



On the type species of the genus *Dendarus* Dejean, 1821 (Coleoptera: Tenebrionidae)

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Abstract

Based on type specimen investigation, the status of *Helops tristis* Rossi, 1790 as the type species of the genus *Dendarus* Dejean, 1821 is confirmed. Lectotypes are designated for *Helops tristis* and *Pandarus coarcticollis* Mulsant, 1854 – both are classified in *Dendarus*. *Pandarus libanicus* Desbrochers des Loges, 1881 is recognised as a junior synonym of *Dendarus calcaratus* Baudi di Selve, 1881. Both taxa share the same *locus typicus* (Mount Lebanon in Lebanon) and are morphologically distinct from the Italian *Dendarus lugens* (Mulsant & Rey, 1854). Finally, *D. lugens* is considered as a synonym of *D. (Dendarus) coarcticollis*.

Key words: Nomenclature, lectotype, synonyms, darkling beetles, Dendarini, Dendarina

Introduction

Dendarus Dejean, 1821 (Coleoptera: Tenebrionidae) is a well-known genus of flightless darkling beetles inhabiting the Western Palearctic Region (Trichas et al. 2020). The genus is represented by 89 species and subspecies classified in six subgenera (Iwan et al. 2020, Bouchard et al. 2021), and is currently placed within the tribe Dendarini Mulsant & Rey, 1854 of the subfamily Blaptinae Leach, 1815 (Kamiński et al. 2020). Throughout history, several contributors questioned the validity of the type species fixation for *Dendarus* (see Löbl et al. 2008, Iwan et al. 2020). However, despite intensive taxonomic work on the genus this problem has not yet been solved. As this threatens the nomenclatural stability of *Dendarus*, the authors of this paper reanalyzed the available data on the genus and introduced new acts to resolve the existing issues associated with the type species fixation.

Material and methods

The present investigation is based on an analysis of diverse literature sources cited throughout the manuscript. This includes the original descriptions of the treated species (see References). Furthermore, historical type materials concerning *Helops tristis* Rossi, 1790 and *Pandarus coarcticollis* Mulsant, 1854 were studied.

Results and discussion

Fixation of type species

Dejean (1821) introduced the genus-group name *Dendarus* [as *Dendarus*. Meg.] and listed four species-group names under it: “*tristis* Rossi” from Italy; “*emarginatus*” from Spain; and “*dalmatinus* Dej.” from Dalmatia with “*emarginatus* Germ.” as a synonym. Only the first two names applied to available species. The first refers to *Helops tristis* Rossi, 1790, while the second refers to *Blaps emarginata* Fabricius, 1792. As Dejean (1821) did not fix the type species, the two available species-group names are originally included nominal species that can be selected for subsequent designation (see Arts 67.2.1, 69.1 of ICZN 1999). Mulsant (1854b) transferred *Blaps emarginata* to the genus *Heliopates* Dejean, 1834, where it remains to this day (Español & Viñolas 1983, 1987a, b, 1990, Trichas et al. 2020). Therefore, taking into consideration the regulations of the ICZN (1999), and the widely accepted taxonomic distinctiveness of *Dendarus* and *Heliopates* (e.g., Español & Viñolas 1983, 1987, 1990, Kamiński et al. 2019), at this point only *Helops tristis* Rossi can be considered as a potential type species of the genus *Dendarus*. In fact, this species has been already fixed as the type species of *Dendarus* by Blanchard (1844: pl. 48, fig. 8).

Blanchard’s decision was not adopted by Seidlitz (1893), Reitter (1904), and Español (1937) who considered *Helops tristis* Rossi as an unidentifiable species since the type series was assumed to be lost. They used “*Dendarus tristis* Laporte, 1840” as a valid name (with *Pandarus coarcticollis* Mulsant, 1854 as a synonym) and considered it to be the type of *Dendarus*. Many subsequent authors followed this concept (Gebien 1938, Español 1961, Medvedev 1968, Chatzimanolis & Löbl 2003, Cherney 2005, Iwan et al. 2020). However, as mentioned before “*D. tristis* Laporte” was not originally included in *Dendarus* by Dejean (1821) and therefore cannot be considered as a type species of that genus. Additionally, “*D. tristis* Laporte” is an unavailable species-group name because it was not described as a new species (Bouchard et al. 2021).

