

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

Новый род из семейства Nesticidae (Arachnida: Aranei) с Кавказа

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

КЛЮЧЕВЫЕ СЛОВА: *Aituaria*, Araneae, *Carpathonesticus*, биоразнообразие, Грузия, Дагестан, новый вид, осыпь, приповерхностная подземная среда обитания.

ABSTRACT. A new genus, *Daginvesticus* gen.n. with the type species, *D. dzhmirzoevi* sp.n. (♂♀) is described from the Caucasus based on morphological and molecular evidences. Three new combinations are proposed: *Daginvesticus tamajevae* (Marusik, 1987) comb.n., *Aituaria borutzkyi* (Reimoser, 1930) comb.n. and *Aituaria eriashvili* (Marusik, 1987) comb.n. (all ex. *Carpathonesticus*). The new genus is closely related to *Aituaria* Eyunin 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.

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РЕЗЮМЕ. На основании морфологических и молекулярных данных, с Кавказа описывается новый род *Daginvesticus* gen.n. с типовым видом *D. dzhmirzoevi* sp.n. (♂♀). Предложены новые комбинации: *Daginvesticus tamajevae* (Marusik, 1987) comb. n., *Aituaria borutzkyi* (Reimoser, 1930) comb. n. и *Aituaria eriashvili* (Marusik, 1987) comb. n. (все исключаются из рода *Carpathonesticus*). Новый род близок к роду *Aituaria* Eyunin et Efimik, 1998, имеет хорошо развитые глаза и пигментацию. Приводятся описание, иллюстрации, диагноз и фотогра-

фия биотопа. Обсуждается структура пальпы 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 [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* Eyunin 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 taxa. The goals of this paper are as follows: (1) to establish the new genus *Daginvesticus* gen.n., (2) to provide a description of *D. dzhamirzoevi* sp.n., (3) to discuss relationships between *Daginvesticus* 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* — radical process, *Rx* — radix, *Sd* — sperm duct, *Sf* — 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 *Daginvesticus* 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

Daginvesticus gen. n.

TYPE SPECIES. *Daginvesticus 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* Eysunin 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 *Daginvesticus* 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

Table 1. Differences between *Daginesticus* gen.n. and *Aituaria*.
Таблица 1. Различия между *Daginesticus* gen.n. и *Aituaria*.

Structures of copulatory organs	<i>Daginesticus</i> gen. n.	<i>Aituaria</i> 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.

Рис. 1–3. Внешний вид самца (1–2) и самки (3) *Daginesticus dzhamirzoevi* sp.n. 1 — сбоку; 2–3 — дорсально. Масштаб: 2 мм.

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-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 (*Cp*) long, weakly sclerotized. Retrolateral

