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Cryptic diversity in the Azorean beetle genus *Tarphius* Erichson, 1845 (Coleoptera: Zopheridae): An integrative taxonomic approach with description of four new species

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Abstract

Recent findings based on molecular data support the occurrence in the Azores of several independently evolving lineages of the beetle genus *Tarphius* Erichson, 1845 (Coleoptera: Zopheridae Solier, 1834) and higher species richness masked by cryptic diversity, needing formal taxonomic description. All *Tarphius* from the Azores are revised using an integrative taxonomic approach, using evidence from morphology, morphometrics and molecular data to delimit species. Our results reveal that Azorean *Tarphius* comprise at least five phyletic lineages, two of which share a similar morphology, despite being divergent at the molecular level. A total of four new species are described grouped into two complexes: i) two new species in the "complex *tornvalli*" with the new taxa *Tarphius relictus* **sp. nov.** (Terceira) and *Tarphius furtadoi* **sp. nov.** (São

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Jorge, Faial and Pico) and; ii) two new species in the "complex *azoricus-wollastoni-depressus*" with the new taxa *Tarphius gabrielae* **sp. nov.** (Pico) and *Tarphius floresensis* **sp. nov.** (Flores). Descriptions, photographs of holotypes and morphological details, and remarks on diagnostic features comparing similar species are presented. Additional information on the distribution and conservation status of the 12 described species in the archipelago is also provided.

Key words: Azores, biodiversity, conservation, Macaronesia, radiation, Zopheridae

Introduction

There is a consensus among biogeographers that the Azorean fauna is poor and disharmonic when compared with the other Macaronesian archipelagos. Indeed this is the basis of an ongoing debate surrounding the causal factors for the low diversification of the Azorean biota, the so-called "Azorean enigma" (Borges 1992; Borges & Hortal 2009; Carine & Schaefer 2010; Schaefer *et al*. 2011; Triantis *et al.* 2012). The Azorean islands are one of the most isolated oceanic volcanic archipelagos on Earth, and the most isolated of the four major Macaronesian archipelagos (Azores, Canary Islands, Madeira and Cape Verde). Beetle diversity is now well known (Borges 1990; Borges *et. al.* 2005b; Oromí *et al.* 2010), but the rate of species discovery has not yet reached a plateau (Borges & Lobo 2010).

Recently, Amorim *et al.* (2012) performed a detailed phylogenetic reconstruction of the beetle genus *Tarphius* Erichson, 1845 (Coleoptera: Zopheridae) in the Azores, and their results support the occurrence of several independently evolving lineages, and a higher richness of taxa than previously recognized, masked by cryptic diversity, requiring formal taxonomic description. This suggests the need for a detailed revision of the beetle genus *Tarphius* in the Azores using an integrated framework to delimit independent species. In the current work we follow an operational strategy for species delimitation: i) first, molecular data is used to provide evidence of lineage separation; and ii) then, morphometric and traditional morphological approaches are used to species delimitation. With this approach we integrate enough lines of evidence to designate a species that reflects a natural group based on the traditional biological concept, i.e., reproductive isolation (Mayr 1942).

The genus *Tarphius* is represented by 74 species (Franz 1967; Dajoz 1977; Ślipiński 1985; Borges *et al.* 2008; Ślipiński & Schuh 2008; Arechavaleta *et al.* 2010; Borges *et al.* 2010; Machado 2012; Serrano *et al*. 2013), with its major richness concentrated in Macaronesia. Species of *Tarphius* exhibit fungivorous feeding habits, a nocturnal activity and are mostly associated with native habitats in Macaronesia. Eight valid species have been assigned to the genus in the Azores (Borges 1991; Oromí *et al.* 2010), which is a low figure when compared with the Macaronesian archipelagos of Madeira (23 spp.) (Borges *et al.* 2008; Machado 2012) and of the Canary Islands (31 spp.) (Arechavaleta *et al.* 2010; Machado 2012).

The first Azorean *Tarphius*, *T. wollastoni*, was described by Crotch (1867) based on specimens collected in Faial Island, and later redescribed by Dajoz (1977, pp. 118) and Gillerfors (1985). Dajoz (1977) also mentions a specimen collected in Flores Island that he assigns to *Tarphius wollastoni.* Therefore, *T. wollastoni* has been consistently listed for Faial and Flores Islands (Borges 1991; Borges *et al.* 2005b; Borges *et al.* 2010). Seven more *Tarphius* species were subsequently described for the Azores: *T. rufonolulosus* Israelson, 1984, *T. depressus* Gillerfors, 1985, *T. pomboi* Borges, 1991, and *T. serranoi* Borges, 1991 from Santa Maria Island; *T. tornvalli* Gillerfors, 1985 from São Miguel Island; *T. azoricus* Gillerfors, 1986 from São Miguel, Pico and Flores Islands; and *T. acuminatus* Gillerfors, 1986 from Pico Island (Israelson 1984; Gillerfors 1985; Gillerfors 1986a; Borges 1991).

Gillerfors (1986b) also recorded *T. tornvalli* for Pico Island and Borges (1990) assigned the first population of *Tarphius* found in Terceira Island to *T. azoricus*. Gillerfors (1986a), after an expedition to Flores Island where he collected many specimens of *Tarphius*, stated that there is some uncertainty as to the type locality of *T. wollastoni* and suggested it was only present on Flores, and not in Faial Island. Borges *et al.* (2005a,b) assigned the first population found in São Jorge to *T. azoricus* and extended the distribution of *T. depressus* to Pico and São Miguel Islands, and of *T. acuminatus* to São Miguel Island. In the most recent checklist of Azorean beetles Oromí *et al.* (2010) assumed that: i) *T. acuminatus* is restricted to Pico Island and that the previous records of *T. acuminatus* from São Miguel Island represent a new species, ii) *T. wollastoni* is restricted to Flores Island, and iii) specimens collected in 2010 in the native forest of Caldeira of Faial, belong to *T. azoricus*, therefore now the only recognized *Tarphius* species of Faial Island. This represents the most updated distribution of *Tarphius* species in the Azores.

For all *Tarphius* species described so far, taxonomy has been strictly based on external morphology, with specimens assigned to species based on diagnostic characters, namely: the number and location of interstriae nodules on the elytra; the shape of setae on elytra, head and pronotum; elytron humeral angle; and aedeagus shape. Amorim *et al.* (2012) performed a detailed phylogenetic reconstruction based on nuclear (elongation factor 1 alpha —EF1α and mitochondrial (cytochrome *c* oxidase subunit I—COI, leucine specific transfer RNA—$tRNA_{Leu}$, cytochrome *c* oxidase subunit II—COII) sequences, and found strong support for the taxonomic entities *T. serranoi*, *T. pomboi*, *T. rufonodulosus* and *T. depressus* from the island of Santa Maria, and for *T. wollastoni* (from Flores Isl.), as all specimens belonging to these species form monophyletic groups with high to maximum clade support. The faster evolving mtDNA genes provide more resolution (Fig. 2 in Amorim *et al.* 2012) and most taxa are grouped according to morphospecies identity. However, for species that occur on multiple islands (*T. azoricus*, *T. tornvalli* and *T. depressus*) even though individuals of the same morphospecies belong to the same major clade, they group by island of origin. For instance, specimens morphologically identified as *T. depressus* belong to the same major clade (clade IV, Fig. 2 in Amorim *et al*. 2012) but are clustered into three groups, according to island of origin (Pico, S. Miguel and S. Maria Isls.). This may suggest that the recently discovered populations in São Miguel and Pico Islands may in fact represent two new species, distinct from *T. depressus* described originally for Santa Maria Island (Gillerfors 1985). Additionally, from Figure 2 in Amorim *et al.* (2012) we may conclude that the species *T. azoricus* and *T. tornvalli* are an even more complex case, where haplotypes group by island of origin irrespective of morphospecies affiliation.

Here we revise *Tarphius* species of the Azores (all species except *T. acuminatus*), resulting in the description of four new species. As stated above, we use an integrative approach combining molecular and morphometric analysis and a classical taxonomic approach using external morphological characters. We show that some of the taxonomic inferences made by previous authors concerning Azorean *Tarphius* were erroneous. We also conclude that the type locality of *Tarphius wollastoni* described by Crotch (1867) is in fact Faial Island and that the specimens found in Flores Island previously assigned to *T. wollastoni* are a distinct species. Information on the distribution and conservation status of the 12 *Tarphius* species currently known from the archipelago is also provided.

Material and methods

Sampling. Beetles were sampled from 1999 through 2010 in different habitats in all Azorean islands, except Graciosa and Corvo islands where the genus has never been recorded. The bulk of our data comes from the BALA project (**B**iodiversity of the **A**rthropods from the **L**aurisilva of the **A**zores), in which arthropods were collected in a standardized way by means of pitfall traps in the native forests (see details in Borges *et al.* 2005a; Gaspar *et al.* 2008; see also http://islandlab.uac.pt/projectos/ver.php?id=65). Species occurring in exotic *Cryptomeria japonica* plantations were collected in four islands (S. Maria, Terceira, Faial and Flores Isls.) in the years 2001, 2004, 2005 and 2009 by means of pitfall traps (see details in Amorim 2005; Cardoso *et al.* 2009; Meijer *et al.* 2011). Specimens of *Tarphius* were also collected from 1999 onwards by manual searching in specific habitats (in decaying wood and under bark of live trees, see Amorim 2005 and Amorim *et al.* 2012).

DNA extraction, PCR amplification and sequencing. The goal was to genetically characterize approximately 10 specimens per species per island for all Azorean islands where the genus occur, expanding on the sampling of Amorim *et al.* (2012) for the Azores. To increase the success of DNA sequencing, the specimens used for DNA analyses were preferentially those captured by manual searching or by pitfall traps containing bread or propylene glycol. Specimens were stored individually in absolute ethanol or acetone, and refrigerated until DNA extraction. Specimens of *Tarphius* from Flores Island previously identified as *T. azoricus* (Gillerfors 1986) were obtained from dried mounted material.

The DNeasy Tissue Kit (Qiagen) was used to extract total genomic DNA. Both mitochondrial and nuclear markers were used in this study: a mitochondrial fragment approximately 1,500 bp comprising part of the COI gene, the tRNA-Leu gene and the complete COII gene; and a nuclear fragment approximately 950 bp of the EF1α gene. These fragments were amplified via the polymerase chain reaction (PCR) using several primers described in the literature (Simon *et al.* 1994; Emerson *et al.* 2000; Whiting 2002; Amorim *et al.* 2012). Purified PCR products were cycle-sequenced in both directions with the PCR amplification primers and internal primers. For details on DNA extraction, PCR amplification, and sequencing see Amorim *et al*. (2012).

Phylogenetic analyses and ancestral range reconstruction. Sequences for the mtDNA and nuclear markers were assembled, edited, aligned and collapsed to unique sequences using the softwares SEQUENCHER 4.8 (Gene Code Corporation), MACCLADE v4.08 (Maddison & Maddison 2005) and DNACOLLAPSER (Villesen 2007). The gametic phase for heterozygous EF1α sequences were inferred manually, as no individual exhibit more than three heterozygous positions. Sequences of mtDNA and EF1α of Azorean *Tarphius* already available from previous studies were also included in the phylogenetic alignments (see Amorim *et al.* 2012).

The mtDNA and EF1α data matrices were analysed separately according to various partitioning schemes (see Amorim *et al.* 2012). Maximum likelihood (ML) and Bayesian inference (BI) methods were used to reconstruct phylogenetic relationships among Azorean specimens using *T. kiesenwetteri* Heiden, 1870 from the Iberian Peninsula as the outgroup (GenBank accession nos. JQ689203 and JQ689284).

The model of evolution that best explains the nucleotide variation within each partition was selected using the program jMODELTEST v0.1.1 (Posada 2008) and used for the parameterization of the ML and BI searches. The software MRBAYES v3.1.2 (Ronquist & Huelsenbeck 2003) was used to perform BI analyses and the ML phylogenetic inferences were performed with RAxML v7.2.8 (Stamatakis 2006; Stamatakis *et al.* 2008). For further details on phylogenetic analyses see Amorim *et al.* (2012). Whenever possible the same specimens were used for morphological and genetic characterization.

The Bayesian Binary MCMC (BBM) Method (Ronquist & Huelsenbeck 2003), as implemented in the software RASP v3.2 (Yu *et al.* 2015), was used to reconstruct ancestral geographic distribution. The probabilities of ancestral ranges was calculated for clades of the the BI mtDNA tree with high support (PP>0.95) that include different species and/or the same species on multiple islands (nodes a–g, Fig. 1). The BMM analysis was run with default options, except for the number of cycles (n=100,000) (see Appendix S3).

Morphological data. The morphological studies, including measurements and drawings, were performed under a Wild M5 stereoscopic microscope equipped with an ocular micrometer and drawing tube. Photographs were taken using a Nikkor lens attached to a Canon EOS 5D Mark II camera, using the software Zerene Stacker v.1.04 to stack the images. Image editing was performed in Photoshop CS6. Measurements, recorded in millimeters, were taken for up to 10 specimens per population in each island ahead of knowing the taxonomic status of that population: head length, from the anterior margin of the frons to the posterior margin of the head; pronotum width at the largest part; pronotum length; elytral length, at the elytral suture from the apex of the scutellum to the posterior margin of the elytra; and elytral width at the widest part. Since all the aforementioned measurements were highly correlated (See Supporting information, Appendix S1), we only evaluate body length (elytral length plus pronotum length) in the following analysis. Moreover, because only one individual of *T. acuminatus* and *T. wollastoni* were available for measurement, we did not include these species in the analysis.

Subsequently, we also calculated four ratios commonly used in previous *Tarphius* descriptions, namely width/length of the pronotum; elytra/pronotum width ratio; ratio length/width of the elytra; and pronotum/elytra length ratio. Prior to analysis, body length and the four ratios were log-transformed to meet the requirements for the statistical analysis with parametric methods and to minimize probable distortion caused by allometric relationships of the variables. We tested for morphological differences between *Tarphius'* species using nonparametric permutational multivariate analysis of variance (PerMANOVA; Anderson 2001) with Euclidean distances calculated among the five morphological variables (body length and the four ratios). If the overall test was significant, *post hoc* tests were performed to identify significant differences among species. P-values of the *post hoc* tests were corrected for multiple comparisons using false discovery rate (FDR, Benjamini & Yekutieli 2001). PerMANOVA were also run for each morphological variable separately. Results were visualized using a non-metric multidimensional scaling analysis (NMDS) using Euclidian distance. All tests were implemented within the R programming environment (R Development Core Team 2010).

Acronyms. The acronyms used for the entomological collections where the type material is placed are as follows: DTPC= University of the Azores, Terceira, Portugal ("Dalberto Teixeira Pombo" Collection); FCULC= *Faculdade de Ciências da Universidade de Lisboa*, Lisbon, Portugal; SNM—*Senckenberg Naturmuseum*, Frankfurt, Germany.

Results

Molecular data. A total of 151 mitochondrial DNA sequences and 89 EF1α sequences of Azorean *Tarphius* were used for the phylogenetic analyses (Appendix S2). The mtDNA alignment consisted of 1,383 bp, comprising 642 bp of the COI gene, 64 bp of the $tRNA_{Leu}$ gene, and 677 bp of the COII gene. The EF1α alignment consisted of 917 bp, comprising two exon regions totalling 711 bp intervened by an intron of 206 aligned nucleotide positions, ranging in sequence length from 196 to 204 bp. Sequences for both markers were collapsed to unique sequences and the final data sets, including one Iberian outgroup, consisted of 109 unique sequences for the mtDNA and 78 for the EF1α fragment (homozygotes plus phased haplotypes), including one Iberian outgroup (Appendix S2).

Among the sequences generated, 52 mtDNA and 11 EF1α sequences are reported for the first time (GenBank accession numbers KU666002-53 and KU679448-58, Appendix S2). The available specimens of *T. acuminatus* of Pico Island, *T. azoricus* of Flores Island and *Tarphius* of São Miguel Island previously identified as *T. acuminatus* (Borges *et al.* 2005a,b) did not yield PCR amplifiable DNA and were thus not sequenced for either marker.

