Research Article

Bringing *Tegenaria boitanii* stat. rev. back to life with a review of the *Tegenaria percuriosa*-complex (Araneae: Agelenidae), description of a new species and insight into their phylogenetic relationships and evolutionary history

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The funnel web spiders (Agelenidae) are a diverse and taxonomically challenging worldwide distributed family. The genus *Tegenaria* Latreille, 1804, includes more than 100 valid species, mostly circumscribed to Europe and western Asia, although some species may have been subsequently introduced to other regions by anthropogenic action. Here we revise and investigate phylogenetic relationships of a group of morphologically similar species from the south-western Black Sea region and Anatolia. We remove the species *Tegenaria boitanii* Brignoli, 1978 stat. rev. and *Tegenaria bithyniae* Brignoli, 1978 from synonymy of *Tegenaria percuriosa* Brignoli, 1972. *Tegenaria boitanii* stat. rev. is restored as a valid species, re-described and re-diagnosed, and *T. bithyniae* syn. nov. is placed as its junior synonym. We also provide an updated diagnosis for *T. percuriosa*, describe a new species, *Tegenaria euxinica* Dimitrov sp. nov. from the mesophilic beech forests (*Fagus orientalis*) in Bulgaria, and review the members of *T. percuriosa* complex. We provide new photographs for selected species, and a map of the updated distribution ranges of all the species in the complex. The phylogenetic position and internal structure of *T. percuriosa* species-complex is investigated by combining available morphological and molecular (target sequencing) data with new data from the species of interest. Finally, we propose to test in future studies the hypothesis that major climatic changes during the Miocene drove diversification of the group and imprinted its biogeography.

http://zoobank.org/urn:lsid:zoobank.org:pub:08A77B59-ACFE-4C16-BBCB-BC45BE981360

Key words: Evolution, faunistic elements, funnel weavers, phylogeny, taxonomy

Introduction

The funnel web spiders (Agelenidae) are a diverse family, consisting of 1350 valid species, classified in 90 genera (World Spider Catalog, 2021). The taxonomy of the family has a long and controversial history, summarized by Bolzern et al. (2013). Although many important taxonomic issues were already resolved (like the position of the subfamily Coelotinae), there are still many gaps to fill. This is especially true for *Tegenaria*, one of the largest genera in the family, which comprises 113 valid species. Many species from the Black Sea region are still known only from their original descriptions and there are very scarce data about their distribution ranges or ecology. *Tegenaria percuriosa* Brignoli, 1972 and its closest congener are a good example of one of such enigmatic complexes. As already stated by Bolzern et al. (2013), the taxonomy of *T. percuriosa* and its related species is confusing. Brignoli (1972) described *T. percuriosa* from Zindan cave, near Isparta, Turkey. Later he reported the species from two more localities: Haci Akif cave, near Beyşehir and Barla cave, near Barla, Turkey (Brignoli, 1978a). The same year the author described *T. bithyniae* and *T. boitanii*, both from Abant, near Bolu, Turkey (Brignoli, 1978b). Delsheva (1982) reported *Tegenaria pagana* C. L. Koch from two caves in Strandzha Mountain, Bulgaria, but later (Delsheva, 1993), he found out that the record was misidentified and actually concerned *T. bithyniae*. Gasparo (2007) synonymized *T. boitanii* with *T. percuriosa* and redescribed *T. percuriosa* based on both sexes, from the
type locality. Finally, Bolzern et al. (2013) synonymized *T. bithyniae* with *T. percuriosa*. Another faunistic record of *T. percuriosa* was published by Demircan and Topçu (2016). Two more species are close to this complex – *Tegenaria bayrami* Kaya et al., 2010 and *Tegenaria angustipalpis* Levy, 1996.

When identifying spider material from Strandzha Mountain, Bulgaria we found a species of *Tegenaria* in which the female epigyne looked similar to the drawings of *T. bithyniae* by Brignoli (1978b) and Deltshew (1993), but clearly different from those of *T. percuriosa*, provided by Gasparo (2007) from the type locality. The male also had some stable differences from those of *T. percuriosa* which prompted us to re-examine the *T. percuriosa* species complex. The comparison of the morphology confirmed that *T. boitanii* and *T. bithyniae* are conspecific, as suggested by Bolzern et al. (2013), but represent a different species from *T. percuriosa*. Therefore, we remove the two species from synonymy of *T. percuriosa*. *T. boitanii* stat. rev. is restored as a valid species and *T. bithyniae* syn. nov. is regarded as its junior synonym. Also, we describe a new species of the same complex, *Tegenaria euxinica* sp. nov. from the mesophilic beech forests (*Fagus orientalis*) of Strandzha Mountain, South-East Bulgaria. In addition, we investigate the phylogenetic position and internal relationships of the complex by taking advantage of the wealth of DNA sequence data of Agelenidae available from public repositories and the morphological data matrix for the family scored by Bolzern and collaborators (Bolzern et al., 2013). We further update the distribution of the *T. percuriosa* species-complex and propose an evolutionary scenario for its origins and biogeographic history.