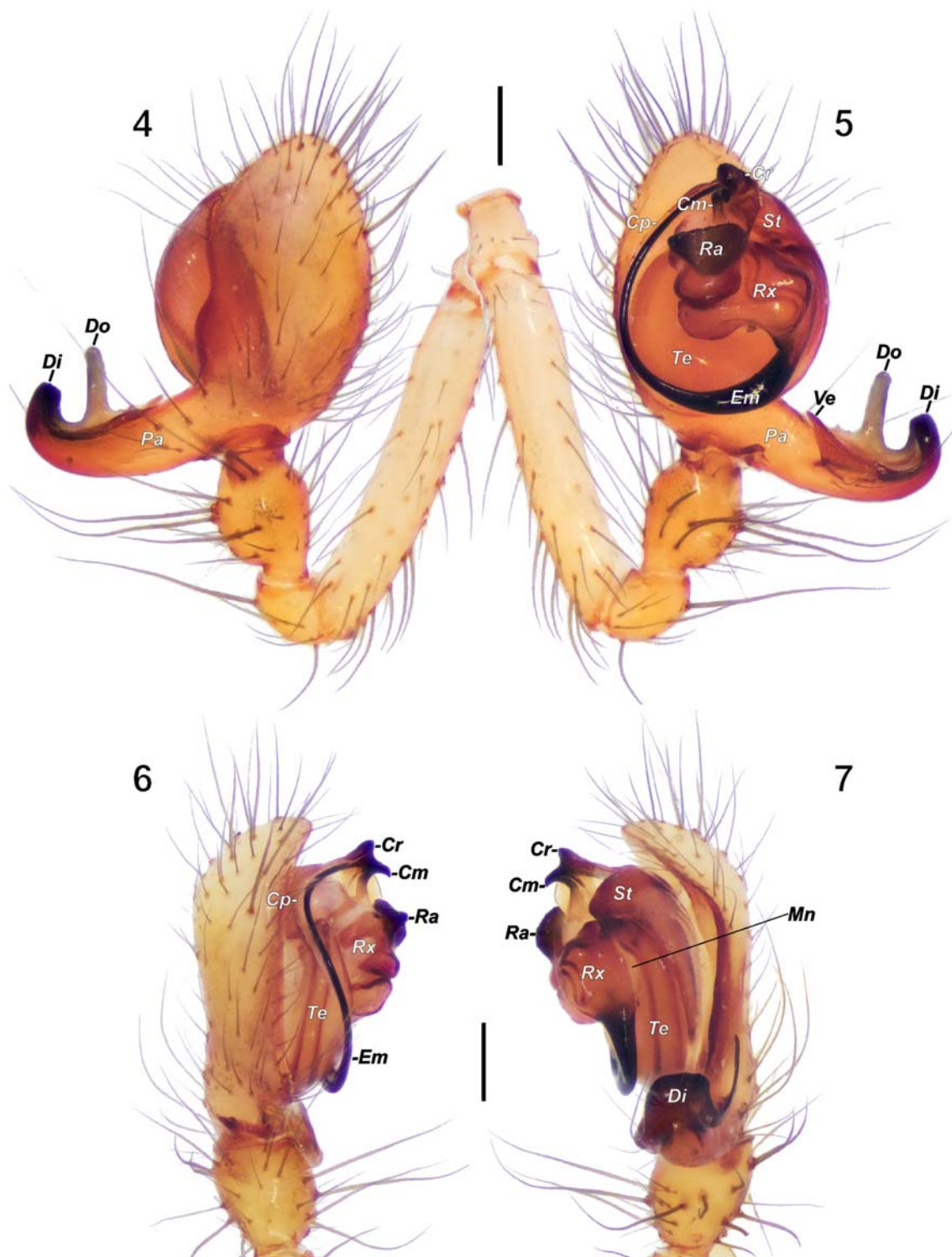
process of conductor (*Cr*) located anteriorly and surpasses the embolus tip. Median process of conductor (*Cm*) curved distally. Embolus (*Em*) whip-like, starting at about 5 o'clock, partially bordering tegulum. Embolus tip not modified.

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.

