A new genus of the family Nesticidae (Arachnida: Aranei) from the Caucasus

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KEY WORDS: Aituaria, Araneae, biodiversity, Carpathonesticus, Dagestan, Georgia, new species, scree, shallow subterranean habitat.

ABSTRACT. A new genus, Daginesticus gen.n. with the type species, D. dzhamirzoevi sp.n. (♂♀) is described from the Caucasus based on morphological and molecular evidences. Three new combinations are proposed: Daginesticus mammajevae (Marusik, 1987) comb.n., Aituaria borutzkyi (Reimoser, 1930) comb.n. and Aituaria eriashvilii (Marusik, 1987) comb.n. (all ex. Carpathonesticus). The new genus is closely related to Aituaria Esyunin et Efimik, 1998 and has unreduced eyes and well-developed body pigmentation. Description, figures, diagnosis and photographs of the habitat are provided. The conformation of the male palp in Nesticini is discussed and new terms are suggested based on homology of different sclerites.


Introduction

Nesticidae Simon, 1894 is a relatively small family, currently numbering 280 extant species belonging to 16 genera, as well as 11 fossil species belonging to four extinct genera [WSC, 2022; Dunlop et al., 2020]. The family is distributed almost worldwide and in all zoogeographical realms [WSC, 2022]. Representatives of this family from temperate regions are often found in caves or in other dark and humid habitats [Dippenaar-Schoeman, Jocqué, 1997]. West Palearctic nesticids are relatively well studied owing to existence of one global [Kratochvíl, 1933] and several regional papers dealing with species from many European countries and the Caucasus: Iberian Peninsula [Ribera, 2018], Italy [Ballarin, 2020], Balkans [Pavlek, Ribera, 2017], Romania [Dumitrescu, 1980; Weiss, Heimer, 1982], Ukraine [Marusik et al., 2017] and the Caucasus [Charitonov, 1947; Marusik, 1987]. Four genera and nine species of Nesticidae are known from the Caucasus: Aituaria Esyunin et Efimik, 1998, Carpathonesticus Lehtinen et Saaristo, 1980, Nesticella Lehtinen et Saaristo, 1980 and Nesticus Thorell, 1869 [Otto, 2020; Mikhailov, 2021; Nentwig et al., 2022]; however, none have been recorded from Dagestan. While studying spiders collected in Dagestan, we found around a dozen specimens of Nesticidae whose morphology do not...
correspond to any known genera. Comparison with other genera led us to the conclusion that they may represent a new genus. Molecular analysis supported this hypothesis. In addition, while analyzing molecular data and morphology of other Caucasian nesticids, it was revealed that one already described species, namely *Carpathonesticus manajevae* Marusik, 1987 from eastern Georgia, appeared to be closely related to the new taxa. The goals of this paper are as follows: (1) to establish the new genus *Daginesticus* gen. n., (2) to provide a description of *D. dzhamirzoevi* sp. n., (3) to discuss relationships between *Daginesticus* gen. n., *Aituaria* and *Carpathonesticus*, (4) to propose new combinations and (5) to discuss homology of different sclerites of the male palp.

**Material and methods**

Spiders were hand-collected and preserved in 70% ethanol. Specimens were photographed with the Olympus DP74 camera attached to the Olympus SZX16 stereomicroscope at the Altai State University (Barnaul, Russia). Photographs were taken in a dish with white cotton at the bottom, filled with ethanol. Digital images were montaged using Helicon Focus and Zerene Stacker software. Epigyne was macerated in a potassium hydroxide aqueous solution. All measurements are given in millimetres. Length of the leg segments was measured on their dorsal sides. Leg measurements are shown as: femur, patella, tibia, metatarsus, tarsus (total length). Terminology of the structures of copulatory organs in Nesticidae is inconsistent: different authors considered the same structures under different names [Marusik et al., 2017]. While studying morphology of the male palp of several nesticids, we realized that terms are not properly homologized, and that even not all parts forming the complex conductor have been detected by preceding authors. Therefore, we are using our own terminology. The studied material is deposited in the Institute of Systematics and Ecology of Animals SB RAS, Novosibirsk, Russia (ISEA; curator G.N. Azarkina), in Zoological Museum of the Moscow State University (ZMMU; curator K.G. Mikhailov) and in E.V. Prokopenko Personal Collection (PCP).

