International Journal for Parasitology xxx (xxxx) xxx

Contents lists available at ScienceDirect

International Journal for Parasitology

journal homepage: www.elsevier.com/locate/ijpara

Updates on subgenus *Ixodes* in the Mediterranean region: validity of *Ixodes festai* Rondelli, 1926, reinstatement of *Ixodes tatei* Arthur, 1959, and a new species closely related to *Ixodes gibbosus* Nuttall, 1916

Sándor Hornok [a,b,*], Adem Keskin [c], Igor Uspensky [d], Jenő Kontschán [e,f], Nóra Takács [a,b], Paulina Lesiczka [g], Tim Warbroek [g], Tijs J.M. van den Bosch [g], Gergő Keve [a,b], Andor Pitó [a,b], Attila D. Sándor [a,b,h]

[a] Department of Parasitology and Zoology, University of Veterinary Medicine, Budapest, Hungary
[b] HUN-REN UVMB Climate Change: New Blood-sucking Parasites and Vector-borne Pathogens Research Group, Budapest, Hungary
[c] Department of Biology, Faculty of Science and Art, Tokat Gaziosmanpaşa University, Tokat, Türkiye
[d] Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Israel
[e] Plant Protection Institute, Hungarian Research Network (HUN-REN) Centre for Agricultural Research, Budapest, Hungary
[f] Department of Plant Sciences, Albert Kázmér Faculty of Mosonmagyaróvár, Széchenyi István University, Mosonmagyaróvár, Hungary
[g] NVWA - Centrum Monitoring Vectoren, Wageningen, the Netherlands
[h] STAR-UBB Institute, Babes-Bolyai University, Cluj-Napoca, Romania

ARTICLE INFO

Article history:
Received 26 April 2025
Received in revised form 9 September 2025
Accepted 18 September 2025
Available online xxxx

Keywords:
Prostriata
Taxonomy
Morphology
Phylogeny
Cox1
16S rRNA

ABSTRACT

The southern part of Europe is one of the most species-rich regions from the point of view of the genus and subgenus *Ixodes*. However, numerous unresolved or questionably interpreted issues exist in the context of tick species indigenous to Mediterranean countries, such as the validity of *Ixodes festai*, synonymy of *Ixodes tatei* with *Ixodes eldaricus* (never tested molecularly) or the haplotype heterogeneity of *Ixodes gibbosus*. In this study, 21 specimens of six tick species from the subgenus *Ixodes* were compared morphologically with high resolution digital microscopy and also analyzed with molecular-phylogenetic methods based on two mitochondrial genetic markers. The nymphs of *I. eldaricus* and *I. tatei* showed differences in the morphology of the scutum and basis capituli. Both the nymph and the females of *I. festai* could be distinguished from those of *I. eldaricus*, *I. ventalloi* and *I. acuminatus*. A female tick resembled *I. gibbosus* but was also different from this species, based on its descriptions. Analysis of phylogenetic relationships confirmed with moderate to strong support that all six species examined in this study represent different taxa of the subgenus *Ixodes*, including a previously unknown sister species to *I. gibbosus*. The latter is recognized and described here as a new species, *Ixodes paragibbosus* Hornok and Kontschán, sp. nov. Based on findings of this study, the tick species *I. tatei* Arthur, 1959 should be resurrected and reestablished. Morphological and phylogenetic comparisons performed here (including the first barcoding sequences of *I. eldaricus* and *I. festai*) confirm that the latter is a valid species, distinct from both *I. eldaricus* and *I. ventalloi*. For the differential diagnosis of the above species, the results highlight the importance of observing (among other structures) the auriculae, the internal spur of coxa I and the hypostome.

1. Introduction

Among hard tick (Acari: Ixodidae) genera, the genus *Ixodes* includes the highest number, i.e. more than one third of all species, approximately 285 (Mumcuoglu et al., 2025). Within the genus *Ixodes*, in the Palearctic Zoogeographic Region, the largest subgenus is *Ixodes*, with over 20 species (Guglielmone et al., 2023). In the European part of the Western Palearctic, the number of indigenous species from the subgenus *Ixodes* tends to increase from the north to the south: in Scandinavia and the Baltic states, two members of the *Ixodes ricinus* complex, *I. ricinus* and *Ixodes persulcatus*, as well as *Ixodes apronophorus* occur, in Central Europe further two species (*Ixodes acuminatus*, *Ixodes laguri*), whereas in Southern Europe (Mediterranean Basin), which lacks *I. persulcatus*, an additional four species are indigenous.

Considering the latter, (1) *Ixodes ventalloi* has a western-central Mediterranean distribution, (2) *Ixodes festai* has a similar geographical range, while (3) *Ixodes gibbosus* is restricted to the

* Corresponding author at: Department of Parasitology and Zoology, University of Veterinary Medicine, Budapest, Hungary.
E-mail address: hornok.sandor@univet.hu (S. Hornok).

https://doi.org/10.1016/j.ijpara.2025.09.002

Please cite this article as: Sándor Hornok, A. Keskin, I. Uspensky et al., Updates on subgenus *Ixodes* in the Mediterranean region: validity of *Ixodes festai* Rondelli, 1926, reinstatement of *Ixodes tatei* Arthur, 1959, and a new species closely related to *Ixodes gibbosus* Nuttall, 1916, International Journal for Parasitology, https://doi.org/10.1016/j.ijpara.2025.09.002

central-eastern Mediterranean countries and (4) *Ixodes eldaricus* can be found in the latter region, extending its occurrence well into the Middle East and central Asia (Guglielmone et al., 2023). However, it is virtually impossible to assign these species to any zoogeographic region, if there are unresolved issues in their taxonomy. In particular, it is widely acclaimed that the name *Ixodes tatei*, under which Arthur discovered and described a new species (Arthur, 1959; 1968) is a junior synonym of *I. eldaricus* (Filippova, 1977; Camicas et al., 1998; Guglielmone et al., 2014). By contrast, despite opinions that *I. ventalloi* should be synonymized with *I. festai* (Arthur, 1961), these two are considered valid, as not only their morphology but their host ranges are also different (Guglielmone et al., 2014; Hornok et al., 2016; Estrada-Peña et al., 2018). Both species were morphologically compared, redescribed and adequately illustrated (Gilot and Perez, 1978).

This study was initiated with the primary aim of clarifying the above uncertainties in the taxonomy of subgenus *Ixodes* in the Mediterranean region. More specifically, it was within the scope of this study to compensate for scarcity of data regarding the following aspects. (1) The morphology of all stages of *I. ventalloi* (Estrada-Peña et al., 2018), and of the male of *I. festai* (Contini et al., 2011) was studied and illustrated with pictures in detail, but key characters of the female and nymph of the latter have not been reported in English or based on high resolution digital photography. (2) The barcoding (*cox1*: cytochrome *c* oxidase subunit I) gene sequence of *I. festai* was never reported, probably because the so-called Folmer primers do not amplify it (Hornok et al., 2016). (3) No *bona fide* mitochondrial sequences of *I. eldaricus* are available in GenBank, particularly not with contemporaneous morphological comparison with other closely related species from its geographical region. Last but not least, (4) based on its 16S rRNA sequence, highly divergent haplotypes of *I. gibbosus* were shown to exist but morphologically these could not have been compared (Hoffman et al., 2020).

2. Materials and methods

2.1. Sample collection and morphological identification of tick species

In this study, 21 *Ixodes* spp. tick specimens were analyzed morphologically and molecularly. These samples were collected from birds, rodents or from the vegetation between 2013–2024 in the Mediterranean region (Israel, Türkiye) and the southern part of central-eastern Europe (Hungary, Romania) (Table 1). The ticks were stored in 96 % ethanol until usage. Tick species were morphologically identified using the best available keys according to their species (for all *Ixodes* species: Estrada-Peña et al., 2017a; for *I. eldaricus*: Filippova, 1974; for *I. festai* females: Gilot and Perez, 1978, Contini et al., 2011; for *I. tatei* nymph: Arthur, 1959 and 1968; for *I. gibbosus* female and nymph: Nuttall, 1916; Saratsiotis, 1970). The nymph of *I. festai* was identified based on its up to 99.1 % (418/422 bp) 16S rRNA gene sequence identity to females of this species. *Ixodes acuminatus* was included only in the illustrations and phylogenetic analyses on account of its morphological similarities to *Ixodes* species studied here. Pictures were made with a Keyence VHX-5000 digital microscope (Osaka, Japan).

2.2. DNA extraction and molecular-phylogenetic analyses

DNA was extracted with the QIAamp DNA Mini Kit (QIAGEN, Hilden, Germany), including an overnight digestion in tissue lysis buffer and Proteinase K at 56 °C. Molecular-phylogenetic relationships were analyzed based on two mitochondrial genetic markers. First, amplification of an approx. 710-bp-long fragment of the cytochrome *c* oxidase subunit I (*cox1*) barcoding gene was attempted with the primer pairs LCO1490 (5′- GGT CAA CAA ATC ATA AAG ATA TTG G –3′) and HCO2198 (5′ – TAA ACT TCA GGG TGA CCA AAA AAT CA- 3′) (Folmer et al. 1994). Samples not yielding PCR product in this test were analyzed further with other primer pairs designed to amplify 680- to 850-bp-long fragments of the same region of this gene (Table 2). As the second genetic marker, an approx. 460-bp-long fragment of the 16S rDNA gene of Ixodidae was also amplified with the primers 16S + 1 (5′-CTG CTC AAT GAT TTT TTA AAT TGC TGT GG-3′) and 16S-1 (5′-CCG GTC TGA ACT CAG ATC AAG T-3′) (Black and Piesman, 1994). Cycling conditions of these PCRs are summarized in Table 2. PCR reaction components included 5 µl of extracted DNA, added to 20 µl of reaction mixture containing 1 U HotStar Taq Plus DNA Polymerase (5U/µl) (QIAGEN, Hilden, Germany), 0.5 µl dNTP Mix (10 mM), 0.5 µl of each primer (50 µM), 2.5 µl of 10x Coral Load PCR buffer (15 mM $MgCl_2$ included) and 15.8 µl PCR water. PCR products were visualized on a 1.5 % agarose gel.

