

Research article

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is a genuine member of the genus *Talavera* (Araneae: Salticidae)**

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Abstract. The small jumping spider *Euophrys petrensis* C. L. Koch, 1837 combines morphological characters of both *Euophrys* s. str. and *Talavera*, and its generic placement has consequently been contentious. After many years of being placed in *Talavera*, the species has recently been transferred back to *Euophrys*. Here, public DNA barcoding data are used to confirm that the species should be placed in the genus *Talavera*, as *T. petrensis*, **stat. rev.**, as is also indicated by several putative morphological synapomorphies identified earlier.

Key words. Araneae, DNA barcoding, phylogenetic systematics.

INTRODUCTION

The taxonomic placement of *Euophrys petrensis* has been problematic for some time, since the revision and major expansion of the genus *Talavera* Peckham & Peckham, 1909, by Logunov (1992). Logunov (1992) transferred four Palaearctic members of *Euophrys* s. lat. to *Talavera* (*T. aequipes*, *T. monticola*, *T. thorelli*, and *T. trivittata*). However, he delayed the transfer of their close relative, *E. petrensis*, as the latter showed ambiguous characters implying a possible closer affinity to *Euophrys* s. str. (e.g., chitinous rings in the epigynum and twisted insemination ducts, as well as a pronounced sexual dimorphism). Logunov (1992) also remarked that *T. aequipes* occupies a similar morphologically intermediate position between *Talavera* and *Euophrys* s. str.

Logunov et al. (1993) then indicated that all species of their *petrensis* group of *Euophrys* s. lat. (*E. petrensis*, *E. aequipes*, and *E. thorelli*) should be included in the genus *Talavera*, without, however, providing additional arguments regarding *E. petrensis* itself.

The transfer of the latter was formalized by Żabka (1997; see also Żabka & Prószyński 1998), and *Talavera petrensis* was generally accepted as the valid combination by subsequent authors. Logunov & Kronstedt (2003) reviewed *Talavera* s. lat. and list the diagnostic characters of the expanded genus: absence of a tibial apophysis; endite tooth on the male maxilla; long white/red hairs on the base of the cymbium; clearly exposed embolus-tegulum membrane; thin, thread-like insemination ducts; and scales with a well-marked keel on carapace and abdomen.

However, most recently, Prószyński et al. (2018) transferred *T. petrensis* back to *Euophrys*, but maintained

other members of the *petrensis* group (sensu Logunov et al. 1993), such as *T. aequipes* and *T. thorelli*, within *Talavera*. This re-transfer was based on Prószyński's non-cladistic approach combined with a different relative weighting of the various characters already highlighted as ambiguous by Logunov (1992): the coiled embolus and colourful frontal hairs of the male. The absence of a tibial apophysis, which Logunov & Kronstedt (2003) describe as one of the most important diagnostic characters of *Talavera*, was considered as non-informative, as the apophysis in *Euophrys* s. str. is typically highly reduced, and the thin copulatory ducts were considered an artefact of observation by optical microscopy, while “they appear much broader” when observed by scanning electron microscopy (Prószyński et al. 2018); this latter argument is not quite convincing, being based on a rather subjective comparison of published figures. The other characters discussed by Logunov & Kronstedt (2003) received no further attention.

Given this controversial history, it was interesting to examine if the publicly available barcoding sequences could be used to supplement the morphological data to resolve the placement of *Euophrys petrensis*, in analogy to the approach taken in Breitling (2017, 2019). In a barcoding study of German spiders, the species had already been shown as sister of *Talavera aequipes*, rather than *Euophrys frontalis* (Astrin et al. 2016: Supplementary Figures S1 and S2); as these results were based on a limited set of species and were not further discussed in the article, the robustness of this relationship remained unclear, but the results certainly indicated that the barcode data should contain relevant phylogenetic information.

MATERIAL AND METHODS

All public Cytochrome Oxidase Subunit 1 5' region barcodes (COI-5P) for members of *Euophrys*, *Talavera* and *Pseudeuophrys* (i.e. *Euophrys* s. lat.), and the closely related genus *Chalcoscirtus* were downloaded in FASTA format from the BOLD database (www.boldsystems.org; Ratnasingham & Hebert 2007) in April 2018. Sequences were aligned in BioEdit v7.2.5 (Hall 1999), and trailing gaps and particularly short sequences were removed to maximize the amount of sequence positions for which all specimens in the analysis had data available. The resulting dataset included 540 residues of the COI-5P barcode for 59 specimens. The BOLD and GenBank accession numbers of all sequences in the final dataset are shown in Figure 1.