Status of *Helops tristis* Rossi, 1790

Rossi (1790) described and illustrated *Helops tristis* from the Central Italian region of Etruria. Type specimens from Rossi’s collection have been considered lost (Seidlitz, 1893), although Horn and Kahle (1937) and Horn et al. (1990) indicated that some of his material went to the Museum für Naturkunde (ZMB - Berlin). Based on contacts with Bernd Jaeger of the ZMB, two historical specimens from Italy under the species name *Helops tristis* were located in the Rossi material. As Rossi (1790) did not specify the number of studied specimens nor designate a holotype while describing *Helops tristis* a lectotype designation is needed in order to fix the taxonomic status of the species. The male specimen presented on the Fig. 1A is hereby designated as the lectotype. The second specimen, a female, is accordingly treated as a paralectotype. Labels indicating the status of these two specimens were added.

Up to now, the following five species of *Dendarus* have been reported from Italy (Aliquo et al. 2007, Trichas 2008, Soldati 2012, Iwan et al. 2020): *D. (Dendarus) carinatus* Mulsant & Rey, 1854, *D. (Dendarus) coarcticollis* Mulsant, 1854, *D. (Pandarinus) dalmatinus* (Germar, 1823), *D. (Pandarinus) peslieri* Soldati, 2012, and *D. (Paroderus) lugens* (Mulsant & Rey, 1854). Italian records of *D. (Pandarinus) coelatus* Brullé, 1832 are artificial, and due to misinterpretation of this species with *D. peslieri* (Aliquò & Soldati 2014). The investigation of the newly designated lectotype of *D. tristis* (Rossi) clearly indicates that it is not synonymous with *D. (Dendarus) coarcticollis* Mulsant, 1854 (Fig. 1). In fact, it is fully convergent with the taxonomic concept of *D. lugens*, and as a result it is hereby considered as a senior synonym of this species.

Status of *Pandarus libanicus* Desbrochers des Loges, 1881

Several authors considered *Pandarus libanicus* Desbrochers des Loges, 1881 as a junior synonym of *D. lugens* Mulsant & Rey, 1854 (e.g., Gebien 1938, Löbl et al. 2008, Iwan et al. 2020). However, as noted by Koch (1948) *Pandarus libanicus* is in fact a synonym of *Dendarus calcaratus* Baudi di Selve, 1881. Both species share the same *locus typicus* (Mount Lebanon in Lebanon) and are morphologically distinct from the Italian *D. lugens* (Mulsant & Rey).

