

The Crimean scorpion, *Euscorprius tauricus* (C.L. Koch, 1837)
(Scorpiones: Euscorpriidae): an endemic species supported
by mitochondrial DNA evidence

Крымский скорпион, *Euscorprius tauricus* (C.L. Koch, 1837)
(Scorpiones: Euscorpriidae): данные митохондриальной ДНК
подтверждают эндемизм вида

V. Ya. Fet
В. Я. Фет

Department of Biological Sciences, Marshall University, Huntington, West Virginia 25755-2510, USA: E-mail: fet@marshall.edu

KEY WORDS: *Euscorprius*, Crimea, scorpion, mitochondrial DNA, phylogeny, endemism.

КЛЮЧЕВЫЕ СЛОВА: *Euscorprius*, Крым, скорпион, митохондриальная ДНК, филогения, эндемизм.

ABSTRACT: New mitochondrial 16S rRNA DNA data support a separate phylogenetic position for the Crimean scorpion *Euscorprius tauricus* (C.L. Koch, 1837), previously considered a subspecies of *E. carpathicus* (L.), in contrast to several other species of the “*E. carpathicus*” complex. Phylogenetic and biogeographic details are discussed.

РЕЗЮМЕ: Новые данные по последовательности гена 16S рРНК митохондриальной ДНК свидетельствуют об обособленном филогенетическом положении крымского скорпиона *Euscorprius tauricus* (C.L. Koch, 1837), который ранее считался подвигом *E. carpathicus* (L.). Приводится сравнение с несколькими видами комплекса “*E. carpathicus*”. Обсуждаются подробности филогении и биогеографии вида.

Introduction

Scorpions of the genus *Euscorprius* Thorell, 1876 (Scorpiones: Euscorpriidae) are very common in southern Europe [Hadži, 1930; Caporiacco, 1950; Kinzelbach, 1975; Fet, 1986; Fet & Sissom, 2000]. Ecologically diverse, they occupy a variety of habitats from xeric to mesic, from the Mediterranean shoreline to the high altitudes of the Alps and Balkans. Numerous species have been described in *Euscorprius*. The traditional taxonomy of this genus, based mainly on morphosculpture and coloration, was complicated and confusing. C.L. Koch [1850: 86–87] gave a synopsis of all the *Euscorprius* species he had described in his series “Die Arachniden”, and clearly divided these species into three groups according to the number of trichobothria (“Grübchen”) on the ventral aspect of pedipalp patella. Birula [1900b: 14] ironically noticed that “the genus *Euscorprius* belongs to such a category of systematic groups, in which the number of species accepted by

a specialist depends on how well developed this specialist’s passion was to compile long columns of synonymous species names”. He quite correctly wrote that “...only studying the morphology of all forms as related to their geographic distribution will we possibly make some positive conclusions about the classification of this genus”.

The most recent development in *Euscorprius* taxonomy was the introduction of molecular techniques by our research team. This started with the pioneering paper of Gantenbein *et al.* [1999] on the application of 16S ribosomal RNA gene sequence analyses for assessing the phylogeny of the genus *Euscorprius*. This study provided the first ever published DNA-based phylogeny for the order Scorpiones. These data revealed a phylogenetic relationship between four species, namely *E. flavicaudis* (DeGeer, 1778), *E. carpathicus* (L., 1767), *E. italicus* (Herbst, 1800) and *E. germanus* (C.L. Koch, 1837). This phylogeny was quite different from the former views on the evolution of this genus, based only on morphology [Birula, 1900b; Hadži, 1930; Caporiacco, 1950; Kinzelbach, 1975]. DNA data helped to reorient morphological analysis towards important character sets. Further work from this team and its collaborators included more detailed genetic and morphological analyses.

As a result of an extensive recent revision by Fet & Soleglad [2002], the European scorpion species *E. carpathicus* (L., 1767) was restricted only to Romania, its type locality. The name *E. tergestinus* (C.L. Koch, 1837) was applied to most of the “western” populations of former *E. carpathicus*. Across the Balkans, several more forms of the “*E. carpathicus*” complex are present. During the revisions of this complex [Gantenbein *et al.*, 2001; Fet & Soleglad, 2002; Fet *et al.*, 2002, 2003] using morphological and molecular information, the following species have been established: *E. balearicus* Caporiacco, 1950 (Balears, Spain), *E. tergestinus*

Table 1. A matrix of genetic distances: uncorrected ("p") distance (below the diagonal); Kimura 2-parameter distance (above the diagonal).
 Таблица 1. Матрица генетических расстояний: ниже диагонали, нескорректированное абсолютное расстояние ("p"); выше диагонали, расстояние Кимуры.