Abbreviations: **Cd** — dorsal process of the conductor, **Cg** — club-like gland, **Cm** — median process of the conductor, **Cn** — connection between **Rx** and **Te**, **Co** — copulatory duct, **Cp** — prolateral process of the conductor, **Cr** — retrolateral process of the conductor, **Ct** — conductor, **Di** — distal apophysis of the paracymbium, **Do** — dorsal apophysis of the paracymbium, **Em** — embolus, **Mn** — membrane between **Rx** and **Te**, **Mp** — median plate, **Pa** — paracymbium, **Re** — receptacle, **Ra** — radical apophysis, **Rm** — radical membrane, **Rp** — radial process, **Rx** — radix, **Sd** — sperm duct, **Sf** — slanting fold of **Re**, **St** — subtegmentum, **Te** — tegulum, **Ve** — ventral apophysis of the paracymbium.

**Molecular analysis**

Aiming to confirm the newly established genus, a molecular analysis was conducted including the type species and other representatives of all the main European nesticid genera. For each voucher two legs were detached and preserved in 96% ethanol for molecular analysis. Total genomic DNA was extracted from leg muscular tissue using a Qiagen DNeasy Blood & Tissue Kit following the standard protocol suggested by the manufacturer. Three gene fragments were preferentially amplified: the mitochondrial genes Cytochrome c oxidase subunit I (COI) and 16S rRNA (16S) and the nuclear gene Histone H3 (H3). DNA extraction and Polymerase Chain Reaction amplification were carried out at the Systematic Zoology Laboratory, Department of Biological Sciences, Tokyo Metropolitan University, Japan (TMU). Sequencing was performed using an ABI PRISM 3130xl (Applied Biosystems) at the same institute. PCR protocols and primers follow Ballarin, Li [2018]. Additional sequences were obtained from GenBank online database (https://www.ncbi.nlm.nih.gov/genbank/). The complete list of species and sequences is reported in the Table 3. *Gaucelmus augustinus* Keyserling, 1884 from North America was selected as outgroup due to the putative distant relationship with other European Nesticidae [Ballarin, 2020].

Sequences were aligned using the online version of MAFFT v.7.450 ([Katoh et al., 2019], available at: https://mafft.cbrc.jp/alignment/server/) under the G-INS-i algorithm and subsequently visually examined to find potential mismatching. Protein coding genes (COI, H3) were further checked by translating the sequences to proteins with the software MEGA X ver. 10.0.5 [Kumar et al., 2018]. A Maximum Likelihood analysis (ML) was carried out using the online version of RAXML v.8.2.12 [Stamatakis, 2014] on CIPRES Science Gateway v.3.3 ([Miller et al., 2010], available at: https://www.phylo.org/). A rapid bootstrap of one thousand replicates were performed twice under a GTR-GAMMA substitution model. Each gene and the 3rd codon of COI were partitioned separately as suggested by the software JModelTest 2 v.2.1.7 [Darriba et al., 2012]. Additionally, an uncorrected pairwise-distance genetic divergence was carried out in MEGA X in order to compare the genetic distance between *Daginesticus* gen. n. and other genera. Standard COI barcode gene fragment of type species of the Nearctic genus *Gaucelmus* Keyserling, 1884 and each of the known European genera were analyzed using 1000 replications under a bootstrap method.

**Taxonomy**

Family Nesticidae Simon, 1894

*Daginesticus* gen. n.

**TYPE SPECIES.** *Daginesticus dzhamirzoevi* sp. n. from Dagestan, Russia.

**ETYMOLOGY.** The generic name is derived from the type locality of the genotype, Dagestan, added to *nesticus*, a common ending for nesticid genera. The gender is masculine.

**DIAGNOSIS.** The new genus is most similar to *Aituaria* Esyunin et Efimik, 1998. The males of the new genus differ from those of *Aituaria* by having a reduced or missing radical process (**Rp**) (vs. well-developed), median process of the conductor (**Cm**) with strongly curved tip (vs. straight or slightly bent) and blunt shape of the radical apophysis (**Ra**) (vs. **Ra** ending with a sharp tip) (cf. Figs 4–5, 8–13 and 25, 27–29). Females of *Daginesticus* gen. n. differ from *Aituaria* by having smaller and longer receptacles (1/3 of median plate width and 2 times longer than wide vs. 0.4 and 1.3) and club-like gland (**Cg**) with head about 3 times wider than stalk (vs. cylindrical with a stalk thinner than head) (cf. Figs 4–5, 8–13 and 25, 27–29).

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Structures of copulatory organs

<table>
<thead>
<tr>
<th></th>
<th>Daginesticus gen. n.</th>
<th>Aituaria spp.</th>
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<tbody>
<tr>
<td>Male</td>
<td></td>
<td></td>
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<tr>
<td>Radical process</td>
<td>Reduced</td>
<td>Well-developed</td>
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<tr>
<td>Radical apophysis</td>
<td>Blunt</td>
<td>With a sharp tip</td>
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<td>Median process of the conductor</td>
<td>With curved tip</td>
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<tr>
<td>Ventral process of the paracymbium</td>
<td>Inclined</td>
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<td>Female</td>
<td></td>
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<tr>
<td>Receptacle</td>
<td>Comma-shaped, 1/3 of median plate’s width and 2 times longer than wide</td>
<td>Ovoid, 0.4 of median plate’s width and 1.3 times longer than wide</td>
</tr>
<tr>
<td>Club-like gland</td>
<td>Located outwards from receptacle</td>
<td>Overlapping with receptacle</td>
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Table 1. Differences between Daginesticus gen.n. and Aituaria.
Таблица 1. Различия между Daginesticus gen.n. и Aituaria.