### Materials and methods

#### Morphological data

The material is preserved in 80% ethanol. The specimens were examined and measured using Wild M5A stereomicroscope. All measurements are in mm. Photographs were taken with Canon EOS 1100 D digital camera, attached to Carl Zeiss Amplitol microscope. The drawings were made with Wacom tablet and Adobe Illustrator graphic design software. The map is generated through the SimpleMappr API. Colour is described from specimens preserved in ethanol. Female epigynes have been cleared with lactic acid. Leg measurements formula: Total length (coxa + trochanter, femur, patella, tibia, metatarsus, tarsus). Leg spination sequence: femur, tibia, metatarsus. Male palp measurements formula: Total length (femur, patella, tibia, cymbium).

The phylogenetic position of the newly described species was investigated using morphological and molecular data. The morphological data matrix of Agelenidae published by Bolzern et al. (2013) was extended by adding one more character and six additional species. The new character (male embolus width) had 3 states (1. long and thin, with approximately equal thickness along its length; 2. short, thick and truncated apically; 3. wider in 2/3, narrowing the last 1/3). The additional species were: *Tegenaria euxinica* sp. nov., *Tegenaria boitanii* stat. rev., *Tegenaria bayrami*, *Tegenaria lazaroii*, *Tegenaria vallei* and *Tegenaria faniapollinis*. The program Mesquite (Maddison & Maddison, 2019) was used for editing the morphological data matrix.

Abbreviations (in alphabetical order): ALE – anterior lateral eyes, AME – anterior median eyes, C – conductor, CD – copulatory ducts, CO – copulatory openings, d – dorsal, DPC – dorsal part of terminal end of the conductor, DTA – dorsal tibial apophyse, E – embolus, FD – fertilization ducts, LMC – lateral margin of conductor, MA – median apophyse, MPE – median plate of epigyne, pl – prolabial, PLE – posterior lateral eyes, PME – posterior median eyes, PSE – posterior sclerite of epigyne, R – receptacles, rl – retrolateral, RTA – retrolateral tibial apophyse, T – tegulum, TC – terminal end of the conductor, v – ventral.

The material is deposited in the following institutional collections: Museo Civico Scienze Naturali Enrico Caffi, Bergamo, Italy (MBCG); Museo Civico di Storia Naturale, Verona, Italy (MCSN); Muséum d’histoire naturelle de Genève, Switzerland (MHNG); National Museum of Natural History, Sofia, Bulgaria (NMNH); Senckenberg Research Institute, Frankfurt, Germany (SMF).

#### Molecular data

DNA sequences were obtained from two individuals of *Tegenaria euxinica* sp. nov. for two gene fragments, the mitochondrial protein-coding gene cytochrome c oxidase subunit I (COI), and the nuclear ribosomal 28S rRNA (28S), using the primer pairs LCO1490 and HCO12198 (Folmer et al., 1994) and 28S-O (Hedin & Maddison, 2001) and 28S-B (Whiting et al., 1997), respectively. Molecular procedures followed those in Macias-Hernández et al. (2020). Chromatograms were edited and sequences manipulated in Geneious Prime 2021.1.1 (https://www.geneious.com).

The newly generated sequences from *Tegenaria euxinica* sp. nov. were combined with sequences available in GenBank for the family Agelenidae and selected outgroups. The bulk of the sequences retrieved were generated in Bolzern et al. (2013) and complemented
with sequences from Zhao and Li (2017). Available sequences of the mitochondrial protein-coding gene NADH dehydrogenase subunit 1 (ND1) were also included in the analyses. Alignments of the protein-coding genes were trivial as no indel mutation were detected. The 28S was aligned with the online version of MAFFT v. 7 (Katoh et al., 2019) using the G-INS-i algorithm.

Phylogenetic analyses

The morphological data matrix was analysed with parsimony under both equal and implied weights, using the software TNT v. 1.5 (Goloboff et al. 2008). Sensitivity of the results to different values of the concavity constant (k) was assessed by conducting analyses using strong (k = 1), mild (k = 3) and light (k = 6) down-weighting of the homoplasious characters. Analyses were conducted using a heuristic search consisting on 1000 Wagner trees and subsequent TBR branch swapping, holding 10 trees per replicate, up to 10,000 total trees. Node support was assessed by means of Bremer support and jackknifing, using 1000 replicates, under implied weights (k = 3). Additionally, model-based analyses were conducted using Maximum likelihood, as implemented in IQ-TREE v. 2.1.2 (Minh et al., 2020). and Bayesian inference, as in MrBayes v.3.2.6 (Ronquist et al. 2012). The best model for the IQ-TREE analysis was selected using ModelFinder (Kalyaanamoorthy et al., 2017). The Mk model with gamma and correction for variable coding was defined in MrBayes. Node support was assessed by parametric bootstraps (1000 replicates) and posterior probabilities, respectively. All trees were rooted using the amaurobid Amaurobius ferox (Walckenaer, 1830) as outgroup.