Purification and sequencing of the PCR products in one direction were done by Eurofins Biomi Ltd. (Gödöllő, Hungary). Quality control and trimming of sequences were performed with the BioEdit program. Obtained sequences were compared to GenBank data by the nucleotide BLASTN program (https://blast.ncbi.nlm.nih.gov). For the phylogenetic analyses, only sequences with high (98–100 %) coverage to sequences from this study were retrieved. Phylogenetic trees were constructed with the Neighbor-Joining method, p-distance model in MEGA11 (Tamura et al., 2021), and sequence datasets were resampled 1,000 times to generate bootstrap values.

2.3. Data accessibility

New sequences were submitted to GenBank under the following accession numbers (*cox*1 gene: PV274492-PV274501, 16S rRNA gene: PV277790-PV277808). Alignment data were deposited in MendeleyData (https://doi.org/10.17632/cyjw6f98c7.1).

3. Results

3.1. Morphological identification of tick species

The most important characters are summarized in Supplementary Table 1. Males of *I. eldaricus* were identified based on the hairy, anteriorly dark conscutum, the caudolaterally pointing cornuae and long (>100 µm) dorsal hair on palpal segment II and trochanter I (Supplementary Fig. 1). Females of this species had 1.5x longer than broad scutum, laterally directed broad and blunt auriculae with caudal corner, laterally curving short internal spur on coxa I (directed towards but not reaching above coxa II), and wavy sides of basis capituli (Fig. 1). Nymphs of *I. eldaricus* showed straight cervical grooves, carinae and sparse punctuation on the posteriorly obtuse-angled scutum, caudolateral concavity of scutal margin directly behind maximum width, few pores and caudolaterally directed cornuae on the basis capituli, and caudally directed, at their tip perpendicular-angled short auriculae and hypostome bearing 2/2 dentition except the anterior third with 3/3 formula (Fig. 2). The nymph of *I. tatei* had curved cervical grooves, very sparse punctuation on the posteriorly rounded scutum, caudolateral concavity of scutal margin at mid-length behind maximum width, caudolaterally directed cornuae on the basis capituli, caudally directed acute-angled prominent auriculae and hypostome bearing 2/2 dentition except the anterior quarter with 3/3 formula (Fig. 3). Females of *I. festai* were identified based on the well-defined, relatively straight cervical grooves, long (>100 µm) hair covering and caudolateral shallow concavity of the scutum; large, compartmented porose areas with narrow (50 µm) interval,

Table 1
Data of tick specimens used in this study.

Tick species	Sex or stage	Country of collection (location, sample code)	Date of collection (D.M.Y)	Origin		Cox1/16S PCR (DNA) code	GenBank accession number of ... gene	
				Environ.	Host		Cox1	16S rRNA
Ixodes eldaricus	male	Israel (Judean Mountains	05.03.2021	X	–	B/D (ELD1)	PV274492	PV277790
	male	20 km west of Jerusalem, 105875)	05.03.2021	X	–	B/D (ELD2)	PV274493	PV277791
	female		05.03.2021	X	–	ns/D (ELD3)	–	PV277792
	female		05.03.2021	X	–	ns/D (ELD4)	–	PV277792
	nymph		05.03.2021	X	–	ns/D (ELD5)	–	PV277793
	nymph		05.03.2021	X	–	ns/D (ELD6)	–	PV277794
Ixodes tatei	nymph	Türkiye (Kızılırmak Delta)	02.04.2016	–	*Turdus merula*	ns/ns (ELD7)	–	–
	nymph	Türkiye (Kızılırmak Delta)	02.04.2016	–	*Turdus merula*	ns/D (ELD8)	–	PV277795
Ixodes acuminatus	male	Hungary (Szeged)	21.10.2024	X	–	A/D (ELD19)	PV274499	PV277806
	female	Hungary (Nyirkai-Hany, PA9)	28.04.2021	–	*Locustella luscinioides*	A/D (ELD16)	PV274498	PV277805
	nymph	Türkiye (Kızılırmak Delta)	16.01.2016	–	*Crocidura suaveolens*	ns/D (ELD9)	–	PV277796
	nymph	Türkiye (Kızılırmak Delta)	16.01.2016	–	*Crocidura suaveolens*	ns/D (ELD10)	–	PV277797
Ixodes festai	nymph	Hungary (Ócsa, 1456)	30.03.2014	–	*Prunella modularis*	ns/D (ELD14)	–	PV277801
	female	Türkiye (Kızılırmak Delta)	04.04.2016	–	*Turdus merula*	ns/D (ELD11)	–	PV277798
	female	Hungary (Ócsa, HS404)	11.07.2019	–	*Acrocephalus arundinaceus*	C/D (ELD12)	PV274494	PV277799
	female	Hungary (Ócsa, 1456)	30.03.2014	–	*Prunella modularis*	B/D (ELD13)	PV274495	PV277800
	female	Hungary (Ócsa, A45)	21.03.2014	–	*Chloris chloris*	ns/D (ELD15)	–	PV277802
	female	Hungary (Sumony, PA229)	22.03.2023	–	*Prunella modularis*	A/D (ELD17)	PV274496	PV277803
	female	Romania (Agigea, 105206)	17.04.2019	–	*Turdus merula*	A/D (ELD18)	PV274497	PV277804
Ixodes paragibbosus sp. nov.	female	Greece (Naxos, 04.2013/57)	07.04.2013	X	–	A/D (Ixin-1)	PV274500	PV277807
Ixodes gibbosus	nymph	Greece (Naxos, Apiranthos, 04.2013/56)	07.04.2013	X	–	A/D (Ixin-2)	PV274501	PV277808

Abbreviations: environ. – environment; ns – PCR amplification was not successful.

Table 2
Oligonucleotide sequences and cycle parameters of taxonomic PCRs used in this study.

PCR code	Target gene	Amplicon length (bp)	Primers (5′-3′)	Cycling conditions						Reference
				initial denaturation	denaturation	annealing	extension	final extension	Number of cycles	
A	**cox1**	710	LCO1490 (GGT CAA CAA ATC ATA AAG ATA TTG G) HCO2198 (TAA ACT TCA GGG TGA CCA AAA AAT CA)	95 °C, 5 m	94 °C, 40 s	48 °C, 1 m	72 °C, 1 m	72 °C, 10 m	40	Folmer et al., 1994
B	**cox1**	850	HCO2064-fw (GGT GGG CTC ATA CAA TAA ATC C) HCO1240-rev (CCA CAA ATC ATA AAG ACA TTG G)	95 °C, 5 m	94 °C, 40 s	48 °C, 1 m	72 °C, 1 m	72 °C, 10 m	40	Kwak et al., 2017
C	**cox1**	680	C1-J-1718 (GGA GGA TTT GGA AAT TGA TTA GTT CC) C1-N-2329 (ACT GTA AAT ATA TGA TGA GCT CA)	95 °C, 5 m	94 °C, 40 s	42 °C, 1 m	72 °C, 1 m	72 °C, 10 m	40	Shao et al., 2001
D	**16S rRNA**	460	16S + 1 (CTG CTC AAT GAT TTT TTA AAT TGC TGT GG) 16S-1 (CCG GTC TGA ACT CAG ATC AAG T)	95 °C, 5 m	94 °C, 40 s	51 °C, 1 m	72 °C, 1 m	72 °C, 10 m	40	Black and Piesman, 1994

short cornuae, palps broadest behind the junction of segments II-III, caudally directed, curved and sharply pointed auriculae, straight internal spur on coxa I, and large goblets in three concentric rows on the spiracular plate (Figs. 4 and 5). The nymph of this species had prominent, caudally directed cornuae, scutum similar to that of female except having short hair (20–40 μm), and rounded auriculae (Fig. 6). The male of *I. acuminatus* had well-developed cornuae, internal spur on coxae I-III, and the nymph 2/2 dentition along the full length of hypostome, and internal spur on coxae I-III (Supplementary Fig. 2) as in the case of female. The nymph of *I. gibbosus* had scattered, deep scutal punctuation, caudolaterally directed, lobe-like cornuae, long (80 μm) medial hair on palpal segment II, long oval hypostome broadest at mid-length, broad and dark auricular ridge, medially straight internal spur on coxa I and obtuse-angled subterminal bump on tarsus I (Fig. 7). Another female tick resembled *I. gibbosus*, but its scutum had dense punctuations and wavy carinae, broad (100 μm) interval between porose areas, mace-shape hypostome broadest at anterior fourth of length, slightly curved internal spur on coxa I, round spiracular plate, as well as ball-like terminal thickening, perpendicular-angled subterminal hump and high (nearly 20) number of ventral hairs on tarsus I (Fig. 8), and 13 ventral hairs on tarsus IV (Supplementary Fig. 3). Owing to these differences from *I. gibbosus*, this specimen is described below as a new species.

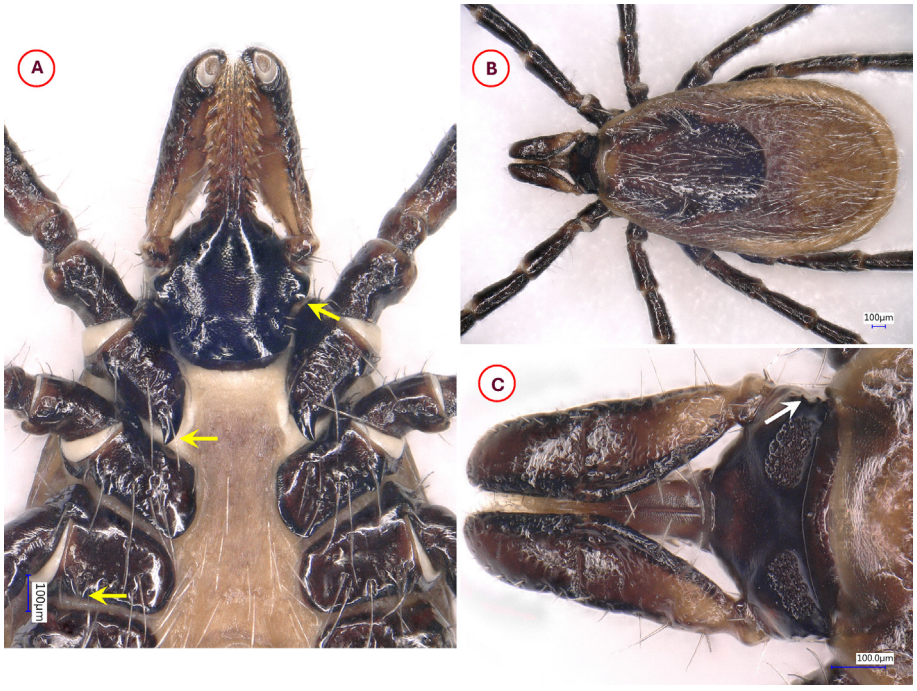

Fig. 1. Morphological characters of *Ixodes eldaricus* female: (A) ventral view (yellow arrow: coxal spurs, white arrow: auricula); (B) habitus, dorsal view; (C) dorsal view of gnathosoma (arrow: wavy sides of basis capituli). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