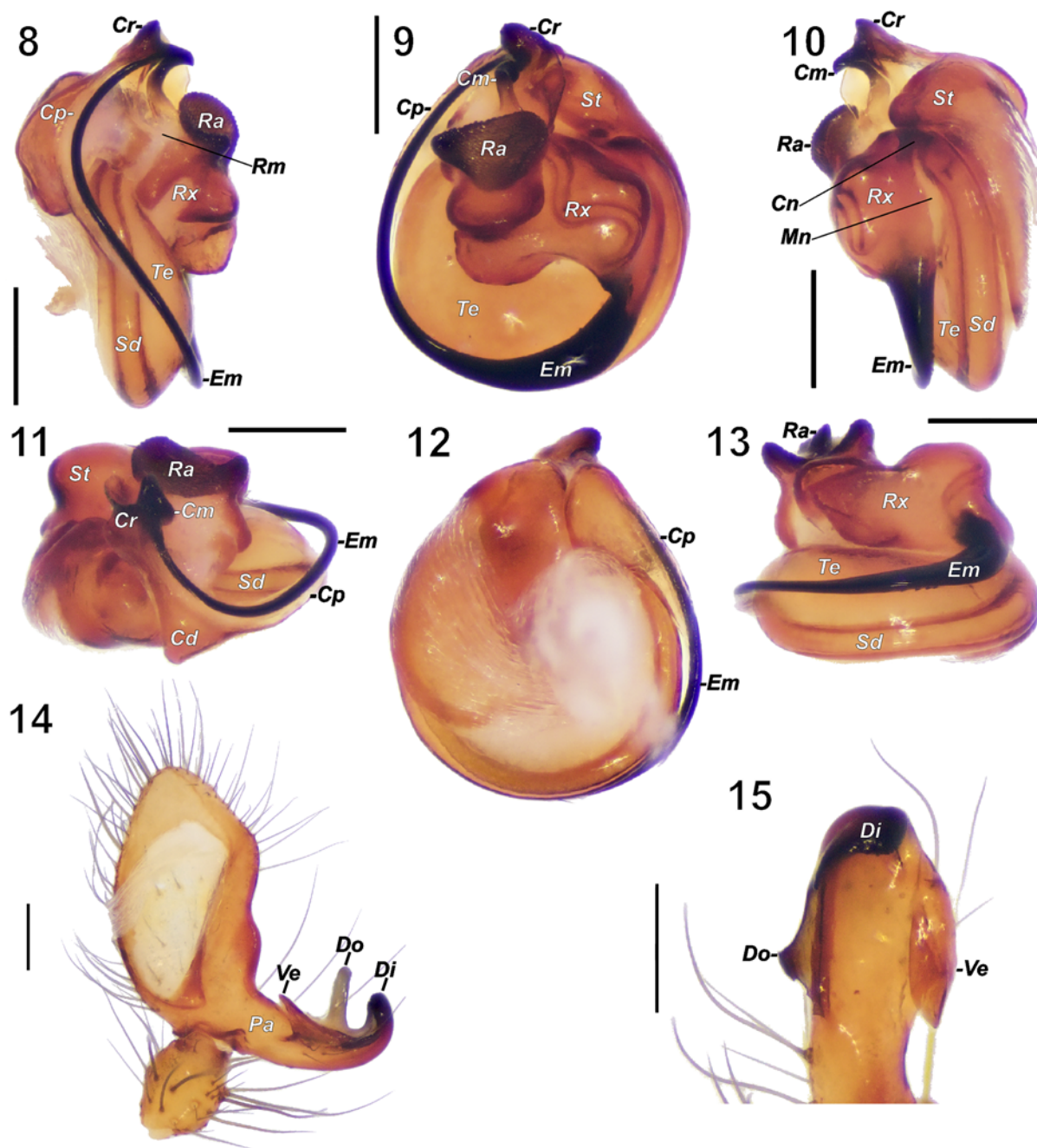
DISTRIBUTION. Known only from the eastern Caucasus (Dagestan, Russia, and eastern Georgia) (Fig. 22).

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 радикакса, *Rx* — радикакс, *St* — субтегулум, *Te* — тегулум, *Ve* — вентральный апофиз парацимбиума.



Figs 8–15. Bulb (8–13), cymbium and tibia (14) and paracymbium (15) of *Daginesticus dzhimirzoevi* 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.

Рис. 8–15. Бульбус (8–13), цимбиум и тибия (14) и парацимбиум (15) *Daginesticus dzhimirzoevi* sp.n. 8 — пролатерально; 9, 14 — вентрально; 10 — ретролатерально; 11, 15 — спереди; 12 — дорсально; 13 — сзади. Масштаб: 0,2 мм. Сокращения: Cd — дорсальный отросток кондуктора, Cm — медиальный отросток кондуктора, Cn — соединение между Rx и Te, Cp — пролатеральный отросток кондуктора, Cr — ретролатеральный отросток кондуктора, Di — дистальный апофиз парацимбиума, Do — дорсальный апофиз парацимбиума, Em — эмболюс, Mn — мембрана между Rx и Te, Pa — парацимбиум, Ra — апофиз радика, Rm — мембрана радика, Rx — радика, Sd — семенной проток, St — субтегулюм, Te — тегулюм.

ship between *D. dzhimirzoevi* 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 dzhmirzoevi sp.n.

Figs 1–22, 30.

TYPES. RUSSIA: *Dagestan*: holotype ♂ (ISEA, 001.8872) and paratypes 1♂ 10♀♀ (ISEA, 001.8873), 1♀ (ISEA, 001.8874), 3 km WNW from Gunib Village (42°24.219'N, 46°55.305'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 Gadzhibek S. Dzhmirzoev (Makhachkala, Russia), a research 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 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 11 o'clock position and its tip bent retrolaterally. 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 (12.05).

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 (♂♀).