Both the concatenated data matrix of the three gene fragments and the combined matrix of the morphological and molecular data were also analysed under parsimony, maximum likelihood and Bayesian inference. For parsimony analyses, all characters were equally weighted and gaps were recoded as absence/presence characters following the simple coding method (Simmons and Ochoterena 2000) as implemented in the computer program SeqState (Müller, 2005). Parsimony search strategy for shortest trees combined sectorial searches, tree fusing, drift and ratchet. Tree searches were driven to hit independently 10 times the optimal scoring, followed by TBR branch swapping, saving up to 1000 trees (Soto et al., 2017). Node support was assessed by jackknifing frequencies derived from 1000 resampled matrices using 20 random addition sequences, retaining 50 trees per replication, followed by TBR, and TBR collapsing to calculate the consensus. Maximum likelihood analyses were conducted as indicated above but assessing the best partition scheme starting by splitting by gene and codon in the case of the protein coding genes and estimating nodal support by means of 1000 replicates of ultrafast bootstrapping (Hoang et al., 2018). For Bayesian analyses, the best partition scheme and evolutionary model was first selected with help of the computer program PartitionFinder v2.1.1 (Lanfear et al., 2017). Analyses were run with MrBayes for 5 million generations, sampling every 1000. Support values were calculated as posterior probabilities. We assessed convergence of the chains, correct mixing and the number of burn-in generations with Tracer v. 1.7 (Rambaut et al., 2018). We ran all model-based analyses remotely at the CIPRES Science Gateway v.3.3 (Müller et al., 2010).

Results

Taxonomy

Agelenidae C. L. Koch, 1837
Tegenaria Latreille, 1804

The Tegenaria percuriosa species-complex consists of T. percuriosa Brignoli, 1972, T. boitanii Brignoli, 1978b stat. rev., T. euxinica Dimitrov sp. nov., T. bayrami Kaya et al., 2010, T. angustipalpis Levy, 1996, T. fanipollinis Brignoli, 1978a, and T. forestieroi Brignoli, 1978a. Males of this complex are characterized by the short thick embolus and the simple conductor with long, narrow base, gradually widening apically. The dorsal part of the conductor is missing. The females have short copulatory ducts (often shaped as a round button), and large, elliptic receptacles.

Tegenaria percuriosa Brignoli, 1972
Figs. 1–2, 7–13, 40–41.

Tegenaria percuriosa Brignoli, 1972: 176, f. 18, 21
Tegenaria percuriosa: Gasparo, 2007: 96, figs 1–8 [part]
Tegenaria percuriosa: Bolzern et al., 2013: 810 [part]

Material examined. 1♀, Zindan mağarası, Isparta, Turkey, 21.05.2007, R. Kaya leg. (from the type locality); 1♀, Kazanpınar mağarası, Bursa, Turkey, 06.06.2009, R. Kaya leg; 1♂♀, Ayvaini mağarası, Bursa, Turkey, 14.10.2012, R. Kaya leg.

Diagnosis. The species fits well in the genus Tegenaria according to Bolzern et al. (2013), judging from the straight trochanters, the absence of dorsal spines on the patellae and the shape of the conductor. It closely resembles T. boitanii stat. rev. and T. euxinica sp. nov.
by (1) the short and wide embolus and the simple narrow conductor in males, (2) the wide receptacles and the short copulatory ducts in females. Differs well by the following set of characters: Male. (1) the shape of conductor, having more narrow and pointed DPC (Figs 7, 42) than *T. percuriosa* (Figs 7, 40) and smaller angle in the LMC than *T. euxinica* sp. nov. (Fig. 44). (2) the shape of MA, wider in its base, gradually narrowing, with slightly curved apical part (Figs 14, 42) vs. twisted and whip-like in *T. percuriosa* (Fig. 40) and much wider and ending with a hook apically in *T. euxinica* sp. nov. (Fig. 44). Female. (3) posterior sclerite wider than long, rectangular, but with rounded edges (Figs 13, 41) vs. oval in *T. boitanii* (Figs 20, 43) and protruding laterally in *T. euxinica* sp. nov. (Figs 30, 45).

**Description.** See Brignoli (1972) and Gasparo (2007).

**Distribution.** Western Anatolia (Fig. 49), in caves.

**Remarks.** The records of *T. percuriosa* from the European part of Turkey by Demircan and Topçu (2016) are doubtful and more likely concern *T. euxinica* sp. nov. They are all from the Turkish part of Strandzha Mountain, from localities very close to the type locality of *T. euxinica* sp. nov. while all the confirmed records of *T. percuriosa* are only from inland Anatolia.

**Tegenaria boitanii** Brignoli, 1978b stat. rev.

Figs 3–4, 14–20, 42–43.