	1	2	3	4	5	6	7	8
1EtMA1	–	0.043	0.077	0.050	0.131	0.074	0.085	0.119
2EtMD1	0.042	–	0.058	0.043	0.119	0.053	0.071	0.099
3EcKA2	0.073	0.055	–	0.054	0.120	0.034	0.075	0.087
4EcRO2	0.048	0.042	0.052	–	0.103	0.043	0.049	0.099
5EfLA	0.120	0.109	0.110	0.096	–	0.114	0.114	0.125
6EcPA1	0.070	0.051	0.034	0.041	0.105	–	0.049	0.096
7EcOS1	0.080	0.067	0.072	0.048	0.105	0.047	–	0.099
8EtaCR1	0.110	0.093	0.082	0.093	0.115	0.090	0.093	–

(C.L. Koch, 1837) (France, Italy, western Balkans), *E. carpathicus* (Linnaeus, 1767) (Romania), *E. hadzii* Caporiacco, 1950 (Balkans), *E. koschewnikowi* Birula, 1900 (Greece) and *E. sicanus* (C.L. Koch, 1837) (Greece, Italy, Malta, North Africa). Several additional forms of this species complex are currently under detailed investigation. One of them inhabits the Southern Coast of the Crimean Peninsula, from where it was first recorded by Pallas [1795], and is usually reported as the species *E. tauricus* (C.L. Koch, 1837) (see Taxonomy section). This paper presents the first molecular (mitochondrial DNA) data for this Crimean scorpion.

Material and methods

Material. An adult female of *E. tauricus* was collected by A. Khaustov in July 2001 at the Nikita Botanical Garden, Crimea, Ukraine. The scorpion was preserved in 96% ethanol and sent for DNA analysis to Marshall University, West Virginia, USA. We also added for comparison specimens of two previously unstudied populations from Greece (Epirus and Thessaly), collected by V. Fet and M. Mylonas; for label data see below.

DNA analysis. Comparative analyses of the mitochondrial 16S ribosomal RNA gene has been recently used for resolving species-level phylogeny of *Euscorpius* [Gantenbein *et al.*, 1999, 2000, 2001; Scherabon *et al.*, 2000; Fet *et al.*, 2002, 2003]. For detailed DNA analysis procedures and phylogenetic tree-building algorithms, see Gantenbein *et al.* [1999, 2000]. Total DNA was extracted from fresh or preserved (95% ethanol) muscle tissue (a leg) using a Qiagen™ DNeasy extraction kit. An approximate 400 bp fragment of the mitochondrial (mt) 16S rRNA gene was amplified by the polymerase chain reaction (PCR) using the primers 16Sbr, or LR-J-12887 (CGATTTGAACTCAGATCA; forward, 18-mer) and a scorpion-specific reverse primer (GTGCAAAGG-TAGCATAATCA, 20-mer). These primers corresponded to the positions 11,173–11,190 and 11,625–11,606 in the *Limulus polyphemus* mitochondrial genome [Lavrov *et al.*, 2000]. The resulting PCR product was verified on 1% agarose electrophoretic gel and purified by Ultrafree MC 30000 cellulose filters (Millipore, Inc.). Automated Sanger dideoxy sequencing of the double-stranded PCR product was performed at the Molecular Genetics Instrumentation Facility, University of Georgia (Athens, GA) on the ABI 9600 Sequencer.

