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

Alexander A. Fomichev1,2, Francesco Ballarin3,4, Yuri M. Marusik5,6
A.A. Фомичев1,2, Ф. Балларин3,4, Ю.М. Марусик5,6

1 Altai State University, Lenina Pr., 61, Barnaul, RF-656049, Russia. E-mail: a.fomichev@mail.ru
2 Tomsk State University, Lenina Pr., 36, Tomsk, RF-634050, Russia.
3 Systematic Zoology Laboratory, Department of Biological Sciences, Tokyo Metropolitan University, 1-1 Minami-Osawa, Hachioji-shi, 192-0397, Tokyo, Japan. E-mail: ballarin.francesco@gmail.com
4 Institute for Biological Problems of the North of the Far Eastern Branch of the Russian Academy of Sciences, Portovaya str., 18, Magadan 685000 Russia. E-mail: yurmar@mail.ru
5 Department of Zoology, Civic Museum of Natural History of Verona, Lungadige Porta Vittoria, 9, I-37129 – Verona, Italy.
6 Department of Zoology and Entomology, University of the Free State, Bloemfontein 9300 South Africa

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 mamajevae (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 Nestici for From the paper: Fomichev A.A., Ballarin F., Marusik Yu.M. 2022. A new genus of the family Nesticidae (Arachnida: Aranei) from the Caucasus // Arthropoda Selecta. Vol.31. No.1. P.99–110. doi: 10.15298/arth.31.1.12

РЕЗЮМЕ. На основании морфологических и молекулярных данных, с Кавказа описывается новый род Daginesticus gen.n. с типовым видом D. dzhamirzoevi sp.n. (♂♂). Предложены новые комбинации: Daginesticus mamajevae (Marusik, 1987) comb. n., Aituaria borutzkyi (Reimoser, 1930) comb. n. и Aituaria eriashvilii (Marusik, 1987) comb. n. (все исключаются из рода Carpathonesticus). Новый род близок к роду Aituaria Esyunin et Efimik, 1998, имеется хорошо развитые глаза и пигментацию. Приводится описание, иллюстрации, диагноз и фотография биотопа. Обсуждается структура пальцы самца у Nesticini, предлагается новая терминология, основанная на гомологии различных склеритов.

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 [Dippnaar-Schoeman, Jocqué, 1997]. West Palaeartic nesticids are relatively well studied owing to existence of one global [Kratochvil, 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 mamajevae* Marusik, 1987 from eastern Georgia, appeared to be closely related to the new taxon. 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** — coxal plate, **Cr** — prolateral process of the conductor, **Cr** — retro-lateral process of the 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, **Rr** — radical process, **Rx** — radix, **Sd** — sperm duct, **St** — slanting fold of **Re**, **St** — subtegulum, **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 Nesticinae 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 generotype, 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 (**Rr**) (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...
A new genus of Nesticidae from the Caucasus

Table 1. Differences between *Daginesticus* gen.n. and *Aituaria*.

| Structures of copulatory organs | *Daginesticus* gen.n. | *Aituaria* spp. |
|---------------------------------|----------------------|-----------------|
| Male                            |                      |                 |
| Radical process                 | Reduced              | Well-developed  |
| Radical apophysis               | Blunt                | With a sharp tip|
| Median process of the conductor | With curved tip      | Straight        |
| Ventral process of the paracymbium | Inclined           | Straight        |
| Female                          |                      |                 |
| Receptacle                      | Comma-shaped, 1/3 of median plate’s width and 2 times longer than wide | Ovoid, 0.4 of median plate’s width and 1.3 times longer than wide |
| Club-like gland                 | Located outwards from receptacle | Overlapping with receptacle |

Figs 1–3. Habitus of *Daginesticus dzhamirzoevi* sp.n., male (1–2) and female (3). 1 — lateral; 2–3 — dorsal. Scale bars: 2 mm.

16–18 and 26). For a list of differences between *Daginesticus* gen.n. and *Aituaria* see Table 1.

