus* s.str. from the representatives of other subgenera. However, the aedeagal configuration is highly characteristic (Fig. 2): Aedeagus rather small, elongated; apex elongated, slender but simple; two copulatory pieces of elongated shape in ventral position, both of similar length, without areas covered by dense scales.

Comments: Beside the extraordinarily widespread, common and winged *T. quadristriatus* (the type species), some exceedingly rare and localized (sub)alpine species of disjunct distribution (e.g., *T. laevipes* from Monte Generoso in the Alps or *T. varendorffi* from Corse) belong to this subgenus. *Trechus* s.str. is closely related to the next two subgenera, *Orinotrechus* and *Nigrinotrechus*.

Trechus (s.str.) *cuniculorum* MEQUIGNON, 1921*

Trechus (s.str.) *gallaecus* JEANNEL, 1921

Trechus (s.str.) *laevipes* JEANNEL, 1927*

Trechus (s.str.) *latebricola* KIESENWETTER, 1850

Trechus (s.str.) *planipennis* ROSENHAUER, 1856*

Trechus (s.str.) *pyreaneus* DEJEAN, 1831

Trechus (s.str.) *quadristriatus* (SCHRANK, 1781)*

Trechus (s.str.) *sessitanus* MONGUZZI, 1985*

Trechus (s.str.) *suturalis* PUTZEYS, 1870

Trechus (s.str.) *varendorffi* SAINTE-CLAIRE DEVILLE, 1903*

Subgenus *Orinotrechus* subgen.n.

= *Trechus* (s.str.) *pertyi* group sensu JEANNEL (1927: 485).

Type species: *Trechus pertyi* HEER, 1837.

Distribution: Alps and northwestern Carpathians, restricted to alpine habitats.

Description: Small (exceptional medium sized) *Trechus* with flattened elytra; striae reduced; hindwings lost, shoulders rounded. Pigmentation dark or moderately reduced to pale reddish. Aedeagus in most species of a common shape within *Trechus* (Fig. 2); apex simple, straight or slightly upcurved. Two copulatory pieces in characteristic position. The larger piece is elongated distally (not ventrally like in most other subgenera), without dense fields of scales. A second copulatory piece of simple, small and elongated shape exists or is totally reduced. Two species from the Austrian Alps (*T. regularis* and *T. noricus*), described and imaged by JEANNEL 1927: 422), show a rather aberrant type of aedeagus, extraordinarily elongated and slender, with strongly reduced copulatory pieces (Fig. 2). This subgenus is described and imaged in detail as the *T. pertyi* group by JEANNEL (1927: 485).

Comments: This speciose clade includes most alpine endemic species from the Alps living close to the surface. Additionally, *T. matejkai*, an alpine and local endemic from the Slovakian Carpathians and two relictual species from the Austrian eastern Alps belong to *Orinotrechus*. Interestingly, *T. pseudopiceus* from the alpine zone in the southeastern Alps (Austria/Slovenia) and *T. laevipes* from the alpine zone of Monte Generoso (Italy) do not belong to this clade as previously suggested; similarities are caused by convergence.

Taxonomic changes: The following species are transferred from *Trechus* (s.str.) to *Trechus* subgen. *Orinotrechus* subgen.n.:

1. *Trechus (Orinotrechus) regularis* group
Trechus (Orinotrechus) noricus MEIXNER, 1911*
Trechus (Orinotrechus) regularis PUTZEYS, 1870*
2. *Trechus (Orinotrechus) matejkai* group
Trechus (Orinotrechus) matejkai VSETECKA, 1938*
3. *Trechus (Orinotrechus) pertyi* group
Trechus (Orinotrechus) barii FOCARILE, 1949*
Trechus (Orinotrechus) danieli HOLDHAUS, 1902*
Trechus (Orinotrechus) dolomitanus JEANNEL, 1931*
Trechus (Orinotrechus) glacialis HEER, 1837*
Trechus (Orinotrechus) hampei GANGLBAUER, 1891*
Trechus (Orinotrechus) insubricus DANIEL & DANIEL, 1898*
Trechus (Orinotrechus) longulus DANIEL & DANIEL, 1898*
Trechus (Orinotrechus) magistrettii FOCARILE, 1950*
Trechus (Orinotrechus) montisarerae FOCARILE, 1950*
Trechus (Orinotrechus) pertyi HEER, 1837*
Trechus (Orinotrechus) pumilus JEANNEL, 1927*
Trechus (Orinotrechus) schaumi PANDELLE, 1867*
Trechus (Orinotrechus) schyberosiae SZALLIES & SCHÜLE, 2011*