*Tegenaria boitanii* Brignoli, 1978b:518, figs 100–101

*Tegenaria bithyniae* Brignoli, 1978b:515, fig. 97, syn. nov. [misidentification, female of *T. boitanii*]

*Tegenaria percuriosa*: Gasparo, 2007: 96 [misidentification]

*Tegenaria percuriosa*: Bolzern et al., 2013: 810, fig. 17W [misidentification]

**Material examined.** Holotype ♂, Turkey, Bolu vill., Abant, 1400 m asl, 17.07.1971, P. Brignoli & A. Vigna leg; 1 ♀ (holotype of *T. bithyniae*), the same data as holotype; 2 ♀ (paratypes of *T. bithyniae*), the same data as holotype.

**Diagnosis.** The species fits well in the genus *Tegenaria* according to Bolzern et al. (2013), judging from the straight trochanters, the absence of dorsal spines on the patellae and the shape of the conductor. It is most close to *T. percuriosa* and *T. euxinica* sp. nov. but differs well by the following set of characters: Male. (1) The shape of conductor, having more narrow and pointed DPC (Figs 14, 42) than *T. percuriosa* (Figs 7, 40) and smaller angle in the LMC than *T. euxinica* sp. nov. (Fig. 44). (2) The shape of MA, wider in its base, gradually narrowing, with slightly curved apical part (Figs 14, 42) vs. twisted and whip-like in *T. percuriosa* (Fig. 40) and much wider and ending with a hook apically in *T. euxinica* sp. nov. (Fig. 44). Female. (3) The oval posterior sclerite (Figs 20, 43) vs. wider than long and with more irregular shape in the other 2 species (Figs 41, 45).

**Redescription.** Male holotype (Figs 3, 14–16, 42).

Measurements. Total length 6.76; carapace length 3.70,
width 2.80; sternum length 1.75, width 1.60; chelicerae length 1.58, width 0.61; clypeus height 0.2; palp – 6.24 (2.65, 0.61, 1.34, 1.64); eye diameters: AME 0.09, ALE 0.15, PME 0.15, PLE 0.13; abdomen length 3.06, width 1.77; leg I – 18.64 (1.66, 4.05, 1.19, 4.64, 4.57, 2.53), leg II – 16.68 (1.58, 3.95, 1.18, 3.73, 4.01, 2.23), leg III – 14.77 (1.50, 3.57, 1.19, 3.07, 3.87, 1.57), leg IV – 19.00 (1.73, 4.35, 1.12, 4.18, 5.40, 2.22). Spination.

Leg I – 1d 2pl, 2pl 1rl, 3pl 3rl; leg II – 3d12pl 2rl, 2v 2pl, 3pl 3rl; leg III – 5d, 1d 2pl 2rl 1v, 2pl 2rl 4v; leg IV – 3d, 1d 2pl 2rl 3v, 1d 2pl 4rl 3v.

Colouration (Fig. 3). Carapace yellow brown, darker in the eye region, gradually lightening posteriorly, without pattern. Fovea visible as thin brown strip. On each side fovea there are three perpendicular brown stripes.

Femur I brown, all the other leg segments yellowish. Chelicerae brown, the same colour as the eye region. Sternum yellow-brown, with pattern. Palpal segments the same colour as the legs. Abdomen yellowish with brown-grey pattern. Other somatic characters. Chelicerae with 2 promarginal and 4–5 retromarginal teeth. The promarginal teeth positioned near the promarginal base of the cheliceral groove. Retromarginal ones positioned on the whole length. Trochanters straight. Colulus narrow.

Palp (Figs 14–16, 42). Femur and tibia long. The retrolateral tibial apophysis with dorsal and lateral branches. The lateral branch smaller, elliptic. The

Figs. 7–13. T. percuriosa. 7. Male palp, ventral view; 8. Male palp, retrolateral view; 9. Male palp, dorsal view; 10. Epigyne, ventral view; 11. Ibid., cleared; 12. Vulva, dorsal view; 13. Epigyne, posterior view. Scale bar: 0.5 mm.
dorsal one higher, pointed at the end (Figs 15, 16). Embolus short, with wide base, starting approximately at 12 o’clock and ending at 13 o’clock. Conductor with narrow connection to the tegulum, starting from the middle of the bulb, widening apically, ending in pointed ventral part of the terminal end. The distal portion is missing. Lateral margin folded. The median apophysis long with wide base and thin and straight apical part, slightly curved at the end (Figs 14–15, 42).

Female (Figs 4, 17–20, 43). Measurements. Total length 5.09; carapace length 2.46, width 1.65; sternum length 1.27, width 1.12; chelicerae length 1.19, width 0.49; clypeus height 0.18; eye diameters: AME 0.08, ALE 0.12, PME 0.13, PLE 0.12; abdomen length 2.63, width 1.75; leg I – 9.71 (1.08, 2.25, 0.81, 2.18, 1.92, 1.47), leg II – 16.68 (0.97, 2.09, 0.79, 1.76, 1.60, 1.29), leg III – 14.77 (0.95, 1.90, 0.55, 1.55, 1.82, 1.16), leg IV – 19.00 (1.03, 2.45, 0.78, 2.24, 2.57, 1.29). Spination and the other somatic characters as in male.