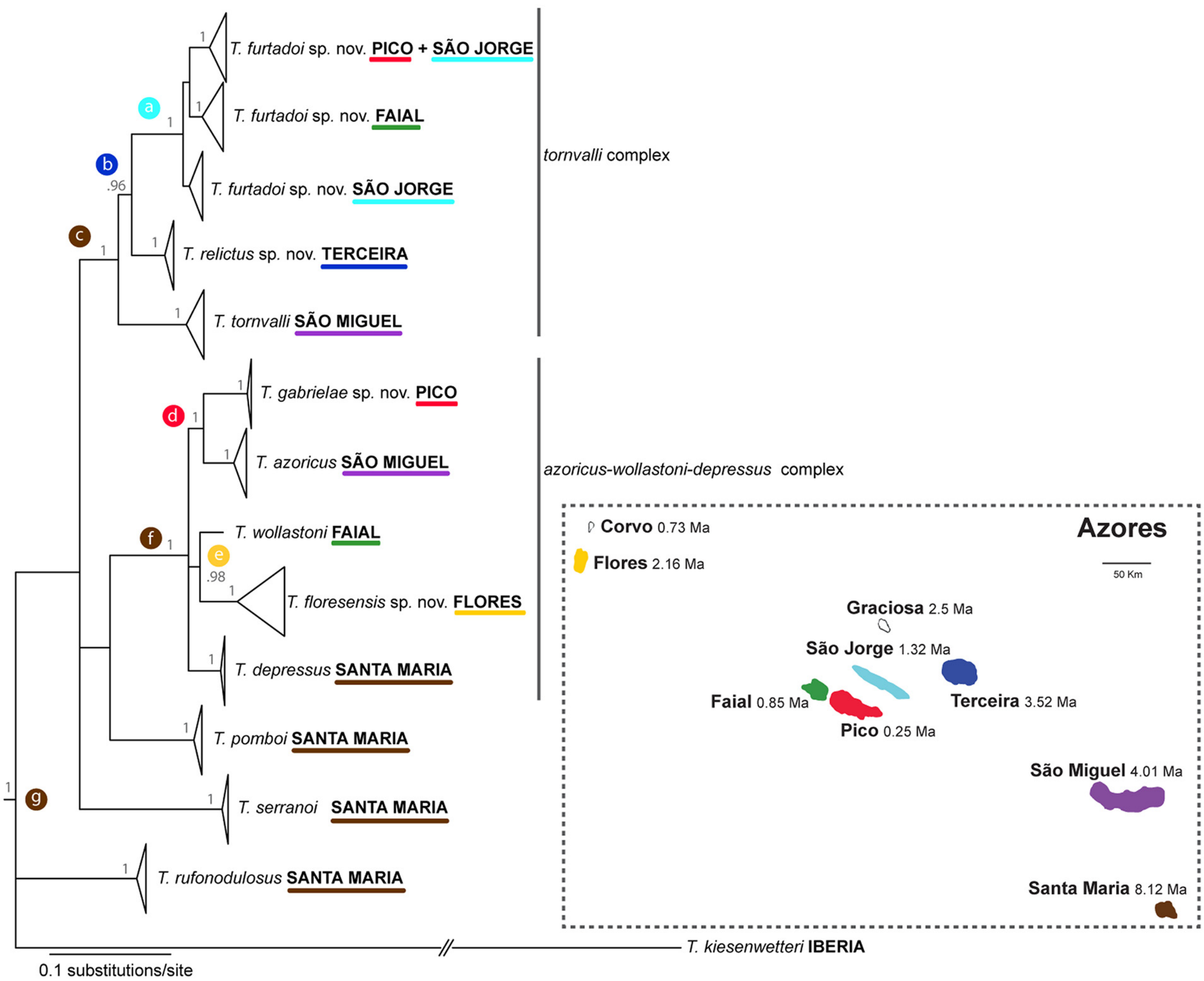

FIGURE 1. Bayesian inference tree for *Tarphius* beetles of the Azores based on 1,383 bp of mitochondrial DNA (COI, tRNA-Leu, COII). Clade credibility values are shown for nodes with a posterior probability ≥ 0.95. Colored circles with lower case letters (a–g) indicate nodes, encompassing the same species on multiple islands and/or different species, for which most likely ancestral ranges were inferred. Color code for ancestral range matches that of current species distribution (see colored bar underneath island name and island colors in inset map). Inset map also shows island maximum geological age in millions of years (Ma).

Note: new taxonomic scheme used in this figure. Corresponding old species names are presented in parenthesis: *T. furtadoi* **sp. nov.**, Pico Isl. (*T. tornvalli* plus *T. azoricus* of Pico Isl.); *T. furtadoi* **sp. nov.**, Faial Isl. (*T. azoricus* of Faial Isl.); *T. furtadoi* **sp. nov.**, São Jorge Isl. (*T. azoricus* of São Jorge Isl.); *T. relictus* **sp. nov.**, Terceira Isl. (*T. azoricus* of Terceira Isl.); *T. tornvalli*, São Miguel Isl. (*T. tornvalli* plus *T. azoricus* of São Miguel Isl.); *T. gabrielae* **sp. nov.**, Pico Isl. (*T. depressus* of Pico Isl.); *T. azoricus*, São Miguel Isl. (*T. depressus* of São Miguel Isl.); *T. wollastoni* Faial Isl. (*T. depressus* of Faial Isl.); *T. floresensis* **sp. nov.**, Flores Isl. (*T. wollastoni* of Flores Isl.).

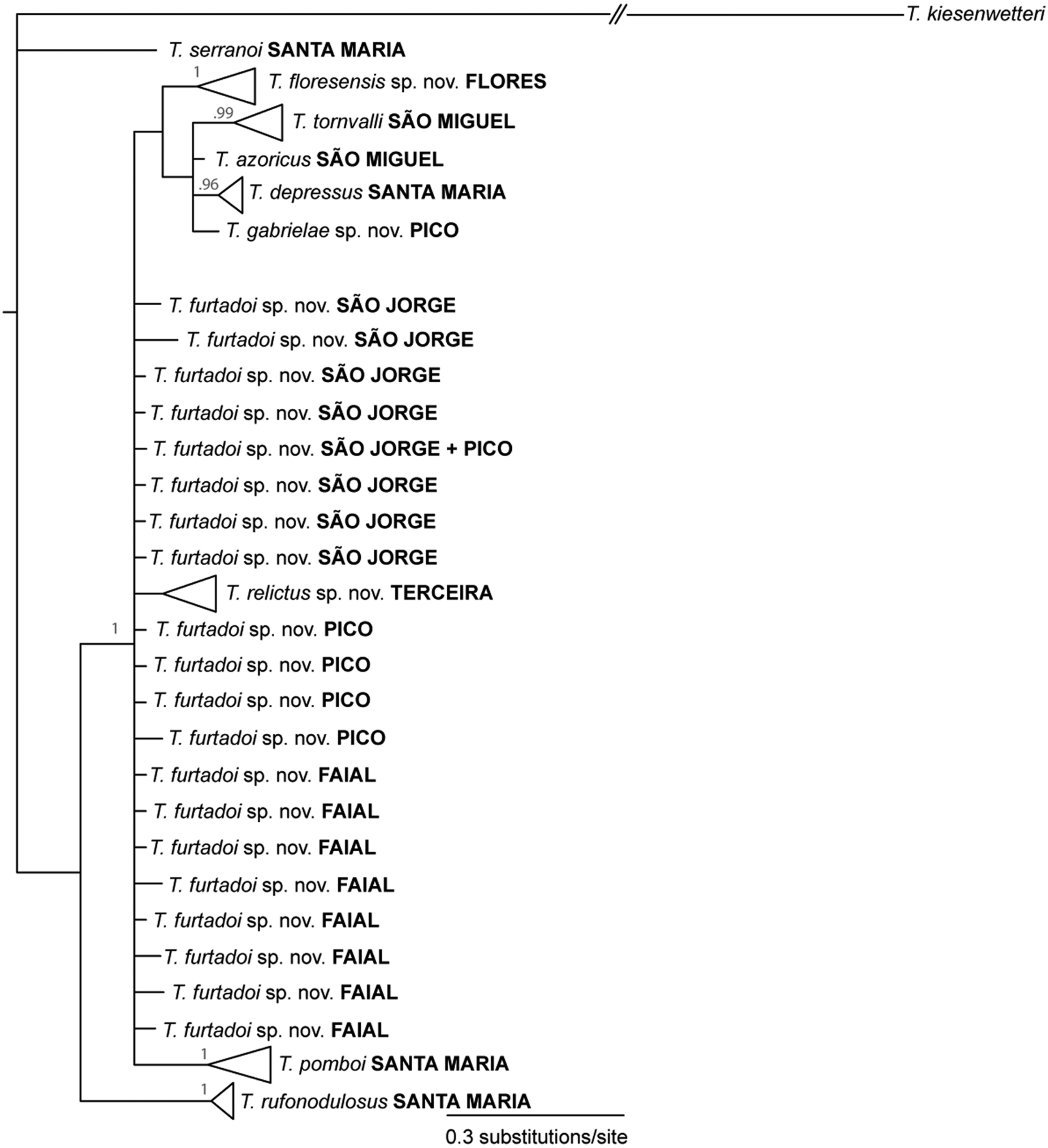

FIGURE 2. Bayesian inference tree for *Tarphius* beetles of the Azores based on 915 bp of nuclear DNA (Elongation Factor 1 alpha). Clade credibility values are shown for nodes with a posteror probability ≥ 0.95.
Note: new taxonomic scheme used in this figure. Corresponding old species names are presented in parenthesis: *T. furtadoi* **sp. nov.**, Pico Isl. (*T. tornvalli* plus *T. azoricus* of Pico Isl.); *T. furtadoi* **sp. nov.**, Faial Isl. (*T. azoricus* of Faial Isl.); *T. furtadoi* **sp. nov.**, São Jorge Isl. (*T. azoricus* of São Jorge Isl.); *T. relictus* **sp. nov.**, Terceira Isl. (*T. azoricus* of Terceira Isl.); *T. tornvalli*, São Miguel Isl. (*T. tornvalli* plus *T. azoricus* of São Miguel Isl.); *T. gabrielae* **sp. nov.**, Pico Isl. (*T. depressus* of Pico Isl.); *T. azoricus*, São Miguel Isl. (*T. depressus* of São Miguel Isl.); *T. wollastoni* Faial Isl. (*T. depressus* of Faial Isl.); and *T. floresensis* **sp. nov.**, Flores Isl. (*T. wollastoni* of Flores Isl.).

For both molecular markers, sequences were in general only shared by conspecific individuals from the same island. The exceptions are: i) *T. azoricus* and *T. tornvalli* of Pico shared one mtDNA sequence; ii) *T. azoricus* and *T. tornvalli* of São Miguel shared one mtDNA sequence; and iii) *T. azoricus* and *T. tornvalli* of Pico, and *T. azoricus* of São Jorge shared one EF1α sequence. The topologies of the ML and BI phylogenetic trees are similar for both the mtDNA and nuclear markers for all partition schemes used. Clades were consistently recovered for *T. rufonodulosus* (S. Maria), *T. serranoi* (S. Maria), *T. pomboi* (S. Maria), *T. depressus* (S. Maria), *T. wollastoni* (Flores), and *T. azoricus* (Terceira) (Figs. 1 and 2). For both molecular markers, lineages from Santa Maria (*T. rufonodulosus*, *T. serranoi* and *T. pomboi*), the oldest island in the archipelago, show the deepest divergences, implicating that Santa Maria is the probable island for the common ancestor of the group. Results of the historical distribution reconstruction (Fig. 1 and Appendix S3) also suggest that the island of Santa Maria is the most likely ancestral range for the major *Tarphius* groups found in the Azores (*tornvalli* and *azoricus/wollastoni/depressus* complexes, and remaining endemic species of Santa Maria Isl.).

As expected based on the faster substitution rate of mitochondrial genes relative to the nuclear EF1α gene, the mtDNA tree provides a finer resolution of phylogenetic relationships. Within the BI tree obtained for the mtDNA region, with no partitioning of the sequence data, most taxa group according to morphospecies identity (Fig. 1). However, within the three species that occur on multiple islands, *T. azoricus*, *T. tornvalli* and *T. depressus*, individuals group by island of origin, rather than by originally identified taxonomic identities. This is clearly in conflict with the accepted taxonomic scheme.

Morphological data. The plots of the NMDS for all individuals included in the analysis are presented in Fig. 3. Results of the PerMANOVA based on the five morphological traits (body length and the four ratios) indicated that species differed significantly in their morphology ($F_{6,165}$ = 8.461, P = 0.001, R^2 = 0.243). Moreover, post-hoc tests revealed that the three species of the complex *tornvalli*, namely *T. tornvalli*, *T. relictus* **sp. nov.** and *T. furtadoi* **sp. nov.**, as well as the species *T. rufonodulosus* (Santa Maria), differed from the other species, while the species *T. gabrielae* **sp. nov.**, *T. azoricus*, *T. depressus*, *T. floresensis* **sp. nov.** (*azoricus-wollastoni-depressus* complex), *T. pomboi* (Santa Maria) and *T. serranoi* (Santa Maria) did not particularly differ between each other (Table 1; detailed data in Appendix S4). However, differences between species for each trait analyzed independently were also significant (Body length: $F_{6,165}$ = 13.158, P = 0.001, R^2 = 0.433; Ratio width Elytra/pronotum: $F_{6,165}$ = 13.745, P = 0.001, R^2 = 0.444; Ratio length Elytra/pronotum: $F_{6,165}$ = 7.329, P = 0.001, R^2 = 0.298; Ratio width / length Elytra: $F_{6,165}$ = 3.707, P = 0.001, R^2 = 0.177; and Ratio width / length pronotum: $F_{6,165}$ = 21.332, P = 0.001, R^2 = 0.553, see Appendix S5 for post-hoc tests).

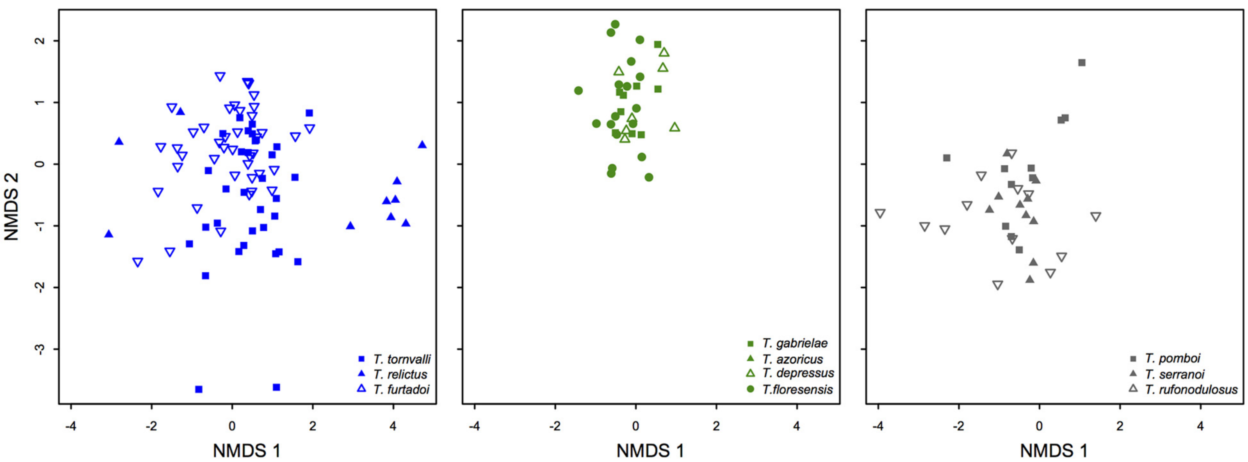

FIGURE 3. Nonmetric multidimensional scaling (NMDS) ordination based on Euclidean distances calculated among log-transformed morphological variables. Symbols represent ten different *Tarphius* species while colours indicate species complex, with blue for "*tornvalli*", green for "*azoricus-wollastoni-depressus*" and grey for the endemic species of Santa Maria. Ordinations were done on all individuals simultaneously, but species complex are illustrated separately for clarity. Statistical tests between species were performed using the PerMANOVA; NMDS two-dimensional stress: 0.17.

Molecular and morphological data. Based on molecular (Figs. 1 and 2) and morphological data (see above and descriptions of species below) we present a taxonomic revision of *Tarphius* species endemic to the Azores. We argue that:

a) The current Azorean *Tarphius* species can be grouped in six major clades, comprising 12 species: *T. rufonodulosus* (restricted to S. Maria Isl.); *T. serranoi* (restricted to S. Maria Isl.); *T. pomboi* (restricted to S. Maria Isl.); *T. acuminatus* (restricted to Pico Isl.); an *"azoricus-wollastoni-depressus"* complex composed of *T. depressus* (restricted to S. Maria Isl.), *T. azoricus* (in S. Miguel and possibly also in Flores Isl.), *T. wollastoni* (restricted to Faial Isl.) and two new species—*Tarphius gabrielae* **sp. nov.** (restricted to Pico Isl.) and *Tarphius floresensis* **sp. nov.** (restricted to Flores Isl.); and a "*tornvalli*" complex composed of *T. tornvalli* (restricted to S. Miguel Isl.) and two new species—*T. relictus* **sp. nov.** (restricted to Terceira Isl.) and *T. furtadoi* **sp. nov.** occurring on three islands (Pico, Faial and S. Jorge Isls). Although different lineages were identified for the islands of Faial, Pico and São Jorge within the "*tornvalli*" complex (Fig. 1), because morphologically specimens are extremely difficult to tell apart, we took the more conservative approach of considering all of them as belonging to the same species, *T. furtadoi* **sp. nov.**;

TABLE 1. P-values of the *post hoc* pairwise PerMANOVA tests based on Euclidean distances calculated among log-transformed morphological variables. P-values are corrected for multiple tests using the false discovery rate (FDR). Significant results are in bold.

	T. tornvalli	*T. relictus* **sp. nov.**	*T. furtadoi* **sp. nov.**	*T. gabrielae* **sp. nov.**
T. relictus sp. nov.	**0.011**			
T. furtadoi sp. nov.	0.500	**0.003**		
T. gabrielae sp. nov.	**0.021**	**0.008**	**0.034**	
T. azoricus	**0.020**	**0.012**	**0.019**	0.786
T. depressus	**0.032**	**0.003**	0.057	0.571
T. floresensis sp. nov.	**0.003**	**0.003**	**0.003**	0.354
T. pomboi	**0.003**	**0.003**	**0.003**	0.298
T. serranoi	**0.003**	**0.003**	**0.003**	0.103
T. rufonodulosus	**0.003**	**0.003**	**0.003**	**0.003**

continued.