Phylogenetic analysis. Eight mtDNA sequences representing different haplotypes were aligned using Clustal X 1.81 [Thompson *et al.*, 1997]. Three new DNA sequences were deposited at GenBank [http://www.ncbi.nlm.nih.gov] with the following accession numbers: Nikita Botanical Garden, Crimea, Ukraine, July 2001, coll. A.A. Khaustov (EtaCR1) (AY193822); Parga, Epirus, Greece, 12 May 2001, coll. V. Fet (EcPA1) (AY193823); and Mt. Ossa (Kissavos), Thessaly, Greece, May 2001, coll. M. Mylonas (EcOS1) (AY193824). Five DNA sequences published earlier by our research group and its collaborators [Gantenbein *et al.*, 1999, 2000, 2001; Huber *et al.*, 2001; Fet *et al.*, 2002] were extracted from the GenBank online database. The corresponding taxa, their geographic origin, abbreviations and accession numbers were: *E. flavicaudis* (DeGeer, 1778): Lauris, Vaucluse, France, EfLA (AJ389381); *E. carpathicus* (Linnaeus, 1767), Baile Herculane, Romania, EcRO2 (AY172338); *E. tergestinus* (C.L. Koch, 1837): Mathis, Alpes-Martimes, France, EtMA1 (AJ389376); Mala Duba, Croatia, EtMD2 (AJ298063); and *E. "carpathicus candiota"* Birula, 1903: Kallikratis, Crete, Greece, EcKA2 (AJ309214). As an outgroup, we used *E. flavicaudis*. The software package PAUP* Version 4.0b10 [Swofford, 1998] was used for sequence analysis to perform genetic distance calculation, Maximum Parsimony (MP), and Neighbor Joining (NJ) algorithms. The statistical support of inner clades of the phylogenetic tree was determined by bootstrapping (1000 pseudoreplicates).

Results

Exhaustive Search under PAUP* found one shortest Maximum Parsimony tree (Fig. 1), 93 steps long (CI=0.81, RI=0.56), under various weightings. Of 319 total characters, 252 characters were constant, 42 variable characters were parsimony-uninformative, and 25 variable characters were parsimony-uninformative. The Crimean population appeared as a sister group to all other studied taxa of "*E. carpathicus*" complex, which formed a highly supported (bootstrap 79%) monophyletic clade: *E. carpathicus* from Romania, *E. tergestinus* from France and Croatia, *E. "carpathicus candiota"* from Crete, and two additional populations from Greece. Within this clade, a high statistical support (72%) was demonstrated by two geographically distant populations of *E. tergestinus* from France and Croatia. The

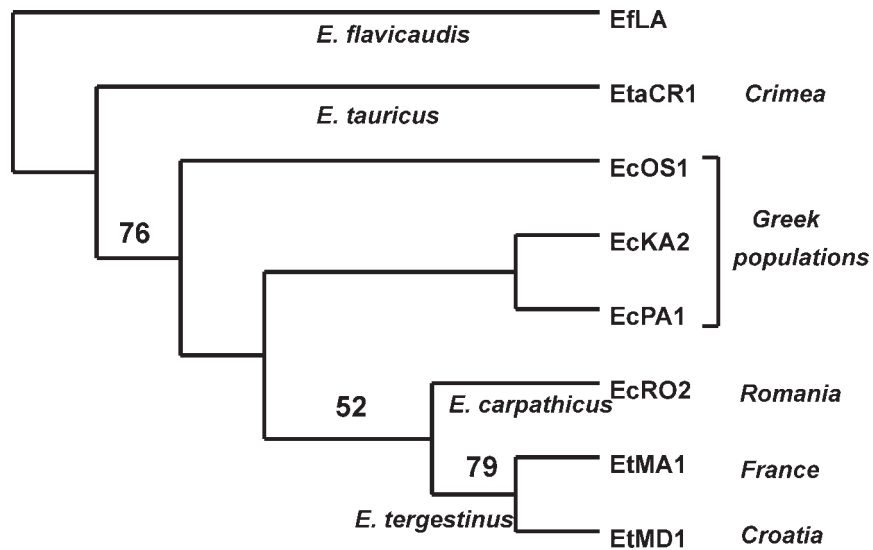


Fig. 1. Maximum Parsimony (MP) cladogram. Numbers designate bootstrap values.

Рис. 1. Филогенетическое дерево (кладограмма), полученное методом максимальной парсимонии. Номера соответствуют показателям бутстреп-анализа.

branching order under all Neighbor Joining distance models studied (absolute distance, Kimura, Felsenstein, Jukes-Cantor, HKY85, Tamura-Nei), was the same as for MP phylogeny, placing the Crimean population as the sister group to all other considered species of the “*E. carpathicus*” complex. Distance data (Table 1) are presented for absolute and Kimura distances. In all cases the genetic distance of the Crimean population from other “*E. carpathicus* complex” taxa was high (8 to 13%).