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-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) long, weakly sclerotized. Retrolateral process of conductor (Cp) 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. mamajeva* (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 паракимбия, Do — дорсальный апофиз паракимбия, Em — эмбол, Mn — мембрана между Rx и Te, Pa — паракимбий, Ra — апофис радика, Rx — радикс, St — субтегулюм, Te — тегулюм, Ve — вентральный апофиз паракимбия.
A new genus of Nesticidae from the Caucasus

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.

ship between D. dzhamirzoevi sp.n. and D. mamajevae 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 dzhamirzoevi** sp.n.

Figs 1–22, 30.

**TYPES. RUSSIA: Dagestan:** holotype ♂ (ISEA, 001.8872) and paratypes 1♂ 1♀ (ISEA, 001.8873), 1♀ (ISEA, 001.8874), 3 km WNW from Gunib Village (42°24′21″N, 46°55′30″E), deep stone scree, 1700 m, 7.05.2021, A.A. Fomichev, Y.V. Dyachkov.

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

**DIAGNOSIS.** The new species differs from *D. mamajevae* in having radial 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 labium pale yellow. Sternum dirty yellow. Palps and labium pale yellow. Cephalic part with thin grey median band. Embolus (Em) the same thickness along its entire length.

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. Spur of the conductor (Cr) curved prolaterally. Median process of the conductor (Cm) starting from the 1 o’clock and its tip bent prolaterally. Dorsal process of conductor (Cdl) 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 (12.05).

Epigyne as in Figs 16–18. Median plate 2 times 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 (Sy) 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 (♂). 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 radial 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 median process of the conductor (Cm) with curved tip. In addition, molecular analysis suggests *D. mamajevae* comb.n. 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 Esyunin et Efimik, 1998**

**Aituaria Esyunin et Efimik, 1998: 145.**

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

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

**DESCRIPTION.** See Esyunin & Efimik [1998].

**COMPOSITION.** *Aituaria borutzkyi* (Reimoser, 1930) comb.n., *A. eriashvilii* (Marusik, 1987) comb.n., *A. iranica* Zamani et Marusik, 2021, and *A. poonagia* (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.**

*Nesticus borutzkyi* Reimoser, 1930: 158, fig 1 (♂).

**Nesticus borutzkyi:** Churentov, 1941: 69, figs 1–2 (♂). **Carpathonesticus borutzkyi** Nadolny, Kobylyuk, 2007: 291, figs 1–6 (♂). MATERIAL EXAMINED. GEORGIA: Imereeti: 2♂♀ 7♀♂ (ZMMU), near Mudzhureti Vill. (42°17′07″N 43°04′28.9″E), cave, 341 m, 24.07.2012, Yu.M. Marusik.

**DIAGNOSIS.** See Nadolny & Kobylyuk [2007].
A new genus of Nesticidae from the Caucasus

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.

Рис. 16–24. Daginesticus spp.: эпигина (16–18), головная часть самца (19), биотоп (20), живая самка *in situ* (21) D. dzhamirzoevi sp. *n.*, пальма самца (23) и эпигина (24) D. mamajevae; карта (22), показывающая типовые местности. 16 — интактная, вентрально; 17 — мацерированная, вентрально; 18 — мацерированная, дорсально; 19 — спереди. Круг — D. dzhamirzoevi sp. *n.*, квадрат — D. mamajevae. 23–24 — по Marusik [1987]. Масштаб: 0,2 мм. Сокращения: *Cg* — булавовидная железа, *Cm* — медиальный отросток кондуктора, *Cp* — пролатеральный отросток кондуктора, *Cr* — ретролатеральный отросток кондуктора, *Co* — копулятивный канал, *Di* — дистальный апофиз парацимбия, *Do* — дорсальный апофиз парацимбия, *Em* — эмбол, *Mp* — медиальная пластинка, *Pa* — парацимбий, *Ra* — апофиз радика, *Re* — receptакуль, *Rx* — радикс, *Sf* — наклонная складка *Re*, *St* — субтегулоом, *Te* — тегулоум, *Ve* — вентральный апофиз парацимбия.
Fig. 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. 26 — 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: 2¹³°₂⁰'₂₀" (ZMMU), Chernivtsi City, Korduby Street 17 (48°16′60″ N 25°56′06″ E), cellar, 25.02.2017, V. Voloshyn & M. Fedoriak; Donetsk Oblast: 1¹⁰°₂³'(ZCP), 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.**