	T. azoricus	*T. depressus*	*T. floresensis* sp. nov.	*T. pomboi*	*T. serranoi*
T. relictus sp. nov.					
T. furtadoi sp. nov.					
T. gabrielae sp. nov.					
T. azoricus					
T. depressus	0.450				
T. floresensis sp. nov.	0.571	0.097			
T. pomboi	0.500	0.097	0.926		
T. serranoi	0.266	**0.018**	0.439	0.468	
T. rufonodulosus	**0.005**	**0.003**	**0.009**	**0.011**	0.222

b) The type locality of *T. wollastoni* is now confirmed to be in the island of Faial. Consequently, all the specimens collected by Gillerfors (1986b) and Borges (2005a) of a very common *Tarphius* in the island of Flores belong to a new species, now named *T. floresensis* **sp. nov.**;

c) As suggested by Gillerfors (1986a), *T. azoricus*, *T. wollastoni* and *T. depressus* are closely related species based upon morphology and the molecular phylogeny (see Fig 1). For instance, for body length, the species *T. gabrielae* **sp. nov.**, *T. azoricus*, *T. depressus* of the *azoricus-wollastoni-depressus* complex were larger than the other species while they displayed smaller ratio width Elytra/pronotum (see Appendix S5);

d) P.A.V. Borges erroneously associated *T. azoricus* with *T. tornvalli*, which created the assumption of higher variability within a potential *T. azoricus–tornvalli* complex, as shown in Fig. 2 of Amorim *et al.* (2012). In fact, all the specimens in question from São Miguel Island belong to the original *T. tornvalli* described by Gillerfors (1985); the high morphological variability in the shape of pronotum and seta observed between the populations of São Miguel and the islands of the Central Group resulted in a new species closely related with *T. tornvalli* that is now described—*T. furtadoi* **sp. nov.** (occurring on three islands: Pico, Faial and São Jorge);

e) In previous publications of P.AV. Borges (see Oromí *et al.* 2010), specimens mentioned as *T. depressus* from Pico and São Miguel Islands were wrongly identified. In fact, *T. depressus* recorded from São Miguel Island is *T. azoricus* and *T. depressus* recorded from Pico Island belongs to a new taxon—*T. gabrielae* **sp. nov.**;

f) *T. azoricus* was originally recorded for three islands (S. Miguel, Pico and Flores) (Gillerfors 1986a), but we consider that the population of Pico Island belongs to a new species *Tarphius furtadoi* **sp. nov.**. The specimens of *T. azoricus* from Flores Island are kept with this status, since we have no molecular data and very few specimens available to support the creation of a new taxon;

g) Common traits among the three species of the "*tornvalli*" complex are their strongly arched body, well developed elytral nodules with a pattern formula of 2, 3, 2, 1 and their hair-like setae, that are needle shaped or sub-obtuse (see Fig. 4). However, different lineages are found in different islands (Fig.1) and the species differ from each other in some details of the shape of the pronotum and morphometrics (see Table 1); and

h) The five species of the *"azoricus-wollastoni-depressus"* complex have a combination of morphological characters in common, namely the shape of the humeral angles, well developed elytral nodules with a pattern formula of 3, 3, 2, 1 and their setae (see Fig. 5). The number of seta on the external row of the lateral margin of the pronotum differs among species (Fig. 6).

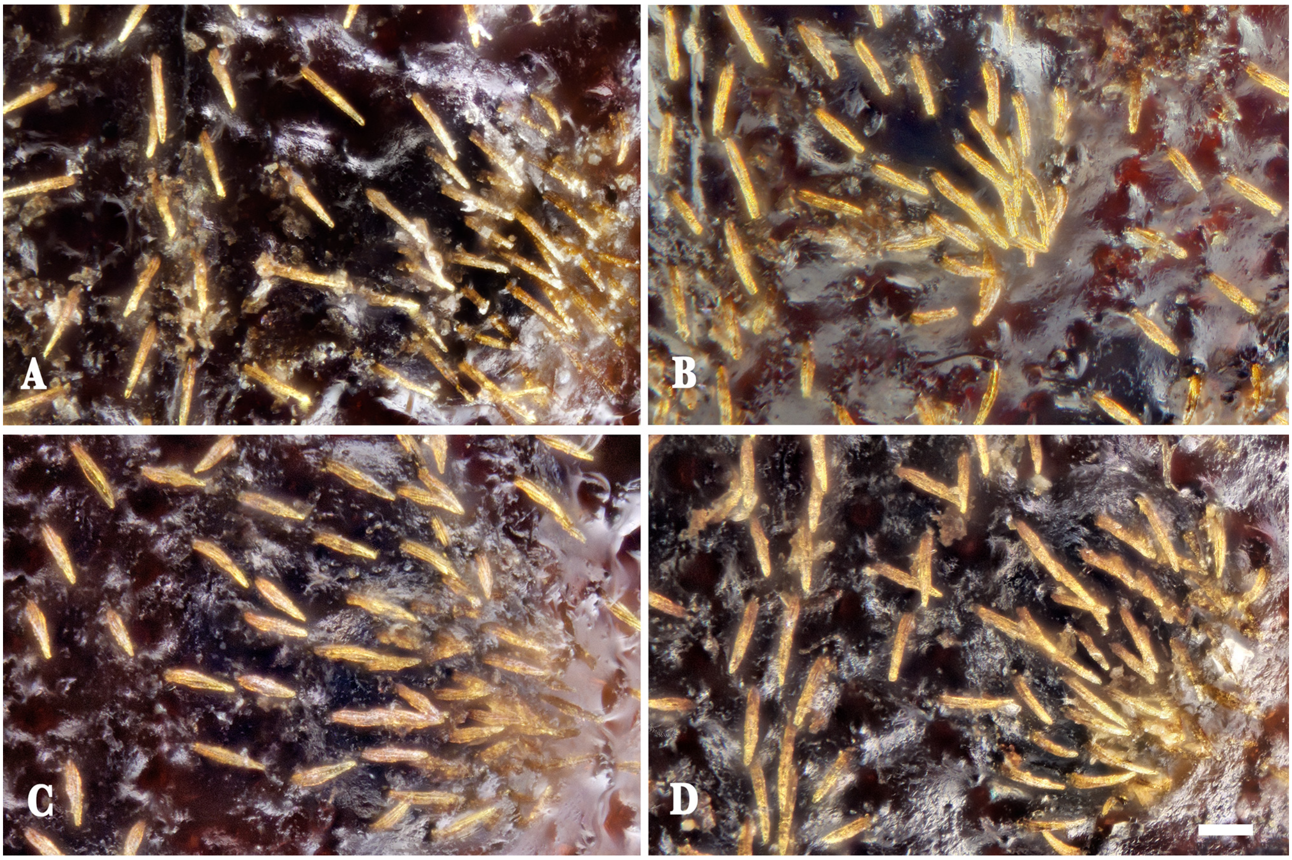

FIGURE 4. Details of setae in elytra for the species in complex "*tornvalli*": *T. tornvalli* (restricted to São Miguel) (A); *Tarphius relictus* **sp. nov.** (restricted to Terceira) (B); and *Tarphius furtadoi* **sp. nov.** (restricted to São Jorge, Pico and Faial) with a specimen of São Jorge (C) and Faial (D). Scale 0.05 mm (Photos: Erno-Endre Gergely).

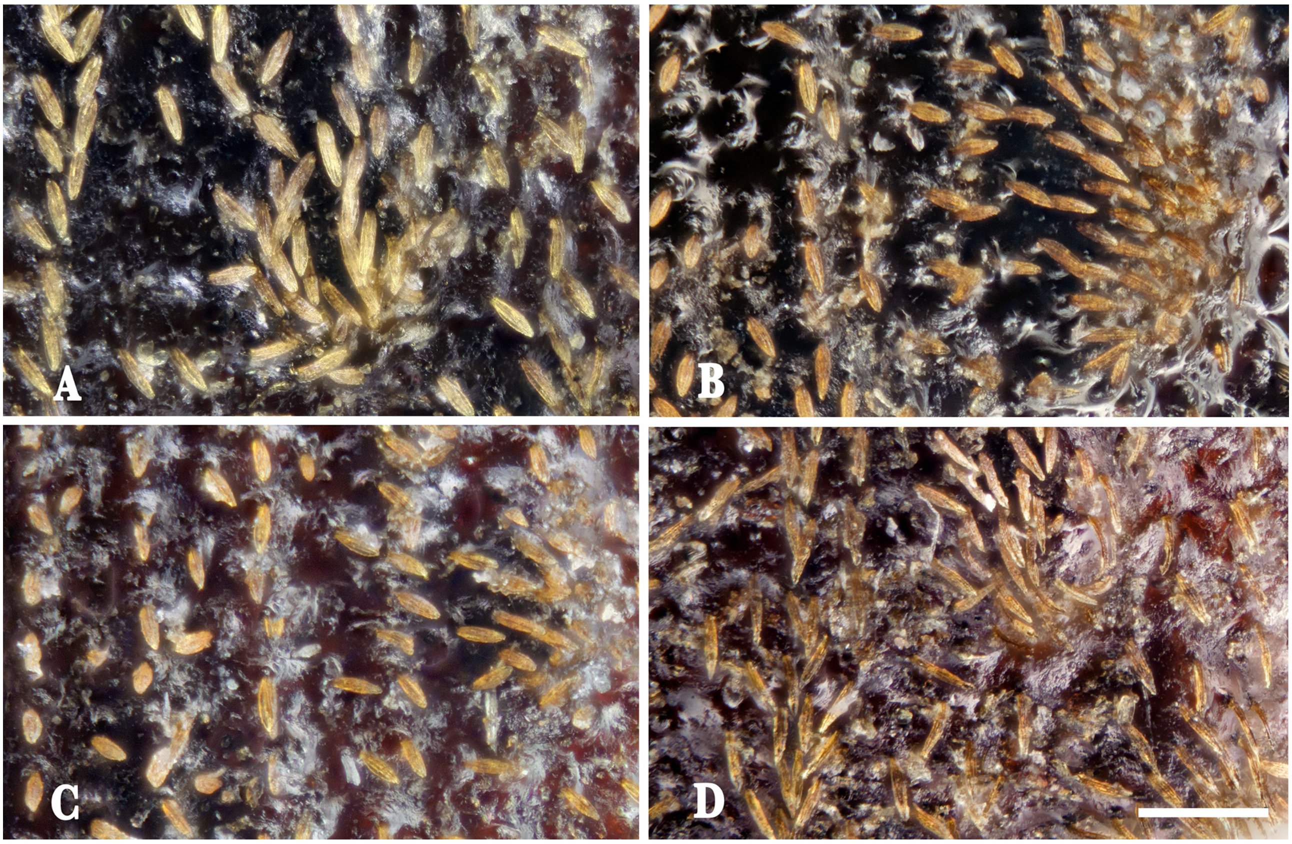

FIGURE 5. Details of setae in elytra for the species in of the complex *"azoricus-wollastoni-depressus"*: *T. azoricus* (restricted to São Miguel and Flores) (A); *Tarphius wollastoni* (restricted to Faial) (B); *Tarphius gabrielae* **sp. nov.** (restricted to Pico) (C); and *Tarphius floresensis* **sp. nov.** (restricted to Flores) (D). Scale 0.1 mm (Photos: Erno-Endre Gergely).

Taxonomy—species descriptions

In this section we revise the taxonomy of *Tarphius* beetles of the Azores in order to better reflect the evolutionary diversity within the group. Four new species are described and *T. tornvalli* Gillerfors, 1985 is redescribed.

Tarphius tornvalli complex

Tarphius tornvalli Gillerfors, 1985
(Fig. 7)

Tarphius tornvalli in Gillerfors (1985, p. 5) (S. Miguel Isl.)
Tarphius tornvalli in Borges (1990, p. 112) (S. Miguel Isl.)
Tarphius tornvalli in Borges (1991, p. 2) (S. Miguel Isl.)
Tarphius tornvalli and *Tarphius azoricus* in Borges *et al.* (2005b, p. 207) (S. Miguel Isl.)
Tarphius tornvalli and *Tarphius azoricus* in Oromí *et al*. (2010, p. 232) (S. Miguel Isl.)
Tarphius tornvalli and *Tarphius azoricus* in Amorim *et al.* (2012, Fig. 2) (S. Miguel Isl.)

Type locality. The Azores, São Miguel Island, Furnas.

Type material. There is one Holotype deposited in *Museu Municipal do Funchal*, Madeira and the remaining type series is deposited in the collection of G. Gillerfors and A. Tornvalli in Gothenburg, Sweden.

Additional material examined. Graminhais, 12/08/1989 (1 ex) (UTM 26S 654557 4185354); Tronqueira, 11–12/08/1989 (5 exx) (UTM 26S 657757 4186138); Santo António, São Miguel, Açores, 12/08/1989 (1 ex) (UTM 26S 656878 4188871) (Paulo A. V. Borges & Fernando Pereira leg.); Miradouro da Tronqueira (T01)

(Natural Forest Reserve of Pico da Vara), VIII.1999 (162 exx), VI.2010 (88 exx) (UTM 26S 659806 4184815); Santo António (T02) (Natural Forest Reserve of Atalhada), VIII.1999 (157 exx) (UTM 26S 656878 4188871); Graminhais (T03) (Natural Forest Reserve of Graminhais), VIII.1999 (58 exx), VI.2010 (2 exx) (UTM 26S 654557 4185354); Miradouro da Tronqueira Inferior (T04) (Natural Forest Reserve of Pico da Vara), VIII.1999 (152 exx), VI.2010 (18 exx) (UTM 26S 659850 4184997); Santo António (T06) (Natural Forest Reserve of Atalhada) VIII.1999 (106 exx) (UTM 26S 656905 4188787); Ribeira dos Graminhais (T07) (Natural Forest Reserve of Graminhais), VIII.1999 (5 exx), VI.2010 (7 exx) (UTM 26S 654838 4185138); Pico da Vara (T08) (Natural Forest Reserve of Pico da Vara), VII.1999 (3 exx) (UTM 26S 657757 4186138); Santo António, Conteiras (T12) (Natural Forest Reserve of Atalhada), VI.2004 (53 exx) (UTM 26S 657009 4188841); Santo António, Precipício (T13) (Natural Forest Reserve of Atalhada), VI.2004 (128 exx) (UTM 26S 657016 4188637); Ribeira dos Graminhais (T14) (Natural Forest Reserve of Graminhais), VI.2004 (5 exx) (UTM 26S 654669 4185360); Graminhais (T15) (Natural Forest Reserve of Graminhais), VI.2004 (13 exx) (UTM 26S 654385 4185571); (Paulo A. V. Borges *et al.* leg.); Material deposited in DTPC.

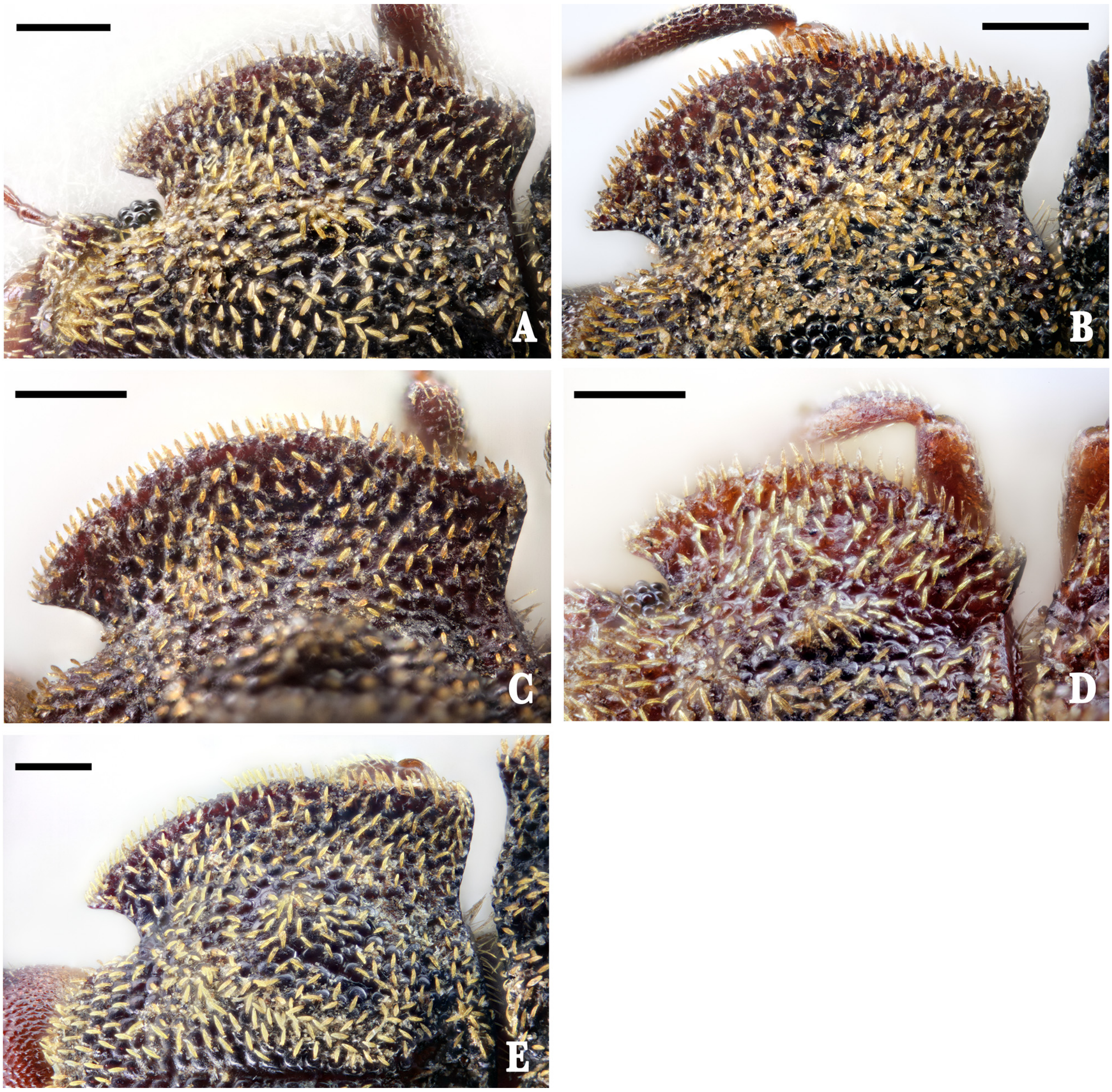

FIGURE 6. Details on the number of seta on the external row of the lateral margin of pronotum in the complex *"azoricus-wollastoni-depressus"*: *T. azoricus* (restricted to São Miguel and Flores) (A); *Tarphius wollastoni* (restricted to Faial) (B); *Tarphius gabrielae* **sp. nov.** (restricted to Pico) (C); *Tarphius floresensis* **sp. nov.** (restricted to Flores) (D); and *T. depressus* (restricted to S. Maria) (E). Scales 0.25 mm (Photos: Erno-Endre Gergely).