The data included barcode sequences for four species of *Talavera* (13 specimens of the type species, *T. minuta*, two specimens of *T. petrensis* and one specimen each of *T. thorelli* and *T. aequipes*). Together, these four species represent all four species groups of *Talavera* s. lat. defined by Logunov & Kronstedt (2003). Also included in the dataset are representatives of *Euophrys* s. str. (17 specimens of the type species, *E. frontalis*, and five of *E. monadnock*), of *Pseudeuophrys* (seven specimens of the type species, *P. erratica*, six specimens of *P. lanigera*, and two of *P. obsoleta*), and two species of *Chalcoscirtus* (two specimens of *C. alpicola*, and three of *C. carbonarius*), which in preliminary analyses of salticid barcodes were consistently nested within *Euophrys* (Breitling 2019).

The plausibility of the identification of the *T. petrensis* specimens critical for this analysis was confirmed using the data deposited in BOLD: the material was collected in Saxony-Anhalt, well within the known range of the species (which extends from Ireland to Central Asia and from Finland to the Mediterranean), identified by Karl-Hinrich Kielhorn, an experienced arachnologist, and is deposited in the Zoologische Staatssammlung München. Both specimens are adult males, which are particularly easy to identify reliably, and the habitus photographs available in BOLD further support the identification.

Phylogenetic trees were reconstructed using phylogeny.fr (Dereeper et al. 2008) as described in Breitling (2017), using the default workflow and parameters to infer Maximum Likelihood (PhyML 3.1; Guindon & Gascuel 2003), Maximum Parsimony (TNT 1.1; Goloboff et al. 2008) and Bayesian trees (MrBayes 3.2.6; Ronquist & Huelsenbeck 2003). Sequences were not partitioned by codon for the analysis. For the Bayesian analysis, the standard (4by4) model of nucleotide substitution was used, while the rate variation across sites was set to “invgamma”. Four Markov Chain Monte Carlo chains were run for 100 000 generations, sampling every 100 generations, with the first 1000 sampled trees discarded as “burn-in”. Finally, a 50% majority rule consensus tree

was constructed. For the Maximum Likelihood analysis, the default substitution model was selected assuming an estimated proportion of invariant sites (of 0.577) and 4 gamma-distributed rate categories to account for rate heterogeneity across sites. The gamma shape parameter was estimated directly from the data (gamma=1.268). Branch support values are based on an Approximate Likelihood-Ratio Test (aLRT; Anisimova & Gascuel 2006) for the Maximum Likelihood results, on 1000 bootstrap replicates for the Maximum Parsimony and Neighbour Joining results, and on posterior probabilities for the Bayesian analysis. Trees were visualized using iTOL (Letunic & Bork 2016) and annotated in Adobe Illustrator.

RESULTS & DISCUSSION

The barcoding data provide unambiguous support for the placement of *Euophrys petrensis* C. L. Koch, 1837, in the genus *Talavera*, as *T. petrensis*, **stat. rev.** The *maximum* interspecies distance between barcodes within the genus *Talavera* is 8.5% (between one of the *T. petrensis* specimens and *T. aequipes*). In contrast, the *minimum* distance between *Talavera* and any member of *Euophrys* is 11.4% (between one of the *T. petrensis* specimens and one specimen of *E. monadnock*). The minimum distance between *T. petrensis* and the type species of *Euophrys*, *E. frontalis*, is 12.2%, and the closest member of *Pseudeuophrys* (*P. obsoleta*) has a distance of 12.9%. This is clearly a much larger barcoding distance, especially when considering that, on average, barcode sequences for species assigned to the same genus differ by 10.5% among Salticidae in the BOLD database, and the numbers are even lower for other families (e.g., 10.0% for Thomisidae, 8.5% for Theridiidae, and 6.2% for Lycosidae; Breitling, unpubl. data). To give a sense of the scale of this difference: of the 72 base pairs shared between *T. petrensis* and either *T. minuta* or *E. frontalis* (but not both), 16 are shared with *E. frontalis*, and 56 with *T. minuta*. Assuming a uniform mutation rate (as would appear reasonable for such a closely related group), this finding is obviously not compatible with a closer relationship between *T. petrensis* and *E. frontalis*. Consequently, all the tree reconstruction methods recover a monophyletic genus *Talavera*, including *T. petrensis*, with strong bootstrap and posterior probability support (99% bootstrap support in the Maximum Parsimony tree, 100% bootstrap support in the Neighbour Joining analysis, 100% posterior probability in the Bayesian analysis, and 100% approximate LRT in the Maximum Likelihood tree), and almost always with the same internal topology (*T. petrensis* as sister to the other three species), as shown in Figure 1. The corresponding node is the most strongly supported interspecific node in the entire tree, with higher support values than the also highly supported node joining the three *Pseudeuophrys* species. None of the trees indicates a closer relationship