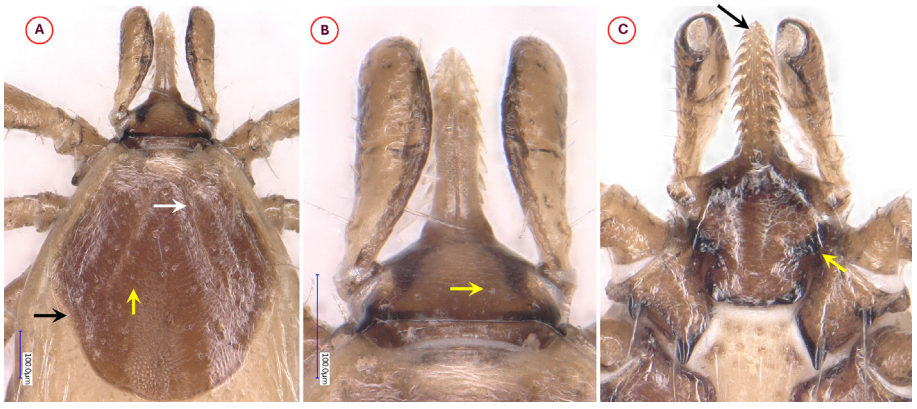

Fig. 2. Morphological characters of *Ixodes eldaricus* nymph: (A) dorsal view of gnathosoma and scutum (yellow arrow: punctuation, black arrow: caudolateral concavity of scutal margin, white arrow: cervical groove); (B) dorsal view of gnathosoma (arrow: pores); (C) ventral view of gnathosoma and coxae I (yellow arrow: auricula, black arrow: tip of hypostome). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Deposition of a neotype and a paraneotype of I. festai

Given the poor condition of the holotype of *I. festai*, one female and the nymph (shown on Figs. 5 and 6) were deposited as neotype and paraneotype, respectively, at the tick collection of the University of Veterinary Medicine, Budapest, Hungary (accession numbers UNIVET-PAR-HS801, UNIVET-PAR-HS802, respectively). The female was collected in Türkiye (Kızılırmak, coordinates: 41°36′ N, 36°05′E) from Common Blackbird (*Turdus merula*) in 2016 (exact date unknown). The nymph was collected in Hungary by bird ringers (Ócsa, coordinates: 47°17′46″N 19°12′35″E) from Dunnock (*Prunella modularis*) on March 30, 2014.

3.3. Molecular-phylogenetic analyses of ticks

All except one tick yielded at least one mitochondrial gene sequence (Table 1). Considering the *cox1* gene, sequences were only amplified successfully from two (male) specimens of *I. eldaricus*, and these showed 99 % (792/800 bp) identity. One of them (PV274493) had the closest, but only 95.1 % (625/657 bp) identity to an *I. ventalloi cox1* sequence available in GenBank (PP047817). Four *I. festai* specimens yielded *cox1* sequence, and these had 97.6 % (638/654 bp) to 100 % *cox1* sequence identities to each other. The closest match to *I. festai* from Hungary (PV274494) was *I. ventalloi* reported in GenBank (OR392440) from a cat sampled in Portugal, having up to 95.5 % (651/682 bp) identity with this species. The nymph of *I. gibbosus* used in this study showed the highest, but only 93.6 % (612/654 bp) *cox1* sequence identity with two specimens reported under this name from Türkiye (MT308590, MT308591). On the other hand, the female tick of the new species had 99.4 % (650/654 bp) sequence identity to the latter.

In the amplified part of the 16S rRNA gene, five specimens of *I. eldaricus* were only 95.9 % (398/415 bp) to 97.6 % (403/413 bp)

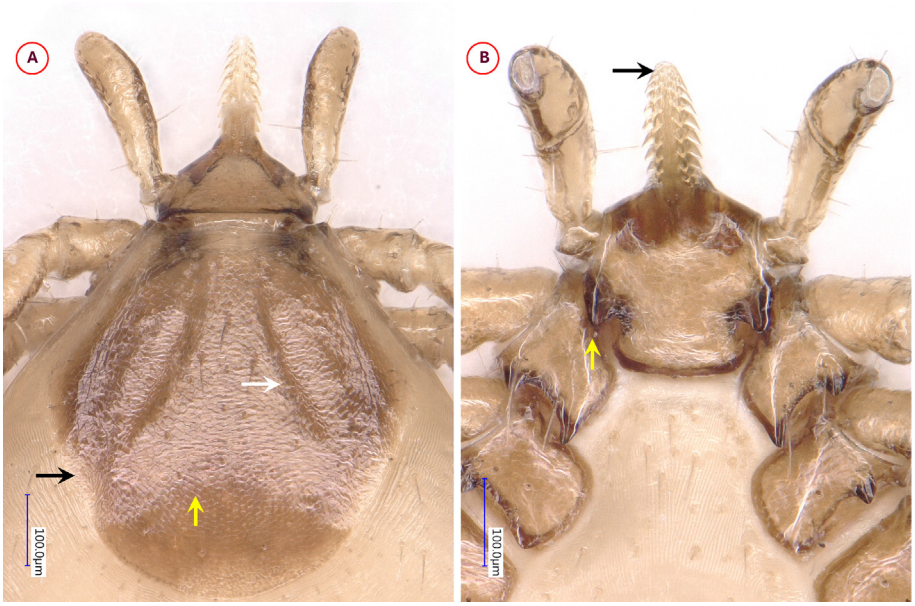

Fig. 3. Morphological characters of *Ixodes tatei* nymph: (A) dorsal view of gnathosoma and scutum (yellow arrow: punctuation, black arrow: caudolateral concavity of scutal margin, white arrow: cervical groove); (B) ventral view of gnathosoma and coxae I-II (yellow arrow: auricula, black arrow: tip of hypostome). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

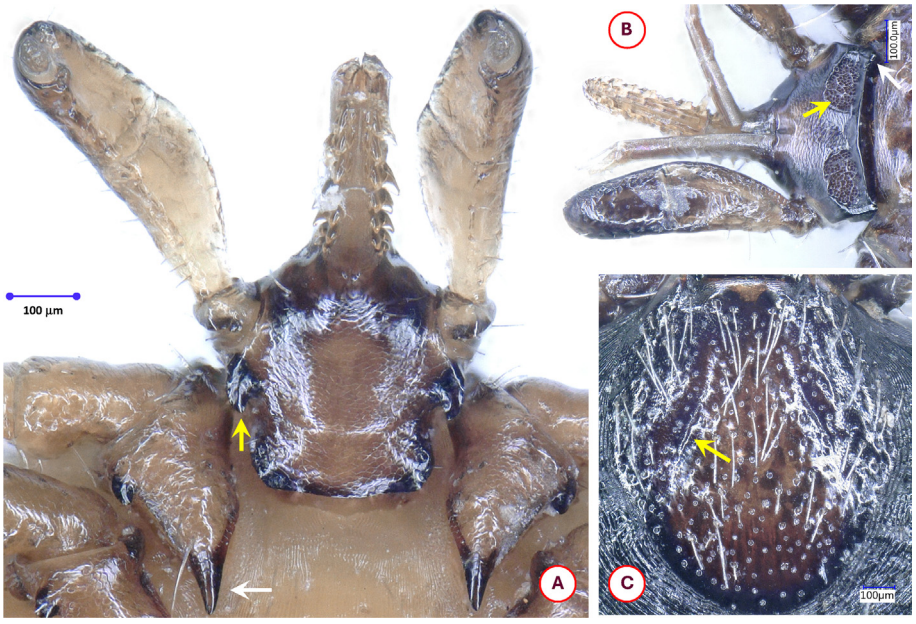

Fig. 4. Morphological characters of *Ixodes festai* female collected in Hungary: (A) ventral view of gnathosoma and coxae I (white arrow: coxal spurs, yellow arrow: auricula); (B) dorsal view of gnathosoma (white arrow: cornua, yellow arrow: compartmented porose area); (C) scutum (arrow: cervical groove). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

identical to each other. The closest match of *I. tatei* reported here (PV277795) to another tick species in GenBank was *I. ventalloi* from Portugal (LC508333) showing 96.4 % (396/411 bp) 16S rRNA gene sequence identity. Corresponding sequences of *I. festai* had 96.9 % (410/423 bp) to 100 % identity to each other, and 96 % (405/422 bp) to 96.7 % (408/422 bp) sequence identities to the neotype of *I. ventalloi* (KY231931). The most significant difference was observed between *I. festai* specimens collected in Türkiye (PV277798) and Romania (PV277804). In the compared part of their 16S rRNA gene, *I. gibbosus* (PV277808) and the closely related new species (PV277807) showed only 95.5 % (399/418 bp) sequence identity to each other.