FIGURE 7. Habitus of *Tarphius tornvalli* Gillerfors. Scale 0.5 mm. (Photo: Erno-Endre Gergely).

FIGURE 8. Detail on the number of seta on the external row of the lateral margin of pronotum in *Tarphius tornvalli* Gillerfors. Scale 0.25 mm (Photo: Erno-Endre Gergely).

Redescription (adapted from Gillerfors 1985).

Diagnosis (Fig. 7). Small to medium species (2.37–3.77 mm; mean: 3.08±0.44); body dorsal surface uniform reddish to reddish brown, antennae, mouth-parts and legs of the same body colour or a slightly clearer hue; body strongly arched (convex); pronotum small and narrower than elytra, disc with dense, large rounded granules, each one with a yellowish erect rigid needle-like acuminate seta (Fig. 4A). Elytra nodules or gibbosities very distinct with a pattern formula 2, 3, 2, 1. Differs from the most related species in some morphometrics (see Appendix S5):

- larger than *T. relictus* **sp. nov.**; and
- differs from *T. furtadoi* **sp. nov.** in having: larger W elytra/pronotum ratio; larger L elytra/pronotum ratio.; smaller ratio W/L elytra; smaller W/L pronotum.

Description. Length 2.37–3.77 mm (mean: 3.08±0.44); width 1.19–1.99 mm (mean: 1.60±0.23), body convex and subquadrate-ovate, reddish to reddish-brown, setose, with large granules.

Head: Genae parallel; anterior clypeal margin straight; vertices protrude under the anterior margin of pronotum; surface reddish dark brown with dense medium granules, except in clypeus which is more or less smooth, each one with one semi-erect fine hair-like seta slightly directed anteriorly; eyes clearly protruding, glabrous; antennae with segment II shorter than III, segment III 1.5x longer than IV, length of IV and V equal, segments VII–IX as long as wide, compact club 2-segmented (segments X and XI); mouth-parts with mandibles brown, the other pieces lighter showing the general morphological pattern of the genus.

Pronotum: Transverse, on average 1.41 times as broad as long, but quite variable (1.22x to 1.59x); surface reddish dark brown, widened in the middle, half posterior-lateral region with a slight nodule; anterior margin deeply bisinuate, anterior angles strongly protrude and acuminate (Fig. 8); hind margin largely bisinuate, in middle broadly produced rearwards; lateral margins arcuate with two irregular rows of long, fine and acuminate setae (20–25 each one) (Fig. 8), slightly sinuate just before the posterior angles which are clearly prominent; disc with a clear median longitudinal sulcus; a distinct transverse channel just before the extreme base between the two lateral notches; lateral surface variable in terms of flatness; dorsal upper surface with dense distinct large rounded granules, gradually diminishing in diameter to the sides, each one with one rigid erect needle-like yellowish seta (Fig. 8); ratios width pronotum/width elytra 0.87±0.04 and length pronotum/length elytra 0.55±0.04 (see Appendix S6).

Elytra: On average 0.90 times as broad as long, but quite variable (0.82x to 1.10x); in general 1.16 times (mean) broader than pronotum, but also quite variable (1.08x to 1.32x); disc concolorous (reddish dark brown), convex, rugosely seriate-punctate, and wrinkled transversally on dorsal surface which is covered with dense granules, each one with an erect rigid needle-like acuminate yellowish seta (Fig. 4A); nodules or gibbosities very distinct with a pattern formula 2, 3, 2, 1, covered with setae more aggregate that confer a pom-pom appearance.

Ventral side. Prosternum as granulose as mesosternum and metasternum; grooves on anterior half of prosternal sides slightly present.

Legs. Tibia normal not expanded apically; tarsi 4-segmented, simple, first three tarsomeres of all legs and in both sexes covered ventrally with several very long hyaline fine setae.

Aedeagus: See Fig. 6 in Gillerfors (1985).

Bionomics. Most specimens were collected in pitfall traps (Borges *et al*. 2005a), but also under the bark of endemic and exotic trees.

Tarphius relictus Borges & Serrano, new species
(Fig. 9)

Tarphius azoricus in Borges (1990, pp. 99, 112) (Terceira Isl.)
Tarphius azoricus in Borges (1991, p. 2) (Terceira Isl.)
Tarphius azoricus in Borges *et al.* (2005b, p. 207) (Terceira Isl.)
Tarphius azoricus in Oromí *et al*. (2010, p. 232) (Terceira Isl.)
Tarphius azoricus Amorim *et al.* (2012, Fig. 2) (Terceira Isl.)

Type locality. The Azores, Terceira Island, Fontinhas.

Type material.Type material. HOLOTYPE, male, deposited at DTPC, labeled: Fontinhas, Terceira, Açores (UTM 26S 488329, 4288597) (Altitude: 208 m), 20/06/2006 (collected by hand; Paulo A. V. Borges leg.). PARATYPES, same locality as holotype, 5/05/1990 (2 exx.), 8/05/1990 (1 ex.), 20/06/2006 (20 exx.), Paulo A. V. Borges & Isabel R. Amorim leg., Material deposited in FCULC, SNM and DTPC.

Etymology. The name refers to the highly reduced area of exotic forest, surrounded by pastureland, where this species lives, the disappearance of which threatens it with extinction.

Diagnosis (Fig. 9). Small to medium species (2.34–3.48 mm; mean: 2.72±0.34 mm); body dorsal surface uniform shining dark brown, antennae, mouth-parts and legs of a slightly clearer hue; body strongly arched (convex); pronotum small and narrower than elytra, disc with dense, large rounded granules, each one with a yellowish or brownish long, thin, erect rigid needle-like acuminate seta (Fig. 4B), but less needled than *T. tornvalli* (Fig. 4A); elytra humeral angle sharply pronounced. Differs from the most related species in some morphometrics (see Appendix S5):

- differs from *T. furtadoi* **sp. nov.** in being smaller, and in having a larger L elytra /L pronotum, W/L elytra and W/L pronotum ratios; and
- differs from *T. tornvalli* in being smaller, and in having a larger W/L elytra and W/L pronotum ratios.

Description. Body length of holotype: 3.10 mm; small to medium size (length 2.34–3.48 mm, mean: 2.72±0.34 mm); width 1.37–1.7 mm (mean: 1.57±0.11 mm), body convex and subquadrate-ovate, dark brown, setose, with rigid setae and large granules.

Head: Genae parallel; anterior clypeal margin straight; vertices protrude under the anterior margin of pronotum; surface dark brown with dense medium granules, except in clypeus which is more or less smooth, each one with one semi-erect fine hair-like seta slightly directed anteriorly eyes clearly protruding, glabrous; antennae with segment II smaller than III, segment III almost 2x longer than IV, IV slightly longer than V, segments VII–IX as long as wide, compact club 2-segmented (segments X and XI); mouth-parts brown or light brown showing the general pattern of the genus.

Pronotum: Highly transverse, on average 1.76 times as broad as long, but quite variable (1.30x to 2.08x); surface dark brown, widened in the middle; in general, shape of pronotum less rounded than *T. tornvalli* (cf. Figs 9, 10 and 7, 8); anterior margin deeply bisinuate, anterior angles strongly protruding and acuminate; hind margin largely bisinuate, in middle broadly produced rearwards; lateral margins arcuate with two irregular rows of long, fine and acuminate setae (20–25 each one, smaller than *T. tornvalli*, and tending to be less acuminated) (Fig. 10), slightly sinuate just before the posterior angles which are clearly prominent; disc with a clear median longitudinal sulcus, half posterior-lateral region with a slight nodule; a distinct transverse channel just before the extreme base between the two lateral notches; lateral surface variable in terms of flatness; dorsal upper surface with dense distinct large rounded granules, gradually diminishing in diameter to the sides, each one with one rigid erect sub-obtuse yellowish seta (Fig. 10); ratios width pronotum/width elytra 0.90±0.04 and length pronotum/length elytra 0.52±0.15 (see Appendix S6).

Elytra: On average 0.98 times as broad as long, but quite variable (0.91x to 1.12x); in general 1.11 times (mean) broader than pronotum, but less variable (1.04x to 1.17x) than in *T. tornvalli*; disc concolorous (reddish dark brown to dark brown), convex, rugosely seriate-punctate, and wrinkled transversally on dorsal surface which is covered with dense granules, each one with an erect rigid needle-like acuminate yellowish or golden seta (Fig. 4B), but less needled than in *T. tornvalli* (Fig. 4A); nodules or gibbosities very distinct with a pattern formula 2, 3, 2, 1, covered with setae more aggregate, conferring a pom-pom appearance.

Ventral side. Prosternum as granulose as mesosternum and metasternum; grooves on anterior half of prosternal sides slightly present.

Legs. Tibia normal not expanded apically; tarsi 4-segmented, simple, first three tarsomeres of all legs and in both sexes covered ventrally with several very long hyaline fine setae.

Aedeagus: Similar to *T. tornvalli* (see Fig. 6 in Gillerfors 1985).

Bionomics. Most specimens were collected under the bark of dead trunks from exotic trees (*Acacia* sp.). Some were collected in pitfall traps using moldy bread as bait.

FIGURE 9. Habitus of *Tarphius relictus* **sp. nov.**. Scale 0.5 mm (Photo: Erno-Endre Gergely).

FIGURE 10. Detail on the number of seta on the external row of the lateral margin of pronotum in *Tarphius relictus* **sp. nov.**. Scale 0.25 mm (Photo: Erno-Endre Gergely).

***Tarphius furtadoi* Borges & Serrano, new species**
(Fig. 11)

Tarphius tornvalli in Gillerfors (1986b, p. 21) (Pico Isl.)
Tarphius tornvalli in Borges (1990, p. 112) (Pico Isl.)
Tarphius tornvalli in Borges (1991, p. 2) (Pico Isl.)
Tarphius tornvalli and *Tarphius azoricus* in Borges *et al.* (2005b, p. 207) (Pico Isl.)
Tarphius tornvalli and *Tarphius azoricus* in Oromí *et al*. (2010, p. 232) (Pico Isl.)
Tarphius tornvalli and *Tarphius azoricus* in Amorim *et al.* (2012, Fig. 2) (Pico Isl.)
Tarphius azoricus in Borges *et al.* (2005b, p. 207) (São Jorge Isl.)
Tarphius azoricus in Oromí *et al*. (2010, p. 232) (São Jorge Isl.)
Tarphius azoricus in Amorim *et al.* (2012, Fig. 2) (São Jorge Isl.)
Tarphius azoricus in Oromí *et al*. (2010, p. 232) (Faial Isl.)
Tarphius azoricus in Amorim *et al.* (2012, Fig. 2) (Faial Isl.)

Type locality. The Azores, Pico Island, Lagoa do Caiado.

Type material. HOLOTYPE, male, deposited at DTPC, labeled: Lagoa do Caiado, Pico, Açores, 4–19/03/1990 (UTM 26S 390266, 4257172); Paulo A. V. Borges & Fernando Pereira leg..

PARATYPES, PICO ISLAND: 280 specimens—Chão Verde Superior (T01) (Natural Forest Reserve of Mistério da Prainha), IX.1999 (4 exx), VII.2010 (1 ex.) (UTM 26S 388838, 4259774); Lagoa do Caiado - Euphorbias (T02) (Natural Forest Reserve of Lagoa do Caiado), IX.1999 (36 exx) (UTM 26S 390266, 4257172); Chão Verde Inferior (T03) (Natural Forest Reserve of Mistério da Prainha) IX.1999 (39 exx) (UTM 26S 388946, 4260693); Picos do Caveiro (T08) (Natural Forest Reserve of Caveiro), IX.1999 (6 exx), VII.2010 (23 exx) (UTM 26S 395274, 4255409); Caveiro Base (T09) (Natural Forest Reserve of Caveiro), IX.1999 (19 exx), VII.2010 (23 exx) (UTM 26S 394341, 4255080); Chão Verde Inferior Cima (T14) (Natural Forest Reserve of Mistério da Prainha), VII.2000 (8 exx) (UTM 26S 389041, 4260364); Chão Verde Superior Perpendicular (T15) (Natural Forest Reserve of Mistério da Prainha), VII.2000 (2 exx) (UTM 26S 389035, 4259508); Lagoa do Caiado—Frente a Lagoa (T16) (Natural Forest Reserve of Lagoa do Caiado), VIII.2000 (21 exx) (UTM 26S 390537, 4257057); Lagoa do Caiado—Frente a Euphorbias (T17) (Natural Forest Reserve of Lagoa do Caiado), VIII.2000 (28 exx) (UTM 26S 390661, 4257058); Caveiro, Prado (T20) (Natural Forest Reserve of Caveiro), VIII.2000 (1 ex) (UTM 26S 394533, 4255179); Caveiro, Morro (T21) (Natural Forest Reserve of Caveiro), VIII.2000 (47 exx) (UTM 26S 394055, 4255376); Caveiro, Meio da Reserva (T22) (Natural Forest Reserve of Caveiro), VIII.2000 (22 exx) (UTM 26S 396643, 4255074) (collected with pitfall traps; Paulo A. V. Borges *et al.* leg.).

FAIAL ISLAND: 142 specimens—Cabeço dos Trinta, IX.2009 (3 exx) (UTM 26S 348327, 4271670), Fernando Pereira, leg.; Cabeço do Fogo (T03) (Natural Forest Reserve of Cabeço do Fogo), IX.2010 (1 ex) (UTM 26S 346239, 4272261); Caldeira do Faial (T10) (Natural Forest Reserve of Caldeira do Faial), IX.2010 (10 exx) (UTM 26S 351110, 4271917); Caldeira do Faial (TB26) (Natural Forest Reserve of Caldeira do Faial), IX.2010 (128 exx) (UTM 26S 350857, 4272272), (collected with pitfall traps; Paulo A. V. Borges *et al.* leg.).

SÃO JORGE ISLAND: 52 specimens—Ribeira Seca, VIII.2003 (32 exx) (UTM 26S 415675, 4273358) (collected by hand; Isabel R. Amorim & Paulo A. V. Borges leg.); Pico Pinheiro Inferior (T13) (Natural Forest Reserve of Pico Pinheiro), VIII.2004 (14 exx) (UTM 26S 409256, 4278677); Topo Euphorbia (T16) (Natural Forest Reserve of Topo), VIII.2004 (1 ex) (UTM 26S 422871, 4271075); Pico Pinheiro Erical (T09) (Natural Forest Reserve of Pico Pinheiro), IX.2010 (5 exx) (UTM 26S 408602, 4277888) (collected with pitfall traps; Paulo A. V. Borges *et al.* leg.).

Deposited at FCULC, SNM and DTPC.

Etymology. The species is named after the Azorean naturalist Francisco Arruda Furtado (1854–1887) who was one of the first Portuguese followers of the Darwin's theory of evolution.

Diagnosis (Fig. 11). Small to medium species (2.60–4.24 mm; mean: 3.23±0.41 mm); body dorsal surface uniform reddish to reddish-brown, antennae, mouth-parts and legs yellowish-brown; body arched (convex); pronotum small and narrower than elytra, transverse, On average 1.45 times as broad as long (1.29x to 1.62x), disc with dense, large rounded granules, each one with a yellowish long, thin, erect rigid long and sub-obtuse seta, with lateral sides slightly rounded and maximum width at middle (Fig. 4C). Differs from the most related species in some morphometrics (see Appendix S5), namely:

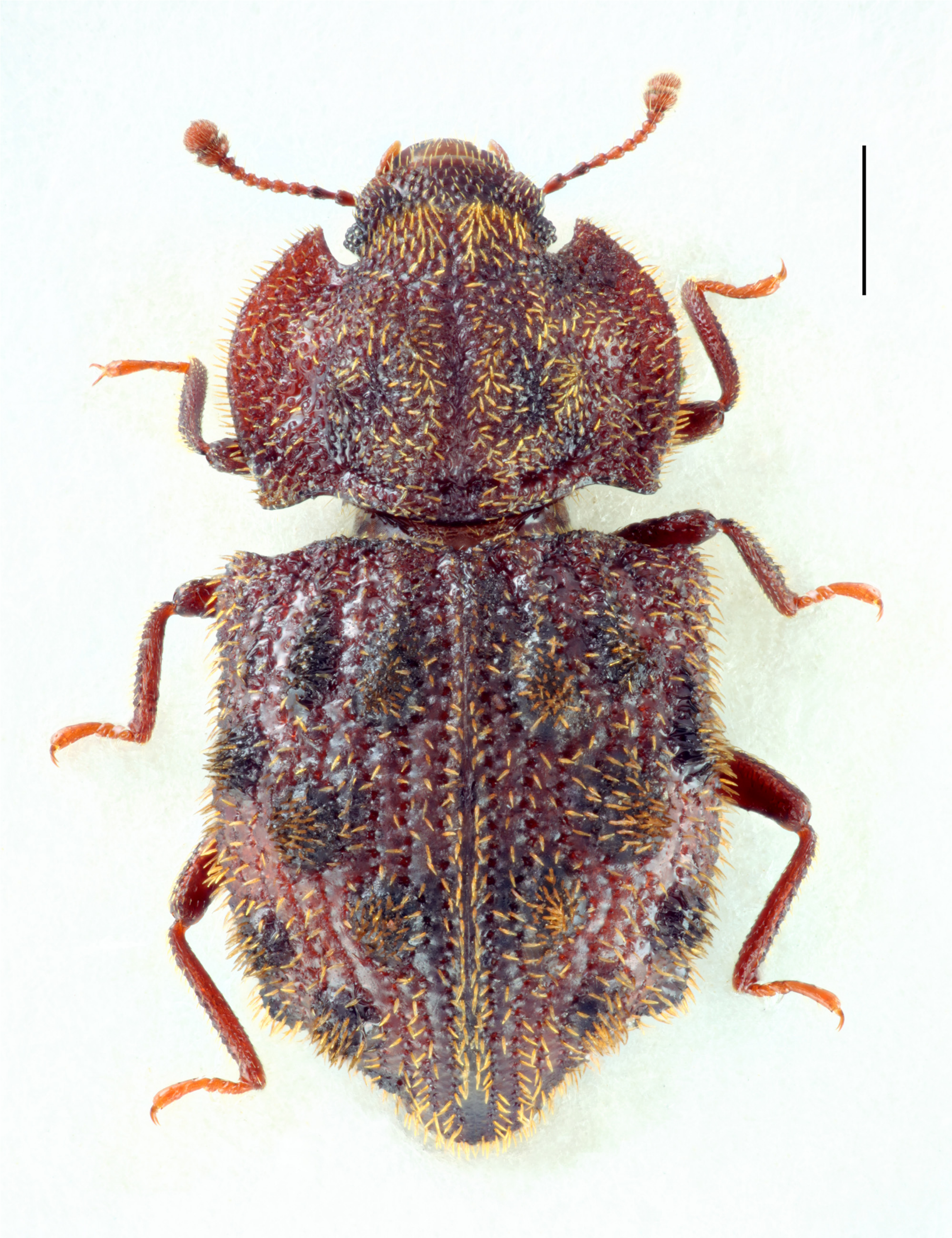

FIGURE 11. Habitus of *Tarphius furtadoi* **sp. nov.**. Scale 0.5 mm. (Photo: Erno-Endre Gergely).