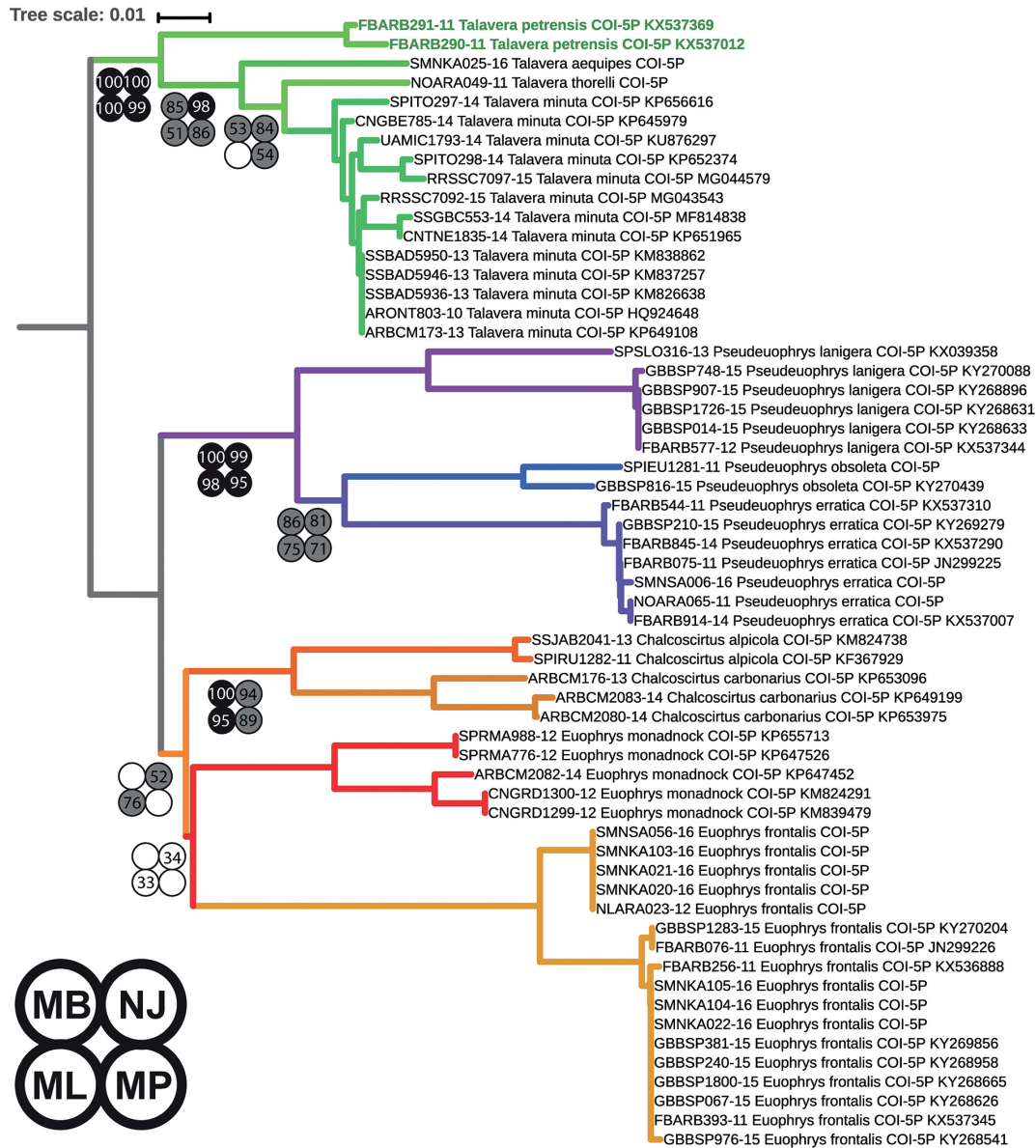


Fig. 1. DNA-Barcode-based tree of *Talavera* and its relatives. The topology and branch lengths are based on the Neighbour Joining tree. The genus *Talavera* forms a very strongly supported monophyletic group, including *T. petrensis*, in all four tree reconstructions, but its relationships to the other members of *Euophrys* s. lat. are not convincingly resolved in the dataset. Black circles indicate more than 95% posterior probability (MB), approximate likelihood (ML), or bootstrap support (MP, NJ); grey circles indicate support values between 50% and 95%. White circles indicate branches that were either not recovered or had a support below 50%. Support values for intraspecific branches are not shown (all species were recovered as monophyletic in all analyses).

of *T. petrensis* to *Euophrys* s. str. or *Pseudeuophrys* with any degree of support. This result is consistent with the barcode-based trees of German spider species shown in the Supplementary Material of Astrin et al. (2016).

