A REVIEW: A NEW SUBGENERIC ARRANGEMENT OF THE GENUS *CHAETOCNEMA* STEPHENS (CHRYSOMELIDAE: GALERUCINAE: ALTICINI) WITH NEW SUBGENERA BASED ON SPERMATHECAL STRUCTURES

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ABSTRACT: Subgeneric classification of the genus *Chaetocnema* Stephens is reviewed. It is clear that the cosmopolitan genus needs a new subgeneric arrengement. As the preliminary studies we have done revealed the spermatecal morphology seems more appropriate and usable than external morphological characters in the subgeneric arrangements for many genera in Chrysomelidae family. The positive results obtained appear to be applicable also for the genus *Chaetocnema* and encouraged us to carry out this study. For this purpose, a new subgeneric arrengement of the *Chaetocnema* genus based on the known spermathecal structures of 83 Palaearctic, 59 Oriental, 37 Afrotropical, 19 Madagascan, 3 Nearctic and 8 Australian species is realized. Data were obtained and evaluated from the previous available studies that have been carried out for a long time and recently accelerated with revisional studies. Therefore, Palaearctic *Chaetocnema* species including Turkish species naturally were firstly evaluated and a total of 8 subgenera including nominative subgenus were identified for these species. Accordingly, except for the nominative subgenus, 5 new subgenera are desribed: *C.* (*Confinoides*) **subgen. nov.**, *C.* (*Hortensoides*) **subgen. nov.**, *C.* (*Majoroides*) **subgen. nov.**, *C.* (*Nigricoides*) **subgen. nov.**, *C.* (*Pseudochaetocnema*) **subgen. nov.** and the status of 2 old names are restored: *C.* (*Plectroscelis*) Dejean, 1836 **stat. rest.**, *C.* (*Udorpes*) Motschulsky, 1845 **stat. rest.**. These subgenera described, also for 59 Oriental species evaluated, were found available. On the contrary the Oriental, Madagascan and Nearctic species, the subgenera described were not found sufficient for all Afrotropical and Australian species and required the description of new subgenera too. Accordingly, 5 new subgenera are also desribed: *C.* (*Biondiana*) **subgen. nov.**, *C.* (*Dalessandroiana*) **subgen. nov.**, *C.* (*Gahanioides*) **subgen. nov.**, *C.* (*Longiconoides*) **subgen. nov.**, *C.* (*Nitidoides*) **subgen. nov.**. According to the results of this study, a total of 4 subgenera were found to be common in each region evaluated. In addition, 2 subgenera occur only in Palaearctic region, while 4 subgenera present only in Afrotropical region and 1 subgenus occurs only in Australian region. With this study, all known *Chaetocnema* species in Palaearctic, Oriental, Madagascan and Nearctic regions, about 39% of all known *Chaetocnema* species in Afrotropical region and about 28% of all known *Chaetocnema* species in Australian region were evaluated. A key to the subgenera of the genus *Chaetocnema* Stephens on the basis of especially spermathecal morphology was also presented.

KEY WORDS: *Chaetocnema*, new subgenera, spermatheca, Alticini, Galerucinae, Chrysomelidae, Coleoptera, Palaearctic region, Oriental region, Afrotropical region, Madagascan region, Australian region

Chaetocnema Stephens, 1831, a member of the tribe Alticini Newman, 1835, is a cosmopolitan genus and includes a large number of species (about 500) that

spread all over the world (Palaearctic, Nearctic, Neotropical, Oriental, Afrotropical, Madagascan and Australian regions). According to Konstantinov et al. (2011), *Chaetocnema* is one of a few flea beetle genera that are cosmopolitan and its known species occur in the Afrotropical (149), Australian (26), Nearctic (36), Neotropical (106), Oriental (76), and Palearctic (75) regions. Nearctic, Madagascan, Palearctic and Oriental faunas of *Chaetocnema* have been recently completely revised (White, 1996; Biondi, 2001; Konstantinov et al., 2011; Ruan et al., 2019). In addition, Biondi (2000, 2002a,b), Biondi & Nardis (2000), Biondi & D'Alessandro (2005, 2006, 2008, 2018) and Samuelson (1967, 1973) on the known species in Afrotropical and Australian regions are available and important recent works in which the data used in this study were obtained.

Until the Nearctic revision of White (1996) also even later, *Chaetocnema* species were traditionally considered within two subgenera as the nominative and *Tlanoma* Motschulsky, 1835. As known, the distinction of two subgeneric groups for *Chaetocnema* is longstanding and not without merits but inadequate and wrong.