Trechus (Orinotrechus) sinuatus SCHAUM, 1860*
Trechus (Orinotrechus) strasseri GANGLBAUER, 1891*
Trechus (Orinotrechus) stricticollis JEANNEL, 1927*
Trechus (Orinotrechus) tenuilimbatus DANIEL & DANIEL, 1898*
Trechus (Orinotrechus) tristiculus DANIEL & DANIEL, 1898*

Subgenus *Nigrinotrechus* subgen.n.

= *Trechus* (s.str.) *obtusiusculus* group sensu JEANNEL (1927: 554); *Trechus* (s.str.) *nigrinus* group sensu JEANNEL (1927: 552).

Type species: *Trechus modestus* PUTZEYS, 1874.

Distribution: Italy, Alps, southeastern Europe, Turkey. In open country (e.g., between grassroots, in leaf litter of shrubs, in alpine meadows), in significantly drier conditions than most other *Trechus*.

Description: Small (sometimes medium sized) *Trechus*, very similar to the previous two subgenera. Hindwings functional or reduced, pigmentation mostly dark, reduced in few species to pale reddish. The aedeagus is characterized by a strongly developed basal bulbus, otherwise elongated in shape, with slightly modified apex (knobbed or hooked). The smaller copulatory piece is lost, the larger one of highly variable shape, frequently elongated ventrally. This group was described and imaged in detail by JEANNEL (1927: 554).

Comments: The members of the *T. obtusiusculus* group share an enlarged basal bulbus of aedeagus. Otherwise, this group is extremely similar to the closely related *Orinotrechus*, but there is a good separation in molecular phylogenies (FAILLE et al. 2013, Fig. 3). Molecular phylogenies indicate that winged and widespread species from the eastern Mediterranean belong here (*T. nigrinus* and *T. melanocephalus*), which is supported by aedeagal characteristics, habitus, colouration, and mode of life. Thus, this subgenus may include several more species from Turkey and the Levante region, which needs further investigations.

Taxonomic changes: The following species are transferred from *Trechus* (s.str.) to *Trechus* subgen. *Nigrinotrechus* subgen.n.:

Trechus (Nigrinotrechus) nigrinus PUTZEYS, 1847*
Trechus (Nigrinotrechus) melanocephalus KOLENATI, 1845*

1. *Trechus (Nigrinotrechus) obtusiusculus* group

Trechus (Nigrinotrechus) albanicus APFLBECK, 1907
Trechus (Nigrinotrechus) bensai JEANNEL, 1927
Trechus (Nigrinotrechus) bergamascus JEANNEL, 1927*
Trechus (Nigrinotrechus) bohemosorum PAWLOWSKI, 1973
Trechus (Nigrinotrechus) bradycelliformis CSIKI, 1906
Trechus (Nigrinotrechus) cephalonicus WINKLER, 1914
Trechus (Nigrinotrechus) delarouzei PANDELLE, 1867*
Trechus (Nigrinotrechus) epirotes COLAS, 1957
Trechus (Nigrinotrechus) gallicaensis GUEORGUIEV & HRISTOVSKI, 2010
Trechus (Nigrinotrechus) hummleri JEANNEL, 1927*
Trechus (Nigrinotrechus) kobingeri APFLBECK, 1902