Based on the phylogenetic analysis of the *cox1* gene, *I. festai* and *I. ventalloi* are sister species with moderate (74 %) support. These two species form a sister group to *I. eldaricus* with high (100 %) support (Fig. 9). In turn, the phylogenetic analysis of the 16S rRNA gene showed that these three species belong to a sister group of *I. tatei*, this relationship also receiving high (100 %) support. The topology of the 16S RNA phylogenetic tree reflected that despite the high genetic heterogeneity (0–3.1 % sequence divergence) within *I. festai*, its morphologically identified specimens, i.e., conspecific sequences clustered together but separately from *I. ventalloi* reported from mammals in Spain, with moderate (63 %) support (Fig. 10). The separation of *I. gibbosus* and the closely related new

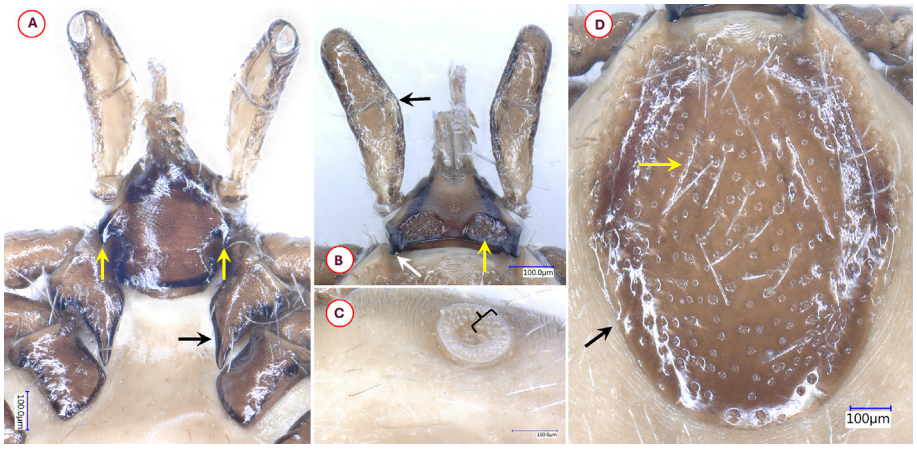

Fig. 5. Morphological characters of *Ixodes festai* female collected in Türkiye: (A) ventral view of basis capituli, palps and coxae I-II (black arrow: coxal spur, yellow arrow: auricula); (B) dorsal view of gnathosoma (white arrow: cornua, yellow arrow: compartmented porose area, black arrow: broadest part of palpal segment II); (C) spiracular plate (curly bracket: three rows of internal, large goblets); (D) scutum (yellow arrow: cervical groove; black arrow: caudolateral margin of scutum). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

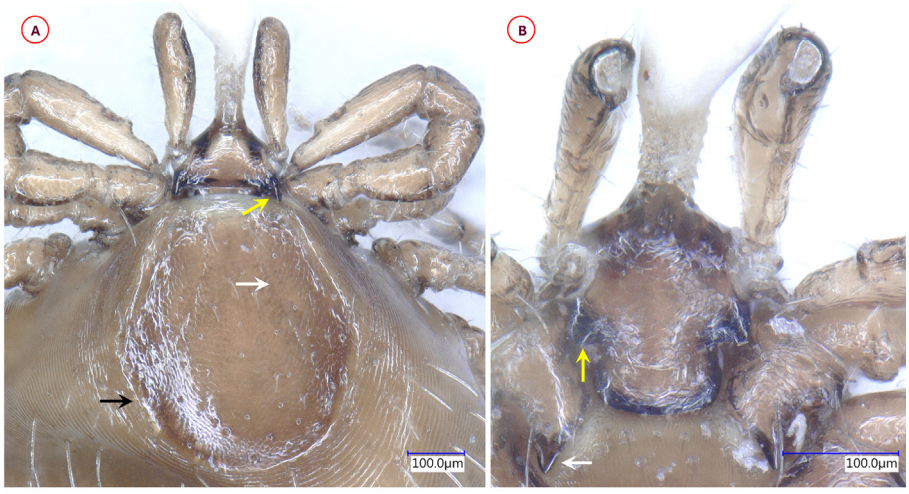

Fig. 6. Morphological characters of *Ixodes festai* nymph: (A) dorsal view of gnathosoma and scutum (yellow arrow: cervical groove, black arrow: caudolateral concavity of scutal margin); (B) ventral view of gnathosoma (yellow arrow: auricula, white arrow: internal spur of coxa I). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species received strong support in both the *cox1* (97 %) and 16S rRNA (89 %) phylogenetic analyses (Figs. 9 and 10).

3.4. Description of the new Ixodes species

Family Ixodidae Koch, 1844.
Genus *Ixodes* Latreille, 1795.
***Ixodes paragibbosus* Hornok and Kontschán sp. nov.**
Type-host: unknown.
Type-locality: Apiranthos (coordinates 37°04′20″N 25°31′20″E or 37.07222°N 25.52222°E), Naxos, Greece.
Type-specimen: Holotype: female from vegetation, collected by Jenő Kontschán on April 7, 2013; deposited at the Department of Parasitology and Zoology, University of Veterinary Medicine, Budapest, Hungary (accession number UNIVET-PAR-HS800).
Representative DNA sequences: Mitochondrial *cox1* and 16S rRNA gene sequences of the holotype are deposited in GenBank under PV274500 and PV277807, respectively.
ZooBank registration: To comply with the regulations set out in article 8.5 of the amended 2012 version of the *International Code of Zoological Nomenclature* (ICZN), details of the new species have been submitted to ZooBank on March 13, 2025. The Life Science Identifier (LSID) of the article is urn:lsid:zoobank.org:pub:EE46CB78-0E6E-4021-9DB5-41163F6B8FD6, and of the new name *Ixodes paragibbosus* urn:lsid:zoobank.org:act:AFF3FC0E-C768-47A6-8FF6-CD470328D262.
Etymology: The name of the new species refers to its sister species, *Ixodes gibbosus*, from which it was separated, thus originates and is phylogenetically closest to (Greek: para).

4. Description

4.1. General

Medium size, yellow inornate prostriate tick. Basis capituli dorsally pentagonal, with rounded triangular porose areas and short cornuae. Scutum is brown, rounded. The hypostome is mace-(club-) shaped. Internal spur on coxa I long, curved. All coxae with short external spur. Spiracle opening round.

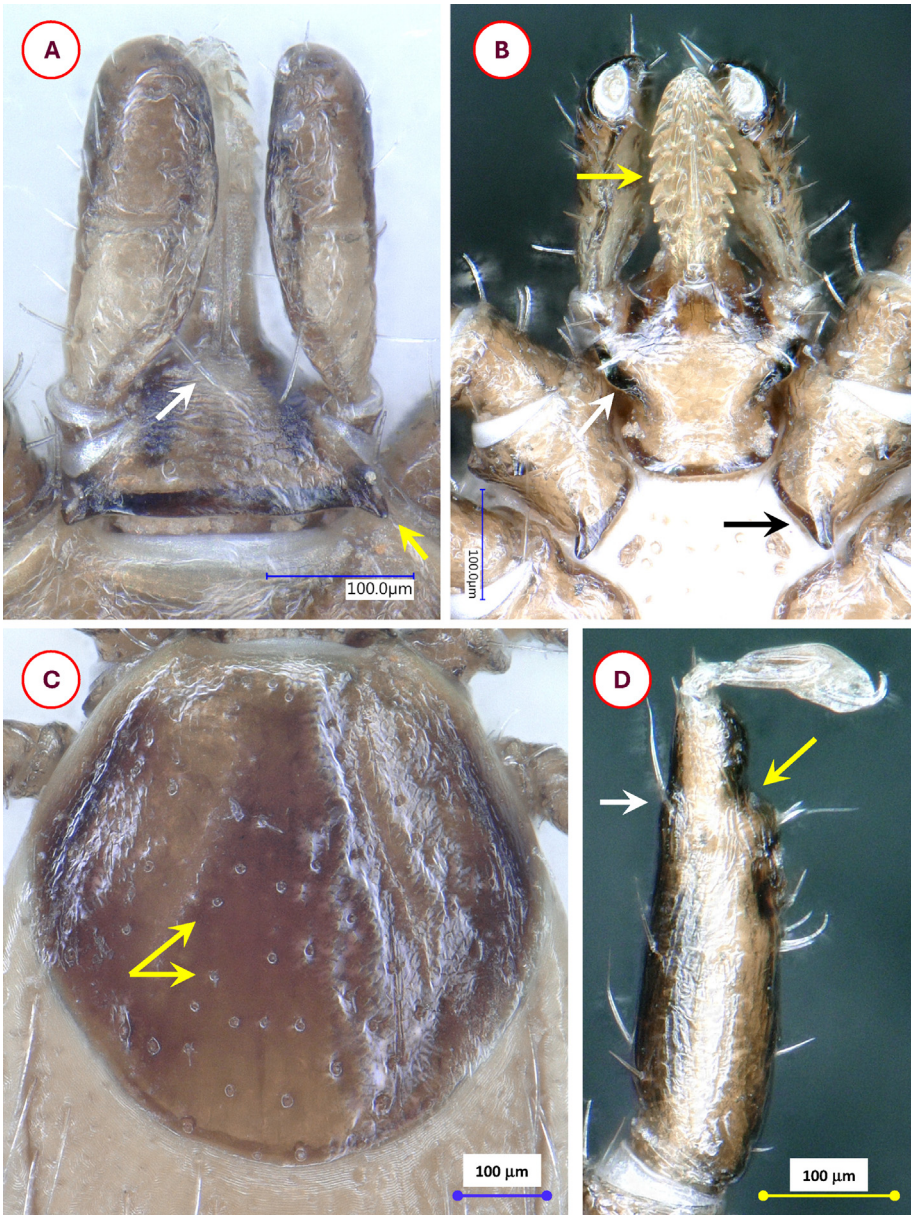

Fig. 7. Morphological characters of *Ixodes gibbosus* nymph: (A) dorsal view of gnathosoma (yellow arrow: cornua, white arrow: long median hair on palpal segment II); (B) ventral view of gnathosoma (yellow arrow: broadest point of hypostome, white arrow: auricula, black arrow: internal spur of coxa I); (C) scutum (yellow arrows: punctuations); (D) tarsus I (yellow arrow: obtuse angle of hump, white arrow: the first of three long ventral hairs). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.2. Female

[Based on the holotype; parameters provided in mm; Fig. 8.A-F, Supplementary Fig. 3].

Length of idiosoma (from the half point between scapular apices to the middle of posterior margin) 2.5, width 1.55, ratio of idiosomal length/width 1.6.

Scutum uniformly brown, heart-shaped, broadest slightly anterior to mid-length, posteriorly rounded, with prominent scapulae (Fig. 8.C). Length of scutum 1.33, maximum width 1.2, ratio length/width 1.11. On the scutum long, curved, shallow cervical grooves, converging backwards in anterior third of scutum, then diverging in S-shape with nearly parallel end fading into caudolateral scutal margin. Lateral carina wavy. Scutal punctuations scattered, small but prominent, evenly distributed (Fig. 8.C). Scutal setae laterally and centrally 0.16, as long as alloscutal setae (Fig. 8.C).

Alloscutum and idiosoma ventrally with long (0.16), sparse hair covering. Genital aperture broad U-shaped, 0.21 broad, 0.08 long, with diverging anterior margins (Fig. 8.G), situated between coxae IV. Preatrial fold longitudinally striated. Surface between preatrial fold and anterior genital groove longitudinally striated (Fig. 8.G). Genital groove anteriorly curved, convex, gradually diverging backwards until the virtual line connecting the anus and spiracular plates, then parallel to caudal margin of idiosoma. Spiracular plates round, with decreasing size goblets toward eccentric spiracle opening surrounded by a lane without aeropyles (Fig. 8.F).