Discussion

The population of *Euscorpium* from Crimea was for a long time considered an endemic species, *E. tauricus* — albeit probably due to its highly isolated geography than to morphological features [Birula, 1900a, 1900b, 1904, 1917a,b; Puzanov, 1927, 1949; Orlov & Vasilyev, 1983, 1984]. It was “lumped” under *E. carpathicus* (L.) as a subspecies only by Caporiacco [1950] who did not actually analyze any specimens from Crimea. Fet [1997] analyzed overall trichobothrial counts and pectinal tooth counts for 71 specimens from Crimea, and tentatively retained the Crimean scorpion as *E. carpathicus tauricus* (C.L. Koch). It was listed in the most recent catalog [Fet & Sissom, 2000] among numerous European subspecies of *E. carpathicus* (L.). However, an ongoing revision of this overly inflated taxon by V. Fet, M.E. Soleglad, B. Gantenbein and their collaborators has already resulted in many changes, determined on the basis of both morphological and molecular criteria [Gantenbein *et al.*, 2001; Fet & Soleglad, 2002; Fet *et al.*, 2002, 2003].

The Crimean population is indeed a very isolated one, probably the most isolated *Euscorpium* population in Europe. The closest populations of *Euscorpium* from

this complex are about 500 km westward in Romania, which is the easternmost boundary of the genus’ continuous range in Europe [Fet *et al.*, 2002]. The Caucasian species *E. italicus* (Herbst) and *E. mingrelicus* (Kessler) are not closely related to the Crimean population, as is clear from their distinct morphologies [Birula, 1917a, b]. Trichobothrial (sensory seta) numbers and patterns unequivocally place the Crimean scorpion in the “*E. carpathicus*” complex. Its standard diagnostic formula for trichobothrial series on the external aspect of pedipalp patella is: $et=6$ (variable, but ca. 90% in the Crimean population [Fet, 1997]), $est=4$, $em=4$, $esb=2$, $eb_a=4$, $eb=4$ [Fet, 1986; Fet & Soleglad, 2002]. These “standard” numbers persist across several species (*E. balearicus*, *E. tergestinus*, *E. koschewnikowi*; see Gantenbein *et al.*, 2001; Fet & Soleglad, 2002; Fet *et al.*, 2002), while in other related species significant diagnostic deviations also exist in the series em , eb_a and eb (*E. carpathicus*, *E. sicanus*, *E. hadzii*; see Fet [2000]; Fet & Soleglad [2002]; Fet *et al.* [2003]). Therefore, the Crimean population, as far as trichobothrial patterns are concerned, shares the conservative “standard” formula with a number of other, not necessarily closely related populations such as, *E. balearicus* from the Balearic Islands, *E. “carpathicus candiota”* from Crete (see Fet [1986], “Group A” of Fet [2000]), and two populations from Epirus and Thessaly used in this paper (the Thessaly population can be assigned to *E. “carpathicus ossae”* Caporiacco, 1950). Obviously, the trichobothrial character set is not diagnostic for all these diverse taxa.

The DNA sequence analysis provides the first insight into a possible ancient origin of the Crimean scorpion. The phylogeny obtained suggests that the Crimean population is drastically different from all previously studied “standard formula” populations of

the “*E. carpathicus*” complex. We can also trace a clear “east-to-west” gradient within the branching pattern of this complex, from Crimea to Greece to the Adriatic and further along the Mediterranean coast. The “westernmost” species of the complex, *E. tergestinus*, is the most derived compared to the Crimean taxon, and Romanian *E. carpathicus* is the sister group to *E. tergestinus*, therefore the Crimean scorpion does not form a monophyletic group with *E. carpathicus*. This is the first information which suggests that the “*E. carpathicus*” complex has an eastern origin, and that the Crimean scorpion is possibly a relict remnant of the Tertiary biota.

The Crimean Peninsula originated as an island in the Tethys Sea during the Mesozoic and throughout the Tertiary period was connected many times to different land masses (Caucasus, Balkan Peninsula, Anatolia, and/or modern Ukraine). There are no Tertiary relicts in the Crimea; and all endemic plants there are generally considered to be very recent [Grosset, 1979]. Golovach [1984] analyzed the diplopod fauna in the Crimea, and suggested that its age is primarily Pleistocene and that the source of migration was the eastern Mediterranean, especially the Balkan Peninsula. It was previously suggested [Fet, 1997] that the existence of the Crimean scorpion was a result of a (possibly recent) migration from the Balkans or Anatolia during Pleistocene interglacials; however, the new DNA data points rather to a more relict status for this taxon. Severe Pleistocene glaciations could have eliminated most of the ancient thermophile and mesophile biota in the Crimea, but it is possible that the Crimean scorpion is indeed a relict of more ancient times. It has to be noted that it is not related to either of the two extant Caucasian species of *Euscorpis*.