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 generotype 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 generotype 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. 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 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. eriashvili* (Marusik, 1987) comb.n., *A. iranica* Zamani et Marusik, 2021, and *A. pontica* (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 (j♀).

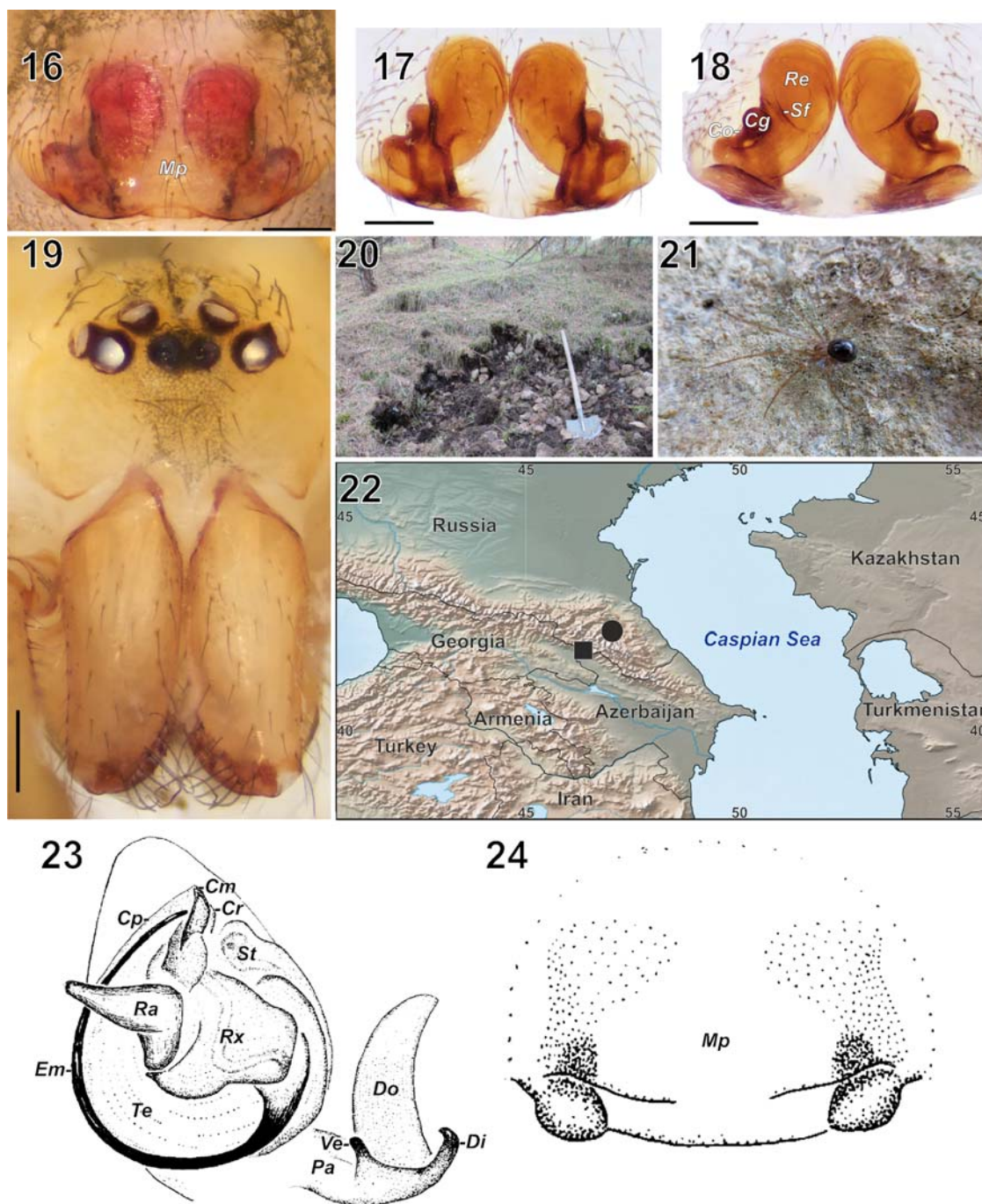
Nesticus borutzkyi: Charitonov, 1941: 69, figs 1–2 (♂).