*Carpathonesticus eriashvilii* Marusik, 1987: 462, fig. 3 (†). *Carpathonesticus eriashvilii* Marusik *et al.*, 2017: 302, figs 1–6, 8–17, 23-33, 38–40 (†).
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. eriashvilii Marusik, 1987 group together with the distant related Aituaria sp.n. and Typhlonesticus Kulczyński, 1914) are determined to form 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).

Notes on morphology of male palp in Nesticidae

Many authors dealing with morphology of the male palp in Nesticidae [Dumitrescu, 1979; Huber, 1993; Nadolny, Kobylyuk, 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 Entelegyneae 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 cellulanus (Clerck, 1757), although two of them, p6 and p5, look like one radical process separated from the radix by a membrane (Fig. 8, Rmn). 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 process directed anti-clockwise. 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-

|              | Domitius | Nesticus | Carpathonesticus | Kryptonesticus | Daginesticus | Aituaria | Typhlonesticus |
|--------------|----------|----------|------------------|---------------|--------------|----------|---------------|
| Domitius     |          |          |                  |               |              |          |               |
| Nesticus     | 0.17     |          |                  |               |              |          |               |
| Carpathonesticus | 0.17 | 0.10     |                  |               |              |          |               |
| Kryptonesticus | 0.15 | 0.13     | 0.12             |               |              |          |               |
| Daginesticus | 0.18     | 0.16     | 0.16             | 0.15          |              |          |               |
| Aituaria     | 0.16     | 0.14     | 0.13             | 0.13          | 0.13         |          |               |
| Typhlonesticus | 0.20 | 0.17     | 0.16             | 0.15          | 0.17         | 0.16     |               |
| Gaucelmus    | 0.23     | 0.22     | 0.22             | 0.22          | 0.21         | 0.21     | 0.24          |

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.

Таблица 2. Нескорректированные попарные генетические дистанции между Daginesticus gen.n. и основными родами европейских Nesticidae, вычисленные для стандартного фрагмента гена COI (ДНК-баркода). Также включен неарктический род Gaucelmus. Для сравнения использованы типовые виды каждого рода.
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), Gadzhibek S. Dzhamirzoev, 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 (Tbilisi, Georgia) 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.