Colouration as in male but paler (Fig. 4).

Epigyne (Figs 17–18, 20, 43). Median plate not clearly separated from the epigynal plate. Posterior sclerite oval (Figs 20, 43). Copulatory openings situated on both sides of the posterior sclerite. Copulatory ducts shaped as a round button (seen from ventral side, Fig. 18). Vulva (Fig. 19). Receptacles large, elliptic. Fertilization ducts small, ribbon-shaped.
Figs. 21–30. *T. euxinica* sp. nov. 21, 24. 21–23. Male holotype, right palp; 24–26. Male paratype, left palp; 27–30. Female paratype. 21, 24 Palp, ventral view; 22, 25. Palp, retrolateral view; 23, 26. Palp, dorsal view; 27. Epigyne, ventral view; 28. Ibid., cleared; 29. Vulva, dorsal view; 30. Epigyne, posterior view. Scale bar: 0.5 mm.
Distribution. Only known from the type locality – Abant, near Bolu, Turkey.

*Tegenaria euxinica* Dimitrov sp. nov.  
Figs 5–6, 21–39, 44–45.

*Tegenaria pagana*: Deltshev, 1982: 101  
[misidentification]

*Tegenaria bihyniae*: Deltshev, 1993: 168, fig. 1  
[misidentification]

Type material examined. 1♂ holotype, Silkosia reserve, Strandzha mountain, Bulgaria, beech forest (*Fagus orientalis*), GPS 42.0821, 27.7586, 25.05.2020, Dragomir Dimitrov leg. (NMNHS); 1♀ paratype, Silkosia reserve, Strandzha mountain, Bulgaria, beech forest (*Fagus orientalis*), GPS 42.0821, 27.7586, 29.06.2020, Dragomir Dimitrov leg. (NMNHS). 2♂ 1♀ paratypes, Gramatikovo vill., Strandzha Mountain, Bulgaria, 04.08.1999, V. Popov leg. (SMF).

Other material examined. 1♂ 1♀ Bulgaria, Strandzha Mountain, Gramatikovo vill., 11.08.2000, V. Popov leg. (NMNHS). 1♂ Golyamata propast cave, Mladzechko village, 14.08.1976, C. Deltshev leg. (NMNHS), (Deltshev, 1982, 1993); 1♀ Slivarovo village, Strandzha mountain, cave, 21.07.1997, C. Deltshev leg. (NMNHS), (Deltshev, 1982, 1993). The material has been kept for a long time in formaline and the specimens are not in good condition – discoloured and with missing legs, thus not included in the type series.

Etymology. From Euxine (relating to the Black Sea).

Diagnosis. The species fits well in the genus *Tegenaria* according to Bolzern *et al.* (2013), judging from the straight trochanters, the absence of dorsal spines on the patellae and the shape of the conductor. It is most close to *T. percuriosa* and *T. boitani* stat. rev. but can be separated by the following characters: Males (1) The specific shape of the conductor, having LMC bent in sharper angle (Figs 24, 31, 34) than in the other two species (Figs 7, 14, 42, 44); (2) the shape of MA with wider apical and ending in a hook (Figs 24, 31, 34) vs. more narrow in *T. percuriosa* and *T. boitani* stat. rev. (Figs 7, 14); (3) the smaller process at the apical part of the MA (Figs 25, 32, 35), missing in the other two species (Figs 21, 24, 31, 34, 44). In *T. euxinica* sp. nov. MA looks forked from retrolateral view (Figs 22, 25, 32, 35). Female. (4) The posterior sclerite trapezoid, protruding laterally (Figs 30, 39, 45) vs. more oval in the other two species (Figs 41, 43).

Description. Male holotype (Figs 5, 21–26, 31–36, 44). Measurements. Total length 8.25; carapace length 3.75, width 3.05; sternum length 1.95, width 1.80; chelicerae length 1.80, width 0.65; clypeus height 0.25; palp – 7.28 (3.00, 0.75, 1.50, 2.03); eye diameters: AME 0.10, ALE 0.18, PME 0.16, PLE 0.16; abdomen length 4.50, width 2.65; leg I – 22.16 (1.95, 5.25, 1.28, 5.48, 5.50, 2.70), leg II – 19.89 (1.80, 4.88, 1.28, 4.58, 4.80, 2.55), leg III – 15.91 (1.80, 3.75, 1.28, 3.15, 3.75, 2.18), leg IV – 22.81 (1.95, 5.55, 1.28, 5.18, 6.30, 2.55). Spination. Leg I – 3d, 4v 1pl, 4v, leg II – 3d 1rl, 3v 1pl, 1d 2pl 2v, leg III – 4d 1pl, 2d 1pl 1rl 2v, 2d 2pl 2rl, leg IV – 2d, 2d 2pl 2rl 2v, 2d 2pl 2rl. Colouration (Fig. 5). Carapace yellow with 2 broad grey-brown dorsal parallel stripes, starting from the posterior eyerow. In the region of fovea there are three perpendicular stripes of the same colour on each side. The margin of the carapace bordered with brown-grey strip. Legs yellowish, with brown-grey spots and rings. Chelicerae orange with brown-grey spots. Sternum yellow, with brown-grey pattern. Palpal segments the same colour as the legs. Abdomen yellow with brown pattern. Other somatic characters. Chelicerae with 3 promarginal and 5 retromarginal teeth. The promarginal teeth positioned near the cheliceral base. Retromarginal ones positioned on the whole length. Fovea deep, well visible. Trochanters straight. Colulus narrow, notched at the middle.