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

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

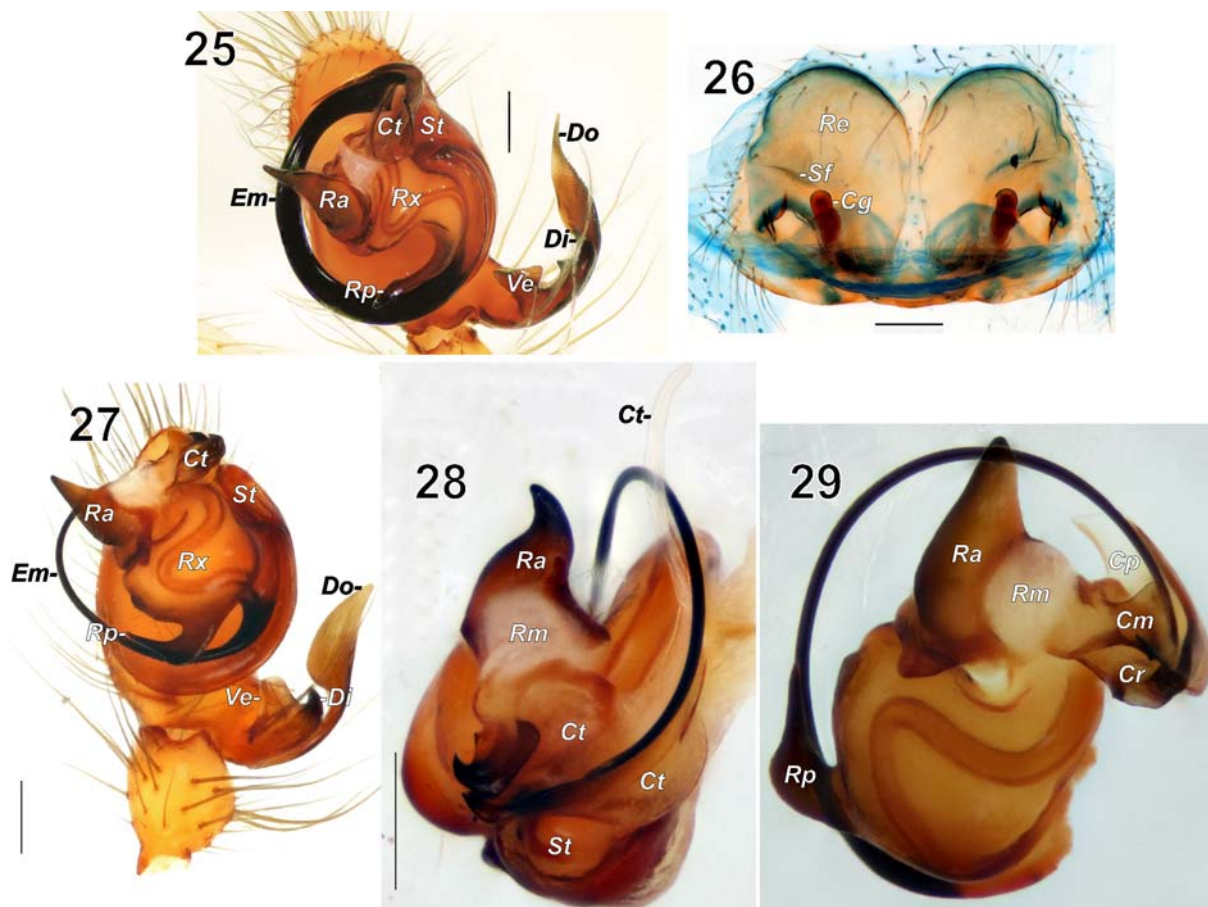
MATERIAL EXAMINED. GEORGIA: *Imereti*: 2♂♂ 7♀♀ (ZMMU), near Mudzhureti Vill. (42°17'07.0"N 43°04'28.9"E), cave, 341 m, 24.07.2012, Yu.M. Marusik.

DIAGNOSIS. See Nadolny & Kovblyuk [2007].