Stephens (1831) described *Chaetocnema* without designating a type species. Westwood (1838) subsequently designated *Chrysomela concinna* Marsham as the type species. The subsequent designation of Westwood (1838) was overlooked by Maulik (1926) who, in turn, designated *Galeruca aridella* Paykull (= *Altica hortensis* Geoffroy) as the type species. However, it was originally not included in *Chaetocnema* and, as a name, is unavailable for this purpose. As Konstantinov et al. (2011) stated that it is unfortunate that Westwood's (1838) type designation for *Chaetocnema* has been overlooked for a long time and many authors, including Döberl (2010), have based the nominal subgenus on *C. aridella* (= *C. hortensis*) rather than *C. concinna*. This makes the name for the other traditionally recognized subgenus, *Tlanoma* Motschulsky, a subjective junior synonym of *Chaetocnema* in the strict sense, while *Chaetocnema* of authors is left without a name. To fill this gap Konstantinov et al. (2011) proposed *Udorpes* Motschulsky as the next available subgeneric name. Unfortunately, this proposal of Konstantinov et al. (2011) is not suitable and not sufficient for all Palaearctic species, as they have stated. In terms of external morphological characters used in this distinction, many species can not be placed in both subgenera. Accordingly, Konstantinov et al. (2011) suggested not to use any subgeneric classification until rigorous phylogenetic analysis has been conducted in this genus. However, the two subgenera were used by Ruan et al. (2019) that they stated the two subgenera is used for practical reasons. The proposed genus group names of *Chaetocnema* genus are based on questionable external characters (usually some only 3-5 adult characters).

Classification systems have mainly based on the external morphological characters, however, most of these classifications change constantly because of homoplasy and symplesiomorphy within these character sets. To provide a more stable classification, therefore, taxonomists have studied internal and genital morphological features in combination with the external morphological characters (e.g. Kasap & Crowson, 1979; Mann & Crowson, 1983; Suzuki, 1988).

Male genitalia have been widely used to differentiate species, while the female internal reproductive organs have been used less frequently (e.g. Arnqvist, 1997; Hernández and Ortuño, 1992; Hernández, 1993; Ferronato, 2000). Their variations are useful in distinguishing species group level and even genus group level (Suzuki, 1988).

Internal reproductive organs of female insects include a pair of ovaries with their respective oviducts, a median ectodermal tube, a vagina, a bursa copulatrix and the spermatheca which is an invagination of the eighth abdominal segment and its number and shape depend on the group of insects .The spermatheca stores and maintains viability of sperm until fertilization and has an important role in copulation and oviposition (Snodgrass 1935; Suzuki 1988; Triplehorn et al. 2005; De Marzo, 2008; Pascini & Martins, 2017; Rodríguez-Mirón et al., 2017).

In Coleoptera, five patterns of spermathecal morphology were distinguished by De Marzo (2008) with the presence, absence or variations of spermathecal capsule, spermathecal duct, and spermathecal gland. The most widespread pattern is to have only one spermathecal capsule (receptacle + pump or velum) connected with the bursa copulatrix by one spermathecal duct, and one spermathecal gland (Suzuki, 1988; Matsumura & Suzuki, 2008; De Marzo, 2008; Rodríguez-Mirón et al., 2017).

Spermathecal structures have been used to separate and diagnose the tribes of Scarabaeinae (López-Guerrero & Halffter, 2000). Also the spermathecae allow the recognition of species and genera in Carabidae and Curculionidae (Aslam 1961, Schuler, 1963). In Chrysomeloidea, the spermatheca has been useful to define subfamilies, genera and species (Reid, 1989; Hernández, 1993; Biondi, 2001; Borowiec & Świętojańska, 2001, Borowiec & Skuza, 2004; Borowiec & Opalinska, 2007; Borowiec & Pomorska, 2009; Rodríguez-Mirón & Zaragoza-Caballero, 2017; Rodríguez-Mirón et al., 2017). According to Rodríguez-Mirón et al. (2017), the spermatheca provides characters to diagnose genera and subgenera, and also they stated that the spermatheca has a high taxonomic value for diagnosing taxa at various ranks.

As can be seen above, it is clear that the *Chaetocnema* genus still needs a subgeneric arrengement. As the preliminary studies we have done on the *Cassida* genus of which aedeagal morphology is not diagnostic while spermathecal morphology is partially diagnostic, revealed the spermathecal morphology seems more available and usable than external morphological characters in the subgeneric arrangements for the genus group. The positive results obtained in the previous studies appear to be applicable also for the genus *Chaetocnema* and encouraged us to carry out this study. We hope that the results obtained in this study will contribute to the subgeneric classification of this genus group. Also as Konstantinov et al. (2011) stated, in fact that *Chaetocnema* clearly needs to be based on a rigorous phylogenetic study for a complete solution in subgeneric reclassification. Until such an analysis is carried out, not using any subgeneric classification is not a solution to the problem and we believe that the positive results obtained in this study will be an available solution for the related problem.