DESCRIPTION. Medium sized (3.75–5.5). Carapace oval in dorsal view. Cephalic region not raised and poorly differentiated from the rest of carapace. Fovea clearly visible, oval. Chelicerae with 3 promarginal teeth. Eyes well-developed. Leg formula I-IV-II-III or I-II-IV-III. Abdomen elliptical in dorsal view, with pattern formed by 2 rows of dark grey spots or scalloped black stipe.

Male palp. Femur twice longer than patella+tibia. Tibia 1.5 times longer than patella. Cymbium oval. Paracymbium (Pa) large, about 2/3 of cymbial length. Paracymbium with 3 robust well-sclerotized apophyses: hooked distal (Di), dorso-ventrally flattened dorsal (Do) and triangular ventral (Ve). Tegulum (Te) round, almost as long as wide, occupies half of the cymbial length. Subtegulum (St) oval in ventral view. Radix (Rx) complex. Radical apophysis (Ra) triangular. Conductor complex with several processes (arms). Prolateral process of conductor (Cr) located anteriorly and surpasses the embolus tip. Median process of conductor (Cm) curved distally. Embolus (Em) whip-like, starting at about 5 o’clock, partially bordering tegulum. Embolus tip not modified.

Epigyne. Median plate (Mp) as long as wide. Receptacle (Re) weakly sclerotized, comma-shaped. Club-like gland (Cg) located on the short copulatory duct (Co) and outwards from the receptacle.

COMPOSITION. Daginesticus dzhamirzoevi sp.n. and D. mamajevae (Marusik, 1987) comb.n.

DISTRIBUTION. Known only from the eastern Caucasus (Dagestan, Russia, and eastern Georgia) (Fig. 22).

COMMENTS. Although the morphology of epigynes of the two Daginesticus species apparently does not show clear similarities, common features can be more easily observed in the male palp (e.g. lack of radical process). Such characters support a putative affinity between the two species included in the genus. In addition, the results of our molecular analysis further suggest a high supported close relation-
Figs 4–7. Male palp of *Daginesticus dzhamirzoevi* sp.n. 4 — dorsal; 5 — ventral; 6 — prolateral; 7 — retrolateral. Scale bars: 0.2 mm.

Abbreviations: Cm — median process of the conductor, Cp — prolateral process of the conductor, Cr — retrolateral process of the conductor, Di — distal apophysis of the paracymbium, Do — dorsal apophysis of the paracymbium, Em — embolus, Mn — membrane between Rx and Te, Pa — paracymbium, Ra — radical apophysis, Rx — radix, St — subtegulum, Te — tegulum, Ve — ventral apophysis of the paracymbium.

Рис. 4–7. Пальпа самца *Daginesticus dzhamirzoevi* sp.n. 4 — дорсально; 5 — вентрально; 6 — пролатерально; 7 — ретролатерально. Масштаб: 0,2 мм. Сокращения: Cm — медиальный отросток кондуктора, Cp — пролатеральный отросток кондуктора, Cr — ретролатеральный отросток кондуктора, Di — дистальный апофиз парацимбиума, Do — дорсальный апофиз парацимбиума, Em — эмболус, Mn — мембрана между Rx и Te, Pa — парацимбиум, Ra — апофиз радика, Rx — радикс, St — субтегулюм, Te — тегулюм, Ve — вентральный апофиз парацимбиума.
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Figs 8–15. Bulb (8–13), cymbium and tibia (14) and paracymbium (15) of Daginesticus dzhamirzoevi sp.n. 8 — prolateral; 9, 14 — ventral; 10 — retrolateral; 11, 15 — anterior; 12 — dorsal; 13 — posterior. Scale bars: 0.2 mm. Abbreviations: Cd — dorsal process of the conductor, Cm — median process of the conductor, Cn — connection between Rx and Te, Cp — prolateral process of the conductor, Cr — retrolateral process of the conductor, Di — distal apophysis of the paracymbium, Do — dorsal apophysis of the paracymbium, Em — embolus, Mn — membrane between Rx and Te, Pa — paracymbium, Ra — radical apophysis, Rm — radical membrane, Rx — radix, Sd — sperm duct, St — subtegulum, Te — tegulum.