FIGURE 12. Detail on the number of seta on the external row of the lateral margin of pronotum in *Tarphius furtadoi* **sp. nov.**. Scale 0.25 mm (Photo: Erno-Endre Gergely).

- differs from *T. tornvalli* in having smaller W elytra/pronotum and L elytra/pronotum ratios, and larger W/L elytra and W/L pronotum ratios; and
- differs from *T. relictus* **sp. nov.** by its larger size and in having smaller L elytra/ Lpronotum, W/L elytra and W/ L pronotum ratios.

Description. Body length of holotype: 3.18 mm; small to medium size (length 2.60–4.24 mm; mean: 3.23±0.41 mm); width 1.42 mm–2.17 mm (mean: 1.71±0.20 mm), body convex and subquadrate-ovate, reddish or reddish-brown, setose, with rigid setae and large granules.

Head: Genae parallel; anterior clypeal margin straight; vertices protrude under the anterior margin of pronotum; surface brown or reddish brown, lighter in clypeus, with dense medium granules, except in clypeus which is more or less smooth, each one with one semi-erect fine hair-like seta slightly directed anteriorly; eyes clearly protruding, glabrous; antennae with segment II smaller than III, segment III 1.3x longer than IV, IV and V equal length, segments VII–IX as long as wide, compact club 2-segmented (segments X and XI); mouth-parts with mandibles brown, the other pieces lighter showing the general morphological pattern of the genus.

Pronotum: Transverse, on average 1.45 times as broad as long, but quite variable (1.29x to 1.62x); surface dark brown, lateral parts reddish, widened in the middle; in general, shape of pronotum as rounded as *T. tornvalli* (cf. Figs 7 and 11) anterior margin deeply bisinuate, anterior angles strongly protruding and acuminate; hind margin largely bisinuate, in middle broadly produced rearwards; lateral margins arcuate with two irregular rows of long, fine and acuminate setae (20–25 each one) (Fig. 12), slightly or without sinuation just before the posterior angles which are prominent; disc with a clear median longitudinal sulcus, half latero-posterior region with a slight nodule; a distinct transverse channel just before the extreme base between the two lateral notches; lateral surface variable in terms of flatness; dorsal upper surface with dense distinct large rounded granules, gradually diminishing in diameter to the sides, each one with one rigid erect sub-obtuse yellowish or golden seta (Fig. 12); ratios width pronotum/width elytra 0.91±0.03 and length pronotum/length elytra 0.58±0.05 (see Appendix S6).

Elytra: On average 0.92 times as broad as long, quite variable (0.84x to 1.09x); in general 1.10 times (mean) broader than pronotum, but less variable than in *T. tornvalli* (1.03x to 1.18x); disc reddish-brown, reddish laterally, convex, rugosely seriate-punctate, and wrinkled transversally on dorsal surface which is covered with dense granules each one with an erect rigid long and sub-obtuse yellowish or golden seta, with lateral sides slightly rounded and maximum width at middle (Figs. 4C and D); nodules or gibbosities very distinct with a pattern formula 2, 3, 2, 1, covered with setae more aggregate which confers a pom-pom appearance.

Ventral side. Prosternum as granulose as mesosternum and metasternum; grooves on anterior half of prosternal sides slightly present.

Legs. Tibia normal not expanded apically; tarsi 4-segmented, simple, first three tarsomeres of all legs and in both sexes covered ventrally with several very long hyaline fine setae.

Aedeagus: Similar to *T. tornvalli* (see Fig. 6 in Gillerfors 1985).

Bionomics. Most specimens were collected in pitfall traps (Borges *et al*. 2005a), but also under the bark of endemic trees and under the bark of dead trunks of exotic trees (*Cryptomeria japonica; Acacia* sp.).

Tarphius azoricus-wollastoni-depressus complex

Tarphius gabrielae Borges & Serrano, new species

(Fig. 13)

Tarphius azoricus in Gillerfors (1986a, p. 21) (Pico Isl.)
Tarphius depressus in Borges *et al.* (2005b, p. 207) (Pico Isl.)
Tarphius depressus in Oromí *et al*. (2010, p. 232) (Pico Isl.)
Tarphius depressus in Amorim *et al.* (2012, Fig. 2) (Pico Isl.)

Type locality. The Azores, Pico Island, Lagoa do Caiado.

Type material. HOLOTYPE, male, deposited at DTPC, labeled: Lagoa do Caiado, 18/08/2003, (UTM 26S 390266, 4257172) (António Machado leg.). PARATYPES, Lagoa do Caiado, 18/08/2003 (7 exx); Lagoa do Caiado, VIII.2009 (2 exx), (UTM 26S 390266, 4257172), (Fernando Pereira leg.). Deposited at FCULC, SNM and DTPC.

FIGURE 13. Habitus of *Tarphius gabrielae* **sp. nov.**. Scale 0.5 mm (Photo: Erno-Endre Gergely).

Etymology. The name refers to the bryologist and naturalist Rosalina Gabriel in honor of her important work in the study of Azorean native forests.

Diagnosis (Fig. 13). Medium to large species (3.24–4.64 mm; mean: 3.72±0.39 mm); body dorsal surface uniform reddish to reddish-brown, antennae, mouth-parts and legs reddish; body arched (convex); lateral margins of pronotum clearly arcuate (Fig. 6C) in contrast with a more straight latera-posterior sides in *T. depressus* (Fig. 6E) small and narrower than elytra, transverse. On average 1.39 times as broad as long (1.35x and 1.42x), disc with dense, medium rounded granules, each one with a yellowish medium, obtuse, semi-erect rigid seta (Fig. 5C); width ratio pronotum/ elytra 0.95±0.15 (see Appendix S6).

Description. Body length of holotype: 4.50 mm; medium to large size (length 3.24–4.64 mm; mean: 3.72±0.39 mm); width 1.61 mm–2.20 mm (mean: 1.82±0.18 mm), body convex and subquadrate-ovate, reddish or reddish-brown, setose, with rigid obtuse setae and medium granules.

Head: Genae parallel; anterior clypeal margin straight; vertices protrude under the anterior margin of pronotum; surface brown or reddish brown, lighter in clypeus, with dense medium granules, except in clypeus which is more or less smooth, each one with one semi-erect fine hair-like seta slightly directed anteriorly; eyes clearly protruding, glabrous; antennae with segment II shorter than III, segment III longer than IV, V a little shorter than IV, VI shorter than V, segments VI–VIII as long as wide, compact club 2-segmented (segments X and XI); mouth-parts with mandibles brown, the other pieces lighter showing the general morphological pattern of the genus.

Pronotum: Transverse, on average 1.39 times as broad as long, little variable (1.35x to 1.42x); surface reddish-brown to reddish, widened in the middle; anterior margin deeply bisinuate, anterior angles strongly protrude and acuminate (Fig. 6C); hind margin largely bisinuate, in middle broadly produced rearwards; lateral margins arcuate (Fig. 6C), contrasting with straight lateral sides in *T. depressus* (Fig. 6E) with two irregular rows of medium, semi-erected obtuse setae (30–32 each one) (Fig. 6C), slightly sinuate just before the posterior angles which are prominent; disc with a clear median longitudinal sulcus, half medium latera-posterior region with a slight nodule; a distinct transverse channel just before the extreme base between the two lateral notches; lateral surface variable in terms of flatness; dorsal upper surface with uniformly dense distinct medium rounded granules, each one with one rigid semi-erect obtuse yellowish seta (Fig. 6C); ratios width pronotum/width elytra 0.95 ±0 .15 and length pronotum/length elytra 0.60±0.02 (see Appendix S6).

Elytra: On average 0.88 times as broad as long, little variable (0.82x to 0.91x); in general 1.06 x (mean) as broad as pronotum, and 1.67x (mean) as long as pronotum (in *T. depressus* 1.5x), at shoulders distinctly broader than pronotum between hind angles; disc reddish to reddish-brown, convex, rugosely seriate-punctate, and wrinkled transversally on dorsal surface which is covered with dense granules each one with a recumbent, obtuse yellowish or golden seta (Fig. 5C); nodules or gibbosities distinct with a pattern formula 3, 3, 2, 1, covered with setae more aggregate conferring a pom-pom appearance.

Ventral side. Prosternum as granulose as mesosternum and metasternum; grooves on anterior half of prosternal sides slightly present.

Legs. Tibia normal not expanded apically; tarsi 4-segmented, simple, first three tarsomeres of all legs and in both sexes covered ventrally with several very long hyaline fine setae.

Aedeagus: Similar to *T. tornvalli* (see Fig. 6 in Gillerfors 1985).

Bionomics. Most specimens were collected in dead twigs of *Euphorbia stygiana*.

Tarphius floresensis **Borges & Serrano, new species**

(Fig. 14)

Tarphius wollastoni in Borges (1990, p. 112) (Flores Isl.)
Tarphius wollastoni in Borges (1991, p. 2) (Flores Isl.)
Tarphius wollastoni in Borges *et al.* (2005b, p. 207) (Flores Isl.)
Tarphius wollastoni in Oromí *et al*. (2010, p. 232) (Flores Isl.)
Tarphius wollastoni in Amorim *et al.* (2012, Fig. 2) (Flores Isl.)

Type locality. The Azores, Flores Island, Morro Alto.

Type material. HOLOTYPE, male, deposited at DTPC, labeled: Lajes, 10/07/1989 (UTM 25S 655803, 4368774), Paulo Borges leg.. PARATYPES, 462 specimens—between Caldeira Funda and Caldeira Comprida

(Altitude: 597 m), 13/08/2013, António Machado leg.; Caldeira Branca, Margem de Ribeira (T03) (Natural Forest Reserve of Morro Alto e Pico da Sé), VIII.1999 (107 exx) (UTM 25S 655883, 4374629); Ribeira da Fazenda (T04) (Natural Forest Reserve of Morro Alto e Pico da Sé), VIII.1999 (18 exx) (UTM 25S 655809, 4377246); Juniperal (T06) (Natural Forest Reserve of Caldeiras Funda e Rasa), VIII.1999 (63 exx), VIII.2010 (15 exx) (UTM 25S 655838, 4370215); Encosta da Caldeira Funda (T07) (Natural Forest Reserve of Caldeiras Funda e Rasa), VIII.1999 (9 exx), VIII.2010 (2 exx) (UTM 25S 655817, 4370019); Morro Alto Este (T08) (Natural Forest Reserve of Morro Alto e Pico da Sé), VIII.1999 (1 ex.) (UTM 25S 655809, 4376293); Caldeira Rasa *Callunetum* (T09) (Natural Forest Reserve of Caldeiras Funda e Rasa), VIII.1999 (3 exx) (UTM 25S 655850, 4371356); Caldeira Comprida (T14) (Natural Forest Reserve of Morro Alto e Pico da Sé), IX.2000 (11 exx) (UTM 25S 655846, 4374777); Pico da Sé (T15) (Natural Forest Reserve of Morro Alto e Pico da Sé), IX.2000 (2 exx) (UTM 25S 655830, 4377715); Ribeira do Cascalho (T16) (Natural Forest Reserve of Morro Alto e Pico da Sé), IX.2000 (57 exx), VIII.2010 (18 exx) (UTM 25S 655899, 4378652); Cross between Lagoas Caldeira Funda e Caldeira Comprida in *Cryptomeria japonica* (TT21) VIII.2009 (2 exx) (UTM 25S 655800, 4373277); Criptomeria plantation near T16 (TT25) VIII.2009 (111 exx) (UTM 25S 655882, 4379185); Regional road in *Cryptomeria japonica* (TT26) VIII.2009 (1 ex.), (UTM 25S 655829, 4372551), Paulo Borges *et al.* leg.. Caveira, Lomba (Z07) VIII.2007 (5 exx) (UTM 25S 655834, 4369258); Ponta Delgada, in Acacia woodland (Z10) VIII.2007 (1 ex) (UTM 25S 655817, 4381525); Ponta Delgada, in Acacia woodland, Km 18 (Z11) VIII.2007 (36 exx), (UTM 25S 655818, 4381526) Paulo Borges & Fernando Pereira leg.. Deposited at FCULC, SNM and DTPC.

Etymology. The name refers to the island of Flores, to where this distribution of this species is restricted.

Diagnosis (Fig. 14). Small to medium species (2.25–3.68 mm; mean: 3.07±0.45 mm), being the smallest species in the complex azoricus-wollastoni-depressus; body dorsal surface reddish or reddish-brown to dark brown, antennae, mouth-parts and legs light reddish; body strong arched (convex); lateral margins of pronotum highly arcuate (Fig. 6D), narrower than elytra between posterior angles, small and transverse, on average 1.35 times as broad as long (1.24x and 1.50x), disc with dense, medium rounded granules, each one with a yellowish, recumbent slightly acuminate seta (Figs. 5D and 6D); width ratio pronotum / elytra 0.92±0.04 (see Appendix S6); the ratio between width and length of the pronotum is smaller than in *T. depressus* Gillerfors, and statistically significant (see Appendix S5).

Description. Body length of holotype: 3.14; small to medium size (length 2.25–3.68 mm; mean: 3.07±0.45 mm); width 1.10 mm–1.76 mm (mean: 1.51±0.19 mm), body convex and subquadrate-ovate, reddish or reddish-brown, setose, with rigid recumbent slightly acuminate setae (Fig. 5D) and medium granules.

Head: Genae parallel; anterior clypeal margin straight; vertices protrude under the anterior margin of pronotum; surface brown or reddish brown, lighter in clypeus, with dense medium granules, except in clypeus which is more or less smooth, each one with one semi-erect fine hair-like seta slightly directed anteriorly; eyes clearly protruding, glabrous; antennae with segment II shorter than III, segment III 1.8x longer than IV, V shorter than IV, segments VI–VII equal length, compact club 2-segmented (segments X and XI); mouth-parts with mandibles brown, the other pieces lighter showing the general morphological pattern of the genus.

Pronotum: Transverse, on average 1.35 times as broad as long, quite variable (1.24x to 1.50x); surface reddish-brown to reddish, widened in the middle; anterior margin deeply bisinuate, anterior angles strongly protrude and acuminate (Fig. 6D); hind margin largely bisinuate, in middle broadly produced rearwards; lateral margins highly arcuate (Fig. 6D), contrasting with straight lateral sides in *T. depressus* (Fig. 6E), with two irregular rows of medium/long, slightly acuminate setae (20–25 each one) (Fig. 6D), slightly sinuate just before the posterior angles which are prominent; disc with a clear median longitudinal sulcus, half medium latera-posterior region with a slight nodule; a distinct transverse channel just before the extreme base between the two lateral notches; lateral surface variable in terms of flatness; dorsal upper surface with uniformly dense distinct medium rounded granules, each one with one rigid semi-erect slightly acuminate yellowish seta (Fig. 6D); ratios width pronotum/width elytra 0.92±0.04 and length pronotum/length elytra 0.61±0.05 (see Appendix S6); ratio between width and length of the pronotum is 1.35±0.07, smaller than *T. depressus* (1.42±0.06), and statistically significant (see Appendix S5).

Elytra: On average 0.90 times as broad as long, quite variable (0.80x to 1.01x); in general, 1.09 x (mean) as broad as pronotum, but also quite variable (1.00 to 1.20) and at shoulders distinctly broader than pronotum between hind angles; disc reddish to reddish-brown, convex, rugosely seriate-punctate, and wrinkled transversally on dorsal surface which is covered with dense granules each one with a recumbent slightly acuminate, yellowish or golden seta (Fig. 5D); nodules or gibbosities distinct with a pattern formula 3, 3, 2, 1, covered with setae more aggregate which confers the appearance of a small pom-pom.

FIGURE 14. Habitus of *Tarphius floresensis* **sp. nov.**. Scale 0.5 mm (Photo: Erno-Endre Gergely).

Ventral side. Prosternum as granulose as mesosternum and metasternum; grooves on anterior half of prosternal sides slightly present.

Legs. Tibia normal not expanded apically; tarsi 4-segmented, simple, first three tarsomeres of all legs and in both sexes covered ventrally with several very long hyaline fine setae.