At the species level, aedeagal morphology in the genus *Chaetocnema* Stephens, 1831 seems to be diagnostic, while spermathecal morphology seems to be not diagnostic or at most partially diagnostic. Similarly, White (1996) stated that the aedeagi have proven to be highly diagnostic at the species level. It must be because of he assumes spermathecae are not diagnostic, however, spermathecae of Nearctic species in revision of White (1996) did not examined. Spermathecae in the genus *Chaetocnema*, like in most genera of the tribe Alticini, are partially uniform and do not offer good diagnostic characters at the species level. Contrary to the partial homogenity of spermathecae, studies on aedeagi suggested quite large diversity of aedeagal structure. For this reason, although there are many species described based on aedeagal structure, while there is no

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species described only based on spermathecal structure. With this study, the above mentioned opinions was supported for the species group. However, so far, genital morphology has been overlooked in the arrangement of the upper categories from species group level in *Chaetocnema* genus. Whereas, according to our study, it can be said that the similarities and differences in spermathecal morphology can be easily used in arrangement of the subgenera.

METHOD

The present study was conducted on the basis of the data obtained from available references: Revisional works of White (1996), Biondi (2001), Konstantinov et al. (2011) and Ruan et al. (2019) mainly and the other works of Biondi (2000, 2002a,b), Biondi & Nardis (2000), Biondi & D'Alessandro (2005, 2006, 2008, 2018) and Samuelson (1967, 1973). Accordingly, spermathecal structures of 209 *Chaetocnema* species in Palaearctic (83), Oriental (59), Afrotropical (37), Madagascan (19), Nearctic (3) and Australian (8) regions were reviewed and evaluated on the basis of these references. Therefore, a new subgeneric arrengement of *Chaetocnema* genus based on the known spermathecal structures of the species was performed. Palaearctic *Chaetocnema* species including Turkish species naturally were firstly evaluated and a total of 8 subgenera including nominative subgenus were identified and described for these species. Later Oriental, Afrotropical, Madagascan, Nearctic and Australian species were reviewed and evaluated respectively. On the contrary the Oriental, Madagascan and Nearctic species, the subgenera described were not found sufficient for all Afrotropical and Australian species and therefore 5 new subgenera were also described for these species. The spermathecal figures given in the study were also cited from the sources given above. The spermathecal terminologies used in the present study is given below (Fig. 1).

Abbreviations: CHA = *Chaetocnema* (s. str.) Stephens, BIO = *C.* (*Biondiana*) subgen. nov., CON = *C.* (*Confinoides*) subgen. nov., DAL = *C.* (*Dalessandroiana*) subgen. nov., GAH = *C.* (*Gahanioides*) subgen. nov., HOR = *C.* (*Hortensoides*) subgen. nov., LON = *C.* (*Longicornoides*) subgen. nov., MAJ = *C.* (*Majoroides*) subgen. nov., NIG = *C.* (*Nigricoides*) subgen. nov., NIT = *C.* (*Nitidoides*) subgen. nov., PLE = *C.* (*Plectroscelis*) Dejean, PSE = *C.* (*Pseudochaetocnema*) subgen. nov., UDO = *C.* (*Udorpes*) Motschulsky.

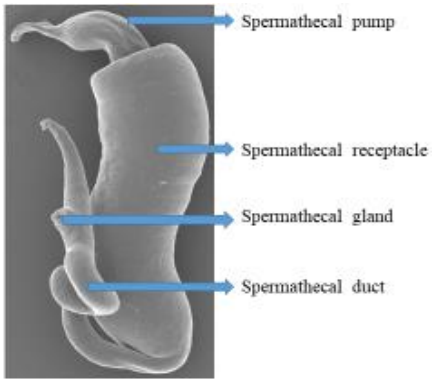

Figure 1. Spermathecal terminologies of *Chaetocnema montenegrina* Heikertinger, 1912.

RESULTS

Genus *CHAETOCNEMA* Stephens, 1831

The genus *Chaetocnema* was established by Stephens (1831: 325) without designating a type species. His work included six species originally (pp. 326-327) as *aridella* (no author given), *sahlbergii* Gyll., *aridula* Gyll., *concinna* Marsham, *picipes* (Kirby manuscript name), and *saltitans* (Kirby manuscript name). Original description of the genus is as follows:

"*Antennae short, 11-jointed: basal joint robust curved; second also robust and short; three following rather slender, equal in length, but longer than the second; the remainder gradually increasing in stoutness, the last being the largest, ovate, subacuminate: head prominent, triangular: thorax short, transverse, the lateral margins rounded, the base obsoletely bisinuate: elytra broad, striated: legs stout, short: anterior tibiae simple: intermediate and posterior with a short acute tooth on the middle of the outer margin, furnished postoriorly with a fringe of hairs or setae: posterior femora very stout: tarsi all short*".