Recently, we demonstrated [Gantenbein *et al.*, 1999] that the phylogeny of *Euscorpis* included vicariant events similar to those detected by Oosterbroeck & Arntzen [1992, Fig. 12] for several other animal groups. These are interpreted as the most ancient split between Iberian/Italian lineages versus younger, Asia Minor-Transmediterranean lineages. While the highly deviant western Mediterranean *Euscorpis* (*Tetratrachobothrius flavicaudis* (DeGeer)) is a good candidate for the Iberian/Italian lineage, the Crimean population could represent one of the relicts of the Asia Minor-Transmediterranean lineage. It is clear from the DNA phylogeny that the Crimean scorpion deserves species status as *Euscorpis tauricus* (C.L. Koch). It remains to be seen if a detailed comparison of morphological characters between this relict and other (especially Balkan) “standard” taxa will provide solid morphological diagnostic characters for *E. tauricus* as a morphospecies.

Taxonomy

Euscorpis tauricus (C.L. Koch, 1837)

Scorpius tauricus C.L. Koch, 1837: 6–8, pl. CXI, fig. 255. Holotype: female (lost), Crimea, Ukraine.

Scorpio carpathicus: Pallas, 1795: 64; 1799: 475.

Scorpio europaeus (unavailable name; see Fet & Sissom, 2000: 356); Kutorga, 1834: 490; Rathke, 1837 (N.V.); Nordmann, 1840: 731; Kessler, 1860: 196.

Scorpio europaeus var. *tauricus*: Nordmann, 1840: 731, pl. I, fig. 3.

Scorpio (*Scorpius*) *tauricus*: Gervais, 1844: 68.

Scorpius tauricus: C.L. Koch, 1850: 86.

Scorpio tauricus: Ferrari, 1872: 658; Kessler, 1874: 23–24; Köppen, 1881: 219.

Euscorpis tauricus: Simon, 1879: 113; Birula, 1896: 230; 1898: 140; 1900a: 250–251; 1900b: 16, 18; 1904: 33; 1917a: 105, 129; 1917b: 168, 208–224, pl. 3, fig. 10, pl. 5, fig. 3–4; Karatygin, 1910: 122; Mokrzehetsky, 1914: 14; Puzanov, 1927: 27; 1949: 22; Orlov & Vasilyev, 1983: 62; 1984: 6, fig. 4; Vasilyev & Orlov, 1983: 72.

Euscorpis italicus (nec *Scorpio italicus* Herbst, 1800; misidentification): Tarnani, 1907: 30 (part: Yalta).

Euscorpis (ISS) *tauricus*: Puzanov, 1929: 104.

Euscorpis carpathicus oligotrichus (nec Hadži, 1929; misidentification): Hadži, 1930: 35 (part: Crimea).

Euscorpis carpathicus tauricus: Caporiacco, 1950: 193, 209; Fet, 1989a: 82–83; 1989b: 124–125; 1997: 106–108; Lacroix, 1991: 19; Fet & Sissom, 2000: 365–366.

Distribution. Ukraine (Crimea, southern coast).

Notes. Simon [1879] erroneously gives «Taurus» (a mountain range in Turkey) as a locality of *E. tauricus* (instead of «Taurie», i. e. Crimea).

ACKNOWLEDGEMENTS. I thank Dr. Alexander A. Khaustov for collecting the specimen of *E. tauricus* for this DNA study and Dr. Kirill G. Mikhailov for handing it over to me. I am grateful to Michael E. Soleglad and Benjamin Gantenbein for their enthusiastic collaboration, expertise and guidance in all the issues related to the genus *Euscorpis*. I thank Moysis Mylonas and Iasmi Stathi (University of Crete, Iraklio, Greece) for supplying a specimen from Mt. Ossa. Elizabeth V. Fet provided skilled assistance in DNA procedures.