As expected, the details of the relationship between *Talavera*, *Euophrys* s. str. and *Pseudeuophrys* are not unambiguously resolved by the barcode data. In the Bayesian and Maximum Likelihood analyses there is some

evidence that the three genera are part of a (monophyletic) clade (*Euophrys* s. lat.), as would be expected on the basis of their morphological similarity, and *Pseudeuophrys* is consistently recovered as monophyletic as well in all analyses. The diversity of *Euophrys* s. str. is not sufficiently represented to assess its monophyly, and its relationship with *Chalcoscirtus* is not convincingly resolved. In several of the reconstructed trees, *Chalco-*

scirtus is nested within a paraphyletic *Euophrys* s. str. As *Chalcoscirtus* appears to be represented only by female specimens in the database, it is not impossible that this finding is due to a misidentification. But, as the case involves multiple specimens from several locations, including material identified by an experienced arachnologist, Gergin Blagoev, the possibility that *Chalcoscirtus* forms a highly derived monophyletic subgroup within a paraphyletic *Euophrys* s. str. as presently defined cannot be discarded outright. The genus *Chalcoscirtus* is defined by a number of characteristic synapomorphies, such as the dark, strongly sclerotized, glabrous prosoma, the male opisthosomal scutum and the absence of retromarginal cheliceral teeth (Cutler 1990). Its key diagnostic character is the presence of a ventral tibial apophysis, but the absence of this apophysis in *Euophrys* is a symplesiomorphy, shared with *Pseudeuophrys* and *Talavera*. Thus, there are currently no convincing synapomorphies for *Euophrys* s. str., and the genitalia of the two genera are obviously very similar in both sexes. Of course, it would also be possible that *Chalcoscirtus* is polyphyletic, and that the two species in the dataset are not closely related to *Chalcoscirtus* s. str., i.e., *C. infimus* and its mostly Central Asian close relatives. However, the large number of convincing synapomorphies supporting the genus makes this hypothesis much less plausible.

It is striking that the barcoding data allow such a clear assignment of “*Euophrys*” *petrensis* to the genus *Talavera*. The ambiguous morphological data had indicated a more “intermediate” position, i.e., a trichotomy or very shallow branching between *Euophrys*, *Talavera* s. str. and *T. petrensis*, which could have been reflected in a much smaller (or non-existent) difference in barcoding distance and possibly an unresolved or ambiguous placement of *T. petrensis* in the various phylogenetic reconstructions. The molecular evidence can stimulate a renewed look at the morphological data as well. It appears that the absence of a tibial apophysis, presence of an endite tooth on the maxilla, exposed embolus–tegulum membrane, long red and white hairs at the base of the cymbium, and keeled scales are indeed synapomorphies of *Talavera* (and, in the case of the missing tibial apophysis, its supposed sister group *Tanzania*; Logunov & Kronstedt 2003, sub *Lilliput*), while the coiled embolus, relatively thick and twisted insemination duct, and pronounced sexual dimorphism, including colourful cymbial setae, are possible symplesiomorphies maintained in the basal *T. petrensis*, and shared with, e.g., *Euophrys*, but lost in the other *Talavera* species, as already suggested by Logunov (1992). More derived *Talavera* species (beyond the *petrensis* and *aequipes* group) are then additionally characterized by a number of derived characters of the male pedipalp (e.g., a more complex sperm duct, a chitinous ligament connecting the embolus and the tegulum, and a distal tegular sclerite; Logunov & Kronstedt 2003).

Of course, the fact that we have been able to refute one of the two alternative hypotheses that we began with does not necessarily mean that the other hypothesis is correct. Thus, while the barcode data do not provide any reason to doubt the taxonomic placement suggested by Logunov & Kronstedt (2003), future studies may well change this assessment. Additional analyses, using larger datasets, will also be required to determine the precise relationships between the various Euophryine genera, including *Chalcoscirtus*. The success of barcode information in suggesting an unambiguous solution to the taxonomic conundrum regarding the generic placement of *Talavera petrensis* should encourage the further use of public barcoding databases as a valuable resource to complement morphological approaches to spider taxonomy, especially in cases where morphological analysis has resulted in ambiguous or controversial placements.

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