Westwood (1838: 42) subsequently designated *Chrysomela concinna* Marsham, 1802 that was included in the first species listed by Stephens after his original description of the genus, as the type species of the genus. Unfortunately, the subsequent designation of Westwood (1838) was overlooked by Maulik (1926) who designated *Galeruca aridella* Paykull, 1799 (= *Altica hortensis* Geoffroy, 1785) as the type species that assuming it was the first species listed by Stephens after his description of the genus. However, it was originally not included in *Chaetocnema* and, as a name, is unavailable for this purpose. Because Stephens (1831) included a name *aridella* without author (see above).

Accordingly, *Chrysomela concinna* Marsham, 1802 was accepted as the type species of the genus by White (1996) and Konstantinov (2011) rightly. Since *Chrysomela concinna* Marsham was one of the original six species included by Stephens under *Chaetocnema* (as is required by the rules), and since there is no prior type species designation, *Chrysomela concinna* is the valid type species of *Chaetocnema*.

On the other side, until White (1996) and even later, the type designation of Westwood's (1838) for *Chaetocnema* has been overlooked for a long time and many authors including Döberl (2010) have based the nominal subgenus on *C. aridella* (= *C. hortensis*) rather than *C. concinna*. Since species of the genus *Chaetocnema* Stephens are often divided into the subgenera *Chaetocnema* s. str. and *Tlanoma* Motschulsky, 1845. Whereas the type species of *Tlanoma* Motschulsky is clearly *Altica dentipes* Koch, 1803 (= *Chrysomela concinna* Marsham, 1802), by original designation. It was synonymized by Heikertinger (1951:211).

Maulik (1926), did not use the subgenus *Tlanoma* Motschulsky in his publication and stated that sometimes *Tlanoma* is regarded as a subgenus of *Chaetocnema*. However, Heikertinger (1951) treated the species of *Chaetocnema* under the two subgenera and mentioned diagnostic characters for them in his study. But he stated that the Palaearctic species lend themselves very nicely to classification under the two subgenera, but that with the exotic species there are difficulties. Since he also assumed that *Galeruca aridella* Paykull, 1799 (= *Altica hortensis* Geoffroy, 1785) is type species of *Chaetocnema* s. str. and *Altica*

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dentipes Koch, 1803 (= *Chrysomela concinna* Marsham, 1802) is type species of *Tlanoma* Motschulsky, 1845. The characters which Heikertinger (1951) sets forth for the two subgenera are below:

***Chaetocnema* s. str.** Type sp.: *Galeruca aridella* Paykull, 1799 (= *Altica hortensis* Geoffroy, 1785)	***Tlanoma* Motschulsky, 1845** Type sp.: *Altica dentipes* Koch, 1803 (= *Chrysomela concinna* Marsham, 1802)
Front between the bases of the antennae and below these broad and flat, sloping obliquely downward generally distinctly punctate to the transverse impression; without carina, and without lateral grooves beside the antennal sockets.	Front between the bases of the antennae with a more or less distinct, mostly smooth, impunctate longitudinal carina or keel which is limited laterally toward the antennal sockets by a groove.
Vertex densely, regularly punctate to the transverse impression (rarely scattered and fine, but even then regularly distributed).	Vertex not punctate anteriorly to the transverse impression, but with a number of coarse punctures near the eyes, which may meet on the posterior part of the vertex.
Pronotum without a longitudinal impression at either side of the base. Body generally strongly convex, of somewhat cylindrical form.	Base of pronotum on each side often with a short, finely impressed longitudinal line or an indistinct, oblique impression in place of it (in the case of the smaller forms, both are usually absent).
Rows of punctures of the elytra regular at the sides, but generally more or less confused on the disc, seldom entirely regular. Metasternum punctate in the middle.	Elytra entirely regularly punctate-striate, even the short scutellar row hardly ever irregular. Metasternum smooth or singly punctate.
Head generally relatively large and broad.	The larger forms possess a relatively broad head, flatter frontal carina, and a more subparallel body-form; the smaller forms are narrow or small headed, and with tapering egg-shaped form.

The nasal keel which is supposed to distinguish the subgenus *Tlanoma* from the nominative subgenus is highly variable and therefore a poor character for grouping species according to White (1996). Also, White (1996) argued that *Tlanoma* cannot be treated as a subgenus of *Chaetocnema* because both have the same type species, *Chrysomela concinna* Marsham, 1802. Instead, he arranged the 59 North American *Chaetocnema* species within twelve species groups defined by several external features. However, this arrangement was not employed by Riley et al. (2003) in their recent catalog of the North American Chrysomelidae rightly. Since, for example, the type species *Chaetocnema concinna* was assigned to the *confinis* group which, among others, is characterized by having only a few large punctures above each eye, the elytral punctures arranged in regular rows, and usually being of small size. Whereas *Chaetocnema confinis* was regarded as the type species of *C.* (*Confinoides*) subgen. nov. in the present study.