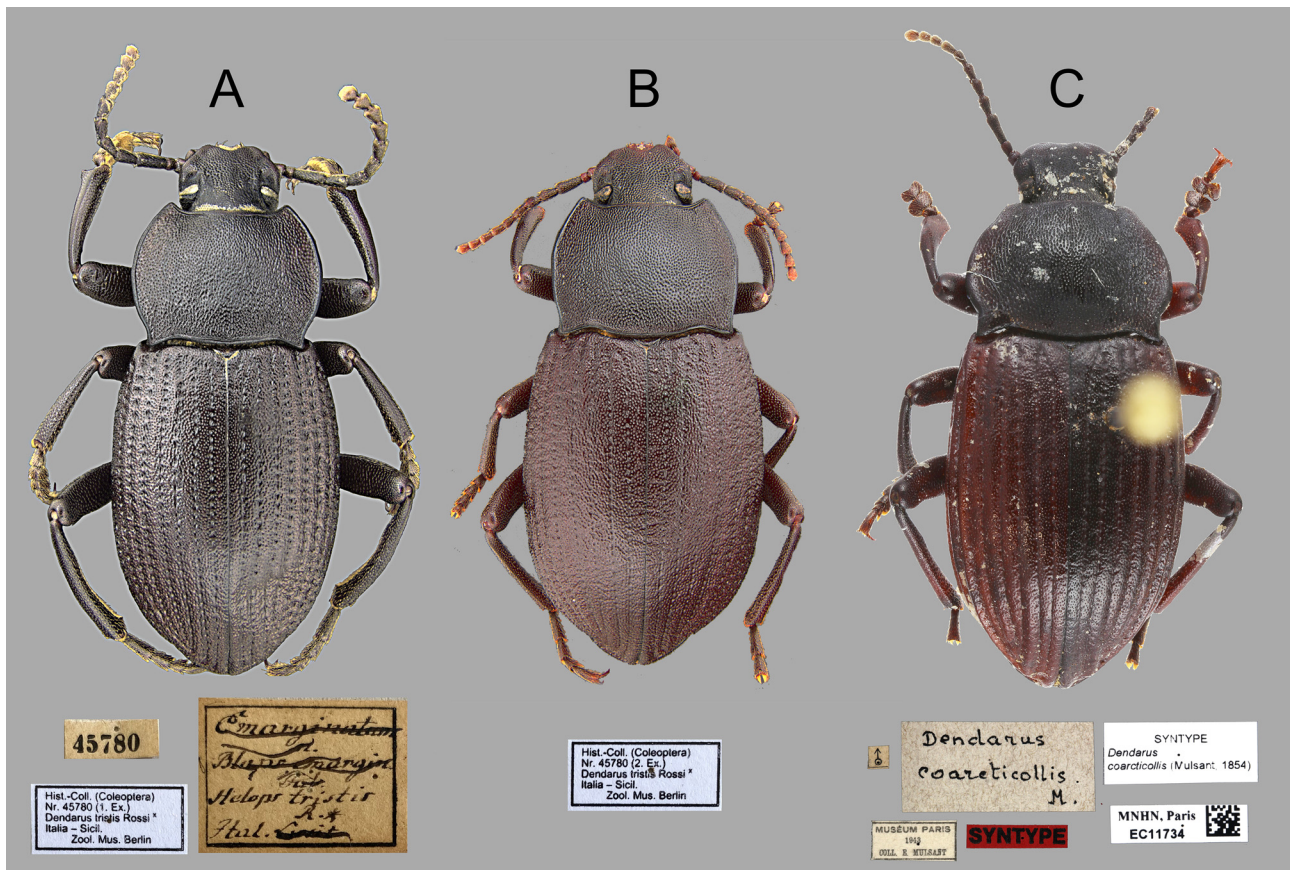


FIGURE 1. Habitus photographs of selected *Dendarus* species. Lectotype (A) and paralectotype (B) of *Helops tristis*, lectotype (C) of *Pandarus coarcticollis* (photos by MNHN/Christophe Rivier).

Lectotype designation for *Pandarus coarcticollis* Mulsant, 1854

During the investigation leading to this note we also studied the type material of additional species of *Dendarus*. One of them was *Pandarus coarcticollis* Mulsant. The name-bearing types of this species represent a small fraction of Mulsant's collection, which was not destroyed over the course of history (Paulian 1944). We use the present opportunity to stabilize the taxonomic concept of this species.

Mulsant (1854a) did not specify the number of studied specimens nor designate a holotype while describing *Pandarus coarcticollis*. Eight syntypes deposited at the Muséum national d'Histoire naturelle (MNHN - Paris) were studied by the authors of this note. In order to fix the taxonomic status of the species the specimen presented in Fig. 1C is hereby designated as the lectotype. The additional seven syntypes are considered paralectotypes. Labels indicating the new status of these specimens were kindly attached by the MNHN curators.

Other implications

Taking into consideration the above presented information it has to be concluded that *Helops tristis* Panzer, 1793, now *Catops tristis* of the family Leiodidae Fleming, 1821, is a junior primary homonym of *Helops tristis* Rossi, 1790. As *Helops tristis* Panzer, 1793 has several synonyms, the introduction of a replacement name is not introduced. The oldest synonym is *Choleva leachii* Spence, 1813.