| Species              | Code  | COI     | 16S     | H3      | Locality                                      |
|----------------------|-------|---------|---------|---------|-----------------------------------------------|
| Altaria pontica      | A193  | OM630576*| OM631938*| OM642843*| Sevastopol, Crimea, Russia                    |
| Altaria borutzkyi    | A231  | OM630577*| OM631940*| OM642848*| Sataple Cave, Imereti, Georgia                |
| Altaria eriashvili   | A250  | OM630578*| OM631939*| OM642847*| Chermitsyi City, cellar, Ukraine              |
| Carpathostenicus fodiunum | Ccod | MK860157 | MK860139 | MK860148 | Small cave along the river, Sighistel, Bihor, Romania |
| Carpathostenicus hungaricus | Chun | KF417412 | KF417402 | KF417419 | Peștera Lilieciul, Chelie Ampoitei Gorges, Romania |
| Carpathostenicus kotriensis | Clot | MK860158 | MK860140 | MK860149 | Humid and shadowed cliff near Lazaret village, Sibiu, Romania |
| Carpathostenicus racovitzaei | Crac | MG201045 | MG200514 | MG201222 | small cave near Peștera Poarta Lui Lonele, Munăca Village, Alba Distr., Romania |
| Carpathostenicus simoni | Csim | KF417408 | KF417398 | KF417417 | cave in Bisbrita Gorges, Stogu-Vinturarita Mts., Romania |
| Dagsteinestes dzhaminrozevi | Ne63 | OM630573*| OM631936*| OM642844*| Gubin Village, Dagestan, Russia               |
| Dagsteinestes dzhamirozevi | Ne64 | OM630574*| OM631937*| OM642845*| Gubin Village, Dagestan, Russia               |
| Dagsteinestes manjevaei | A201 | OM630575*| OM631941*| OM642846*| Lagodekhi, Georgia                            |
| Domitius baeticus    | Dbae  | MF693114 | MF693118 | MF693106 | Cueva del Castillo. Siles, Jaén, Spain       |
| Domitius calu         | Dcul  | MK860152 | MK860134 | MK860143 | Tana delle Fate, Coreglia Antelminelli, Tuscany, Italy |
| Domitius fuscipennis | Dluq  | MF693112 | EU746439 | MF693104 | Cave de la Picona, San Pedro de Carmona, Cantabria, Spain |
| Domitius lusitanicus | Dlus  | MF693113 | EU746429 | MF693105 | Algar de Marradinhas II, Concebedo de Alcancena, Portugal |
| Domitius menozzii     | Dnca  | MK860151 | MK860133 | MK860142 | Tana da Suja, Prati di Bavari, Liguria, Italy |
| Domitius scabrosoni   | Dsbo  | MF693110 | MF693116 | MF693102 | Tana degli orchetti, Supino, Lazio, Italy     |
| Domitius speluncarum  | Dipe  | MK860153 | MK860135 | MK860144 | Tana di Magnano, Caniggiano, Lecce, Tuscany, Italy |
| Kryptostenicus delemelmae | Kdil | KX632167 | KX632160 | KX611237 | Samogorska śpilja, Biskova Mt., Croatia       |
| Kryptostenicus dimonensis | Kdim | MK860155 | MK860137 | MK860146 | Dim cave, Antalya, Turkey                     |
| Kryptostenicus eremita | Kere | MK860156 | MK860138 | MK860147 | Grotta di Ponte Subiolo, Mori, Veneto, Italy |
| Kryptostenicus fagei  | Kfag  | KX632166 | KX632159 | KX611236 | Bjelaca, Popovo polje, Bosnia and Herzegovina |
| Nesticus cellulosus   | Ncel  | MK860154 | MK860136 | MK860145 | Cave of Koufovouno, Didimoticho, Thurace, Greece |
| Typhlostenicus gacemoni | Tgoc | KF939310 | KF939307 | KF939313 | Keloğlan Cave, Dodurgaşlar, Denizli Prov., Turkey |
| Typhlostenicus idriacus | Tidr | MG201050 | MG200521 | MG201227 | Grotta Pre Oreak, Nimis, Udine, Friuli Venezia Giulia, Italy |
| Typhlostenicus oecaceactus | Tobe | KF939309 | EU746437 | MF693109 | Cueva del Molino de Aso, Boliana, Huesca, Spain |
| Typhlostenicus asperculi | Tabl | KF417410 | KF417397 | KF417416 | Baba Tuša Cave, Tmnovo, Virpazar Distr., Montenegro |
| Typhlostenicus monilis | Tmor | KF939311 | KF939308 | / | Sottotanei del Forte di Vernante, Cuneo, Piedmont, Italy |
| Gauicelus augustinus | Gaul | MK860159 | MK860141 | MK860150 | Climax cave, Bainbridge, Georgia, USA         |
manuscript. The work of Alexander A. Fomichev was supported in the framework of “Priority-2020” Program by the Altai State University. The English of the final draft was edited by Alireza Zamani.

References

Ballarin F. 2020. Domitius caulis sp. nov. (Araneae, Nesticidae), a new troglobiont spider from Italy with notes on Italian nesticids of the genus Domitius Ribera, 2018 // Journal of Cave and Karst Studies. Vol.82. No.2. P.82–94. doi.org/10.4311/2\textsc{1911}\textsc{SC010}.