Palp (Figs 21–26, 31–36, 44). Femur and tibia long. The retrolateral tibial apophysis with dorsal and lateral branches. The lateral branch smaller, elliptic (Figs 22, 25, 32, 35). The dorsal one higher, folded (Figs 21, 24, 34). From retrolateral view it looks pointed (Figs 22, 25, 32, 35). Embolus short and massive, starting with wide base approximately at 12 o’clock and ending in 14 o’clock. Conductor narrow. The connection to the tegulum more wide, narrowing in the middle. Lateral margin very slightly folded. Terminal end pointed. The distal portion is missing. The median apophysis long and wide, slightly narrowing at the middle, widening again apically and ending in a hook. On the ventral side of the apical part there is a small, weakly sclerotized pointed process (Figs 21, 24, 31, 34, 44).

Female paratype (Figs 6, 27–30, 37–39, 45). Measurements. Total length 7.75; carapace length 3.75, width 2.70; sternum length 1.90, width 1.58; chelicerae length 1.80, width 0.65; clypeus height 0.26; eye diameters: AME 0.11, ALE 0.18, PME 0.16, PLE 0.16; abdomen length 4.00, width 2.65; leg I – 16.81 (1.65, 3.83, 1.20, 3.75, 3.38, 3.00), leg II – 14.93 (1.45, 3.38, 1.20, 3.80, 3.15, 1.95), leg III – 13.31 (1.45, 3.15, 1.20, 2.63, 3.15, 1.73), leg IV – 17.05 (1.65, 4.15, 1.2, 3.60, 4.35, 2.10). Spinations as in male. Colouration as in male (Fig. 6). Other somatic characters. Chelicerae with 3 promarginal and 5 retromarginal teeth. The promarginal teeth...
positioned near the cheliceral base. Retromarginal ones positioned on the whole length. Median eyes round, median eyes elliptic. Fovea visible, but not as deep as in male. Trochanters straight. Colulus narrow, notched at the middle.

Epigyne (Figs 27–28, 30, 37, 39). Median plate not clearly separated from the epigynal plate. Posterior sclerite trapezoid, narrow, notched, protruding laterally (Figs 30, 39, 45). Copulatory openings situated on both sides of the posterior sclerite. Copulatory ducts shaped as a round button (seen from ventral side, when lightened; Figs 28, 37). Vulva (Figs 29, 38). Receptacles large, elliptic. Fertilization ducts small, ribbon-shaped.

Distribution. Mesophilic forests and caves in Strandzha mountain, South-East Bulgaria (Fig. 49).

Remarks. The altitude of ~1200 m provided by Deltchev (1993: 168) for the two caves in Strandzha
mountain where the species was collected could not be correct. The highest point in the Bulgarian part of the mountain is Golyamo Gradishte peak (709 m), while the altitude of both Slivarovo and Mladezhko villages and the surrounding areas do not exceed 400 m. The species probably occurs in the European part of Turkey too. The records of *T. percuriosa* by Demircan and Topçu (2016) are more likely to be *T. euxinica* sp. nov. but this needs to be confirmed by examining the material. For now, it is shown on the map as unconfirmed record.

*Tegenaria bayrami* Kaya et al., 2010: 3, figs 1–16

**Material examined.** 1♂, Köprülü Canyon, Beşkonak, Turkey, 08.06.2011, R. Kaya & K. Kunt leg.

**Distribution.** Southern Turkey, Aegean region.

**Remarks.** The species is morphologically close to those of *T. percuriosa* complex, but the male has much longer cymbium, more sclerotized embolus and more thin and sclerotized DPC (Figs 46-47). The DTA is distinctly shorter (Figs 47–48). The longer cymbium is typical to *Tegenaria ariadnae* species-complex. It looks like *T. bayrami* combines features from the two complexes.

**Tegenaria angustipalpis** Levy, 1996

*Tegenaria angustipalpis* Levy, 1996: 107, f. 82–87

**Remarks.** The species is closely related to *T. bayrami* and the male also combines features of both *T. percuriosa* and *T. ariadnae* species-complexes. The female however is distinctly different and in our opinion is not conspecific with the male. Moreover, the two sexes in the type series are collected from different localities and are tentatively considered as a pair by Levy (1996: 107). The female has long and twisted copulatory ducts and small receptacles which is not typical for any of the two groups, mentioned above. Although we could not examine the species, judging from the description and the drawings the female looks closer to *Tegenaria*
The species needs revision in the future and if it confirms that the two sexes are incorrectly matched, the female should be described as a separate species.