Conclusions

Subgenus *Dendarus* Dejean, 1821: 65

Type species. *Helops tristis* Rossi, 1790: 236; subsequent designation by Blanchard (1844: pl. 48, fig. 8)

calcaratus Baudi di Selve, 1881: 281

= *Pandarus libanicus* Desbrochers des Loges, 1881: 116 [syn. by Koch 1948: 350; **syn. rest.**]

Notes. *Pandarus libanicus* Desbrochers des Loges, 1881 is a junior secondary homonym of *Dendarus (Pandarinus) pauper* var. *libanicus* Baudi di Selve, 1875: 697, which is now considered as a synonym of *Dendarus reitteri* Seidlitz, 1893.

coarcticollis (Mulsant, 1854a: 142) *Pandarus* [comb. by Gebien, 1938: 421]

Type data. Lectotype, male (MNHN), here designated: “Dendarus / coarcticollis. / M.”, “SYNTYPE”, “SYNTYPE / Dendarus / coarcticollis (Mulsant, 1854)”, “MNHN, Paris / EC11734”, “MUSÉUM PARIS / 1943 / COLL. E. MULSANT” (Fig. 1C). **Paralectotypes** (MNHN): female: “Type / de Mulsant.”, “coarcticollis-Muls”, “MUSÉUM PARIS / 1922 / Coll. L. Bedel”, “Syntype”, “Syntype / Dendarus / coarcticollis (Mulsant, 1854)”, “TYPE”, “MNHN, Paris / EC11733”; male: “SYNTYPE”, “SYNTYPE / Dendarus / coarcticollis (Mulsant, 1854)”, “MUSÉUM PARIS / 1943 / COLL. E. MULSANT”, “MNHN, Paris / EC11735”; female: “Pandarus / coarcticollis ♀ / Mls T / [unreadable] / Du66.”, “coarc / ticollis”, “Pandarus / coarcticollis”, “MUSEUM PARIS / COLL. DE MARSEUL / 2842-90”, “SYNTYPE”, “SYNTYPE / Dendarus / coarcticollis (Mulsant, 1854)”, “MNHN, Paris / EC11736”; female: “Pedemont”, “coarc / ticollis”, “MUSEUM PARIS / COLL. DE MARSEUL / 2842-90”, “SYNTYPE”, “SYNTYPE / Dendarus / coarcticollis (Mulsant, 1854)”, “MNHN, Paris / EC11737”, “coarcticollis-Muls. 60. F I / tristis Rossi I.236. / v bipunctuatus CristgVillaCat.461S”, “Pandarus / coarcticollis [unreadable] / Du66.”; female: “Pedemont”, “Pandarus / coarcticollis ♀ / T Mls / [unreadable] / Du66.”, “coarc / ticollis”, “Pandarus / coarcticollis”, “MUSEUM PARIS / COLL. DE MARSEUL / 2842-90”, “SYNTYPE”, “SYNTYPE / Dendarus / coarcticollis (Mulsant, 1854)”, “MNHN, Paris / EC11738”; male: “Pedemont”, “Type Mulsant”, “Pandarus / coarcticollis ♂ / Mls T / Piémont / Du66.”, “MUSEUM PARIS / COLL. DE MARSEUL / 2842-90”, “SYNTYPE”, “SYNTYPE / Dendarus / coarcticollis (Mulsant, 1854)”, “MNHN, Paris / EC11740”; male: “Pandarus / emarginatus. Dej. / Hispania.”, “Pandarus / coarcticollis ♂ / T Mls / emarginatus / T Dej / E / Du66.”, “coarc / ticollis”, “MUSEUM PARIS / COLL. DE MARSEUL / 2842-90”, “SYNTYPE”, “SYNTYPE / Dendarus / coarcticollis (Mulsant, 1854)”, “MNHN, Paris / EC11739”.

tristis (Rossi, 1790: 236) *Helops* [comb. by Dejean, 1821]

Type data. Lectotype, male (ZMB), here designated: “45780”, “Emarginatum / Blaps emargin. / Helops tristis / R. / Ital. Sicil.”, “Hist.Coll. (Coleoptera) / Nr. 45780 (1. Ex.) / Dendarus tristis Rossi / Italia - Sicil. / Zool. Mus. Berlin” (Fig. 1A).