This makes the name for the other traditionally recognized subgenus, *Tlanoma* Motschulsky, a subjective junior synonym of *Chaetocnema* in the strict sense, while *Chaetocnema* of authors is left without a name. To fill this gap Konstantinov et al. (2011) proposed *Udorpes* Motschulsky as the next available subgeneric name with the following characters:

***Chaetocnema* s. str.** Type sp.: *Galeruca aridella* Paykull, 1799 (= *Altica hortensis* Geoffroy, 1785)	***Udorpes* Motschulsky, 1845** Type sp.: *Udorpes splendens* Motschulsky, 1845
Frontal ridge narrow and convex	Frontal ridge wide and flat.
Vertex unevenly and sparsely covered with usually small punctures.	Vertex evenly and mostly densely covered with usually large punctures.

Unfortunately, this proposal is not suitable and not sufficient for all Palaearctic species, as Konstantinov et al. (2011) have stated. In terms of external morphological characters used in this distinction, many species cannot be placed in both subgenera certainly. Accordingly, Konstantinov et al. (2011) suggested not to use any subgeneric classification until rigorous phylogenetic analysis has been conducted in this genus. However, the two subgenera were used by Ruan et al. (2019) that they stated the two subgenera is used for practical reasons.

As seen above, it is clear that the *Chaetocnema* genus still needs a subgeneric arrengement and the proposed genus group names of *Chaetocnema* are based on questionable external characters (usually some only 3-5 adult characters). As a fact revealed by the efforts briefly mentioned above, a subgeneric arrangement based solely on external morphological characters will not be available and sufficient for *Chaetocnema* species. Whereas the spermateca structure, which we assume to be available and usable for this purpose, has been overlooked by the authors to date for various reasons.

Consequently, a new subgeneric arrengement of *Chaetocnema* genus based on the known spermathecal structures of 83 Palaearctic, 59 Oriental, 37 Afrotropical, 19 Madagascan, 3 Nearctic and 8 Australian species was conducted and presented below. Moreover, 16 Palaearctic, 26 Oriental, 3 Afrotropical, 1 Madagascan, 57 Nearctic and 19 Australian species of which spermathecal stuructures are unknown are also evaluated and placed in possible subgenera based on their aedeagal structures and external characters, and they are presented at the end of each subgenus. However, I would like to state that in fact, it should not be forgotten that the exact determination of the subgenus to which these species belong is only possible by examining their spermathecal morphology.

Subgenus *CHAETOCNEMA* Stephens, (Plate I)

***Chaetocnema* Stephens, 1831: 325** (type species: *Chrysomela concinna* Marsham, 1802, subsequent designation by Westwood, 1838: 42).

Odontocnema; Stephens (1831: 285), incorrect original spelling, unavailable under Article 19.3.

Tlanoma Motschulsky, 1845a: 108 (type species: *Haltica dentipes* Koch, 1803 = *Chrysomela concinna* Marsham, 1802, by original designation; synonymized by White, 1996: 22, subjective synonym of *Chaetocnema*).

Brinckaltica Bechyne, 1959: 237 (type species: *Chaetocnema subaterrima* Jacoby 1900, by original designation; Scherer 1961:259, subjective synonym of *Chaetocnema*).

Description. Spermathecal pump much shorter than receptacle. Apex of spermathecal pump cylindrical or rounded. Spermathecal receptacle relatively shortened, more or less narrowed or widened, cylindrical or pyriform, but not sinuate. Spermathecal pump attached to middle of receptacle top. Maximum width of receptacle situated basally or at about middle. Basal part of receptacle about as wide as apical, wider than apical or narrower than apical. Minimum

width of receptacle usually situated apically. Spermathecal duct shorter than receptacle, but relatively long. Apex of spermathecal duct up to about 2/3 or 3/4 of receptacle, but spermathecal gland at about middle or near middle basally of receptacle. Basal part of spermathecal duct straight or corrugated. Apical part of spermathecal duct more or less straight. General shape of spermatheca more or less cylindrical or pyriform.

The subgenus is included a total of 24 species in Palaearctic region (see below) that most of them were placed by Warchalowski (2010) and Döberl (2010) in the subgenera *Tlanoma* Motschulsky, 1845. It can be divided into 3 groups on the basis of their spermathecal morphology as Group A (basal part and apical part of spermathecal duct more or less straight); Group B (basal part of spermathecal duct straight, apical part of spermathecal duct more or less corrugated); Group C (basal part of spermathecal duct more or less corrugated, apical part of spermathecal duct more or less straight) (Table 1).

The subgenus is represented in all regions evaluated in this study.