Ballarin F., Li S.Q. 2015. Three new genera of the family Nesticidae (Arachnida: Araneae) from Tibet and Yunnan, China // Zoological Systematics. Vol.40. No.2. P.179–190.

Ballarin F., Li S.Q. 2018. Diversification in tropics and subtropics following the mid-Miocene climate change: a case study of the spider genus Nesticella // Global Change Biology. Vol.24. No.2. P.1365–2486. doi.org/10.1111/geb.13958.

Charitonov D.E. 1941. [On the cave fauna of Caucasus] // Izvestiya Biologicheskogo NII pri Permskom Universitete. Vol.12. No.2. P.67–71 [in Russian].

Charitonov D.E. 1947. [Spiders and harvestmen from the caves of the Black Sea coast of the Caucasus] // Byulleten Moskovskogo Oshcheshctva Isspyateli Prirody (N.S., Biol.). Vol.52. No.2. P.15–28 [in Russian].

Darrida D., Taboada G.I., Doallo R., Posada D. 2015. jModelTest 2: more models, new heuristics and parallel computing // Nature methods. Vol.9. No.8. P.772–772. doi.org/10.1038/nmeth.2109.

Dumitrescu M. 1979. La monographie des représentants du genre Nesticus des grottes de Roumania. I note // Travaux de l’Institut de Spéologie “Émile Racovitza”. Vol.18. P.53–84.

Dumitrescu M. 1980. La monographie des représentants du genre Nesticus des grottes de Roumanie, II note // Travaux de l’Institut de Spéologie “Émile Racovitza”. Vol.19. P.77–101.

Dunlop J.A., Penney D., Jekel D. 2020. A summary list of fossil spiders and their relatives. In World Spider Catalog. Natural History Museum Bern, online at http://wsc.nmbe.ch, version 20.5, accessed on January, 2022.

Eysunin S.L. 2017. New data on Actiaura pontica (Spasky, 1932) (Araneae: Nesticidae) // Arthropoda Selecta. Vol.26. No.3. P.241–243. doi.org/10.51258/arhsecl.26.3.05.

Eysunin S.L., Efimov V.E. 1998. Remarks on the Ural spider fauna, 8. New and unidentified species from steppe landscapes of the south Urals (Arachnida: Araneae) // Arthropoda Selecta. Vol.7. No.2. P.145–152.

Garrison N.L., Rodríguez J., Agnarsson I. et al. 2016. Spider phylogenomics: untangling the Spider Tree of Life // PeerJ. Vol.4. No.1. p.e1719. doi.org/10.7717/peerj.1719.

Huber B.A. 1993. Genital mechanics and sexual selection in the spider Nesticus cellulanus (Araneae: Nesticidae) // Canadian Journal of Zoology. Vol.71. P.2437–2447.

Katoh K., Rozewicz J., Yamada K.D. 2019. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization // Briefings in Bioinformatics. Vol.20. P.1160–1166. doi.org/10.1093/bib/bbx108.

Kratochvíl J. 1933. Evropské druhy čeledi Nesticidae Dahl // Práce Moravské Přírodovědecké Společnosti. Vol.8. No.10. P.1–69.

Kumar S., Stecher G., Li M., Knyaz C., Tamura K. 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms // Molecular Biology and Evolution. Vol.35. No.6. P.1547–1549. doi.org/10.1093/molbev/msy096.

Lin Y.C., Ballarin F., Li S.Q. 2016. A survey of the family Nesticidae (Arachnida, Araneae) in Asia and Madagascar, with the description of forty-three new species // ZooKeys. Vol.627. P.1–168.

López-Panzorico A., Ribera C. 2011. Nesticus baeticus sp. n., a new troglobitic spider species from south-west Europe (Araneae, Nesticidae) // ZooKeys. Vol.89. P.1–13. doi.org/10.3897/zooneks.89.921.