Length of gnathosoma (from palpal apices to posterior margin of basis capituli) 0.9, width of basis capituli dorsally 0.54. Ratio of gnathosomal length to basis capituli width 1.67. Length of basis

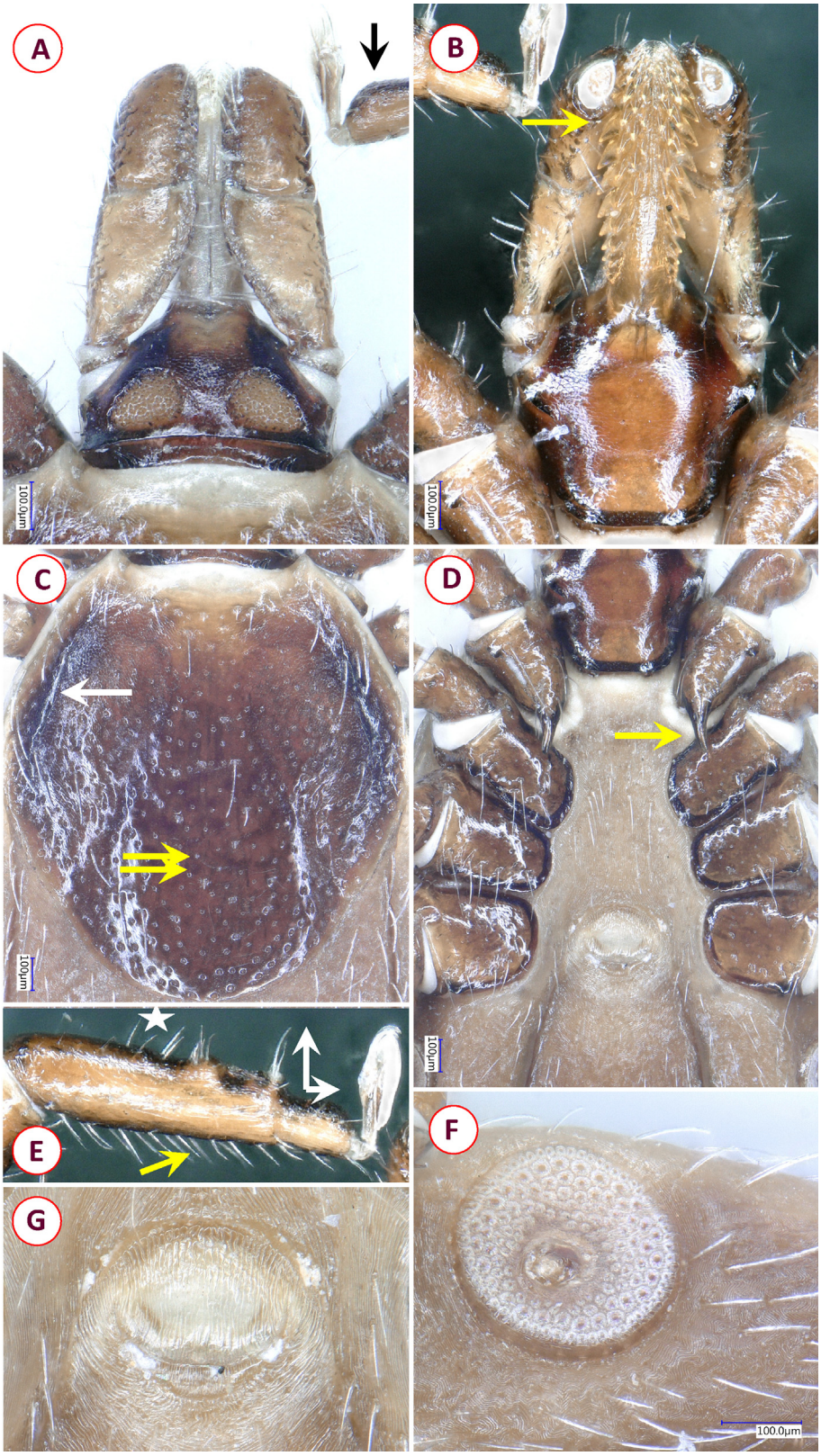

Fig. 8. Morphological characters of *Ixodes paragibbosus* female: (A) dorsal view of gnathosoma (black arrow: distal swelling of tarsus I); (B) ventral view of gnathosoma (yellow arrow: broadest point of hypostome); (C) scutum (yellow arrows: punctuations, white arrow: lateral carina); (D) ventral view of idiosoma (yellow arrow: internal spur of coxa I); (E) tarsus I (white arrows: perpendicular angle of hump, white star: proximal long dorsal hairs, yellow arrow: numerous ventral hairs); (F) spiracular plate; (G) genital aperture and preatrial fold. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

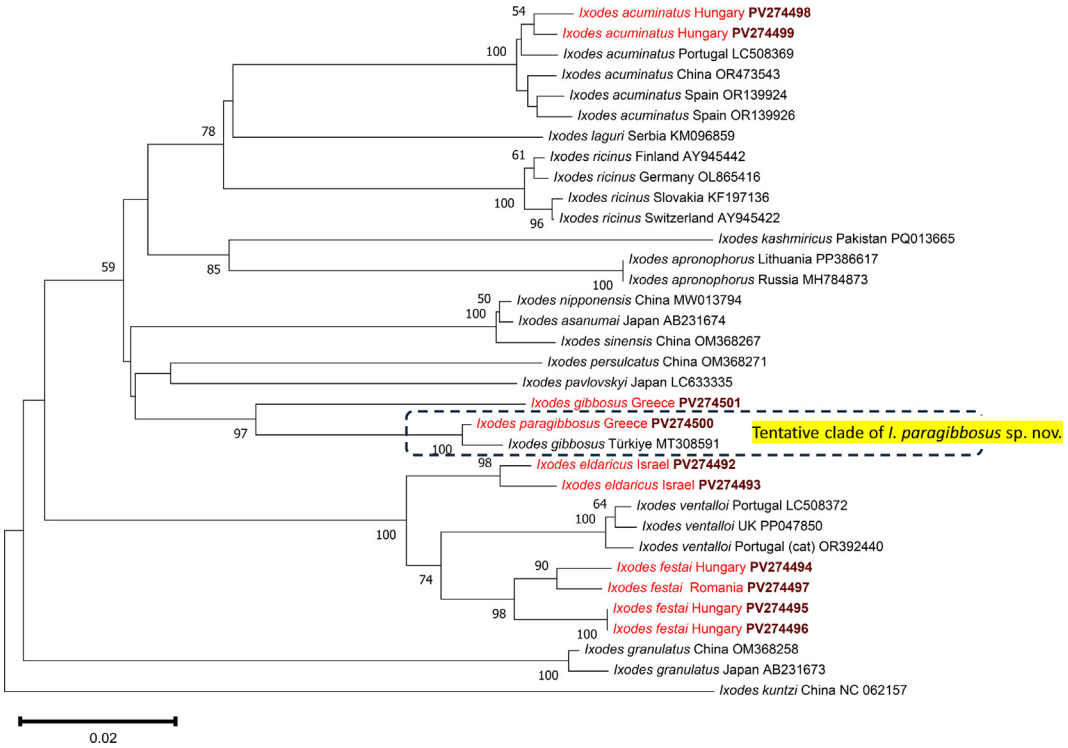

Fig. 9. Phylogenetic tree of Eurasian species from subgenus *Ixodes*, based on the cox1 gene. In each row of individual sequences, the country of origin and the GenBank accession number are shown after the species name. The sequences from this study are indicated with red fonts and bold, maroon accession numbers. Both sequences that probably represent *Ixodes paragibbosus* sp. nov. are surrounded by dashed line. The evolutionary history was inferred by using the Neighbor-Joining method and p-distance model. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown next to the branches. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 34 nucleotide sequences and there were a total of 629 positions in the final dataset. Evolutionary analyses were conducted in MEGA11. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

capituli (from base of hypostome to posterior margin of basis capituli) 0.3, ratio of width to length of basis capituli 1.8. Shape of basis pentagonal, sides nearly parallel (Fig. 8.A). Caudal edge of basis dorsally straight, caudolaterally continuing in cornuae which extend ventrally as ridge/collar flanking the basis (Fig. 8.A). Porose areas large, rounded triangular, length 0.13, width 0.15, interval 0.1. Caudal edge of basis ventrally reverse trapezoid, auriculae broad and slightly elevated, forming a ridge from palpal bases and directed medially to opposite caudolateral corner of basis (Fig. 8.B).

Palps (dorsal view) long, anteriorly oblique straight, sides parallel backward till broadest part behind junction of segments II-III. Length of palpal segments II and III 0.29, 0.23, respectively. Lateral field rugose. Three palpal hairs anteriomedially long, 0.07–0.08; lateral hair on segments II-III 0.05–0.06, with two longer ones (0.14) medially on segment II protruding over the basis of chelicerae above the hypostome (Fig. 8.B). Palpal hair along ventral edge up to 0.13 on segment II, 0.1 on segment III. Hypostome mace-shaped, with broadly rounded tip and maximum width at anterior third of length. Dentition 3/3 in anterior half, 2/2 in posterior half (Fig. 8.B).

Coxae I triangular, coxae II-IV rectangular with rounded medial edge. Internal spur on coxa I long, slightly curved, reaching coxa II (Fig. 8.D). Coxae II-IV without internal spur, but all coxae with short, broad, well-defined external spur. One long hair laterally on coxae I-II in excess of 0.2, further long hairs (0.1–0.18) on coxae II-IV number 3–4 in caudal half of surface. All trochanters with caudolateral rounded bump. All tarsi with subterminal hump (stepped, before tapering to claw). On tarsus I abrupt reduction in diameter near claw forms a step perpendicular to tarsal axis. Between this step and the claw tarsus I terminates with ball-like swelling (Fig. 8.A, 8.E). On tarsus I, ventral hairs (0.06–0.08) number approx. 20, dorsally long hairs present both proximally (tuft and four individual hairs) and distally (forming another tuft) from Haller's organ. On tarsus IV, ventral hairs number 13 (Supplementary Fig. 3).