Bulb (8–13), cymbium and tibia (14) and paracymbium (15) of Daginesticus dzhamirzoevi sp.n. 8 — prolateral; 9, 14 — ventral; 10 — retrolateral; 11, 15 — anterior; 12 — dorsal; 13 — posterior. Scale bars: 0.2 mm. Abbreviations: Cd — dorsal process of the conductor, Cm — median process of the conductor, Cn — connection between Rx and Te, Cp — prolateral process of the conductor, Cr — retrolateral process of the conductor, Di — distal apophysis of the paracymbium, Do — dorsal apophysis of the paracymbium, Em — embolus, Mn — membrane between Rx and Te, Pa — paracymbium, Ra — radical apophysis, Rm — radical membrane, Rx — radix, Sd — sperm duct, St — subtegulum, Te — tegulum.

ship between D. dzhamirzoevi sp.n. and D. mamajeva which are resolved as part of the same monophyletic clade. Additional revisions of nesticid species from the Caucasus and surrounding areas may help to extend the list of morphological diagnostic characters of Daginesticus gen.n. and its differences with Aituaria.
Daginesticus dzhamirzoievii sp.n.
Figs 1–22, 30.

TYPES. RUSSIA: Dagastan: holotype ♀ (ISEA, 001.8872) and paratypes 1♂ 10♀♀ (ISEA, 001.8873), 1♂ (ISEA, 001.8874), 3 km WNW from Gunib Village (42°24′21.9″N, 46°55′30.5″E), deep stone screes, 1700 m, 7.05.2021, A.A. Fomichev, Y.V. Dyachkov.

ETYMOLOGY. The specific name is a patronym in honour of Gadzhikhe S. Dzhamirzoev (Makhachkala, Russia), a research fellow of the Dagestan Nature Reserve, who helped to organize an expedition to Dagastan in which the types of this new species were collected.

DIAGNOSIS. The new species differs from D. mamajevae in having radical apophysis (Ra) equal in length and width (vs. twice longer than wide), retrolateral process of the conductor (Cr) significantly larger than the median process of the conductor (Cm) (vs. equal in size), and dorsal process of the paracymbium (Do) as long as ventral (Ve) (vs. 5 times longer) (cf. Figs 5, 9, 14 and 23). Female of new species can be differed from that of D. mamajevae by the median plate (Mp) with concave posterior edge (vs. convex) (cf. Figs 16 and 24).

DESCRIPTION. Male (holotype). Total length 3.75. Carapace: 1.75 long, 1.45 wide. Coloration. Carapace pale yellow with grey edges. Cephalic part with thin grey median band and grey bands around the edges. Chelicerae, maxillae and labium pale yellow. Sternum dirty yellow. Palps and legs pale yellow. Abdomen beige dorsally, with pattern formed by 2 rows of dark grey spots. Venter of abdomen dirty beige. Spinnerets yellow. Leg measurements. I: 3.8, 0.75, 3.9, 3.8, 1.4 (13.65). II: 3.05, 0.7, 2.9, 2.85, 1.15 (10.65). III: 2.45, 0.55, 1.85, 2.0, 0.85 (7.7). IV: 3.35, 0.65, 2.85, 2.75, 1.1 (10.7).

Palp as in Figs 4–15. Cymbium 1.5 times longer than wide, covered with long setae in the distal area near the tip. Distal process of the paracymbium (Di) square-shaped in the lateral view. Dorsal apophysis (Do) finger-like. Ventral apophysis (Ve) inclined. Sperm duct (Sd) encircles whole tegulum (Te). Radical apophysis (Ra) with serrated surface. Retrolateral process of the conductor (Cr) curved prolaterally. Median process of the conductor (Cm) originating at an 1 o’clock position and its tip bent prolaterally. Dorsal process of conductor (Cd) triangular. Embolus (Em) slightly widened in basal part.

Female. Total length 5.5. Carapace: 2.05 long, 1.7 wide. Coloration as in male, but carapace with grey median band. Grey spots on abdomen larger than in male. Leg measurements. I: 4.15, 0.95, 4.55, 4.3, 1.7 (15.65). II: 3.55, 0.85, 3.3, 3.2, 1.4 (12.3). III: 2.8, 0.7, 2.1, 2.25, 1.1 (8.95). IV: 3.9, 0.8, 3.2, 2.9, 1.25 (10.05).

Epigyne as in Figs 16–18. Median plate 2 time wider than long, translucent. Receptacles (Re) clearly visible even in intact epigyne. Copulatory duct (Co) shorter than length of club-like gland (Cg). Slanting fold (Sf) of receptacle curved posteriorly.

HABITAT. Specimens were collected in deep layer of scree formed by large stones (diameter ~20 cm) (Fig. 20) located in a pine forest. It was covered with a coniferous litter and layer of soil 5–15 cm thick. Spiders were found on the underside of the stones (Fig. 21).