Paralectotype, female (ZMB): “Hist.Coll. (Coleoptera) / Nr. 45780 (2. Ex.) / Dendarus tristis Rossi / Italia - Sicil. / Zool. Mus. Berlin” (Fig. 1B).

= *Pandarus lugens* Mulsant & Rey, 1854: 77 **syn. nov.**

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References

- Aliquò, V., Rastelli, M., Rastelli, S. & Soldati, F. (2007) *Coleotteri Tenebrionidi d'Italia—Darkling Beetles of Italy. Piccole Faune II*. Museo Civico di Storia Naturale di Carmagnola, Torino, Associazione Naturalistica Piemontese, Torino and Progetto Biodiversità, Comitato Parchi, Roma. [CD-ROM]
- Aliquò, V. & Soldati, F. (2014) Updating the CD-ROM on Coleoptera Tenebrionidae of Italy and the check-list of the same family. *Biodiversity Journal*, 5, 429–442.
- Baudi di Selve, F. (1875) Catalogo dei tenebrioniti della fauna europea e circummediterranea appartenenti alle collezioni del Museo Civico di Genova. Parte seconda. *Annali del Museo Civico di Storia Naturale di Genova*, 7, 684–703.

- Baudi di Selve, F. (1881) *Heteromerum* species ex Aegypto, Syria et Arabia. *Deutsche Entomologische Zeitschrift*, 25, 273–296.
<https://doi.org/10.1002/mmnd.48018810223>
- Blanchard, É. (1844) Zoologie. Insectes recueillis à l'Himalaya par Victor Jacquemont. In: *Voyage dans l'Inde par Victor Jacquemont pendant les années 1828 à 1832. Publié sous les auspices de M. Guizot, Ministre de l'Instruction Publique. Descriptions des collections par MM. Isidore Geoffroy Saint-Hilaire.—Milne Edwards.—Émile Blanchard. Valenciennes.—Cambessèdes.—J. Decaisne. Tome quatrième.* Typographie de Firmin Didot Frères, Paris, pp. 13–31. [issued in parts].
- Bouchard, P., Bousquet, Y., Aalbu, R.L., Alonso-Zarazaga, M.A., Merkl, O. & Davies, A.E. (2021) Review of genus-group names in the family Tenebrionidae (Insecta, Coleoptera). *ZooKeys*, 1050, 1–633.
<https://doi.org/10.3897/zookeys.1050.64217>
- Chatzimanolis, S., Trichas, A., Giokas, S. & Mylonas, M. (2003) Phylogenetic analysis and biogeography of the Aegean taxa of the genus *Dendarus* (Coleoptera: Tenebrionidae). *Insect Systematics and Evolution*, 34, 295–312.
<https://doi.org/10.1163/187631203788964773>
- Cherney, L.S. (2005) *Darkling-beetles (Coleoptera, Tenebrionidae). Fauna of Ukraine. Vol. 19. Beetles. Issue 10.* Naukova Dumka, Kiev, 341 pp. [in Russian]
- Dejean, P.F.M.A. (1821) *Catalogue de la collection de Coléoptères de M. le Baron Dejean.* Crevot, Paris, viii + 138 + 2 (errata) pp.
<https://doi.org/10.5962/bhl.title.11259>
- Desbrochers des Loges, J. (1881) Insectes Coléoptères du Nord de l'Afrique nouveaux ou peu connus. *Bulletin de l'Académie d'Hippone*, 16, 51–168.
- Español, F. (1937) Assaig Monogràfic del Subgènere *Dendarus* s. str. (Col. Tenebrionidae). *Treballs del Museu de Ciències Naturals de Barcelona*, 11, 1–89.
- Español, F. (1961) Revisión de los *Dendarus* s. str. (Col. Tenebrionidae). *Eos, Revista Española de Entomología*, 37, 41–70.
- Español, F. & Viñolas, A. (1983) Revisión del género *Heliopathes* Muls. 1854 (Col. Tenebrionidae). 1: Grupo del *strigicollis*. *Nouvelle Revue d'Entomologie*, 13, 213–217.