**Phylogenetic analyses. Morphological data set (Fig. 50).** The morphological data set included 106 characters scored for 75 terminals. Results of the phylogenetic analyses are summarized in Fig. 50. Analyses of the morphological data set under equally weight parsimony resulted in 37 trees of 596 steps. Analyses under implied weight yielded three trees of 635 steps with $k=1$ (fit = 62.33) and $k=3$ (fit = 46.08), and one tree of 609 with $k=6$ (fit = 33.82). The *percuriosa* species-complex is recovered monophyletic in parsimony analyses under $k=3$ and 1, and in some of the tree under equal weights, albeit with no supports.

Maximum likelihood analysis contradicts this result by considering the *percuriosa* species complex as a grade with regard to the rest of the *Tegenaria* species included with the exception of the *ariadnae* species complex. Internal relationships are not supported except for the sister group relationship of *T. boitani* stat. rev and *T. percuriosa*. Bayesian analyses included members of the *percuriosa* complex in a polytomy at the base of the *Tegenaria* clade. The remaining relationships within Agelenidae mostly mirrored those in Bolzern et al. (2013).

**Molecular dataset (Fig. 51).** Final molecular data matrix included 81 terminals for the three genes analysed. Parsimony analyses with gaps scored as absence/presence characters (62 additional characters) yielded 828
Fig. 50. Strict consensus of the tree fittest trees under implied weights $k = 3$. Support values on branches in numbers correspond to the jackknife support (JS) and Bremer support (BS). Boxes on branches indicate support for analyses under alternative analytical conditions, namely implied weights with $k = 6$ (above, left), implied weights with $k = 1$ (below, left), maximum likelihood (above, middle), Bayesian inference (below, middle) and parsimony under equal weights (right). For parsimony analyses, black indicates that the clade was recovered, while for model-based analyses black denotes support $>0.95$ and $>75$ for PP, ML-BS, respectively and grey indicates clade recovered but below former threshold values. In all cases, white indicates the clade was not retrieved in this analysis. Specimens newly scored in the present study in bold.
Review and new species of funnel web spider
trees of 6041 steps. All analyses agreed in supporting members of the percuriosa species-complex as part of a larger clade consisting of species from the Black Sea, Anatolia and the Aegean, most of them members of the ariadnae species-complex. Model-based analyses further supported this clade, hereafter referred as the percuriosa/ariadnae clade to be sister to T. domestica and both groups in turn sister to the remaining Tegenaria species analysed. The remaining relationships within Agelenidae mostly mirrored those in Bolzern et al. (2013).

Combined data set (Fig. 52). Final combined data matrix included 107 terminals for the three genes and the morphological data set analysed. Parsimony analyses with gaps scored as absence/presence characters yielded 1,152 trees of 6687 steps. All analyses recovered the clade including members of the percuriosa and ariadnae species complexes, albeit with no support. Similarly, they also agreed in considering percuriosa as paraphyletic with regard to the ariadnae species complex, although with different arrangements. Surprisingly, the species T. racovitza Simon, 1907, which was only scored for morphology, was also included in the clade, although neither overall morphology nor biogeography seem to support this result. The model-based combined analyses agreed with molecular analyses in considering T. domestica, and its sister species T. rhodiensis, sister to the percuriosa/ariadnae clade, albeit with no support, and both lineages in turn to be sister to the remaining Tegenaria species. The remaining relationships within Agelenidae, mostly mirrored those in Bolzern et al. (2013).

Discussion

Although morphological data (Fig. 50) recovered monophyly of the T. percuriosa complex under some weighting schemes albeit with no support, both the molecular and combined analyses (Figs 51–52) agreed that the T. ariadnae complex renders T. percuriosa complex paraphyletic. This may suggest that some of the putative diagnostic characters of the complex (e.g. the short and thick embolus) are plesiomorphic for the clade. In fact, the Mediterranean species of the percuriosa complex — T. bayrami, T. faniapollinis and T. angustipalpis – share morphological features with the ariadnae complex too (e.g. the longer cymbium), which support the latter suggestion. Potential synapomorphies for the percuriosa/ariadnae clade would include the shape of the conductor in males and the large elliptical receptacles in females.

The T. percuriosa complex comprises species distributed around the southwestern Black Sea coastal areas, inland western Anatolia and coastal areas of south-eastern Greece, southern Anatolia and the Levant. The Black Sea species inhabit the mesophilic deciduous forests, while the ones from inland Anatolia and the Mediterranean are found mostly in caves. Similarly, all the species of the T. ariadnae complex, which is circumscribed to Crete, coastal localities in southern Anatolia and Libya (Dimitrov, 2020, fig. 19), are known from caves. The distribution patterns strongly support a preference of the percuriosa/ariadnae clade for humid and secluded habitats, which in combination with the narrow distributional ranges of the species may point to the key role of climatic changes in shaping present-day diversity and distribution patterns of this group.