4.3. Morphological characters distinguishing the female of I. paragibbosus sp. nov. from females of other species in subgenus Ixodes

The long and narrow palps (length to width exceeding 3), long internal spur on coxa I and genital opening between coxae IV of female *I. paragibbosus* sp. nov. classify it as a member of the subgenus *Ixodes* (as was also confirmed phylogenetically). Within this group, *I. paragibbosus* sp. nov. is different from all other species except *I. gibbosus* based on the subapical hump on all tarsi. In comparison with *I. gibbosus*, of which the females have 2-3x longer scutal than alloscutal setae (Estrada-Peña et al., 2017a), in the case of *I. paragibbosus* sp. nov., these are approx. equal in length (Fig. 8.C). The scutum of female *I. gibbosus* is as long as wide (Nuttall, 1916; Saratsiotis, 1970), but longer than wide in *I. paragibbosus* sp. nov. (Fig. 8.C). The hypostome of *I. gibbosus* female is long oval, broadest at mid-length, with narrow tip (Saratsiotis, 1970; Estrada-Peña et al., 2017a), unlike in *I. paragibbosus* sp. nov. where it is mace-like or club-shaped, broadest at anterior third with broad, rounded tip (Fig. 8.B). The interval of porose areas is approx. two thirds of their width (Fig. 8.A), whereas it is one third in *I. gibbosus* (Saratsiotis, 1970). The subapical hump of tarsus I has obtuse angle and tapering towards the claw in *I. gibbosus* (Saratsiotis, 1970; Estrada-Peña et al., 2017a), but it has perpendicular angle to the axis of tarsus I in *I. paragibbosus* sp. nov., with subterminal

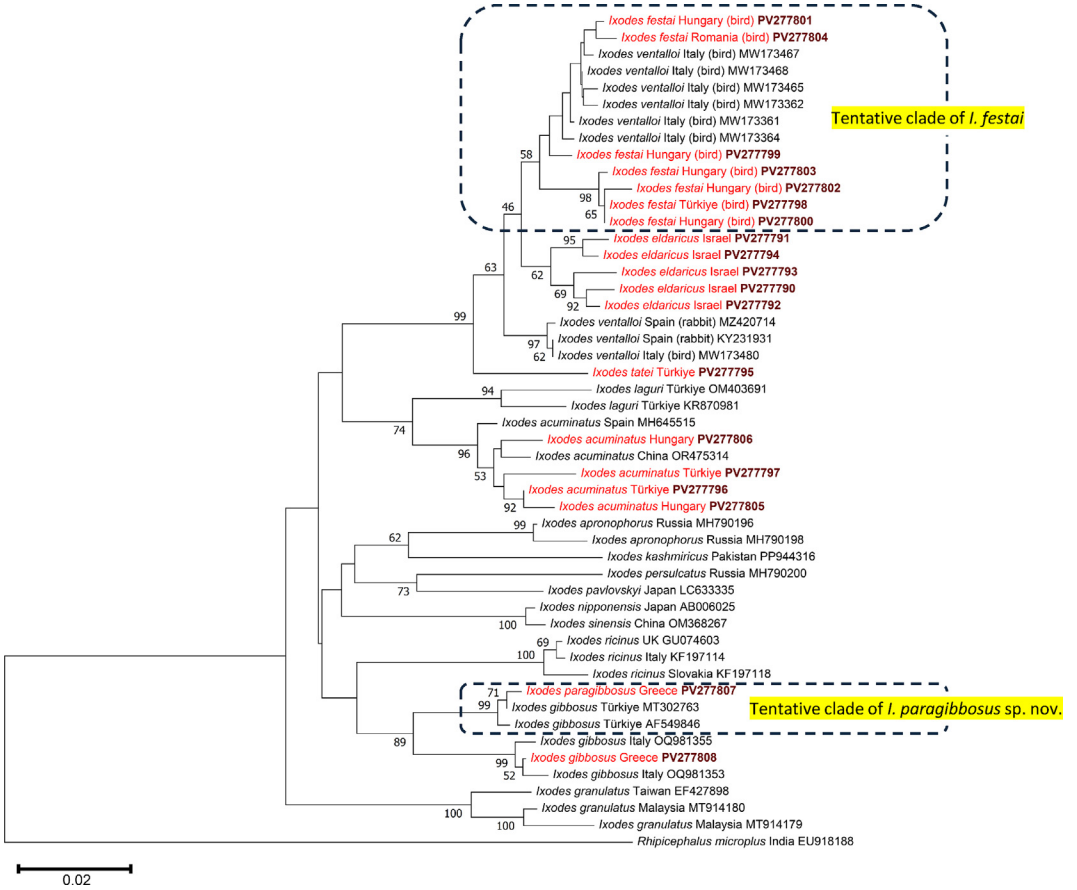

Fig. 10. Phylogenetic tree of Eurasian species from subgenus *Ixodes*, based on the 16S rRNA gene. In each row of individual sequences, the country of origin and the GenBank accession number are shown after the species name. For *Ixodes festai* and *Ixodes ventalloi* the generic name of host is also included in parentheses. The sequences from this study are indicated with red fonts and bold, maroon accession numbers. Sequences that are probably conspecific but were reported under different names are surrounded by dashed line. The evolutionary history was inferred by using the Neighbor-Joining method and p-distance model. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown next to the branches. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 50 nucleotide sequences and there were a total of 425 positions in the final dataset. Evolutionary analyses were conducted in MEGA11. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ball-like distention. The spiracular plate of female *I. gibbosus* is ovoid, elongated (Estrada-Peña et al., 2017a), but round in *I. paragibbosus* sp. nov. Tarsal hairs on the front leg number up to 10 ventrally on female *I. gibbosus* (Saratsiotis, 1970; Manilla, 1998), without similarly long hair proximally to the Haller's organ (Saratsiotis, 1970), whereas on the tarsus I of *I. paragibbosus* sp. nov. female, the ventral long hairs number approx. 20, and dorsally long hairs are present both proximally and distally from Haller's organ. On tarsus IV of *I. paragibbosus* sp. nov. female the ventral hairs number approx. twice as many (Supplementary Fig. 3) as in *I. gibbosus* (Nuttall, 1916; Saratsiotis, 1970).

5. Discussion

Although amplification of part of the *cox1* gene was attempted with several primers for all ticks in this study, some samples did not yield PCR product. This was particularly the case for *I. eldaricus*, *I. tatei* and *I. festai*, the latter already observed previously (e.g., Hornok et al., 2022). However, at least one mitochondrial marker was successfully amplified for all species studied here morphologically, allowing to draw final conclusions in a taxonomical context.

This is the first report of any *cox1* sequences of *I. festai* that allowed its comparison with *bona fide I. ventalloi*, collected from mammals in Southwestern Europe (Rosa et al., 2024). These results confirm the formerly reported phylogenetic divergence between the two species when the neotype of *I. ventalloi* (Estrada-Peña et al., 2018) was compared with *I. festai* based on the 16S rRNA gene (Hornok et al., 2022), also analyzed here. These genetic data add to the well-established morphological differences between the two species (Gilot and Perez, 1978; Senevet and Rodhain, 1968). While the male and larva of *I. festai* were described and illustrated with pictures before (Contini et al., 2011; Hornok et al., 2022), this is done here for the nymph and the female.

Based on Guglielmone et al. (2023), *I. festai* has been widely confused with *Ixodes ventalloi* because Arthur (1958) described the former using specimens of the latter. In addition, *I. festai* may have been mistakenly identified not only as *I. ventalloi,* but also as *I. ricinus* and *I. eldaricus* (Estrada-Peña et al., 2017b), as also elaborated below. At the same time, this was a difficult issue to clarify, as the poor condition of the holotype (engorged female of *I. festai* without capitulum) has rendered morphological comparison of these species difficult (Estrada-Peña et al., 2017b). In this study, synonymy of *I. festai* and *I. ventalloi* is confuted. Nevertheless, it is worth mentioning that even if in the future taxonomists would raise evidence that *I. festai* and *I. ventalloi* should be synonymous, that species should be called *I. festai* based on the rule of priority (ICZN), i.e. earlier establishment of the name.

Concerning geographical data, as one of the northernmost records in Europe, *I. festai* was reported previously in the UK (Hillyard, 1996), where genetically confirmed identification stands

only for *I. ventalloi* (Gillingham et al., 2020). Other countries were either regarded as providing questionable information, or data from migratory birds only while outside the geographical range of *I. festai*, as exemplified by Germany, Switzerland, Hungary, Poland (Petney et al., 2012; Papadopoulos et al., 2002; Hornok et al., 2016; Nowak-Chmura and Siuda, 2012) or Romania (this study). These uncertainties could be resolved in the future by using the barcoding (*cox1*) and 16S rRNA sequences of these species, as made available here for *I. festai* and previously for *bona fide I. ventalloi* (Estrada-Peña et al., 2018; Rosa et al., 2024). This is particularly important since *I. festai* is dispersed with migratory birds along the Adriatic flyway (Malta, Hungary, Poland, Romania) and hitherto no data attest its established status north of the Mediterranean Basin.

Regarding host ranges, while *I. ventalloi* typically infests lagomorphs, carnivores and rodents, as well as ground-living bird species (partridges) (Estrada-Peña et al., 2018), *I. festai* is typically a parasite of passeriform birds, as exemplified by Turdidae (Papadopoulos et al., 2002; Contini et al., 2011; Hornok et al., 2016). Nevertheless, several studies reported migratory passeriform birds infested with *I. ventalloi* either not illustrating the morphology of collected ticks (Toma et al., 2021) or showing pictures that are morphologically *I. festai* (Peňazziová et al., 2024). Based on the above results, the great majority of records of *I. ventalloi* from passerine birds in Italy (Toma et al., 2021; Fig. 10: accession numbers starting with MW173…) and probably all such data originating north of Italy (e.g. Slovakia: Peňazziová et al., 2024) maybe in fact *I. festai*.

In another study (Latrofa et al., 2017) *I. ventalloi* was reported from cats in Italy. While carnivores are among the well-known hosts of this tick species, the pictures provided in that study are not useful for comparison with stereomicroscope or digital pictures, because the ticks were made semitransparent with lactophenol. The sequeces in Latrofa et al. (2017) have very low (cox1 gene: 55–67 %, 16S rRNA gene: 58 %) coverage with sequences used in this study, therefore could not be included in the phylogenetic analysis here. However, in the comparable part the cox1 and 16S rRNA sequences from this study, *I. ventalloi* in Latrofa et al. (2017) had only 95.5–95.9 % and 95.1–96.3 % sequence identities to *I. festai*. These values are similar to the above comparisons between *I. festai* and *bona fide I. ventalloi*, and together with 99.6 % identity to the neotype of *I. ventalloi* support the diagnosis as the latter species.