Diagnosis. Spermathecal structure of this subgenus is very similar to that of *Chaetocnema* (*Pseudochaetocnema*) subgen. nov. at first glance, but can be easily distinguished from it mainly by the cylindrical or rounded apex of spermathecal pump.

Some external characters for the subgenus. Frontal ridge between antennal sockets narrow and convex. Frons with only relatively long setae on sides present. Vertex flat, situated about on same level as orbit. Surface of vertex sparsely and unevenly covered with varying number of punctures near eye only. Punctures about as large as or slightly larger than pronotal punctures. Pronotum with evenly but relatively sparsely punctures. Diameter of pronotal punctures 2–4 times smaller than distance between them. Pronotal punctures distinctly smaller than elytral punctures. Basal stria of punctures on pronotum absent. Base of pronotum without longitudinal impressions or with two well-developed longitudinal impressions, both near basal margin and further anteriorly. Elytra with convex sided. Elytral punctures regular including periscutellar rows.

Table 1. Palaearctic species in this subgenus.

Palaearctic Species	Subgenus under the present study	Subgenus under the previous studies*
Group A		
C. batophiloides Abeille, 1909	*Chaetocnema*	*Tlanoma*
C. cheni Ruan et al., 2014	*Chaetocnema*	*Chaetocnema*
C. concinna (Marsham, 1802)	*Chaetocnema*	*Tlanoma*
C. constricta Ruan et al., 2014	*Chaetocnema*	*Chaetocnema*
C. depressa (Boieldieu, 1859)	*Chaetocnema*	*Tlanoma*
C. fortecostata Chen, 1939	*Chaetocnema*	*Chaetocnema*
C. heptapotamica Lubischev, 1963	*Chaetocnema*	*Tlanoma*
C. kimotoi Gruev, 1980	*Chaetocnema*	*Tlanoma*
C. koreana Chûjô, 1942	*Chaetocnema*	*Tlanoma*
C. picipes Stephens, 1831	*Chaetocnema*	*Tlanoma*
C. salixis Ruan et al., 2014	*Chaetocnema*	*Chaetocnema*
C. semicoerulea (Koch, 1803)	*Chaetocnema*	*Tlanoma*
C. transbaicalica Heikertinger, 1951	*Chaetocnema*	*Tlanoma*
Group B		
C. bilunulata Demaison, 1902	*Chaetocnema*	*Tlanoma*
C. lubischevi Konstantinov et al., 2011	*Chaetocnema*	
C. nebulosa Weise, 1886	*Chaetocnema*	*Tlanoma*

C. simplicifrons (Baly, 1876)	*Chaetocnema*	*Chaetocnema*
Group C		
C. breviuscula (Faldermann, 1837)	*Chaetocnema*	*Tlanoma*
C. delarouzeei (Brisout, 1884)	*Chaetocnema*	*Tlanoma*
C. duvivieri Jacoby, 1892	*Chaetocnema*	*Chaetocnema*
C. puncticollis (Motschulsky, 1858)	*Chaetocnema*	*Tlanoma* or *Chaetocnema*
C. scheffleri (Kutschera, 1864)	*Chaetocnema*	*Tlanoma*
C. sticta Maulik, 1926	*Chaetocnema*	*Tlanoma* or *Chaetocnema*
C. tibialis (Illiger, 1807)	*Chaetocnema*	*Tlanoma*

* Warchalowski (2010), Döberl (2010), Ruan et al. (2019).

This subgenus includes also the following 15 Oriental, 6 Afrotropical, 8 Madagascan, 1 Nearctic and 1 Australian species, of which spermathecal structures have been studied by cited references:
Oriental *Chaetocnema* (s. str.) species: *C. baoshanica* Ruan et al., 2019; *C. cheni* Ruan, Konstantinov & Yang, 2014; *C. constricta* Ruan, Konstantinov & Yang, 2014; *C. deqinensis* Ruan et al., 2014; *C. duvivieri* Jacoby, 1892; *C. fortecostata* Chen, 1939; *C. kingpinensis* Ruan et al., 2014; *C. puncticollis* (Motschulsky, 1858); *C. purerulea* Ruan et al., 2019; *C. salixis* Ruan et al., 2014; *C. simplicifrons* (Baly, 1876); *C. sticta* Maulik, 1926; *C. wallacei* Baly, 1877; *C. yulongensis* Ruan et al., 2014 and *C. yunnanica* Heikertinger, 1951. **Afrotropical *Chaetocnema* (s. str.) species:** *C. bilunulata* Demaison, 1902; *C. convexicollis* (Boheman, 1859); *C. gregaria* Weise, 1910; *C. picipes* Stephens, 1831; *C. rutovuensis* Bechyné, 1955 and *C. tibialis* (Illiger, 1807). **Madagascan *Chaetocnema* (s. str.) species:** *C. bilunulata* Demaison, 1902; *C. cachani* Biondi, 2001; *C. gregaria* Weise, 1910; *C. madagascariensis* Baly, 1877; *C. malgascia* Biondi, 2001; *C. orophila* Biondi, 2001; *C. picipes* Stephens, 1831 and *C. vadoni* Bechyné, 1948. **Nearctic *Chaetocnema* (s. str.) species:** *C. concinna* (Marsham, 1802). **Australian *Chaetocnema* (s. str.) species:** *C. littoralis* (Broun, 1893).