Aedeagus: Similar to *T. tornvalli* (see Fig. 6 in Gillerfors 1985).

Bionomics. Most specimens were collected by pitfall trapping in natural forests and *Cryptomeria japonica* stands (Borges *et al*. 2005a).

Key for identification of Azorean species of *Tarphius*

1. Elytral nodules well developed with a pattern formula 3, 3, 2, 1; "*azoricus*+*wollastoni*+*depressus*" complex. 2
- Elytral nodules well developed with a pattern formula 2, 3, 2, 1; "*tornvalli*" complex 6
- Elytral nodules well or not so well developed with a different pattern formula; other species 8
2. First three tarsomeres of all legs with one pair of long hyaline hair-like setae on ventral side; anterior margin of clypeus straight or slightly arcuate inwards; external row of the lateral margin of pronotum with 30–34 setae (Fig. 5A); pronotal and elytral setae short and obtuse (leaf shaped) (Fig. 5A); aedeagus as in Fig. 7 (in Gillerfors 1986a); São Miguel and Flores Islands . . . . *T. azoricus* Gillerfors (Fig. 15)
- First three tarsomeres of all legs with two or more pairs of long hyaline hair-like setae on ventral side resembling a brush; anterior margin of clypeus straight 3
3. Pronotal and elytral setae recumbent and slightly acuminate (Fig. 5D); external row of the lateral margin of pronotum with 27–28 setae (Fig. 6D); Flores Island . . . . *T. floresensis* **sp. nov.** (Fig. 14)
- Pronotal and elytral setae short and leaf shaped (broad obtuse setae); external row of the lateral margin of pronotum with 30 or even more setae 4
4. Lateral margins of pronotum straight and sub-parallel in the posterior half (Fig. 6E); aedeagus as in Fig. 5 (in Gillerfors 1985); Santa Maria Island. . . . . *T. depressus* Gillerfors (Fig. 16)
- Lateral margins of pronotum arcuate since the anterior angles to the posterior ones, slightly sinuate before the hind angles . . 5
5. Lateral margins of pronotum slightly arcuate between the anterior and the hind angles (Fig. 6C); pronotal setae obtuse, rigid and semi-erect (Fig. 5C); Pico Island . . . . *T. gabrielae* **sp. nov.** (Fig. 13)
- Lateral margins of pronotum arcuate between the anterior and the hind angles (Fig. 6B); pronotal setae obtuse, rigid and decumbent (Fig. 5B); Faial Island. . . . . *T. wollastoni* Crotch
6. Setae acuminate with lateral sides slightly rounded and maximum width at middle (Figs. 4C and D); external row of the lateral margin of pronotum with 30 or more setae; Faial, Pico and São Jorge Islands . . . . *T. furtadoi* **sp. nov.** (Fig. 11)
- Pronotal and elytral setae long and needle shaped (Figs 4A and B) 7
7. Lateral margins of pronotum slightly arcuate and sub-parallel in the posterior half; setae less needle shaped (Fig. 4B); Terceira Island. . . . . *T. relictus* **sp. nov.** (Fig. 9)
- Lateral margins of pronotum arcuate since the anterior angles to the posterior ones, slightly sinuate before the hind angles; setae strongly needle-like (Fig. 4A); aedeagus as in Fig. 6 (in Gillerfors 1985); São Miguel Island . . . . *T. tornvalli* Gillerfors (Fig. 7)
8. First three tarsomeres of all legs with one pair of long hyaline hair-like setae on ventral side; anterior margin of clypeus markedly arcuate inwards; elytral nodules fair developed with a pattern formula 3/2, 3, 1/2, 0; external row of the lateral margin of pronotum with more or less 15 setae; pronotal and elytral setae long and acuminate (needle shaped); aedeagus as in Fig. 8 (in Gillerfors,1986a); Pico Island . . . . *T. acuminatus* Gillerfors (Fig. 17)
- First three tarsomeres of all legs with two or more pairs of long hyaline hair-like setae on ventral side resembling a brush . . .9
9. Anterior margin of clypeus arcuate inwards; humeral angle of elytron very protrude upwards resembling a nodule or a gibbositie; elytral nodules fair developed with a pattern formula 1, 3, 3, 2, 0; aedeagus as in Fig. 9 (in Borges 1991); Santa Maria Island . . . . *T. pomboi* Borges (Fig. 18)
- Anterior margin of clypeus straight; humeral angle of elytron not protrude upwards 10
10. Body surface sparingly covered with setae; external row of lateral margin of pronotum with about 30 short and leaf shaped setae; elytrae with pale pattern enclosing nodules; elytral nodules developed with a pattern formula 1, 2/3, 2, 2, 1; aedeagus as in Fig. 7 (in Gillerfors 1985); Santa Maria Island. . . . .*T. rufonodulosus* Israelson (Fig. 19)
- Body surface covered with more dense setae; external row of lateral margin of pronotum with 15–16 almost leaf shaped setae; elytral nodules evanescent with a pattern formula 3/2, 3, 2, 0/1; aedeagus as in Fig. 10 (in Borges 1991); Santa Maria Island . . . . *T. serranoi* Borges (Fig. 20)

FIGURE 15. Habitus of *Tarphius azoricus* Gillerfors. Scale 0.5 mm (Photo: Erno-Endre Gergely).

FIGURE 16. Habitus of *Tarphius depressus* Gillerfors. Scale 0.5 mm (Photo: Erno-Endre Gergely).

FIGURE 17. Habitus of *Tarphius acuminatus* Gillerfors. Scale 0.5 mm (Photo: Erno-Endre Gergely).

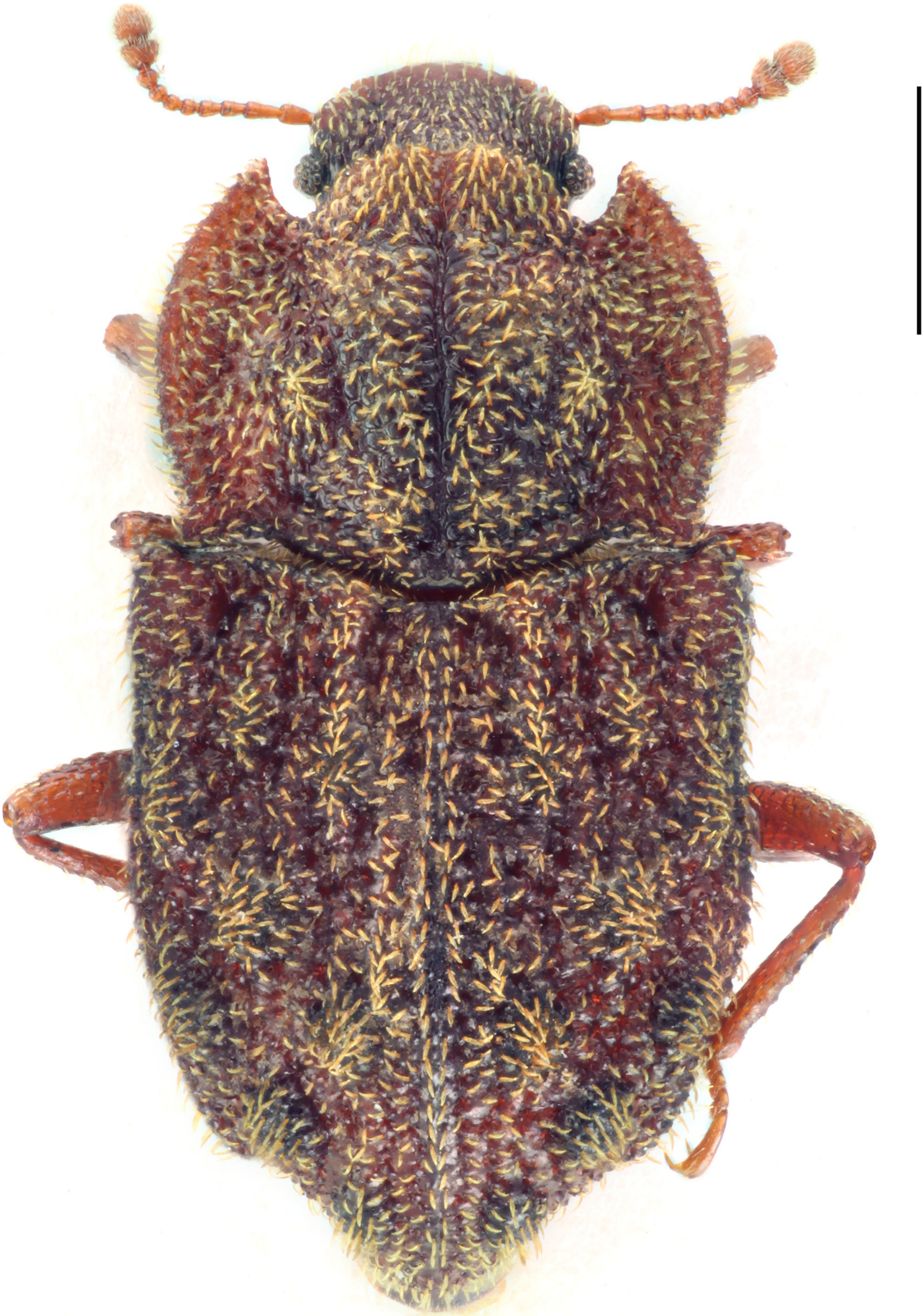

FIGURE 18. Habitus of *Tarphius pomboi* Borges. Scale 0.50 mm (Photo: Erno-Endre Gergely).

FIGURE 19. Habitus of *T. rufonodulosus* Israelson. Scale 0,50 mm (Photo: Enésima Mendonça).

FIGURE 20. Habitus of *Tarphius serranoi* Borges. Scale 0.5 mm (Photo: Erno-Endre Gergely).

Discussion

Taxonomy. Amorim *et al.* (2012) published the first phylogeny of the Azorean beetle genus *Tarphius*. In our work we present an updated version of that phylogeny, adding new taxa and correcting the taxonomic nomenclature of the species. After almost twenty years sampling and studying Azorean *Tarphius* we can now interpret more correctly the taxonomy of this diverse genus in the Azores and propose taxonomic entities that better reflect natural groups. This effort was only possible due to the use of an integrative taxonomic approach in which we resolved taxonomic uncertainties based on multiple lines of evidence such as morphological, molecular and ecological information. Similar approaches for Macaronesian arthropods are scarce (but see Lopez *et al*. 2013).

In Table 2 we summarize the known distribution of Azorean *Tarphius*, showing three groups of species described herein: i) a group composed of basally divergent species (see Fig. 1) restricted to Santa Maria Island, the geologically oldest island of the archipelago; ii) a group composed of five species, the *"azoricus-wollastoni-depressus"* complex identified in the phylogenetic analysis (Fig. 1), which recovers the group previously identified by Gillerfors (1986a) with the addition of *T. gabrielae* **sp. nov.** and *T. floresensis* **sp. nov.**; and iii) a group designated the "*tornvalli*" complex, including the taxa derived from the most recent speciation events, with three species occurring on five different islands (*T. furtadoi* **sp. nov.** of Pico, Faial and S. Jorge Isls., *T. relictus* **sp. nov.** of Terceira Isl., and *T. tornvalli* of S. Miguel Isl.). Because we were unsuccessful in generating molecular data for *Tarphius acuminatus*, its position in the phylogeny of Azorean *Tarphius* is unknown. We argue therefore for the occurrence of at least five phyletic lineages in the archipelago: "*rufonodulosus*", "*serranoi*", "*pomboi*", "*azoricus-wollastoni-depressus*" complex and "*tornvalli*" complex. The islands of Faial, Pico and São Miguel have one representative of each of the large species complexes, i.e., island species assemblages are not monophyletic (Fig. 1), suggesting at least two colonization events to each island.

TABLE 2. List and distribution of Azorean *Tarphius*. Taxonomic entities are based on molecular and morphological characters (exception: *T. acuminatus*—no molecular data).
AZ—Azores, COR—Corvo Isl., FLO—Flores Isl., FAI—Faial Isl., PIC—Pico Isl., GRA—Graciosa Isl., SJO—São Jorge Isl., SMG—São Miguel Isl., SMR—Santa Maria Isl.

	AZ	COR	FLO	FAI	PIC	GRA	SJG	TER	SMG	SMR
Ancestral species										
Tarphius rufonodulosus Israelson, 1984										SMR
Tarphius serranoi Borges, 1991										SMR
Tarphius pomboi Borges, 1991										SMR
"*azoricus-wollastoni-depressus*" Group										
Tarphius azoricus Gillerfors, 1986			FLO						SMG	
Tarphius depressus Gillerfors, 1985										SMR
Tarphius wollastoni Crotch, 1867				FAI						
Tarphius gabrielae sp. nov.					PIC					
Tarphius floresensis sp. nov.			FLO							
"*tornvalli*" Group										
Tarphius furtadoi sp. nov.				FAI	PIC		SJG			
Tarphius relictus sp. nov.								TER		
Tarphius tornvalli Gillerfors, 1985									SMG	
Unknown status										
Tarphius acuminatus Gillerfors, 1986					PIC					
Total number of species	12	0	2	2	3	0	1	1	2	4

Four different lineages are represented in Santa Maria Island; Terceira Island has only one species belonging to the "*tornvalli*" complex; Flores Island has two species of the "*azoricus-wollastoni-depressus*" complex; and São Jorge Island has two mtDNA lineages for *T. furtadoi* **sp. nov.**, possibly the result of two colonization events, where for the most recent one, molecular divergence from Pico populations is still incomplete (Fig.1). The presence of two species in Flores (one of the most isolated islands) may indicate either within island speciation or two independent colonization events.

Albeit a few exceptions, there is a general congruence between the major phylogenetic lineages and some key morphological characters, namely the shape of the body, and setae distribution and type: (a) the three species derived from the earliest divergence events occur on Santa Maria Island and are all easily morphologically distinguishable. A fourth species that occurs in the same island, *T. depressus*, is also easy to differentiate from the other three. Given that the earliest divergence events within the genus all involve the island of Santa Maria, it would seem likely that the species of the *"azoricus-wollastoni-depressus"* complex are derived from an ancestral species on Santa Maria island, which is also supported by the ancestral range reconstruction; (b) Species in this *"azoricus-wollastoni-depressus"* complex share well developed elytral nodules with a pattern formula 3, 3, 2, 1, a more depressed body and the shape of setae, more obtuse and generally almost decumbent (Fig. 5). *Tarphius wollastoni* (Faial Isl.), *T. depressus* (S. Maria Isl.) and *T. gabrielae* **sp. nov.** (Pico Isl.) are more similar, and differ from *T. floresensis* **sp. nov.** (Flores Isl.) in the size and shape of setae. Remarkably, those former three species plus *T. azoricus* also differ from *T. floresensis* **sp. nov.** in their ecology, where the species from Flores Island is mainly a soil species, and the other species in this complex tend to occur under the bark of trees (both native and exotic). Based on morphology and ecology, *T. floresensis* **sp. nov.** (Flores Isl.) segregates from the remaining fours species of the *"azoricus-wollastoni-depressus"* complex, but this is not supported by the molecular data (according to the mtDNA molecular data, *floresensis* and *wollastoni* are the closest relatives; Fig. 1). This incongruence between molecular data *versus* morphological plus ecological data can be explained by an adaptation of *T. floresensis* to a soil habitat instead of the "under the bark of trees" habitat that favours the depressed body and obtuse and generally almost decumbent setae of the remaining four species (Fig. 5). The status of *T. azoricus* from Flores Island is still dubious, since there is no molecular information and not enough specimens to decide if it should be considered as an independent species from *T. azoricus* of São Miguel Island; (c) all the species in the "*tornvalli*" complex have well developed elytral nodules exhibiting a 2-3-2-1 formation, tend to have rigid semi-erect or erect acuminate setae (Fig. 4), and have a similar ecology, occurring in the soil associated with dead wood. The morphological separation of the three species in this complex is somewhat difficult due to their similarity and high intraspecific variation. However, with a careful examination of the shape of pronotum, morphometry, and shape and size of setae, it is possible to distinguish them. In particular, *T. tornvalli* from São Miguel Island and *T. relictus* **sp. nov.** from Terceira Island are distinguishable by the shape of the pronotum and setae with *T. relictus* **sp. nov.** having a habitus more similar to *T. azoricus*, which originated the confusion in the past identification of this taxon (Borges 1990, 1991). Despite the occurrence of different mtDNA lineages for *T. furtadoi* **sp. nov.** in each island, it is, at best, extremely difficult to separate the species from Faial, Pico and São Jorge Islands based on morphology, and therefore we took the more conservative approach of considering them as belonging to the same species. However, the populations of *T. furtadoi* **sp. nov.** from Faial, Pico and S. Jorge are isolated and possibly will generate new species in evolutionary time.

Diversity, ecology and conservation. Due to the high sampling effort performed in the last three decades in most of the Azorean islands, the 12 species of endemic *Tarphius* should be close to the real number of extant species in the archipelago. The species accumulation curve (Appendix S7) may suggest that many more species will be found, however the curve after 1991 is mainly a consequence of the discovery of cryptic species that are now described. Currently there are 12 *Tarphius* species recorded for the Azores (13 if *T. azoricus* from Flores Isl. is considered a different species from *T. azoricus* from S. Miguel Isl.), 23 species for the Madeiran archipelago (Borges *et al*. 2008; Machado 2012) and 31 species for the Canary Islands (Arechavaleta *et al*. 2010; Machado 2012). However, there is evidence that the taxonomy of species from Madeira and the Canaries is also complex (see Emerson *et al*. 2000; Emerson & Oromí 2005) and cryptic speciation may also increase the diversity of *Tarphius* in these archipelagos. The last figures indicate that about 66 species of *Tarphius* are known in Macaronesia, which is 85% of the total number of species known worldwide (see Appendix in Serrano *et al*. 2013). The overall *Tarphius* species richness per Azorean island is shown in Table 2, from which it is obvious that Santa Maria Island is the richest. Interestingly, the most recent island, Pico, is the second most diverse, which may be due to the fact that this island has still a large area of well-preserved native forest. The small number of *Tarphius* species in most of the Azorean islands may be due to historical extinction associated with major land-use changes that have resulted in the current poor representation of native forest in those islands (Gaspar *et al*. 2008; Triantis *et al.* 2010; Terzopoulou *et al.* 2015). The total number of *Tarphius* species endemic to the Azores is difficult to assess accurately, as we do not know the number of species that may now be extinct, and there is the possibility that more species will be discovered in geographically limited areas. In fact, some of the described species only occur in very small patches, such as *T. relictus* **sp. nov.** from Terceira Island, *T. serranoi* and *T. pomboi* from Santa Maria Island, and *Tarphius gabrielae* **sp. nov.** from Pico Island. The very restricted distribution of these taxa puts them at a high risk of extinction.