- Español, F. & Viñolas, A. (1987a) s.n. In: *Revisión del género Heliopathes Muls. 1854 (Col. Tenebrionidae). 2: Grupos del strigosus, del cribratostrigatus y del escaleraí. Publicaciones del Departamento de Zoología, Facultad de Biología, Universidad de Barcelona 13.* Universidad de Barcelona, Barcelona, pp. 83–88.
- Español, F. & Viñolas, A. (1987b) s.n. In: *Revisión del género Heliopathes Muls. 1854 (Col. Tenebrionidae). 3: Grupo de emarginatus. Publicaciones del Departamento de Zoología, Facultad de Biología, Universidad de Barcelona 13.* Universidad de Barcelona, Barcelona, pp. 83–88.
- Español, F. & Viñolas, A. (1990) Revisión del género *Heliopathes* Mulsant, 1854 (Col. Tenebrionidae). 4: Grupo de *H. lusitanicus* (Herbst, 1797). *Eos, Revista Española de Entomología*, 66, 43–47.
- Gebien, H. (1938) Katalog der Tenebrioniden. Teil II. *Mitteilungen der Münchner Entomologischen Gesellschaft*, 28, 283–428.
- Horn, W. & Kahle, I. (1937) “Über entomologische Sammlungen, Entomologen und Entomo-Museologie”. Issued in 3 pts. as: *Sonderdruck von Entomologische Beihefte, Bd. 2–4. Dec. 1935, Oct. 1936, Aug. 1937.* Dahlem, Berlin, 536 + 12 + 38 b/w pls.
- Horn, W., Kahle, I., Friese, G. & Gaedike, R. (1990) *Collectiones Entomologicae. Ein Kompendium über den Verbleib entomologischer Sammlungen der Welt bis 1960. Teil 1. A bis K.* Akademie der Landwirtschaftswissenschaften der Deutschen Demokratischen Republik, Berlin, 573 pp.
- ICZN (1999) *International Code of Zoological Nomenclature, Fourth Edition, adopted by the International Union of Biological Sciences.* International Trust for Zoological Nomenclature, London, xxix + 306 pp.
- Iwan, D., Löbl, I., Bouchard, P., Bousquet, Y., Kamiński, M., Merkl, O., Ando, K. & Schawaller, W. (2020) family Tenebrionidae Latreille, 1802. In: Iwan, D. & Löbl, I. (Eds.), *Catalogue of Palaearctic Coleoptera. Vol. 5. Tenebrionoidea. Revised and Updated 2nd Edition.* I. Brill NV, Leiden, pp. 1–969.
<https://doi.org/10.1163/9789004434998>
- Kamiński, M.J., Kanda, K., Lumen, R., Smith, A.D. & Iwan, D. (2019) Molecular phylogeny of Pedinini (Coleoptera, Tenebrionidae) and its implications for higher-level classification. *Zoological Journal of the Linnean Society*, 185, 77–97.
<https://doi.org/10.1093/zoolinnean/zly033>
- Kamiński, M.J., Lumen, R., Kanda, K., Iwan, D., Johnston, M.A., Kergoat, G., Bouchard, P., Bai, X.-L., Li, X.-M., Ren, G.-D. & Smith, A.D. (2020) Reevaluation of Blapimorpha and Opatrinae: addressing a major phylogeny-classification gap in darkling beetles (Coleoptera: Tenebrionidae: Blaptinae). *Systematic Entomology*, 46, 140–156.
<https://doi.org/10.1111/syen.12453>
- Koch, C. (1948) Die Tenebrioniden Kretas (Col.). *Mitteilungen der Münchner Entomologischen Gesellschaft*, 34, 255–363.
- Löbl, I., Ando, K., Bouchard, P., Egorov, L.V., Iwan, D., Lillig, M., Masumoto, K., Merkl, O., Nabozhenko, M.V., Novák, V., Petterson, R., Schawaller, W. & Soldati, F. (2008) Family Tenebrionidae Latreille, 1802. In: Löbl, I. & Smetana, A. (Eds.), *Catalogue of Palaearctic Coleoptera. Vol. 5. Tenebrionoidea.* Apollo Books, Stenstrup, pp. 105–352.
- Medvedev, G.S. (1968) Coleoptera. Darkling-beetles (Tenebrionidae), subfamily Opatrinae, tribes Platynotini, Dendarini, Pedinini, Dissonomini, Pachypterini, Opatrini (part) and Heterotarsini. *Fauna of USSR, Zhestkokrylye, Leningrad*, 19, 1–285.