References

- Birula A.A. 1896. Miscellanea scorpologica. I. Zur Synonymie der russischen Skorpione // Ann. Mus. Zool. Acad. Imp. Sci. St.-Petersbourg. T.1. P.229–245.
- Birula A.A. 1898. Ein Beitrag zur Kenntniss der Skorpionenfauna Kleinasiens // Horae Soc. Entomol. Ross. Vol.33. No.1–2. P.132–140 [preprint: October 1898; collated issue: 1901].
- Birula A.A. 1900a. Miscellanea scorpologica. IV. Zur Synonymie der russischen Skorpione (Schluss) // Ann. Mus. Zool. Acad. Imp. Sci. St.-Petersbourg. T.5. P.248–256.
- Birula A.A. 1900b. Scorpiones mediterranei Musei Zoologici mosquensis // Izv. Imper. Obsch. Lyub. Prir., Ist., Antropol. Etnogr. Vol.98. Pt.3. No.1. P.8–20 [in Russian].
- Birula A.A. 1904. Miscellanea scorpologica. VII. Synopsis der russischen Skorpione // Ann. Mus.Zool.Acad. Imp. Sci. St.-Petersbourg. T.9. P.28–38.
- (Birula A.A.) Byalynitskii-Birulya A.A. 1917a. Arachnoidea Arthrogastra Caucasica. Pars I. Scorpiones // Zap. Kavkaz. Muz. [Mém. Mus. Caucase], Tiflis: Imprimerie de la Chancellerie du Comité pour la Transcaucasie. Ser.A. Vol.5. 253 p. [in Russian; published August 1917]. English translation: Byalynitskii-Birulya A.A. 1964. Arthrogastric Arachnids of Caucasia. 1. Scorpions. Jerusalem: Israel Program for Scientific Translations. 170 pp.
- (Birula A.A.) Byalynitskii-Birulya A.A. 1917b. Faune de la Russie et des pays limitrophes fondée principalement sur les collections du Musée Zoologique de l'Académie des Sciences de Russie. Arachnides (Arachnoidea). Petrograd. Vol.1. No.1. xx, 227 p. [in Russian; Introduction dated October 1917]. English translation: Byalynitskii-Birulya A.A. 1965. Fauna of Russia and Adjacent Countries. Arachnoidea. Vol. I. Scorpions.