Despite intensive collecting effort in Terceira Island, *T. relictus* **sp. nov.** was only found in a small, disturbed site covered by exotic trees at low altitude (Fontinhas), which makes it the most endangered *Tarphius* species in the Azores. Terceira Island, as was the case for most of the Azores, was entirely covered by forest before human settlement almost 600 years ago, which suggests that other *Tarphius* species may have existed and gone extinct, particularly in the first centuries of massive land-use changes (see also Triantis *et al.* 2010). Fortunately, Fontinhas is now a protected area included in the Nature Park of Terceira Island.

Some Azorean *Tarphius* species are particularly abundant, namely those living in the soil and occurring in some of the larger and well preserved patches of native forest: *Tarphius floresensis* **sp. nov.** (Flores Isl.), *Tarphius furtadoi* **sp. nov.** (Pico, Faial and S. Jorge Isls.), and *Tarphius tornvalli* (São Miguel Isl.). However, even those species may be threatened due to the rapid advance of invasive plants in Azorean native forests, which are changing the structure of the forest soil with unknown impact on endemic arthropod communities. In fact, in 2010 we observed disturbance in many sites compared to the observations made a decade earlier, with the spread of invasive plants. In two of the islands, Corvo and Graciosa, there is no native forest remaining, and all sampling efforts in exotic vegetation were unsuccessful in collecting *Tarphius* specimens.

Ecological knowledge of Azorean *Tarphius* has been updated. Only two species (*T. rufonodulosus* and *T. serranoi*) were found so far associated with lichens in tree canopies both in Santa Maria Island, but only *T. rufonodulosus* was found both in endemic (*Picconia azorica*) and exotic (*Pittosporum undulatum*) trees, whereas *T. serranoi* was only associated with *Picconia azorica.* Several species of the *"azoricus-wollastoni-depressus"* complex are commonly found under the bark of living trees, while; all species of the "*tornvalli*" complex are mainly found in the soil and dead wood, and are easily captured with pitfall trapping. Habitat loss and invasive species are the principal threats to Azorean native fauna (Borges *et al*. 2009), including arthropods in general and *Tarphius* in particular. Many of the Azorean *Tarphius* species seem to have adapted to exotic trees, mainly if their populations occur near patches of native vegetation (Meijer *et al.* 2011). We also observed that non-managed *Cryptomeria japonica* plantations favours the occurrence of *Tarphius* species, which is explained by the abundance of resources, i.e. fallen trees and dead wood.

Until recently only few species of *Tarphius* were known from the Azores (Borges 1991; Borges *et al.* 2005b). However, in the past three decades efforts to survey the arthropod fauna in remote places (e.g. dense laurel forest in high altitude and inaccessible places) have challenged this view (see also Borges & Wunderlich 2008). Twelve species of *Tarphius* are now recorded for the Azores, including four new species described in this contribution. This work highlights the importance of combining long-term field work, standardized sampling covering many habitats and islands, natural history observations, morphometrics, and molecular studies for the understanding of a complex genus with many species.

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Supplementary information

Multi-approach taxonomic revision of *Tarphius* Erichson, 1845 (Coleoptera: Zopheridae) of the Azores

APPENDIX S1. Pearson's pairwise correlation between the five measurements taken on *Tarphius*' individuals. Pron = pronotum; Ely = elytra; L = length; W = width.

	W Ely	W Pron	L Pron	L Ely
W Pron	0.962			
L Pron	0.859	0.904		
L Ely	0.910	0.903	0.827	
L Body	0.929	0.942	0.931	0.975

APPENDIX S2. Sample origin, species affiliation and GenBank accession numbers for the mtDNA (COI, tRNA-Leu, COII) and nuclear EF1α sequences of the specimens used in the phylogenetic reconstructions. All entries are *Tarphius* species of the Azores, except for the outgroup *T. kiesenwetteri*. GenBank accession numbers for new sequence submissions are in bold (KU666002-53 and KU679448-58). n.s.—not sequenced; s.s.—same sequence as

Species	Species complex	Origin		GenBank accession nos. (mtDNA / EF1α)	
T. kiesenwetteri Heiden, 1870		Melgaço,	North Portugal	JQ689203	/ s.s. JQ689284
T. azoricus Gillerfors, 1991	*azoricus-wollastoni-depressus*	Furnas,	São Miguel	s.s. KU666041	/ n.s.
T. azoricus Gillerfors, 1991	*azoricus-wollastoni-depressus*	Furnas,	São Miguel	**KU666042**	/ n.s.
T. azoricus Gillerfors, 1991	*azoricus-wollastoni-depressus*	Furnas,	São Miguel	s.s. KU666042	/ n.s.
T. azoricus Gillerfors, 1991	*azoricus-wollastoni-depressus*	Furnas,	São Miguel	**KU666041**	/ n.s.
T. azoricus Gillerfors, 1991	*azoricus-wollastoni-depressus*	Furnas,	São Miguel	s.s. KU666042	/ n.s.
T. azoricus Gillerfors, 1991	*azoricus-wollastoni-depressus*	Ponta da Madrugada,	São Miguel	**KU666043**	/ s.s. JQ689382
T. azoricus Gillerfors, 1991	*azoricus-wollastoni-depressus*	Ponta da Madrugada,	São Miguel	JQ689274	/ JQ689382
T. azoricus Gillerfors, 1991	*azoricus-wollastoni-depressus*	Ponta da Madrugada,	São Miguel	JQ689275	/ s.s. JQ689382
T. azoricus Gillerfors, 1991	*azoricus-wollastoni-depressus*	Ponta da Madrugada,	São Miguel	JQ689276	/ s.s. JQ689382
T. azoricus Gillerfors, 1991	*azoricus-wollastoni-depressus*	Ponta da Madrugada,	São Miguel	n.s.	/ s.s. JQ689382
T. azoricus Gillerfors, 1991	*azoricus-wollastoni-depressus*	Ponta da Madrugada,	São Miguel	s.s. JQ689274	/ n.s.
T. azoricus Gillerfors, 1991	*azoricus-wollastoni-depressus*	Ponta da Madrugada,	São Miguel	s.s. JQ689274	/ n.s.
T. azoricus Gillerfors, 1991	*azoricus-wollastoni-depressus*	Ponta da Madrugada,	São Miguel	s.s. JQ689274	/ n.s.
T. azoricus Gillerfors, 1991	*azoricus-wollastoni-depressus*	Ponta da Madrugada,	São Miguel	**KU666044**	/ n.s.
T. depressus Gillerfors, 1985	*azoricus-wollastoni-depressus*	Alto da Nascente,	Santa Maria	**KU666046**	/ n.s.
T. depressus Gillerfors, 1985	*azoricus-wollastoni-depressus*	Pico Alto,	Santa Maria	JQ689248	/ JQ689365
T. depressus Gillerfors, 1985	*azoricus-wollastoni-depressus*	Pico Alto,	Santa Maria	JQ689249	/ s.s. JQ689365
T. depressus Gillerfors, 1985	*azoricus-wollastoni-depressus*	Pico Alto,	Santa Maria	JQ689250	/ JQ689366
T. depressus Gillerfors, 1985	*azoricus-wollastoni-depressus*	Pico Alto,	Santa Maria	JQ689251	/ s.s. JQ689365
T. depressus Gillerfors, 1985	*azoricus-wollastoni-depressus*	Pico Alto,	Santa Maria	**KU666047**	/ n.s.
T. depressus Gillerfors, 1985	*azoricus-wollastoni-depressus*	Pico Alto,	Santa Maria	**KU666048**	/ n.s.
T. depressus Gillerfors, 1985	*azoricus-wollastoni-depressus*	Pico Alto,	Santa Maria	s.s. JQ689251	/ n.s.
T. floresensis Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Caldeira Funda,	Flores	JQ689227	/ JQ689351
T. floresensis Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Caldeira Funda,	Flores	JQ689228	/ JQ689352
T. floresensis Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Caldeira Funda,	Flores	**KU666045**	/ n.s.
T. floresensis Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Caldeira Funda,	Flores	JQ689225	/ JQ689349
T. floresensis Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Lombas,	Flores	JQ689230	/ JQ689353
T. floresensis Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Morro Alto,	Flores	JQ689226	/ JQ689350

……*continued on the next page*

APPENDIX S2. (Continued)

Species	Species complex	Origin		GenBank accession nos. (mtDNA / EF1α)	
T. floresensis Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Morro Alto,	Flores	JQ689229	/ s.s. JQ689350
T. floresensis Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Morro Alto,	Flores	JQ689224	/ s.s. JQ689350
T. floresensis Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Morro Alto,	Flores	JQ689223	/ JQ689348
T. gabrielae Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Reserva da Lagoa do Caiado,	Pico	JQ689238	/ JQ689359
T. gabrielae Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Reserva da Lagoa do Caiado,	Pico	s.s. JQ689238	/ n.s.
T. gabrielae Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Reserva da Lagoa do Caiado,	Pico	n.s.	/ s.s. JQ689359
T. gabrielae Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Reserva da Lagoa do Caiado,	Pico	JQ689239	/ s.s. JQ689359
T. gabrielae Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Reserva da Lagoa do Caiado,	Pico	JQ689240	/ s.s. JQ689359
T. gabrielae Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Reserva da Lagoa do Caiado,	Pico	**KU666010**	/ n.s.
T. gabrielae Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Reserva da Lagoa do Caiado,	Pico	s.s. JQ689240	/ s.s. JQ689359
T. gabrielae Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Reserva da Lagoa do Caiado,	Pico	s.s. JQ689238	/ s.s. JQ689359
T. gabrielae Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Reserva da Lagoa do Caiado,	Pico	s.s. JQ689238	/ n.s.
T. gabrielae Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Reserva da Lagoa do Caiado,	Pico	**KU666009**	/ n.s.
T. gabrielae Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Reserva da Lagoa do Caiado,	Pico	s.s. JQ689240	/ n.s.
T. gabrielae Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Reserva da Lagoa do Caiado,	Pico	s.s. KU666009	/ n.s.
T. gabrielae Borges & Serrano, sp. nov.	*azoricus-wollastoni-depressus*	Reserva da Lagoa do Caiado,	Pico	s.s. JQ689240	/ n.s.
T. wollastoni Crotch, 1867	*azoricus-wollastoni-depressus*	Caldeira,	Faial	**KU666028**	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Caveiro,	Pico	JQ689235	/ JQ689356
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Caveiro,	Pico	JQ689237	/ JQ689358
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Caveiro,	Pico	**KU666006**	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Caveiro,	Pico	JQ689234	/ JQ689355
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Caveiro,	Pico	s.s. JQ689231	/ s.s. JQ689357
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Caveiro,	Pico	s.s. JQ689231	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Caveiro,	Pico	s.s. JQ689231	/ s.s. JQ689357
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Caveiro,	Pico	**KU666004**	/ s.s. JQ689357
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Chão Verde,	Pico	JQ689231	/ s.s. JQ689357
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Chão Verde,	Pico	s.s. JQ689231	/ s.s. JQ689357
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Chão Verde,	Pico	JQ689236	/ JQ689357
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Chão Verde,	Pico	**KU666003**	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Chão Verde,	Pico	**KU666008**	/ **KU679451**
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Chão Verde,	Pico	s.s. JQ689236	/ s.s. JQ689357

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APPENDIX S2. (Continued)

Species	Species complex	Origin		GenBank accession nos. (mtDNA / EF1α)	
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Reserva da Lagoa do Caiado,	Pico	JQ689232	/ s.s. JQ689357
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Reserva da Lagoa do Caiado,	Pico	JQ689233	/ JQ689354
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Reserva da Lagoa do Caiado,	Pico	**KU666002**	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Reserva da Lagoa do Caiado,	Pico	**KU666007**	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Reserva da Lagoa do Caiado,	Pico	s.s. JQ689232	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Reserva da Lagoa do Caiado,	Pico	s.s. JQ689236	/ s.s. JQ689357
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Reserva da Lagoa do Caiado,	Pico	s.s. JQ689236	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Reserva da Lagoa do Caiado,	Pico	s.s. JQ689231	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Reserva da Lagoa do Caiado,	Pico	**KU666005**	/ **KU679452**
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Reserva da Lagoa do Caiado,	Pico	s.s. JQ689236	/ s.s. JQ689357
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Ribeira Seca,	São Jorge	JQ689260	/ JQ689370
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Ribeira Seca,	São Jorge	JQ689261	/ JQ689371
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Ribeira Seca,	São Jorge	s.s. JQ689260	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Ribeira Seca,	São Jorge	s.s. JQ689268	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Ribeira Seca,	São Jorge	**KU666011**	/ **KU679449**
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Ribeira Seca,	São Jorge	JQ689262	/ JQ689372
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Ribeira Seca,	São Jorge	JQ689263	/ s.s. JQ689357
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Ribeira Seca,	São Jorge	JQ689264	/ s.s. JQ689357
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Ribeira Seca,	São Jorge	JQ689265	/ JQ689373
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Ribeira Seca,	São Jorge	JQ689266	/ JQ689374
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Ribeira Seca,	São Jorge	JQ689267	/ JQ689375
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Caldeira,	Faial	**KU666023**	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Caldeira,	Faial	**KU666024**	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Caldeira,	Faial	**KU666025**	/ **KU679455**
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Caldeira,	Faial	**KU666026**	/ **KU679456**
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	Caldeira,	Faial	**KU666027**	/ **KU679457**
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	near Cabeço dos 30,	Faial	JQ689220	/ JQ689345
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	near Cabeço dos 30,	Faial	JQ689221	/ JQ689346
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	near Cabeço dos 30,	Faial	JQ689222	/ JQ689347
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	near Cabeço dos 30,	Faial	**KU666012**	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	near Cabeço dos 30,	Faial	**KU666013**	/ n.s.

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APPENDIX S2. (Continued)

Species	Species complex	Origin		GenBank accession nos. (mtDNA / EF1α)	
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	near Cabeço dos 30,	Faial	**KU666014**	/ **KU679453**
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	near Cabeço dos 30,	Faial	**KU666015**	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	near Cabeço dos 30,	Faial	s.s. KU666016	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	near Cabeço dos 30,	Faial	**KU666017**	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	near Cabeço dos 30,	Faial	**KU666018**	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	near Cabeço dos 30,	Faial	**KU666019**	/ **KU679454**
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	near Cabeço dos 30,	Faial	**KU666020**	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	near Cabeço dos 30,	Faial	**KU666021**	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	near Cabeço dos 30,	Faial	**KU666022**	/ n.s.
T. furtadoi Borges & Serrano, sp. nov.	*tornvalli*	near Cabeço dos 30,	Faial	**KU666016**	/ n.s.
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	JQ689277	/ JQ689383
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	JQ689278	/ JQ689384
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	**KU666029**	/ n.s.
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	s.s. KU666030	/ n.s.
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	**KU666030**	/ n.s.
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	s.s. JQ689280	/ n.s.
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	s.s. KU666029	/ n.s.
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	s.s. KU666029	/ n.s.
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	JQ689279	/ JQ689385
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	**KU666031**	/ n.s.
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	JQ689280	/ JQ689386
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	s.s. JQ689278	/ s.s. JQ689386
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	**KU666032**	/ n.s.
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	s.s. JQ689278	/ s.s. JQ689386
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	**KU666033**	/ **KU679450**
T. relictus Borges & Serrano, sp. nov.	*tornvalli*	Biscoito das Fontinhas,	Terceira	JQ689281	/ JQ689387
T. tornvalli Gillerfors, 1985	*tornvalli*	Furnas,	São Miguel	**KU666034**	/ n.s.
T. tornvalli Gillerfors, 1985	*tornvalli*	Furnas,	São Miguel	JQ689272	/ JQ689380
T. tornvalli Gillerfors, 1985	*tornvalli*	Lagoa do Fogo,	São Miguel	JQ689269	/ JQ689377
T. tornvalli Gillerfors, 1985	*tornvalli*	Lagoa do Fogo,	São Miguel	JQ689270	/ JQ689378
T. tornvalli Gillerfors, 1985	*tornvalli*	Pico da Vara,	São Miguel	**KU666039**	/ n.s.