Marusik Yu.M. 1987. [Three new species of the family Nesticidae (Aranei) from the fauna of the USSR] // Zoologicheskii Zhurnal. Vol.66. No.3. P.461–463 [in Russian].

Marusik Yu.M., Fedorich M.M., Konponen S., Prokopenko E.V., Voloshyn V.L. 2017. Taxonomic notes on two species of Nesticidae (Arachnida: Araneae) in the Ukraine, with the first description of the male of Carpathnesticus eriashivili // Arachnology. Vol.17. Pt.6. P.302–308. doi.org/10.13156/arac.2017.6.302.

Mikhailov K.G. 2021. Advances in the study of the spider fauna (Aranei) of Russia and adjacent regions: a 2017 update // Invertebrate Zoology. Vol.18. No.1. P.25–35, Supplements 1.01–1.15, 2.01–2.24. doi.org/10.15298/invertzool.18.1.03.

Miller M.A., Pfeiffer W., Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees // Proceedings of the Gateway Computing Environments Workshop (GCE). 14 Nov. 2010, New Orleans. P.1–8. doi.org/10.1109/GCE.2010.5676129.

Nadolny A.A., Kobylyuk M.M. 2007. Carpathnesticus borutskyi, the first record of Nesticidae from the Crimea (Aranei: Nesticidae) // Arthropoda Selecta. Vol.15. No.4(2006). P.291–294.

Nentwig W., Blick T., Bosmans R., Gloor D., Hänggi A., Krof C. 2022. Spiders of Europe. Version 01.2022. Online at https://www.araneae.nmbe.ch, accessed on January 2022. doi.org/10.24436/1

Otto S. 2020. Caucasian spiders: A faunistic database on the spiders of the Caucasus Ecoregion. Database version 03.2020. Online at caucasian-spiders.info

Pavlek M., Ribera C. 2017. Kryptostenicus deeleemanae gen. et sp. nov. (Araneae, Nesticidae), with notes on the Mediterranean cave species // European Journal of Taxonomy. Vol.262. P.1–27. doi.org/10.15298/invertzool.18.1.03.

Reimoser E. 1930. Eine neue Nesticus-Art aus dem Kaukasus // Zoologischer Anzeiger. Bd.88. S.158–159.

Ribera C. 2018. A new genus of nesticid spiders from western European Peninsulas (Araneae, Nesticidae) // Zootaxa. Vol.4407. No.2. P.229–240. doi.org/10.11646/zootaxa.4407.2.4.

Ribera C., Elverici M., Kunt K.B., Özkütük R.S. 2014. Typhonesticus gocmeni sp. n., a new cave-dwelling blind spider species from the Aegean region of Turkey (Araneae, Nesticidae) // Zootaxa. Vol.419. P.87–102. doi.org/10.11646/zootaxa.419.5.739.

Stamatakis A. 2014. RAXML, version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies // Bioinformatics. Vol.30. No.9. P.1312–1313. doi.org/10.1093/bioinformatics/btu333.

Weiss I., Heimer S. 1982. Zwei neue Carpathnesticus-Arten aus Rumänien nebst Betrachtungen über Kopulationsmechanismen und deren Evolution (Arachnida, Araneae, Nesticidae) // Reichenbachia. Bd.20. S.167–174.

Wheeler W.C., Coddington J.A., Crowley et al. 2017. The spider tree of life: phylogeny of Araneae based on target-gene analyses from an extensive taxon sampling // Cladistics. Vol.33. No.6. P.574–616. doi.org/10.1111/cla.12182.

WSC. 2022. World Spider Catalog. Version 22.5. Natural History Museum Bern, online at http://wsc.nmbe.ch (accessed on January 2022). https://doi.org/10.24436/2

Zamani A., Marusik Yu.M. 2021. New taxa of six families of spiders (Arachnida: Araneae) from Iran // Zoology in the Middle East. Vol.67. No.1. P.81–91. doi.org/10.1080/09397410.2021.1877382

Responsible editor K.G. Mikhailov