- ons. Jerusalem: Israel Program for Scientific Translations, xix, 154 p.
- Caporiacco L., di. 1950. Le specie e sottospecie del genere "*Euscorpium*" viventi in Italia ed in alcune zone confinanti // Atti Accad. naz. Lincei Memor. Ser.8. No.2. P.159–230.
- Ferrari J.A. 1872. Ueber das Vorkommen der Skorpione in Erzherzogthum Oesterreich // Verh. Zool.-Bot. Ges. Wien. Vol.22. S.655–658.
- Fet V.Ya. 1986. Notes on some *Euscorpium* (Scorpiones: Chactidae) from Greece and Turkey // Riv. Mus. Civ. Sci. Natur. „Enrico Caffi“ (Bergamo). Vol.9 (for 1985). P.3–11.
- Fet V.Ya. 1989a. [A catalog of scorpions of the USSR. Families Chactidae and Iuridae] // Lange A.B. (ed.). Fauna i ekologiya paukov i skorpionov [Fauna and Ecology of Spiders and Scorpions]. Moscow: Nauka. P.76–98 [in Russian].
- Fet V. 1989b. A catalogue of scorpions (Chelicerata: Scorpiones) of the USSR // Riv. Mus. Civ. Sci. Natur. „Enrico Caffi“ (Bergamo). Vol.13 (for 1988). P.73–171.
- Fet V. 1997. A note on *Euscorpium carpathicus* (Scorpiones: Chactidae) from the Crimea // J. Arachnol. Vol.25. No.1. P.106–108.
- Fet V. 2000. Scorpions (Arachnida, Scorpiones) from the Balkan Peninsula in the collections of the National Museum of Natural History, Sofia // Hist. Natur. Bulgar. Vol.11. P.47–60.
- Fet V., Gantenbein B., Fet E.V. & Popa V. 2002. *Euscorpium carpathicus* (Linnaeus, 1767) (Scorpiones: Euscorpiidae) from Romania: mitochondrial DNA data // Biogeographica. Vol.78. No.4. P.141–147.
- Fet V. & Sissom W.D. 2000. Family Euscorpiidae // Fet V., Sissom W.D., Lowe G. & Braunwalder M.E. Catalog of the Scorpions of the World (1758–1998). New York: New York Entomological Society. P.355–381.
- Fet V. & Soleglad M.E. 2002. Morphology analysis supports presence of more than one species in the "*Euscorpium carpathicus*" complex (Scorpiones: Euscorpiidae) // Euscorpium. No.3. P.1–51.
- Fet V., Soleglad M.E., Gantenbein B., Vignoli V., Salomone N., Fet E.V. & Schembri P. 2003. New molecular and morphological data on the "*Euscorpium carpathicus*" species complex (Scorpiones: Euscorpiidae) from Italy, Malta, and Greece justify the elevation of *E. c. siccaus* (C.L. Koch, 1837) to the species level // Rev. suisse Zool. T.110. Fasc.2. P.355–379.
- Gantenbein B., Fet V., Barker M. & Scholl A. 2000. Nuclear and mitochondrial markers reveal the existence of two parapatric scorpion species in the Alps: *Euscorpium germanus* (C.L. Koch, 1837) and *E. alpha* Caporiacco, 1950, stat. nov. (Scorpiones, Euscorpiidae) // Rev. suisse Zool. T.107. Fasc.4. P.843–869.
- Gantenbein B., Fet V., Largiadur C.R. & Scholl A. 1999. First DNA phylogeny of *Euscorpium* Thorell, 1876 (Scorpiones: Euscorpiidae) and its bearing on taxonomy and biogeography of this genus // Biogeographica. Vol.75. No.2. P.49–65.
- Gantenbein B., Soleglad M.E. & Fet V. 2001. *Euscorpium balearicum* Caporiacco, 1950, stat. nov. (Scorpiones: Euscorpiidae): molecular (allozymes and mtDNA) and morphological evidence for an endemic Balearic Islands species // Org. Div. Evol. Vol.1. No.4. P.301–320.
- Gervais P.M. 1844. Scorpions // Walckenaer C.A. (ed.). Histoire naturelle des Insectes. Aptères. Librairie Encyclopédique de Roret, Paris. Vol.3. Pt.8. P.14–74.
- Golovach S.I. 1984. [Distribution and faunogenesis of the Diplopoda of the European USSR] // Chernov Yu.I. (ed.). Faunogenez i filotsenogenez [Faunogenesis and phylocenogenesis] Moscow: Nauka. P.92–138 [in Russian].
- Grosset G.E. 1979. [On the origin of flora of the Crimea] // Byulleten Moskovsk. Obshch. Ispyt. Prirody [Bull. Moscow Soc. Natur.], Otdel Biol. Vol.84. P.35–55, 64–84 [in Russian].
- Hadži J. 1930. Die europäischen Skorpione des Polnischen Zoologischen Staatsmuseums in Warszawa // Ann. Mus. Zool. Polon. Vol.9. No.4. P.29–38.
- Karatygin V.G. 1910. [Vegetation and animal life] // Rossiya. Polnoye geograficheskoye opisaniye nashego otechestva [Russia. The complete geographical description of our motherland]. St. Petersburg. Vol.14. P.72–125 [in Russian].
- Kessler K.F. 1860. Puteshestvie s zoologicheskoi tselyu k severnomu beregu Chernogo morya i v Krym v 1858 Godu [A zoological trip to the northern coast of the Black Sea and to the Crimea in 1858]. Kiev. 248 p. [in Russian].
- Kessler K.F. 1874. [On Russian scorpions] // Tr. Russk. Entomol. Obshch. St.-Peterb. [Trans. Rus. Entomol. Soc. St. Petersburg]. Vol.8. No.1. P.3–27 [in Russian].
- Kinzelbach R. 1975. Die Skorpione der Agäis. Beiträge zur Systematik, Phylogenie und Biogeographie // Zool. Jb. (Syst.). Bd.102. H.1. S.12–50.
- Koch C.L. 1837. Die Arachniden. Nürnberg: C.H. Zeh'sche Buchhandlung. Bd.4. Lief. 1–5. S.1–108.
- Koch C.L. 1850. Scorpione // Uebersicht des Arachnidensystems. Nürnberg: C.H. Zeh'sche Buchhandlung. Bd.5. S.86–92.
- Kondaraki V.Kh. 1875. Universal'noye opisaniye Kryma [The Universal description of the Crimea]. St. Petersburg. Vol.2. 444 p. [in Russian].
- Köppen F. 1861. Ueber einige in Russland vorkommende giftige und vermutlich giftige Arachniden // Beitrag zur Kenntniss des Russischen Reich. Vol.4. S.179–226.
- Kutorga S. 1834. [A general view on the Taurian Peninsula (excerpt from a 1833 trip)] // Zh. Min. Nar. Obraz. [J. Dept. Public Educ.]. Vol.2. No.6. P.484–494 [in Russian].
- Kraepelin K. 1899. Scorpiones und Pedipalpi. Dahl F. (ed.) Das Tierreich. Berlin: R. Friedländer und Sohn Verlag. Lfg.8 (Arachnoidea). 265 S.
- Lacroix J.-B. 1991. Faune de France; Arachnida: Scorpionida. 5e note. Sub-genus (*Euscorpium*) Thorell, 1876 // Arachnides. No.8. P.7–36.
- Lavrov D.V., Boore J.L. & Brown W.M. 2000. The complete mitochondrial DNA sequence of the horseshoe crab *Limulus polyphemus* // Mol. Biol. Evol. Vol.17. P.813–824.
- Linnaeus C. (C. von Linné). 1767. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 12. Holmiae (Stockholm): Laurentii Salvii. Vol.1. Pt. 2. P.533–1327.
- Mokrzhefsky S.A. 1914. [The fauna of Crimea]. Krym: Putevoditel' [Crimea: A travel guide]. Simferopol: Crimean Society of Naturalists. 32 p [in Russian].
- Nordmann A. 1840. Notice sur les Scorpions de la faune pontique // Voyage dans la Russie méridionale et la Crimée, par la Hongrie, la Valachie et la Moldavie, exécuté en 1837, sous la direction de M. Anatole de Demidoff, par Mm. de-Sainson, Le-Play, Huot, Léleveille, Raflet, Rousseau, de Nordmann et du Ponceau; dédié a S. M. Nicolas 1-er, Empereur de toutes les Russies. Paris. Vol.3. P.751–752.
- Oosterbroek P. & Arntzen J.W. 1992. Area-cladograms of Circum-Mediterranean taxa in relation to Mediterranean palaeogeography // J. Biogeogr. Vol.19. P.3–20.
- Orlov B.N. & Vasilyev N.F. 1983. [Scorpions of the European part of the USSR] // Nazemnye i vodnye ekosistemy [Terrestrial and Aquatic Ecosystems]. Gorky: Gorky State University. Vol.6. P.60–65 [in Russian].
- Orlov B.N. & Vasilyev N.F. 1984. Skorpiony i ikh yad. Chast' II. Opredelitel' skorpionov fauny SSSR, ontogenez, okhrana [Scorpions and their venom. Part 2. A key to the scorpions of the USSR fauna; development; conservation]. Gorky State University, Gorky. 32 p. [in Russian; date on the cover 1983; published January 16, 1984].
- Pallas P.S. 1795. Kratkoe fizicheskoe i topograficheskoe opisaniye Tavricheskoi Oblasti [Brief physical and topographical description of the Taurian Region]. St. Petersburg, 72 p. [in Russian].
- Pallas P.S. 1799. Bemerkungen auf einer Reise in die südlichen Statthalterschaften des Russisches Reiches in den Jahren 1793 und 1794. Leipzig: Martini. Vol.2. 460 S.
- Puzanov I.I. 1927. Fauna Kryma [Fauna of the Crimea]. Simferopol. 37 p. [in Russian].
- Puzanov I.I. 1929. [Fauna of the Crimea] // Krym. Putevoditel' [The Crimea. A travel guide]. 3d Ed. Simferopol: Krymgosizdat. P.81–111 [in Russian].
- Puzanov I.I. 1949. [Specificity of the Crimean fauna and its origin]