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APPENDIX S2. (Continued)

Species	Species complex	Origin		GenBank accession nos. (mtDNA / EF1α)	
T. tornvalli Gillerfors, 1985	*tornvalli*	Pico da Vara,	São Miguel	JQ689273	/ JQ689381
T. tornvalli Gillerfors, 1985	*tornvalli*	Pico da Vara,	São Miguel	**KU666040**	/ **KU679448**
T. tornvalli Gillerfors, 1985	*tornvalli*	Pico da Vara,	São Miguel	**KU666038**	/ n.s.
T. tornvalli Gillerfors, 1985	*tornvalli*	Reserva da Atalhada,	São Miguel	**KU666035**	/ n.s.
T. tornvalli Gillerfors, 1985	*tornvalli*	Reserva da Atalhada,	São Miguel	s.s. KU666035	/ n.s.
T. tornvalli Gillerfors, 1985	*tornvalli*	Reserva da Atalhada,	São Miguel	**KU666036**	/ n.s.
T. tornvalli Gillerfors, 1985	*tornvalli*	Reserva da Atalhada,	São Miguel	JQ689271	/ JQ689379
T. tornvalli Gillerfors, 1985	*tornvalli*	Tronqueira,	São Miguel	**KU666037**	/ n.s.
T. pomboi Borges, 1991		Pico Alto,	Santa Maria	JQ689252	/ JQ689367
T. pomboi Borges, 1991		Pico Alto,	Santa Maria	JQ689253	/ s.s. JQ689367
T. pomboi Borges, 1991		Pico Alto,	Santa Maria	JQ689254	/ JQ689368
T. pomboi Borges, 1991		Pico Alto,	Santa Maria	**KU666049**	/ **KU679458**
T. pomboi Borges, 1991		Pico Alto,	Santa Maria	JQ689255	/ s.s. JQ689367
T. rufonodulosus Israelson, 1984		Barreiros,	Santa Maria	JQ689244	/ s.s. JQ689362
T. rufonodulosus Israelson, 1984		Barreiros,	Santa Maria	**KU666051**	/ n.s.
T. rufonodulosus Israelson, 1984		Barreiros,	Santa Maria	**KU666052**	/ n.s.
T. rufonodulosus Israelson, 1984		Glória,	Santa Maria	**KU666050**	/ n.s.
T. rufonodulosus Israelson, 1984		Glória,	Santa Maria	JQ689241	/ JQ689360
T. rufonodulosus Israelson, 1984		Glória,	Santa Maria	JQ689242	/ JQ689361
T. rufonodulosus Israelson, 1984		Glória,	Santa Maria	JQ689243	/ JQ689362
T. rufonodulosus Israelson, 1984		Glória,	Santa Maria	s.s. JQ689241	/ n.s.
T. rufonodulosus Israelson, 1984		Pico Alto,	Santa Maria	JQ689245	/ JQ689363
T. rufonodulosus Israelson, 1984		Pico Alto,	Santa Maria	JQ689246	/ JQ689364
T. rufonodulosus Israelson, 1984		Pico Alto,	Santa Maria	JQ689247	/ s.s. JQ689362
T. rufonodulosus Israelson, 1984		Pico Alto,	Santa Maria	**KU666053**	/ s.s. JQ689363
T. rufonodulosus Israelson, 1984		Pico Alto,	Santa Maria	s.s. JQ689246	/ s.s. JQ689362
T. serranoi Borges, 1991		Pico Alto,	Santa Maria	JQ689256	/ JQ689369
T. serranoi Borges, 1991		Pico Alto,	Santa Maria	JQ689257	/ s.s. JQ689369
T. serranoi Borges, 1991		Pico Alto,	Santa Maria	JQ689258	/ s.s. JQ689369
T. serranoi Borges, 1991		Pico Alto,	Santa Maria	s.s. JQ689258	/ s.s. JQ689369
T. serranoi Borges, 1991		Pico Alto,	Santa Maria	JQ689259	/ s.s. JQ689369
T. serranoi Borges, 1991		Pico Alto,	Santa Maria	s.s. JQ689258	/ n.s.

APPENDIX S3. Reconstructed ancestral range for nodes a-g of the BI mtDNA tree (see Fig. 1) obtained with the BMM method as implemented in RASP. The analysis was run with default options, except for the number of cycles (n=100,000): i) Area—Max. no. of areas = 4; ii) MCMC analysis—No. of cycles = 100,000, No. of chains = 10, Sample freq. = 100, Discard samples = 100, Temp. = 0.1; and iii) Model—State freq. = Fixed (JC), Among-Site rate var. = equal. The analysis was run three times (data not shown) and the most likely ancestral areas recovered for each node were the same. Probabilities for the most likely and alternative distributions for one of the runs are presented in percentage following the range and the range code, respectively.

Range code: A—Iberia (Northern Portugal), B—São Miguel Isl., C—Santa Maria Isl., D—Pico Isl., E—Faial Isl., F—São Jorge Isl., G—Terceira Isl., H—Flores Isl.

Node	Most likely ancestral range & probability (%)	Alternative ancestral range & probability (%)
a	São Jorge Isl. 91.44	E 2.58; EF 1.76; G 0.97; D 0.81; FG 0.66; DF 0.55; C 0.19; B 0.18; H 0.14; A 0.14; CF 0.13; BF 0.12; FH 0.10; AF 0.10; EG 0.02; DE 0.02; EFG 0.01; DEF 0.01; DG 0.01
b	Terceira Isl. 50.48	F 31.95; C 3.86; FG 3.66; B 3.24; E 1.96; D 1.11; A 0.68; H 0.67; CG 0.44; BG 0.37; CF 0.28; BF 0.24; EG 0.22; EF 0.14; DG 0.13; DF 0.08; AG 0.08; GH 0.08; AF 0.05; FH 0.05; CFG 0.03; BC 0.03; BFG 0.03; CE 0.02; EFG 0.02; BE 0.01; CD 0.01; DFG 0.01; BD 0.01; AC 0.01; CH 0.01; AFG 0.01; FGH 0.01; AB 0.01
c	Santa Maria Isl. 43.94	B 37.47; G 6.63; F 3.74; BC 3.48; E 0.66; A 0.65; CG 0.62; D 0.55; BG 0.53; H 0.47; CF 0.35; BF 0.30; CE 0.06; AC 0.06; BE 0.05; FG 0.05; AB 0.05; CD 0.05; BCG 0.05; CH 0.04; BD 0.04; BH 0.04; BCF 0.03; EG 0.01; AG 0.01; DG 0.01; GH 0.01; EF 0.01; AF 0.01
d	Pico Isl. 35.68	B 33.28; C 19.80; BD 3.71; CD 2.21; BC 2.06; H 0.59; E 0.52; A 0.43; G 0.39; F 0.39; BCD 0.23; DH 0.07; BH 0.06; DE 0.06; BE 0.05; AD 0.05; AB 0.04; DG 0.04; DF 0.04; BG 0.04; BF 0.04; CH 0.04; CE 0.03; AC 0.03; CG 0.02; CF 0.02; BDH 0.01; BDE 0.01; ABD 0.01
e	Flores Isl. 39.83	E 34.40; C 14.66; EH 3.78; CH 1.61; CE 1.39; D 1.02; B 0.75; G 0.53; A 0.49; F 0.49; CEH 0.15; DH 0.11; DE 0.10; BH 0.08; BE 0.07; GH 0.06; AH 0.05; FH 0.05; EG 0.05; AE 0.05; EF 0.05; CD 0.04; BC 0.03; CG 0.02; AC 0.02; CF 0.02; DEH 0.01; BEH 0.01; EGH 0.01; AEH 0.01; EFH 0.01
f	Santa Maria Isl. 97.37	BC 0.67; CE 0.41; CH 0.32; CD 0.29; B 0.24; E 0.15; H 0.11; D 0.10; CG 0.07; AC 0.07; CF 0.07; G 0.03; A 0.03; F 0.03
g	Santa Maria Isl. 72.54	A 21.93; AC 3.51; B 0.52; G 0.24; F 0.23; H 0.22; E 0.22; D 0.22; BC 0.08; CG 0.04; CF 0.04; CH 0.04; CE 0.04; CD 0.04; AB 0.03; AG 0.01; AF 0.01; AH 0.01; AE 0.01; AD 0.01

APPENDIX S4. Mean, standard error (se), minimum (min) and maximum (max) values for five morphometric traits (body length + four ratios) for 10 *Tarphius* species of the Azores. The number of individuals measured per species are given in parentheses.

		Body Length	Ratio Width elytra / Width pronotum	Ratio Length elytra / Length pronotum	Ratio Width elytra / Length elytra	Ratio Width pronotum / Length pronotum
T. rufonodulosus (12)	mean	2.397	1.040	1.649	0.865	1.365
	se	0.086	0.008	0.034	0.014	0.008
	min	1.950	0.985	1.360	0.811	1.301
	max	2.980	1.074	1.790	0.971	1.398
T. serranoi (13)	mean	2.389	1.114	1.555	0.940	1.297
	se	0.083	0.010	0.044	0.034	0.010
	min	2.040	1.050	1.239	0.783	1.244
	max	3.130	1.196	1.788	1.178	1.347
T. pomboi (10)	mean	2.535	1.142	1.625	0.904	1.286
	se	0.078	0.010	0.022	0.011	0.010
	min	2.220	1.098	1.510	0.863	1.241
	max	2.980	1.215	1.694	0.974	1.340
T. depressus (18)	mean	3.254	1.059	1.641	0.916	1.419
	se	0.097	0.010	0.018	0.008	0.014
	min	2.570	0.975	1.508	0.874	1.282
	max	4.170	1.137	1.798	1.010	1.555
T. floresensis sp. nov. (11)	mean	2.734	1.095	1.651	0.896	1.348
	se	0.123	0.014	0.040	0.019	0.022
	min	2.000	1.007	1.351	0.792	1.239
	max	3.290	1.200	1.829	1.013	1.506
T. azoricus (7)	mean	3.303	1.065	1.712	0.854	1.371
	se	0.112	0.009	0.042	0.015	0.022
	min	2.950	1.036	1.600	0.793	1.315
	max	3.640	1.108	1.912	0.902	1.480

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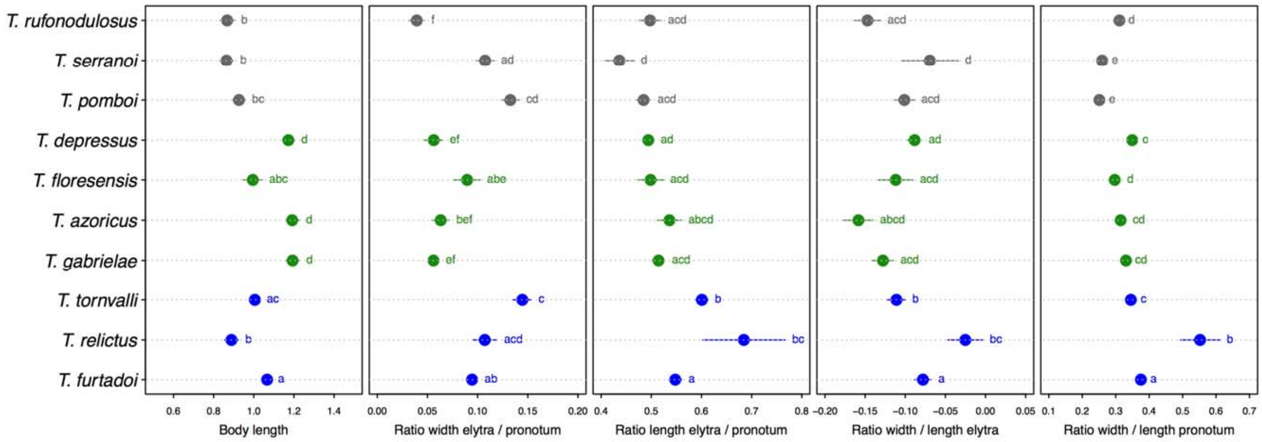
APPENDIX S4. (Continued)

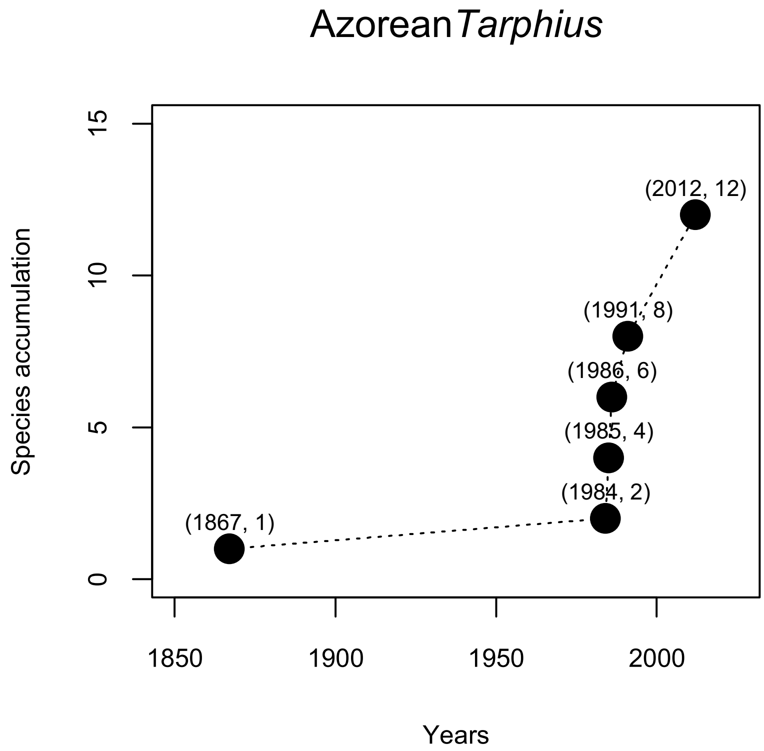
		Body Length	Ratio Width elytra / Width pronotum	Ratio Length elytra / Length pronotum	Ratio Width elytra / Length elytra	Ratio Width pronotum / Length pronotum
T. gabrielae sp. nov. (9)	mean	3.313	1.058	1.674	0.881	1.392
	se	0.118	0.006	0.021	0.011	0.008
	min	2.900	1.029	1.590	0.821	1.350
	max	4.110	1.087	1.758	0.912	1.425
T. tornvalli (33)	mean	2.759	1.157	1.828	0.897	1.414
	se	0.067	0.011	0.022	0.010	0.012
	min	2.120	1.087	1.593	0.821	1.216
	max	3.380	1.322	2.118	1.106	1.588
T. relictus sp. nov. (10)	mean	2.445	1.114	2.039	0.977	1.763
	se	0.088	0.013	0.149	0.022	0.096
	min	2.120	1.038	1.327	0.909	1.304
	max	3.070	1.171	2.459	1.115	2.081
T. furtadoi sp. nov. (42)	mean	2.927	1.100	1.735	0.927	1.457
	se	0.056	0.006	0.021	0.010	0.010
	min	2.310	1.027	1.432	0.840	1.294
	max	3.790	1.178	2.113	1.088	1.619



APPENDIX S5. Results of the PerMANOVA testing the difference between species for each morphological trait separately (Body Length and four ratios). For each trait and for each species, the mean (circle) and its associated standard error (horizontal line) is given. Traits were log-transformed before analyses. Species accompanied by a different letter are significantly different from each other (post hoc tests; P < 0.05). Colours indicate species complex: blue for tornvalli, green for azoricus-wollastoni-depressus and grey for the three endemic species of Santa Maria Island.

APPENDIX S6. Mean, standard deviation, maximum and minimum values for several morphometric measures for the described species. Pron = pronotum; ely = elytra; L = length; W = width.

	L pron	W pron	L ely	W ely	L_pron+L_ely	Total		Ratio	Ratio	Ratio	Ratio	Ratio
						Head	Length	W/L pron	W/L ely	W ely/W pron	L pron /L ely	W pron/W ely
	Tarphius tornvalli											
Mean	0,98	1.38	1.78	1.60	2.76	0.32	3.08	1.41	0.90	1.16	0.55	0.87
sd	0.14	0.22	0.25	0.23	0.38	0.05	0.43	0.07	0.06	0.06	0.04	0.04
Max	1.23	1.75	2.19	1.99	3.38	0.41	3.77	1.59	1.11	1.32	0.63	0.92
Min	0.74	0.90	1.34	1.19	2.12	0.24	2.37	1.22	0.82	1.09	0.47	0.76
	***Tarphius relictus* sp. nov.**											
Mean	0.83	1.41	1.61	1.57	2.45	0.27	2.72	1.76	0.98	1.11	0.52	0.90
sd	0.21	0.13	0.17	0.11	0.28	0.07	0.34	0.30	0.07	0.04	0.15	0.04
Max	1.25	1.63	1.82	1.70	3.07	0.41	3.48	2.08	1.12	1.17	0.75	0.96
Min	0.66	1.22	1.30	1.37	2.12	0.22	2.34	1.30	0.91	1.04	0.41	0.85
	***Tarphius furtadoi* sp. nov.**											
Mean	1.07	1.56	1.86	1.71	2.93	0.35	3.23	1.45	0.92	1.10	0.58	0.91
sd	0.13	0.20	0.25	0.20	0.37	0.04	0.41	0.06	0.06	0.04	0.05	0.03
Max	1.37	2.00	2.42	2.17	3.79	0.45	4.24	1.62	1.09	1.18	0.70	0.97
Min	0.85	1.23	1.36	1.42	2.31	0.28	2.60	1.29	0.84	1.03	0.47	0.85
	***Tarphius gabrielae* sp. nov.**											
Mean	1.24	1.72	2.07	1.82	3.31	0.41	3.72	1.39	0.88	1.06	0.60	0.95
sd	0.12	0.17	0.24	0.18	0.35	0.04	0.39	0.02	0.03	0.02	0.02	0.01
Max	1.49	2.07	2.62	2.20	4.11	0.49	4.60	1.42	0.91	1.09	0.63	0.97
Min	1.06	1.51	1.84	1.61	2.90	0.35	3.25	1.35	0.82	1.03	0.57	0.92
	***Tarphius floresensis* sp. nov.**											
Mean	1.03	1.38	1.70	1.52	2.73	0.34	3.07	1.35	0.90	1.09	1.12	0.61
sd	0.14	0.17	0.28	0.19	0.41	0.05	0.45	0.07	0.06	0.05	0.08	0.05
Max	1.19	1.61	2.11	1.76	3.29	0.39	3.68	1.51	1.01	1.20	1.26	0.74
Min	0.76	1.03	1.24	1.10	2.00	0.25	2.25	1.24	0.79	1.01	0.99	0.55



APPENDIX S7. Accumulated number of *Tarphius* species known from the Azores.