Figs 16–24. *Daginesticus* spp.: epigyne (16–18), cephalic part of the male (19), habitat (20), live female of *D. dzhimirzoevi* 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. dzhimirzoevi* 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. dzhimirzoevi* sp.n.; пальпа 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. dzhimirzoevi* sp.n., квадрат — *D. mamajevae*. 23–24 — по Marusik [1987]. Масштаб: 0,2 мм. Сокращения: Cg — булабовидная железа, Cm — медиальный отросток кондуктора, Cp — пролатеральный отросток кондуктора, Cr — ретролатеральный отросток кондуктора, Co — копулятивный канал, Di — дистальный апофиз парацимбиума, Do — дорсальный апофиз парацимбиума, Em — эмболус, Mp — медиальная пластинка, Pa — парацимбиум, Ra — апофиз радикса, Re — рецептакула, Rx — радикс, Sf — наклонная складка Re, St — субтегулум, Te — тегулум, Ve — вентральный апофиз парацимбиума.



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. 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, Ct — 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.

Рис. 25–29. Пальпа самца (25, 27), радикс (28–29) и эпигина (26) *Aituaria pontica* (25–26) и *A. borutzkyi* (27–29). 25, 27, 29 — вентрально; 26 — дорсально; 28 — спереди. 26 — по Zamani, Marusik [2021]. Масштаб: 0,2 мм. Сокращения: Cg — булабовидная железа, Cm — медиальный отросток кондуктора, Cp — prolateral process of the conductor, Cr — ретролатеральный отросток кондуктора, Ct — кондуктор, Di — дистальный апофиз парацимбиума, Do — дорсальный апофиз парацимбиума, Em — эмболус, Ra — апофиз радикса, Re — рецептакула, Rm — мембрана радикса, Rp — отросток радикса, Rx — радикс, Sf — наклонная складка Re, St — субтегулюм, Ve — вентральный апофиз парацимбиума.

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.**

Carpatonesticus eriashvilii Marusik, 1987: 462, fig. 3 (♀).

Carpathonesticus eriashvilii: Marusik *et al.*, 2017: 302, figs 1–6, 8–17, 23–33, 38–40 (♂♀).

MATERIAL EXAMINED. UKRAINE: *Chernivtsi Oblast*: 2♂♂ 1♀ (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♂ 2♀♀ (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.

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.

	<i>Domitius</i>	<i>Nesticus</i>	<i>Carpatho- nesticus</i>	<i>Krypto- nesticus</i>	<i>Dagi- nesticus</i>	<i>Aituaria</i>	<i>Typhlo- nesticus</i>
<i>Domitius</i>							
<i>Nesticus</i>	0.17						
<i>Carpathonesticus</i>	0.17	0.10					
<i>Kryptonesticus</i>	0.15	0.13	0.12				
<i>Daginesticus</i>	0.18	0.16	0.16	0.15			
<i>Aituaria</i>	0.16	0.14	0.13	0.13	0.13		
<i>Typhlonesticus</i>	0.20	0.17	0.16	0.15	0.17	0.16	
<i>Gaucelmus</i>	0.23	0.22	0.22	0.22	0.21	0.21	0.24

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* Eyunin 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 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. dzhmirzoevi* sp.n. and *D. mamajevae* cluster together in a monophyletic clade distinct from the clade formed by *A. pontica*, *C. borutzkyi* and *C. eriashvilii* (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 fol-

lows 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, Kovblyuk, 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 Entelegynae 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 regular 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, *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 anticlockwise. *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-