Following the Miocene Climatic Optimum (MCO) (17–15 My), which interrupted long-term Cenozoic cooling (Methner et al., 2020), climatic conditions in Anatolia, the whole Levantine region and even on a global scale rapidly changed. The Miocene Climatic transition (14.7–13.8 Ma), and succeeding phases, were characterized by a gradual cooling and a change in the rainfall seasonality. Specifically, in Anatolia these climatic changes resulted in an increase in open habitats (Bouchal et al., 2018). Interestingly, analyses involving molecules and evolutionary models recovered close affinities of the percuriosa/ariadnae clade to T. domestica (Clerck, 1757). The latter species is cosmopolitan, but the fact that (1) T. rhodiensis Caporiacco, 1948, from Greece and Turkey, was recovered as sister to it and (2) its closest known relative, Tegenaria adomestica Guseinov et al., 2005 (not analysed here), is known from Azerbaijan, may hint to an eastern origin of the whole clade. T. domestica shares the same short, thick and truncated embolus with the fossil species T. obtusa Wunderlich, 2004, which was described from the Baltic

Fig. 51. Majority rule consensus tree of the Bayesian inference of the concatenated molecular only data. Dots at specimen labels indicate if the 28S, COI and ND1 were sequenced for the specimen (black) or not (white), respectively. Pie charts on branches denote support for the specific clade as follows: upper left slice is posterior probability (BI-PP); upper right is maximum likelihood ultrafast bootstraps (ML-ufBS) and lower slice is parsimony jackknifing (MP-JS). Black indicates support $>0.95$, $>0.95$ and $>0.75$ for PP, ML-ufBS and MP-JS, respectively, grey indicates clade recovered but below former threshold values, white indicates the clade was not retrieved in this analysis. In the case of MP, because of the large number of equally parsimonious trees recovered, not all trees were inspected, which may have resulted in clades being considered as not recovered when they were present among some of the most parsimonious trees. Outgroups are indicated in grey. Specimens added in the present study are in bold.
Amber, dated about 43–47.8 million years ago (My) (Ritzkowski, 1997). If the inferred relationships hold true, the origins of the *percuriosa/ariadnae* clade and its presence in the region would trace back at least to the Eocene. With the data at hand, we could speculate that as the result of the cooling and increasing rainfall seasonality during the middle Miocene, the ancestors of the *percuriosa/ariadnae* clade were forced to migrate either north to the Black Sea or south to the Mediterranean, which would have resulted in the split of the extant lineages and the subsequent relictualization of their distributions, following the remanent of the mesophilic deciduous forests at the north or caves at the south or inland western Anatolia. Subsequently, Quaternary glacial cycles would have further contributed to the separation of the extant species, as for example those distributed around the Black Sea – *T. boitanii* stat. rev. and *T. euxinica* sp. nov.

Incidentally, we consider the position of the cave-dwelling *T. racovitzai* within the *percuriosa-ariadnae* clade in the combined analyses (Fig. 52) as dubious, and probably due to the lack of data. It is a western Mediterranean species with quite different genital morphology. According to the present analyses, it shares with the other species in the clade mostly the colour pattern, which is usually convergently reduced in the cave species and therefore not reliable. Sequencing this species in the future will help in finding its correct phylogenetic relationships.

In conclusion, the species discussed in the present study provide an interesting study system for understanding the role of climatic changes in the origin, diversification and, in some cases, relictualization of the fauna from the eastern Mediterranean, the Black Sea region and the Near East. A more thorough, better supported and time-informed phylogeny is required to further test the evolutionary scenario here proposed. Specifically, we could only include DNA sequences for two out of the six species of the *T. percuriosa* complex. Sequencing the Western Mediterranean *T. racovitzai* and extending the sampling to include information of some other related eastern species like *Tegenaria longimana* Simon, 1898 and its relatives will help to delimit the clade and confirm its circumscription to the eastern-most part of the distribution of the genus.

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**Supplemental material**

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**Fig. 52.** Majority rule consensus tree of the Bayesian inference of the combined (morphology + concatenated molecular) data. Diamonds on specimen labels indicate if morphology was scored (black) or not (white), and dots if the 28S, COI and ND1 were sequenced for the specimen (black) or not (white), respectively. Pie charts on branches denote support for the specific clade as follows: upper left slice is posterior probability (BI-PP); upper right is maximum likelihood ultrafast bootstraps (ML-ufBS) and lower slice is parsimony jackknifing (MP-JS). Black indicates support >0.95, >95 and >75 for PP, ML-ufBS and MP-JS, respectively, grey indicates clade recovered but below former threshold values, white indicates the clade was not retrieved in this particular analysis. In the case of MP, because of the large number of equally parsimonious trees recovered, not all trees were inspected, which may have resulted in clades being considered as not recovered when they were present among some of the most parsimonious trees. Outgroups are indicated in grey. Specimens added in the present study are in bold.
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