Furthermore, when *I. eldaricus* was reported from two migratory bird species, the Dunnock (*Prunella modularis*) and European Robin (*Erithacus rubecula*) in Poland (Nowak-Chmura, 2012), no illustrations were provided. However, the former bird species is a common host of *I. festai* (Papadopoulos et al., 2002; Hornok et al., 2016), and the morphological description of the female tick from Poland appears to be more relevant to *I. festai* rather than *I. eldaricus*. For instance, the latter can be excluded based on the shape of female auriculae: "acutangular, pointed and long, directed slightly medially and down", because auriculae of *I. eldaricus* female are not long, rather laterally directed and blunt with caudal corner as illustrated here (Fig. 1) and also earlier (Filippova, 1974). Therefore, this record should also enrich data on the occurrence of *I. festai* on migratory birds north of the Mediterranean Basin, similarly to another report from Poland (Siuda and Szymanski, 1991).

The geographical range of *I. eldaricus* includes the Middle East and Asia (Filippova, 1974; Yeruham et al., 1995; Uspensky, 2021). The typical hosts of this species are birds, rodents, occasionally insectivores and bats (Yeruham et al., 1995; Uspensky, 2021). While rock partridges (*Alectoris chukar* in the Middle East and *Alectoris barbara* in North Africa) appear to be a common host for *I. eldaricus* and *I. tatei*, the latter is also found on red fox (*Vulpes vulpes*) (Arthur, 1959). Among the most important morphological differences between the two species are the following: females of *I. eldaricus* have (1) 1.5x longer than broad scutum, (2) laterally wavy basis capituli, (3) broad and blunt lateral auriculae with caudal corner, (4) laterally curving short internal spur on coxa I (directed towards but not reaching above coxa II) (Fig. 1) *vs* in *I. tatei* female (1) the scutum is only 1.3x longer than broad, (2) the basis capituli is laterally straight, (3) auriculae are caudally directed as tapering spurs, (4) and the internal spur on coxa I is directed backwards (not above the center of coxa II) (Arthur, 1959). Considering nymphs of *I. eldaricus*, they have (1) straight cervical grooves, carinae and sparse punctuation on the scutum, which is posteriorly obtuse-angled, (2) caudolateral concavity of scutal margin directly behind maximum width, (3) caudolaterally perpendicular-angled auriculae and (4) hypostome bearing 2/2 dentition except the anterior third with 3/3 formula (Fig. 2) *vs* the nymph of *I. tatei* has (1) curved cervical grooves, very sparse punctuation on the scutum, which is posteriorly rounded, (2) caudolateral concavity of scutal margin at mid-length behind maximum width, (3) caudally directed, acute-angled, prominent auriculae and (4) hypostome bearing 2/2 dentition except the anterior quarter with 3/3 formula (Fig. 3; Arthur, 1968).

Hitherto the taxonomic view persisted that the name *Ixodes tatei*, under which Arthur discovered and described a new species (Arthur, 1959; 1968) is a junior synonym of *I. eldaricus* (Filippova, 1977; Camicas et al., 1998). However, based on the results of this study, this concept should be revised and *I. tatei* Arthur, 1958 resurrected. The morphological comparison with and difference from *I. eldaricus* and closely related species, as illustrated here, and the phylogenetic analysis based on the 16S rRNA gene fully justify this.

In the case of *I. gibbosus*, highly divergent 16S rRNA haplotypes have already been shown to exist, but morphologically these variants could not have been compared (Hoffman et al., 2020). This study provided an opportunity for this. No holotype of *I. gibbosus* is available, therefore differential diagnostic characters listed above were based on the characters illustrated and written by the author of *I. gibbosus* (Nuttall, 1916), as well as on the first detailed and adequate morphological description of the species (Saratsiotis, 1970) and on its characters shown in Estrada-Peña et al. (2017a) and Manilla (1998).

Based on Nuttall (1916) the (lecto)types of *I. gibbosus* were collected in Türkiye, but its geographical range also covers southern countries of the Balkan Peninsula, Italy and Israel (Saratsiotis, 1970; Manilla, 1998). Both *I. gibbosus* and *I. paragibbosus* examined in this study originate in Naxos (Greece), therefore the two species are probably sympatric in at least part of their respective geographical ranges.

The most important hosts of *I. gibbosus* are goats (Nuttall, 1916), as also reported in the westernmost part of its geographical range, Italy (Cringoli et al., 2005), but it can also infest other ungulates, carnivores, insectivores, lagomorphs, birds as well as humans (Guglielmone et al., 2014). Since previously it was not morphologically recognized that there are two species sharing the key character (tarsal hump) of *I. gibbosus* and several other traits, specimens that belonged to the new species described here as *I. paragibbosus* sp. nov. could have been sometimes misidentified as *I. gibbosus* (Figs. 9 and 10). Therefore, it needs further evaluation, if (and how) these two species differ in their geographical distribution, ecology and host ranges. This is especially relevant to countries nearby Greece, the type locality of *I. paragibbosus* sp. nov., because in the 16S rRNA gene phylogenetic analysis of the present study (Fig. 10) sequences reported as *I. gibbosus* from Türkiye clustered with *I. paragibbosus* sp. nov. and, therefore, are probably conspecific with the latter.

Last but not least, the authors of this study would like to note that they are aware of the limitations of this study. These include

the small sample size and the absence of complete mitochondrial genome sequences. The latter could not be yielded owing to low concentrations of probably fragmented DNA extracted from tick legs, especially because nearly half (n = 10) of the specimens were collected 9–12 years ago, and some of them were unique, indispensable. However, these are also relevant to most of the recent taxonomical works including descriptions of new species or re-establishment of outdated species among Ixodidae. Here, at least one traditionally used genetic marker confirmed well-illustrated morphological analyses, while numerous recent tick species descriptions completely lack molecular data (e.g., Aftisse et al., 2024) or only the 16S rRNA gene was sequenced originally (Onofrio et al., 2020). Optimally, in the near future, it will be necessary to analyze a larger set of relevant samples, and to obtain the complete mitogenome of all Palearctic species in the subgenus *Ixodes*.

6. Conclusions

Based on the above results, the species *I. tatei* Arthur, 1959 should be resurrected and reestablished. The first barcoding sequences of *I. eldaricus* and *I. festai* confirm that the latter is a separate, valid species, distinct from both *I. eldaricus* and *I. ventalloi*. Two species existed under the name *I. gibbosus*, and the one different from the description and redescription of this species was recognized, characterized and named here as *I. paragibbosus* sp. nov. For the differential diagnosis of the above species, the results provided here highlight the importance of observing the auriculae and internal spur of coxa I (i.e., while comparing *I. eldaricus*, *I. tatei* and *I. festai*) and the hypostome (e.g., between *I. eldaricus*, *I. tatei* and *I. acuminatus*, or between *I. gibbous* and *I. paragibbosus* sp. nov.).

CRediT authorship contribution statement

Sándor Hornok: Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Adem Keskin:** Investigation, Formal analysis, Data curation. **Igor Uspensky:** Investigation, Formal analysis, Data curation. **Jenő Kontschán:** Methodology, Investigation, Formal analysis, Data curation. **Nóra Takács:** Methodology, Data curation. **Paulina Lesiczka:** Data curation, Investigation, Methodology. **Tim Warbroek:** Data curation, Investigation, Methodology. **Tijs J.M. van den Bosch:** Data curation, Investigation, Methodology. **Gergő Keve:** Methodology, Data curation. **Andor Pitó:** Resources, Data curation. **Attila D. Sándor:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Conceptualization.

Acknowledgements

The authors are grateful to Regina Kovács for her assistance in administration.

Ethics approval

Permission for bird ringing in Hungary was issued by the Pest County Government Office, Department of Environmental Protection and Nature Conservation (No. TMF-1034/2016., 389/2023). Permission number in Romania was COR 828265/2018. In Türkiye, bird ringing and all collections were made with the permission of the Ministry of Forestry and Water Affairs, General Directorate of Nature Conservation and National Parks, according to the protocol number 72784983-488.04-241348. This study has been conducted under the Ethical Principles in Animal Research which was approved by the Ondokuz Mayis University Animal Ethical Committee with the B.30.2.ODM.0.20.09.00-050.04-96 ethical number.

Availability of data and materials

The sequences obtained during this study are deposited in GenBank under the following accession numbers: *cox*1 gene: PV274492-PV274501, 16S rRNA gene: PV277790-PV277808. Alignment data were deposited in MendeleyData (https://doi.org/10.17632/cyjw6f98c7.1). All other relevant data are included in the manuscript and the supplementary material or are available upon request by the corresponding author.

Funding

Molecular work was supported by the Office for Supported Research Groups, Hungarian Research Network (HUN-REN), Hungary (Project No. 1500107).

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpara.2025.09.002.

References

Aftisse, L., Merabet, S., Keskin, A., Apanaskevich, D.A., 2024. Description of a new species of *Ixodes* Latreille, 1795 (Acari: Ixodidae), a parasite of rodents (Rodentia: Muridae) in Algeria. Syst. Parasitol. 102, 5. https://doi.org/10.1007/s11230-024-10197-6.

Arthur, D.R., 1958. *Ixodes festai* Rondelli 1926 (Ixodoidés, Ixodidés). Redescription de la femelle, description du male et des estades impairfaits et notes sur leur biologie. Archives De L'institut Pasteur Du Maroc 5, 475–492 (in French).

Arthur, D.R., 1959. *Ixodes tatei* n. sp. from Iraq (Acarina: Ixodidae). Parasitol 49, 108–110. https://doi.org/10.1017/S0031182000026743.

Arthur, D.R., 1961. The synonymy of *Ixodes festai* Rondelli 1926. Parasitol 51, 497.

Arthur, D.R., 1968. The immature stages of *Ixodes tatei* Arthur (Ixodidae). Parasitol 58, 165–169. https://doi.org/10.1017/s0031182000073510.

Black, W.C., Piesman, J., 1994. Phylogeny of hard and soft-tick taxa (Acari: Ixodida) based on mitochondrial 16S rDNA sequences. Proc Nat Acad Sci. USA 91, 10034–10038. https://doi.org/10.1073/pnas.91.21.10034.

Camicas, J.L., Hervy, J.P., Adam, F., Morel, P.C., 1998. Les tiques du monde. Nomenclature, stades decrits, hotes, repartition (Acarida, Ixodida). Orstom, Paris, 233 pp. (in French).