DISTRIBUTION. Known from the type locality only (Fig. 22).

Daginesticus mamajevae (Marusik, 1987) comb.n.
Figs 23–24, 30.

Carpathonesticus mamajevae Marusik, 1987: 461, figs 1–2 (Cm).

MATERIAL EXAMINED. GEORGIA: Kakheti: 12♂♂ 5♀♀ (ZMMU), Lagodekhi Town (41°51′N 46°20′E), cellar, 1834 m, 27.07.2012, Yu.M. Marusik.

DIAGNOSIS. Daginesticus mamajevae differs from the genotype in having radical apophysis (Ra) twice longer than wide (vs. equal in length and width), retrolateral and median processes of the conductor (Cr and Cm) equal in size (vs. Cr significantly larger than Cm) and dorsal process of the paracymbium (Do) about 5 times longer than the ventral (Ve) (vs. equal in length) (cf. Figs 5, 9, 14 and 23) in males. Female of D. mamajevae can be differed from that of the genotype by the median plate (Mp) with convex posterior edge (vs. concave) (cf. Figs 16 and 24).

DESCRIPTION. Male. See Marusik [1987]. Palp as in Fig. 23. Dorsal apophysis of the paracymbium (Do) extremely large, as long as tegulum. Retrolateral process of the conductor (Cr) straight. Median process of the conductor (Cm) started from the 1 o’clock and its tip bent prolaterally. Embolus (Em) the same thickness along its entire length.

Female. See Marusik [1987]. Epigyne as in Fig. 24.

DISTRIBUTION. Known from the type locality only (Fig. 22).

COMMENTS. The new combination is proposed based on molecular evidence (Fig. 30) and the combination of following characters: reduced radical process (Rp) and medium process of the conductor (Cm) with curved tip. In addition, molecular analysis suggests D. mamajevae comb.n. not to be closely related to the genus Carpathonesticus, but instead nested with high support within the monophyletic clade of the genus Daginesticus gen.n. (Fig. 30).

Aituaria Eysunin et Efimik, 1998


TYPE SPECIES: type A. nataliae Eysunin et Efimik, 1998 (considered as synonym of Nesticus ponticus Spassky, 1932).

DIAGNOSIS. See Eysunin [2017] and the diagnosis of Daginesticus gen.n. For list of differences between Daginesticus gen.n. and Aituaria see Table 1.

DESCRIPTION. See Eysunin & Efimik [1998].

COMPOSITION. Aituaria borutzkyi (Reimoser, 1930) comb.n., A. eriashvilii (Marusik, 1987) comb.n., A. iranica Zamani et Marusik, 2021, and A. poniatowskii (Spassky, 1932). Belonging of A. iranica to the genus was doubt by the authors [Zamani, Marusik, 2021]

DISTRIBUTION. From coastal areas of the Black Sea to the Caucasus and northern Iran.

Aituaria borutzkyi (Reimoser, 1930) comb.n.
Figs 27–29.


Carpathonesticus borutzkyi Zamani, Kovblyuk, 2007: 291, figs 1–6 (♂♀).

For the complete list of references see WSC [2022].

MATERIAL EXAMINED. GEORGIA: Imereti: 2♂♂ 7♀♀ (ZMMU), near Mudzheureti Vill. (42°17′07.0″N 43°04′28.9″E), cave, 341 m, 24.07.2012, Yu.M. Marusik.

DIAGNOSIS. See Nadolny & Kovblyuk [2007].
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Figs 16–24. *Daginesticus* spp.: epigyne (16–18), cephalic part of the male (19), habitat (20), live female of *D. dzhamirzoevi* sp.n. *in situ* (21); male palp (23) and epigyne (24) of *D. mamajevae*; map (22), showing type localities. 16 — intact, ventral; 17 — macerated, ventral; 18 — macerated, dorsal; 19 — anterior. Circle — *D. dzhamirzoevi* sp.n., square — *D. mamajevae*. 23–24 — after Marusik [1987]. Scale bars: 0.2 mm. Abbreviations: Cg — club-like gland, Cm — median process of the conductor, Cp — prolateral process of the conductor, Cr — retrolateral process of the conductor, Co — copulatory duct, Di — distal apophysis of the paracymbium, Do — dorsal apophysis of the paracymbium, Em — embolus, Mp — median plate, Pa — paracymbium, Ra — radical apophysis, Re — receptacle, Rx — radix, Sf — slanting fold of Re, St — subtegulum, Te — tegulum, Ve — ventral apophysis of the paracymbium.