- Mulsant, E. (1854a) Latigènes. Histoire naturelle des Coléoptères de France. [Tome 5]. Maisson, Paris, x + 396 pp.
<https://doi.org/10.5962/bhl.title.51567>
- Mulsant, E. (1854b) *Opuscules entomologiques. Cinquième Cahier*. L. Maisson, Paris, x + 255 pp.
<https://doi.org/10.5962/bhl.title.2682>
- Paulian, R. (1944) Les types d'Insectes de Mulsant de Muséum de Paris. Bulletin de Muséum, 2 Série, 16 (2), 117–121.
- Reitter, E. (1904) Bestimmungs-Tabelle der Tenebrioniden. Unterfamilien: Lachnogyini, Akidini, Pedinini, Opatrini und Trachyscelini aus Europa und den angrenzenden Ländern. *Verhandlungen des naturforschenden Vereines in Brünn*, 42, 25–189.
- Rossi, P. (1790) *Fauna Etrusca sistens insecta quae in provinciis Florentina et Pisana praesertim collegit. Tomus primus*. Thomae Masi & Sociorum, Liburni, xxii + [1] + 272 pp.
<https://doi.org/10.5962/bhl.title.15771>
- Seidlitz, G. von (1893) Tenebrionidae. Pp. 201–400. In: Kiesenwetter, H. von & Seidlitz, G. von: *Naturgeschichte der Insecten Deutschlands. Erste Abtheilung. Coleoptera. Fünfter Band. Erste Hälfte*. Nicolaische Verlags-Buchhandlung, Berlin, xxviii + 877 pp.
- Soldati, F. (2012) A new species of the genus *Dendarus* Dejean, 1821 from Greece. Une nouvelle espèce du genre *Dendarus* Dejean, 1821 décrite de Grèce (Coleoptera, Tenebrionidae). *R.A.R.E.*, 21, 52–59.
- Trichas, A. (2008) The genus *Dendarus* Latreille, 1829 (Coleoptera, Tenebrionidae: Dendarini) in Greece. (A systematic account of the genus with description of a new species and four new systematic combinations.). In: Makarov, S.E. & Dimitrijević, R.N. (Eds.), *Advances in arachnology and developmental biology. Papers dedicated to Prof. Dr. Božidar Čurčić*. Institute of Zoology, Belgrade, BAS, Sofia, Faculty of Life Science, Vienna, SASA, Belgrade and UNESCO MAB Serbia, Belgrade, pp. 417–462.
- Trichas, A., Smirli, M., Papadopoulou, A., Anastasiou, I., Keskin, B. & Poulakakis, N. (2020) Dispersal versus vicariance in the Aegean: combining molecular and morphological phylogenies of eastern Mediterranean *Dendarus* (Coleoptera: Tenebrionidae) sheds new light on the phylogeography of the Aegean area. *Zoological Journal of the Linnean Society*, 190, 824–843.
<https://doi.org/10.1093/zoolinnea/zlaa022>