Contini, C., Palmas, C., Seu, V., Stancampiano, L., Usai, F., 2011. Redescription of the male of *Ixodes festai* Rondelli, 1926 (Ixodida: Ixodidae) on specimens from Sardinia (Italy). Parasite 18, 235–240. https://doi.org/10.1051/parasite/2011183235.

Cringoli, G., Iori, A., Rinaldi, L., Veneziano, V., Genchi, C., 2005. Mappe Parassitologiche – Zecche. Series Edit. Giuseppe Cringoli, Napoli, pp 308. (in Italian).

Estrada-Peña, A., Mihalca, A., Petney, T. (Eds.), 2017a. Ticks of Europe and North Africa. Springer, Cham, Switzerland, p. 404.

Estrada-Peña, A., Pfäffle, M., Baneth, G., Kleinerman, G., Petney, T.N., 2017b. Ixodoidea of the western palaearctic: a review of available literature for identification of species. Ticks Tick Borne Dis. 8, 512–525. https://doi.org/10.1016/j.ttbdis.2017.02.013.

Estrada-Peña, A., Venzal, J.M., Nava, S., 2018. Redescription, molecular features, and neotype deposition of *Rhipicephalus pusillus* Gil Collado and *Ixodes ventalloi* (Acari: Ixodidae). Zootaxa 4442, 262–276. https://doi.org/10.11646/zootaxa.4442.2.4.

Filippova, N.A., 1974. *Ixodes eldaricus* i ego rasprostranenie na iuge SSSR [*Ixodes eldaricus* and its distribution in the southern USSR]. Parazitologiia 8, 504–514 (in Russian).

Filippova, N.A., 1977. Ixodid ticks (Ixodinae). Fauna USSR New Series 4, 1–316 (in Russian).

Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome C oxidase subunit I from diverse metazoan invertebrates. Mel Marine Biol Biot. 3, 294–299.

Gillingham, E.L., Hansford, K.M., Meadows, S., Henney, J., Wieckowski, F., Hernández-Triana, L.M., Muscat, I., Muscat, J., Beckert, C., Nikolova, N.I., Cull, B., Medlock, J.M., 2020. Ticks on the Channel Islands and implications for public health. Ticks Tick Borne Dis. 11, 101405. https://doi.org/10.1016/j.ttbdis.2020.101405.

Gilot, B., Perez, C., 1978. Individualisation. caractérisation de deux *Ixodes* actuellement confondus: *I. festai* Rondelli, 1926, *I. ventalloi* Gil Collado, 1936 (Acarina, Ixodoidea). Rev. Suisse Zool. 85, 143–149 (in French).

Guglielmone, A.A., Robbins, R.G., Apanaskevich, D.A., Petney, T.N., Estrada-Peña, A., Horak, I.G., 2014. The hard ticks of the world. Springer, Dordrecht, p. 738.

Guglielmone, A.A., Nava, S., Robbins, R.G., 2023. Geographic distribution of the hard ticks (Acari: Ixodida: Ixodidae) of the world by countries and territories. Zootaxa 5251, 1–274. https://doi.org/10.11646/zootaxa.5251.1.1.

Hillyard, P.D., 1996. Ticks of North-West Europe, Synopses of the British Fauna No. 52 (New Series). The Linnean Society of London, London, p. 178.

Hoffman, T., Wilhelmsson, P., Barboutis, C., Fransson, T., Jaenson, T.G.T., Lindgren, P. E., Von Loewenich, F.D., Lundkvist, Å., Olsen, B., Salaneck, E., 2020. A divergent *Anaplasma phagocytophilum* variant in an *Ixodes* tick from a migratory bird; Mediterranean Basin. Infect Ecol. Epidemiol. 10, 1729653. https://doi.org/10.1080/20008686.2020.

Hornok, S., Flaisz, B., Takács, N., Kontschán, J., Csörgő, T., Csipak, Á., Jaksa, B.R., Kováts, D., 2016. Bird ticks in Hungary reflect western, southern, eastern flyway connections and two genetic lineages of *Ixodes frontalis* and *Haemaphysalis concinna*. Parasit. Vectors 9, 101. https://doi.org/10.1186/s13071-016-1365-0.

Hornok, S., Cutajar, B., Takács, N., Galea, N., Attard, D., Coleiro, C., Galea, R., Keve, G., Sándor, A.D., Kontschán, J., 2022. On the way between Africa and Europe: molecular taxonomy of ticks collected from birds in Malta. Ticks Tick Borne Dis. 13, 102001. https://doi.org/10.1016/j.ttbdis.2022.102001.

Kwak, M.L., Beveridge, I., Koehler, A.V., Malipatil, M., Gasser, R.B., Jabbar, A., 2017. Phylogenetic analysis of the Australasian paralysis ticks and their relatives (Ixodidae: *Ixodes*: *Sternalixodes*). Parasit. Vectors 10, 122. https://doi.org/10.1186/s13071-017-2045-4.

Latrofa, M.S., Giannelli, A., Persichetti, M.F., Pennisi, M.G., Solano-Gallego, L., Brianti, E., Parisi, A., Wall, R., Dantas-Torres, F., Otranto, D., 2017. *Ixodes ventalloi*: morphological and molecular support for species integrity. Parasitol. Res. 116, 251–258. https://doi.org/10.1007/s00436-016-5286-9.

Manilla, G., 1998. Fauna d'Italia. Acari, Ixodida. Edizioni Calderini, 280 pp.

Mumcuoglu, K.Y., Keskin, A., Mans, B.J., Dantas-Torres, F., 2025. Ticks of the Middle East Taxonomy, Biology, Ecology, Medical, and Veterinary Significance. Academic Press, Elsevier.

Nowak-Chmura, M., 2012. *Ixodes eldaricus* Djaparidze, 1950 (Ixodidae) on migrating birds – reported first time in Poland. Vet. Parasitol. 186, 399–402. https://doi.org/10.1016/j.vetpar.2011.11.029.

Nowak-Chmura, M., Siuda, K., 2012. Ticks of Poland. Review of contemporary issues and latest research. Annals Parasitol. 58, 125–155.

Nuttall, G.H.F., 1916. Notes on Ticks. IV. Relating to the Genus *Ixodes* and including a description of three new Species and two new Varieties. Parasitology 8, 294–337. https://doi.org/10.1017/S0031182000010623.

Papadopoulos, B., Humair, P.F., Aeschlimann, A., Vaucher, C., Büttiker, W., 2002. Ticks on birds in Switzerland. Acarologia 42, 3–19.

Peňazziová, K.L., Chitimia-Dobler, L., Csank, T., Peťko, B., Ondrejková, A., Halán, M., Schusterová, P., Pivka, S., Korytár, Ľ., 2024. First detection and a new avian host of the tick *Ixodes ventalloi* Gil Collado, 1936, in Slovakia. Parasitol. Res. 123, 268. https://doi.org/10.1007/s00436-024-08286-y.

Petney, T.N., Pfäffle, M., Skuballa, J., 2012. An annotated checklist of the ticks (Acari: Ixodidae) of Germany. Syst. Appl. Acarol. 17, 115–170. https://doi.org/10.11158/saa.17.2.2.

Onofrio, V.C., Guglielmone, A.A., Barros-Battesti, D.M., Gianizella, S.L., Marcili, A., Quadros, R.M., Marques, S., Labruna, M.B., 2020. Description of a new species of Ixodes (Acari: Ixodidae) and first report of *Ixodes lasallei* and *Ixodes bocatorensis* in Brazil. Ticks Tick Borne Dis. 11, 101423. https://doi.org/10.1016/j.ttbdis.2020.101423.

Rosa, F., Silva, C., Rodrigues, R., Esteves-Vieira, M., Barbosa, I., Rosa, S., Dias, D., Pina-Martins, F., 2024. Island hitchhikers: pathogen agents of Madeira and Azores ticks. Parasitol. Res. 123, 261. https://doi.org/10.1007/s00436-024-08278-y.

Saratsiotis, A., 1970. Etude morphologique et observations biologiques sur *Ixodes gibbosus* Nuttall, 1916 [Morphological study and biological observations on *Ixodes gibbosus* Nuttall, 1916]. Ann. Parasitol. Hum. Comp. 45, 661–675. https://doi.org/10.1051/parasite/1970455661 (in French).

Senevet, G., Rodhain, F., 1968. Larves des principales esp'eces du genre Ixodes d'Europe Occidentale et Centrale. Description de la larve d'*Ixodes festai* Rondelli 1926 [Larvae of the principal species of the genus *Ixodes* of Central and Occidental Europe. Description of the larva of *Ixodes festai* Rondelli 1926]. Ann. Parasitol. Hum. Comp. 43, 513–523 (in French).

Shao, R., Campbell, N.J., Barker, S.C., 2001. Numerous gene rearrangements in the mitochondrial genome of the wallaby louse, *Heterodoxus macropus* (Phthiraptera). Mol. Biol. Evol. 18, 858–865. https://doi.org/10.1093/oxfordjournals.molbev.a003867.

Siuda, K., Szymanski, S., 1991. A case of transfer to Poland a Mediterranean tick *Ixodes* (*Ixodes*) *festai* Rondelli, 1926 (Acari: Ixodida: Ixodidae). Wiad. Parazytol. 37, 25–29.

Tamura, K., Stecher, G., Kumar, S., 2021. MEGA11: molecular evolutionary genetics analysis version 11. Mol. Biol. Evol. 38, 3022–3027. https://doi.org/10.1093/molbev/msab120.

Toma, L., Mancuso, E., d'Alessio, S.G., Menegon, M., Spina, F., Pascucci, I., Monaco, F., Goffredo, M., Di Luca, M., 2021. Tick species from Africa by migratory birds: a 3-year study in Italy. Exp. Appl. Acarol. 83, 147–164. https://doi.org/10.1007/s10493-020-00573-4.

Uspensky, I., 2021. The Eldari tick *Ixodes eldaricus* (Acari: Ixodidae) in Israel: its occurrence, morphometric and biological characteristics. Acarol Stud. 3, 9–15. https://doi.org/10.47121/acarolstud.844856.

Yeruham, I., Hadani, A., Galker, F., Rosen, S., 1995. The occurrence of *Ixodes eldaricus* (Dzhaparidze, 1950) (Acarina: Ixodidae) in Israel. Acarologia 36, 191–193.