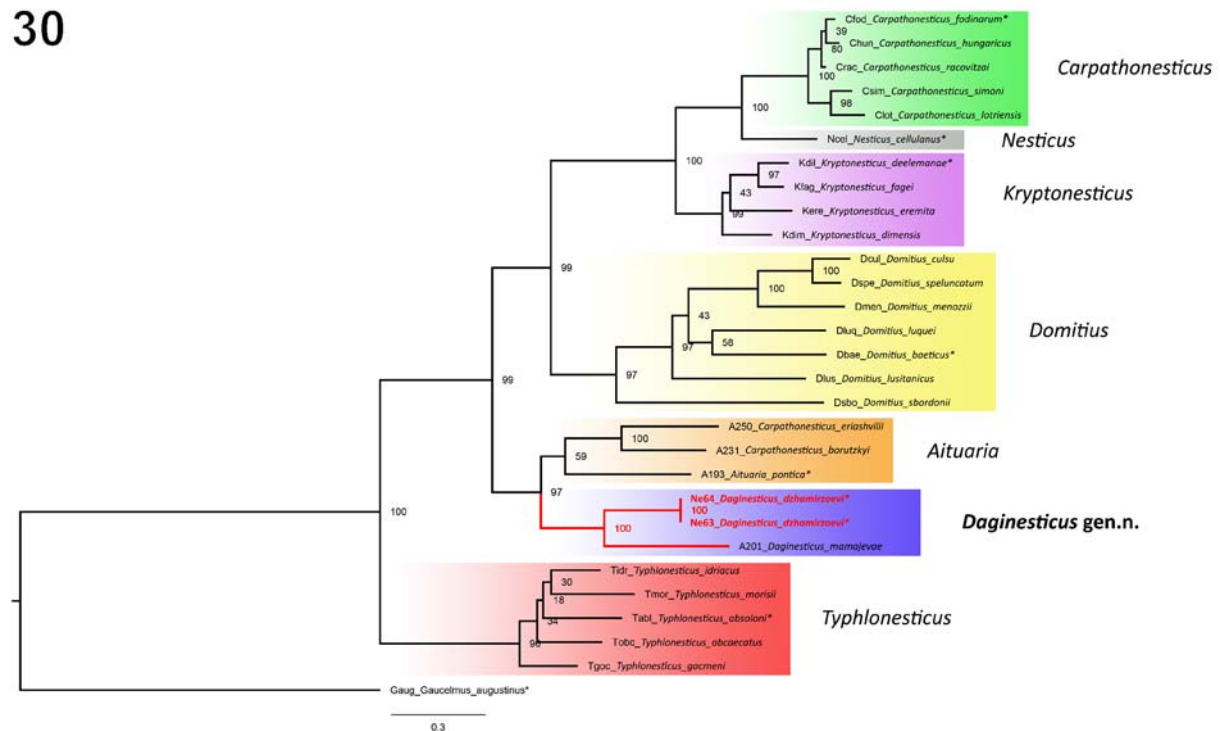


Fig. 30. Maximum likelihood phylogenetic tree of the main Nesticidae genera in Europe inferred from three concatenated gene fragments (COI, 16S, H3). Type species of each genus is indicated by an asterisk. The newly established genus is highlighted in red. Numbers at each node indicate bootstrap support. Lengths of branches are scaled in relation to the number of substitutions per site. Sequence of *Gaucelmus augustinus* Keyserling, 1884 was used as an outgroup to root the phylogram.

Рис. 30. Филогенетическое древо основных европейских родов Nesticidae, построенное методом максимального правдоподобия на основе конкатенированных фрагментов генов COI, 16S, и H3. Типовой вид каждого рода отмечен звёздочкой. Новый род выделен красным цветом. Числами в узлах дерева обозначена бутстреп-поддержка. Длины ветвей масштабируются в зависимости от количества замен на сайт. Нуклеотидная последовательность *Gaucelmus augustinus* Keyserling, 1884 использована в качестве внешней группы для укоренения филограммы.

defined genus, separated from other West Palearctic 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 genotype 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 *borutzkyi*-group *sensu* Lehtinen, Saaristo [1980] and Esysunin [2017] (*C. birsteini* (Charitonov, 1947), *C. caucasicus* (Charitonov, 1947), *C. zaitzevi* (Charitonov, 1939), and *C. ljovuschkini* (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 phyloge-

netic 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.

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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.

Таблица 3. Список видов и нуклеотидных последовательностей, депонированных в базе данных GenBank, использованных в молекулярном анализе. Последовательности, полученные в данной работе, отмечены звездочкой.