Figs 25–29. Male palp (25, 27), radix (28–29) and epigyne (26) of *Aituaria pontica* (25–26) and *A. borutzkyi* (27–29). 25, 27, 29 — ventral; 26 — dorsal; 28 — anterior. 25, 27, 29 — after Zamani, Marusik [2021]. Scale bars: 0.2 mm. Abbreviations: Cg — club-like gland, Cm — median process of the conductor, Cp — prolateral process of the conductor, Cr — retrolateral process of the conductor, Di — distal apophysis of the paracymbium, Do — dorsal apophysis of the paracymbium, Em — embolus, Ra — radical apophysis, Re — receptacle, Rm — radical membrane, Rp — radical process, Rx — radix, Sf — slanting fold of Re, St — subtegulum, Ve — ventral apophysis of the paracymbium.

**MATERIAL EXAMINED.** UKRAINE: Chernivtsi Oblast: 2 ## (ZMMU), Chernivtsi City, Korduby Street 17 (48°16′60″ N 25°56′06″ E), cellar, 25.02.2017, V. Voloshyn & M. Fedoriak; Donetsk Oblast: 1 # (PCP), Donetsk (48°00′ N 37°48′ E), cellar, 18.10.2012, V. V. Martynov.

**DIAGNOSIS.** See Marusik et al. [2017].

**DESCRIPTION.** Male and female. See Nadolny & Kovblyuk [2007]. Male palp as in Figs 27–29.

**DISTRIBUTION.** Crimea, Turkey, Georgia.

**COMMENTS.** Esyunin [2017] suggested a closer relationship between *Aituaria pontica* and *Carpathonesticus* species belonging to the *borutzkyi*-group from the Caucasus. Our molecular analysis supports this affinity (Fig. 30). In addition to molecular evidence, the new combination is proposed on the basis of the following morphological characters in male palp: well-developed radical process (Rp), median process of the conductor (Cm) with strait tip, radical apophysis (Ra) ending in a sharp tip.

*Aituaria eriashvilii* (Marusik, 1987) **comb.n.**


**MATERIAL EXAMINED.** UKRAINE: Chernivtsi Oblast: 2 ♀ ♀ (ZMMU), Chernivtsi City, Korduby Street 17 (48°16′60″ N 25°56′06″ E), cellar, 25.02.2017, V. Voloshyn & M. Fedoriak; Donetsk Oblast: 1 ♀ ♀ (PCP), Donetsk (48°00′ N 37°48′ E), cellar, 18.10.2012, V. V. Martynov.

**DIAGNOSIS.** See Marusik et al. [2017].

**DESCRIPTION.** Male and female. See Marusik et al. [2017].

**DISTRIBUTION.** Ukraine and Georgia.

**COMMENTS.** The new combination is proposed on the basis of molecular evidence (Fig. 30). Although females of *A. eriashvilii* comb. n. and *A. pontica* show a rather different shape of the epigyne, the new combination is also supported by the following morphological characters shared by the male palps of the two species: well-developed radical process (Rp), median process of the conductor (Cm) with strait tip, radical apophysis (Ra) ending in a sharp tip.
Phylogenetic analysis

The final matrix formed by the concatenated sequences numbers 32 terminals and a total length of 2029 bp partitioned as follows: COI = 1197 bp, 16S = 490 bp, and H3 = 342 bp. The resulting ML tree is illustrated in Fig. 30. It shows a well-resolved phylogeny of the European genera of the family Nesticidae which topology is in line with the results of previous studies (see Pavlek & Ribera [2017]; Ballarin [2020]). All the European genera (Aituaria Esyunin et Efimik, 1998, Carpathonesticus Lehtinen et Saaristo, 1980, Domitius Ribera, 2018, Kryptonesticus Pavlek et Ribera, 2017, Nesticus Thorell, 1869, and Typhlonesticus Kulczyński, 1914) are determined as separate clades with high bootstrap support value (BS = 97–100%), Carpathonesticus however represents a special case. Although its generotype and other species from the Carpathian Mountains form a distinct, highly supported monophyletic clade (BS = 100%), some Carpathonesticus species outside this geographic region like C. borutzkyi (Reimoser, 1930) and C. eriashvili Marusik, 1987 group together with the distant related sp.n. and Typhlonesticus Kulczyński, 1914) are determined as separate clades with high bootstrap support value (BS = 97–100%). Carpathonesticus however represents a special case. Although its generotype and other species from the Carpathian Mountains form a distinct, highly supported monophyletic clade (BS = 100%), some Carpathonesticus species outside this geographic region like C. borutzkyi (Reimoser, 1930) and C. eriashvili Marusik, 1987 group together with the distant related Aituaria pontica (Spassky, 1932), suggesting an affinity with this genus.