In addition, the following 3 Palaearctic, 9 Oriental, 1 Afrotropical and 21 Nearctic species of which spermathecal structures are unknown, it is possible that may be belonging to this subgenus based on their aedeagal structures and external morphological characters:
Possible Palaearctic *Chaetocnema* (s. str.) species: *C. bicolorata* Kimoto, 1971; *C. granulosa* (Baly, 1874) and *C. septentrionalis* Kimoto, 1963. **Possible Oriental *Chaetocnema* (s. str.) species:** *C. furthi* Medvedev, 1996; *C. granulosa* (Baly, 1874); *C. laotica* Medvedev, 2009; *C. malaisei* Bryant, 1939; *C. melonae* Chen, 1934; *C. montivaga* Maulik, 1926; *C. nagpurensis* Duvivier, 1892; *C. sumatrana* Jacoby, 1896 and *C. yonyonae* Chen, 1934. **Possible Afrotropical *Chaetocnema* (s. str.) species:** *C. purpurea* Jacoby, 1906. **Possible Nearctic *Chaetocnema* (s. str.) species:** *C. aenigmatica* White, 1996; *C. alutacea* Crotch, 1873; *C. arizonica* White, 1996; *C. bicolor* Gentner, 1928; *C. blatchleyi* Csiki, 1940; *C. crenulata* Crotch, 1873; *C. densa* White, 1996; *C. dispar* Horn, 1889; *C. ectypa* Hom, 1889; *C. elongatula* Crotch, 1873; *C. extenuata* White, 1996; *C. fulvida* White, 1996; *C. gentneri* Cziki, 1940; *C. labiosa* White, 1996; *C. livida* White, 1996; *C. magnipunctata* Gentner, 1928; *C. obliterata* White, 1996; *C. opulenta* Horn, 1889; *C. rileyi* White, 1996; *C. subconvexa* White, 1996 and *C. vesca* White, 1996.

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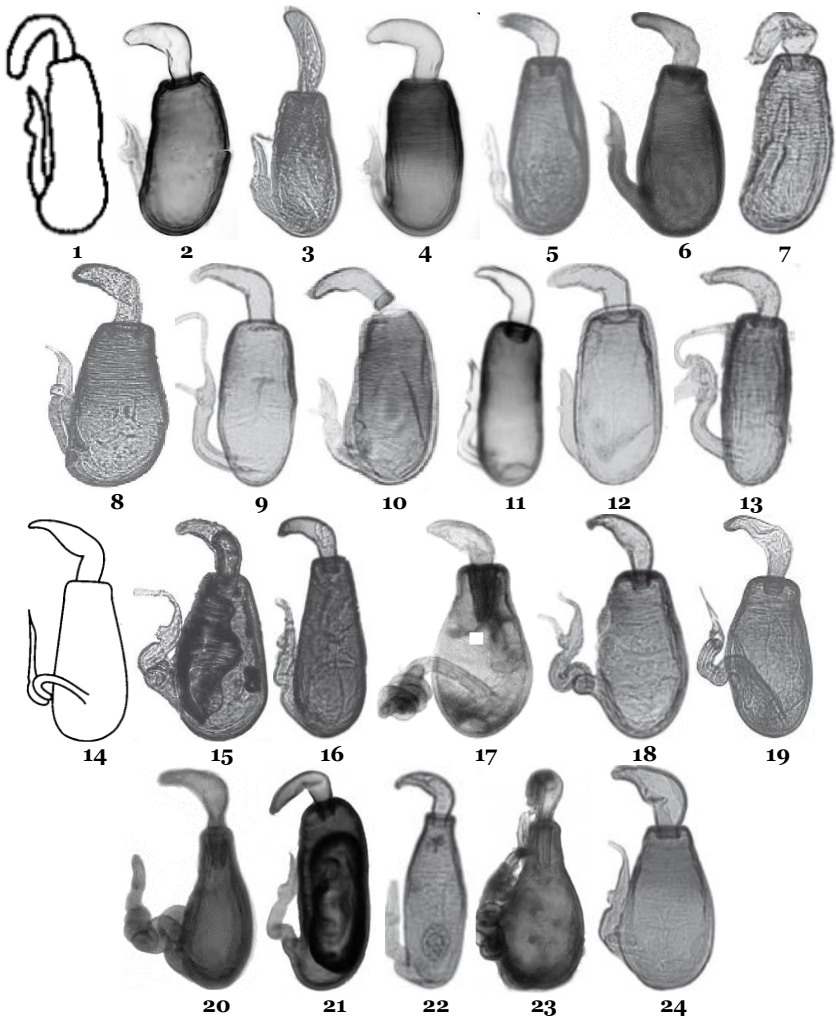