Species	Code	COI	16S	H3	Locality
<i>Aituaria_pontica</i>	A193	OM630576*	OM631938*	OM642843*	Sevastopol, Crimea, Russia
<i>Aituaria_borutzkyi</i>	A231	OM630577*	OM631940*	OM642848*	Sataple Cave, Imereti, Georgia
<i>Aituaria_eriashvili</i>	A250	OM630578*	OM631939*	OM642847*	Chernivtsi City, cellar, Ukraine
<i>Carpathonesticus_fodinarum</i>	Cfod	MK860157	MK860139	MK860148	Small cave along the river, Sighistel, Bihor, Romania
<i>Carpathonesticus_hungaricus</i>	Chun	KF417412	KF417402	KF417419	Peștera Liliecilor, Cheile Ampoitei Gorges, Romania
<i>Carpathonesticus_lotriensis</i>	Clot	MK860158	MK860140	MK860149	Humid and shadowed cliff near Lazaret village, Sibiu, Romania
<i>Carpathonesticus_racovitza</i>	Crac	MG201045	MG200514	MG201222	small cave near Peștera Poarta Lui Lonele, Munună Village, Alba Distr. Romania
<i>Carpathonesticus_simoni</i>	Csim	KF417408	KF417398	KF417417	cave in Bisbrita Gorges, Stogu-Vinturaria Mts., Romania
<i>Dagonesticus_dzhamirzoevi</i>	Ne63	OM630573*	OM631936*	OM642844*	Gunib Village, Dagestan, Russia
<i>Dagonesticus_dzhamirzoevi</i>	Ne64	OM630574*	OM631937*	OM642845*	Gunib Village, Dagestan, Russia
<i>Dagonesticus_mamajevae</i>	A201	OM630575*	OM631941*	OM642846*	Lagodekhi, Georgia
<i>Domitius_baeticus</i>	Dbac	MF693114	MF693118	MF693106	Cueva del Castillo. Siles, Jaén. Spain
<i>Domitius_culsi</i>	Dcul	MK860152	MK860134	MK860143	Tana delle Fate, Coreglia Antelminelli, Tuscany, Italy
<i>Domitius_luquei</i>	Dluq	MF693112	EU746439	MF693104	Cueva de la Picon, San Pedro de Carmona, Cantabria, Spain
<i>Domitius_lusitanicus</i>	Dlus	MF693113	EU746429	MF693105	Algar de Marradinhas II, Concelho de Alcanena, Portugal
<i>Domitius_menozzii</i>	Dmen	MK860151	MK860133	MK860142	Tanna da Suja, Prati di Bavari, Liguria, Italy
<i>Domitius_sbordonii</i>	Dsbo	MF693110	MF693116	MF693102	Tana degli orchetti, Supino, Lazio, Italy
<i>Domitius_speluncarum</i>	Dspe	MK860153	MK860135	MK860144	Tana di Magnano, Canigiano, Lucca, Tuscany, Italy
<i>Kryptonesticus_deelemanae</i>	Kdil	KX632167	KX632160	KX611237	Samogorska špilja, Biokova Mt., Croatia
<i>Kryptonesticus_dimensis</i>	Kdim	MK860155	MK860137	MK860146	Dim cave, Antalya, Turkey
<i>Kryptonesticus_eremita</i>	Kere	MK860156	MK860138	MK860147	Grotta di Ponte Subiolo, Mori, Veneto, Italy
<i>Kryptonesticus_fagei</i>	Kfag	KX632166	KX632159	KX611236	Bjelušica, Popovo polje, Bosnia and Herzegovina
<i>Nesticus_cellulanus</i>	Ncel	MK860154	MK860136	MK860145	Cave of Koufovouno, Didymoticho, Thrace, Greece
<i>Typhlonesticus_gocmeni</i>	Tgoc	KF939310	KF939307	KF939313	Keloğlan Cave, Dodurgalar, Denizli Prov., Turkey
<i>Typhlonesticus_idriacus</i>	Tidr	MG201050	MG200521	MG201227	Grotta Pre Oreak, Nimis, Udine, Friuli Venezia Giulia, Italy
<i>Typhlonesticus_obcaecatus</i>	Tobc	KF939309	EU746437	MF693109	Cueva del Molino de Aso, Boltana, Huesca, Spain
<i>Typhlonesticus_absoloni</i>	Tabl	KF417410	KF417397	KF417416	Baba Tusha Cave, Tmovo, Virpazar Distr., Montenegro
<i>Typhlonesticus_morisii</i>	Tmor	KF939311	KF939308	/	Sotterranei del Forte di Vernante, Cuneo, Piedmont, Italy
<i>Gaucelmus_augustinus</i>	Gaug	MK860159	MK860141	MK860150	Climax cave, Bainbridge, Georgia, USA

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