- // Uch. Zap. Gor'kovsk. Gos. Univ. [Sci. Trans. of the Gorky State Univ.], Vol.14. P.5–32 [in Russian].
- Rathke H. 1837. Zur Entwicklungsgeschichte des Scorpions // H. Rathke. Zur Morphologie: Reisebemerkungen aus Taurien. Riga & Leipzig: Frantzen. Vol.2. P.17–34.
- Simon E. 1879. 3e Ordre. — Scorpiones. Les Arachnides de France. VII. Contenant les Ordres des Chernetes, Scorpiones et Opiliones. Paris: Roret. P.79–115.
- Swofford D.L., 1998. PAUP* Phylogenetic analysis using parsimony (*and other methods). Version 4 // Sunderland: Sinauer Associates.
- Tarnani I.K. 1907. Nashi yadovitye zhivotnye [Our venomous animals] . St. Petersburg, 127 p. [in Russian].
- Thompson J.D., Gibson T.J., Plewniak F., Jeanmougin F. & Higgins D.G. 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools // Nucl. Acids Res. Vol.24. P.4876–4882.
- Vasilyev N.F. & Orlov B.N. 1983. [Scorpions of the USSR, their use and conservation]. Mekhanizmy deistviya zootoksinov [The mechanisms of the zootoxin activity] // Gorky: Gorky State University. P.71–80 [in Russian].