Trechus (Nigrinotrechus) majusculus DANIEL, 1902
Trechus (Nigrinotrechus) maritimus DEVILLE, 1908*
Trechus (Nigrinotrechus) matrismeae PAWLOWSKI, 1972
Trechus (Nigrinotrechus) meixneri JEANNEL, 1924
Trechus (Nigrinotrechus) merkli PAWLOWSKI, 1973
Trechus (Nigrinotrechus) midas JEANNEL, 1927
Trechus (Nigrinotrechus) modestus PUTZEYS, 1874*
Trechus (Nigrinotrechus) montispennae JEANNEL, 1927
Trechus (Nigrinotrechus) montiscusnae FOCARILE, 1952
Trechus (Nigrinotrechus) naldii GHIDINI, 1932
Trechus (Nigrinotrechus) nezlobinskyi HRISTOVSKI, 2014
Trechus (Nigrinotrechus) obtusiusculus GANGLBAUR, 1889
Trechus (Nigrinotrechus) ormayi GANGLBAUR, 1891
Trechus (Nigrinotrechus) orobicus MONGUZZI, 2015*
Trechus (Nigrinotrechus) osellai BATTONO & VIGNA TAGLIANTI, 1993
Trechus (Nigrinotrechus) pennisii MAGRINI, 1984
Trechus (Nigrinotrechus) pirinicus PAWLOWSKI, 1972
Trechus (Nigrinotrechus) ravasinii JEANNEL, 1925
Trechus (Nigrinotrechus) rotundatus DEJEAN, 1831*
Trechus (Nigrinotrechus) salassus JEANNEL, 1927*
Trechus (Nigrinotrechus) solarii JEANNEL, 1921*
Trechus (Nigrinotrechus) straneoi JEANNEL, 1931*
Trechus (Nigrinotrechus) vallestis DANIEL & DANIEL, 1898*
Trechus (Nigrinotrechus) weiratheri JEANNEL, 1929
Trechus (Nigrinotrechus) winkleri JEANNEL, 1927
Trechus (Nigrinotrechus) zangherii JEANNEL, 1927*

Discussion

The first step towards a fundamental taxonomic reorganization of former *Trechus* is completed. Most European taxa of the megadiverse genus *Trechus* are arranged in a way that reflects the published phylogenies significantly better than in former times, because polyphyletic and paraphyletic lineages were resolved according to current knowledge. Molecular methods showed that convergences are a frequent phenomenon within *Trechus* and taxonomic placement of taxa in supraspecific groups based on morphology alone is difficult and frequently error-prone. Similar actions are needed for at least two other clades of European Trechini, where molecular phylogenies contradict the current generic and subgeneric taxonomy: the *Aphaenops* clade (FAILLE et al. 2010) and the *Duvalius* clade (FAILLE et al. 2013).

Some open questions about the European *Trechus* fauna remain; especially several *Trechus* from the Balkan Peninsula or the fascinating giant *Anchotrechus punctipennis* from Tenerife, Canary Islands, could not be integrated yet. Furthermore, molecular data of the highly diverse and interesting fauna of the Caucasus will provide deeper insight into the extraordinary radiation of *Trechus* in the Western Palearctic region. Nothing is

published about the molecular phylogeny of *Trechus* sensu lato from the Eastern Palearctic and Ethiopian regions.

Further studies are needed to find reliable morphological characteristics to distinguish genera and subgenera within Trechini. The taxonomic actions taken here may be criticised because it is not yet clear, how some genera and subgenera can be morphologically distinguished. So far, genetic methods seem to be the sole reliable provider of phylogenies within Trechini. At least, the new arrangement of *Trechus* is supported by distributional patterns, ecological preferences and aedeagal similarities of related taxa. However, characteristics frequently used for separation of (sub)genera in the past, could be identified as “homoplastic” by molecular phylogenies. Some examples are pubescent elytra, reduction of pigmentation, reduction of wings (and consecutive modification of elytral convexity around shoulders), reduction of eyes, body size, position and presence of setae. The highly varied shape of the male aedeagi is valuable for species delimitation, but of limited support for higher taxonomy.

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