Although the support of A. pontica is still resolved as low (BS = 59%), in our analysis D. dzhamirzoevi sp.n. and D. mamajevae cluster together in a monophyletic clade distinct from the clade formed by A. pontica, C. borutzkyi and C. eriashvili (BS = 97%). The two groups clearly share the same evolutionary line. The outcome also corroborates the attribution of D. mamajevae to the new genus, genetically far from the genus Carpathonesticus in which it was previously included.

The uncorrected pairwise-distance analysis shows a genetic distance among the European genera ranging between 10–20% with a mean around 13–17%. The newly established genus Daginesticus gen.n. also follows this rule, having an estimated genetic divergence of 13% with its sister genus Aituaria (Table 2).

### Table 2. Uncorrected pairwise-distance between Daginesticus gen.n. and the main genera of the family Nesticidae in Europe based on standard barcode COI gene fragment. The Nearctic genus Gaucelmus is also included. The type species of each genus were used for the comparison.

<table>
<thead>
<tr>
<th></th>
<th>Domitius</th>
<th>Nesticus</th>
<th>Carpathonesticus</th>
<th>Kryptonesticus</th>
<th>Daginesticus</th>
<th>Aituaria</th>
<th>Typhlonesticus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Domitius</td>
<td>0.17</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
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<td></td>
<td></td>
<td>0.18</td>
<td>0.16</td>
<td>0.18</td>
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<tr>
<td>Carpathonesticus</td>
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<td>0.10</td>
<td></td>
<td>0.12</td>
<td>0.13</td>
<td>0.14</td>
<td>0.13</td>
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<tr>
<td>Kryptonesticus</td>
<td>0.18</td>
<td>0.16</td>
<td>0.16</td>
<td>0.15</td>
<td>0.13</td>
<td>0.13</td>
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<tr>
<td>Daginesticus</td>
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<td>0.14</td>
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<td>0.13</td>
<td>0.13</td>
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<tr>
<td>Aituaria</td>
<td>0.20</td>
<td>0.17</td>
<td>0.16</td>
<td>0.15</td>
<td>0.17</td>
<td>0.17</td>
<td>0.16</td>
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<tr>
<td>Typhlonesticus</td>
<td>0.23</td>
<td>0.22</td>
<td>0.22</td>
<td>0.22</td>
<td>0.21</td>
<td>0.21</td>
<td>0.24</td>
</tr>
</tbody>
</table>

Notes on morphology of male palp in Nesticidae

Many authors dealing with morphology of the male palp in Nesticidae [Dumitrescu, 1979; Huber, 1993; Nadjoliny, Kovalyuk, 2007; López-Pancorbo, Ribera, 2011; Ribera et al., 2014; etc.] indicate the process originated from the base of the embolus (radix, embolic division) as median apophysis while in all Entelegyne spiders it originates from the tegulum. A clear membranous connection (Mn) between base of embolus and tegulum can be observed (see Figs 7, 10).

In addition, some authors use the term “Theridioid tegular apophyses 1, 2” to indicate the branches of the conductor. Recent studies (e.g. Garrison et al. [2016]; Wheeler et al. [2017]) suggest a distant phylogenetic relationship between Theridiidae and Nesticidae, thus not supporting a possible homology between the structures of the conductor in these two families. Huber [1993, figs 1, 3a] indicates six processes as parts of the conductor in Nesticus cellulamus (Clerck, 1757), although two of them, p6 and p5, look like one radical process separated from the radix by a membrane (Fig. 8, Rm). It was found [Marusik et al., 2017] that conductor in Aituaria has more complicated structure than documented before and besides terminal branches, it has a weakly sclerotized prolateral arm directed anteclockwise. Daginesticus gen.n., all Aituaria examined, as well as other genera like Nesticella and Nescina Ballarin et Li, 2015 have the same type of conductor with prolateral, retrolateral and ventral branches [Lin et al., 2016].

Discussion

Both morphology and molecular evidences support the establishment of Daginesticus gen.n. as a well-
defined genus, separated from other West Palaearctic Nesticidae. Its affinity with *Aituaria*, with which it shares a close geographic distribution, is also corroborated by our results.

Our molecular analysis confirms the other previously-established European nesticid genera as distinct clades. However, *Carpathonesticus*, with its current composition, appears to be paraphyletic. The species from the Caucasus and neighboring areas currently included in this taxon appear to be not closely related to the generotype of *Carpathonesticus*. Instead, they show a closer relationship with *Aituaria* or *Daginesticus* gen.n. Nevertheless, we included only three former *Carpathonesticus* species in our present work. It is likely that other species included in the borutzyi-group sensu Lehtinen, Saaristo [1980] and Esyunin [2017] (*C. birsteini* (Charitonov, 1947), *C. caucasicus* (Charitonov, 1947), *C. zaitzevi* (Charitonov, 1939), and *C. liovuschkini* (Pichka, 1965)) should also be transferred to *Aituaria* or *Daginesticus* although we did not have enough material to properly support this hypothesis. A wider revision of the Caucasian species, using both molecular and morphological data, may further elucidate the correct phylogenetic position of these species within the family Nesticidae.

**Compliance with ethical standards**

**CONFLICTS OF INTEREST**: The authors declare that they have no conflicts of interest.

**Acknowledgements**. We thank Roman V. Yakovlev (Barnaul, Russia), Gadzhibeik S. Dzharmirzoev, Magomed-Rasul D. Magomedov, Kurban M. Kuniev, Abdulgamid A. Teimurov, Oleg V. Kravets (all five from Makhachkala, Russia), and Zagirbek M. Asadulaev (Gunib, Russia) for organizing and undertaking an expedition to Dagestan in which the material treated in this paper was collected. Thanks also go to Yuri V. Dyachkov (Barnaul, Russia) for being a great help in collecting, to Nazar A. Shapoval (Saint-Petersburg, Russia) for the linguistic help and to Sergei V. Reshetnikov (Novosibirsk, Russia) for his help in preparing the illustrations. YM thanks Shuqiang Li (Beijing, China) for accompanying in the collecting trip to Georgia, Alexander Abuladze (Tallinn, Estonia) and Andrei S. Kandaurov (Tbilisi, Georgia) for their help in organization of the trip. We also wish to thank the editor Kirill G. Mihailov (Moscow, Russia), and the reviewers Alireza Zamani (Turku, Finland), Martina Pavlek (Zagreb, Croatia) and anonymous reviewer and for their critical comments which helped improving the
Table 3. List of species, gene fragments and related GenBank accession numbers used in the molecular analysis. Sequences obtained in the present study are indicated by an asterisk.

<table>
<thead>
<tr>
<th>Species</th>
<th>Code</th>
<th>COI</th>
<th>I6S</th>
<th>H3</th>
<th>Locality</th>
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<tbody>
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<td><em>Altaria pontica</em></td>
<td>A193</td>
<td>OM630576*</td>
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<td>OM642843*</td>
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<td><em>Altaria borutzkyi</em></td>
<td>A231</td>
<td>OM630577*</td>
<td>OM631940*</td>
<td>OM642848*</td>
<td>Sataple Cave, Imereti, Georgia</td>
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<td><em>Altaria eriashvilli</em></td>
<td>A250</td>
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<td>OM631939*</td>
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<tr>
<td><em>Carpathonesticus fodmarum</em></td>
<td>Cod</td>
<td>MK860157</td>
<td>MK860139</td>
<td>MK860148</td>
<td>Small cave along the river, Sighiștel, Bihor, Romania</td>
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<tr>
<td><em>Carpathonesticus hungaricus</em></td>
<td>Chun</td>
<td>KF417412</td>
<td>KF417402</td>
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<td>Clot</td>
<td>MK860158</td>
<td>MK860140</td>
<td>MK860149</td>
<td>Humid and shadowed cliff near Lazaret village, Sibiu, Romania</td>
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<tr>
<td><em>Carpathonesticus racovitzaei</em></td>
<td>Crac</td>
<td>MG201045</td>
<td>MG200514</td>
<td>MG201222</td>
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<td><em>Carpathonesticus simoni</em></td>
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<td>KF417398</td>
<td>KF417417</td>
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<td>OM631936*</td>
<td>OM642844*</td>
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<td>MF693118</td>
<td>MF693106</td>
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<td>MK860134</td>
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<td>MF693104</td>
<td>Cueva de la Pica, San Pedro de Carmona, Cantabria, Spain</td>
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<td>MF693113</td>
<td>EU746429</td>
<td>MF693105</td>
<td>Algar de Marradiñas II, Concello de Alcancena, Portugal</td>
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<td>MF693116</td>
<td>MF693102</td>
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<tr>
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<td>MK860153</td>
<td>MK860135</td>
<td>MK860144</td>
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<td>Kdl</td>
<td>KX632167</td>
<td>KX632160</td>
<td>KX611237</td>
<td>Samarogorska šipila, Biskova Mt., Croatia</td>
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<tr>
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<td>MK860137</td>
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<td>KX632166</td>
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<td>KX611236</td>
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<td><em>Nesticus cellulans</em></td>
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<td>MK860154</td>
<td>MK860136</td>
<td>MK860145</td>
<td>Cavel di Koufouanou, Didimoticho, Thrace, Greece</td>
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<td>KF393915</td>
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manuscript. The work of Alexander A. Fomichev was supported in the framework of “Priority-2030” Program by the Altai State University. The English of the final draft was edited by Alireza Zamani.

References


Responsibles editor K.G. Mikhailov