Plate I. Spermathecal morphology of Palaearctic species of the subgenus *Chaetocnema* (s. str.) Stephens: **Group A 1-13:** 1. *C. batophiloides* Abeille (taken from Furth, 1985), 2. *C. cheni* Ruan et al., 3. *C. concinna* (Marsham), 4. *C. constricta* Ruan et al., 5. *C. depressa* (Boieldieu), 6. *C. fortecostata* Chen, 7. *C. heptapotamica* Lubischev, 8. *C. kimotoi* Gruev, 9. *C. koreana* Chûjô, 10. *C. picipes* Stephens, 11. *C. salixis* Ruan et al., 12. *C. semicoerulea* (Koch), 13. *C. transbaicalica* Heikertinger; **Group B 14-17:** 14. *C. bilunulata* Demaison (taken from Biondi, 2001), 15. *C. lubischevi* Konstantinov et al., 16. *C. nebulosa* Weise, 17. *C. simplicifrons* (Baly), **Group C 18-24:** 18. *C. breviuscula* (Faldermann), 19. *C. delarouzeei* (Brisout), 20. *C. duvivieri* Jacoby, 21. *C. puncticollis* (Motschulsky), 22. *C. scheffleri* (Kutschera), 23. *C. sticta* Maulik, 24. *C. tibialis* (Illiger) (taken from Konstantinov et al., 2011; Ruan et al., 2019).

Subgenus *BIONDIANA* subgen. nov. (Plate II)

***Biondiana* subgen. nov.** (type species: *Chaetocnema zulu* Biondi & Nardis, 2000).

Description. Spermathecal pump much longer than receptacle. Apex of spermathecal pump more or less cylindrical or rounded. Spermathecal receptacle very shortened, widened, globose, not sinuate. Spermathecal pump attached to middle of receptacle top. Maximum width of receptacle situated medially. Basal part of receptacle about as wide as apical. Minimum width of receptacle situated apically or basally. Spermathecal duct much shorter than receptacle, distinctly shortened. Apex of spermathecal duct up to about middle of receptacle, spermathecal gland at basal 1/4 of receptacle. Basal and apical parts of spermathecal duct straight. Spermatheca long-handled gourd-shaped in general.

The subgenus is included only 2 species in Afrotropical region (see below) now (Table 2).

The subgenus is represented only in Afrotropical region evaluated in this study.

Diagnosis. Spermathecal structure of this subgenus is unique.

Etymology. The name is dedicated to Maurizio Biondi who has made important contributions to the Afrotropical *Chaetocnema* species.

Some external characters for the subgenus. Frontal ridge between antennal sockets narrow and convex. Frons with only relatively long setae on sides present. Vertex flat, situated about on same level as orbit. Surface of vertex sparsely and unevenly covered with some weakly impressed punctures (3-5) near upper ocular margins. Punctures about as large as pronotal punctures. Pronotum with evenly but relatively sparsely punctures. Diameter of pronotal punctures at least 2-4 times smaller than distance between them. Pronotal punctures smaller than elytral punctures. Basal stria of punctures on pronotum absent. Base of pronotum without longitudinal impressions. Elytra with convex sided. Elytral punctures regular including periscutellar rows.

Table 2. Afrotropical species in this subgenus.

Afrotropical Species	Subgenus under the present study
C. mapumalangaensis Biondi & Nardis, 2000	*Biondiana*
C. zulu Biondi & Nardis, 2000	*Biondiana*

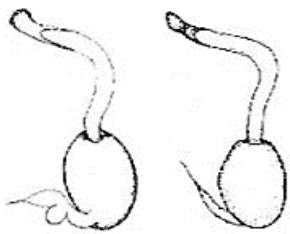


Plate II. Spermathecal morphology of Afrotropical species of the subgenus *C.* (*Biondiana*) subgen. nov.: 1. *C. mapumalangaensis* Biondi & Nardis, 2. *C. zulu* Biondi & Nardis (taken from Biondi & Nardis, 2000).

In addition, the following 1 Afrotropical species of which spermathecal structure is unknown, it is possible that may be belonging to this subgenus based on their aedeagal structure and external morphological characters:

Possible Afrotropical *C.* (*Biondiana*) species: *C. mariobiondii* Biondi & Nardis, 2000.

Subgenus *CONFINOIDES* subgen. nov. (Plate III)

***Confinoides* subgen. nov.** (type species: *Chaetocnema confinis* Crotch, 1873).

Description. Spermathecal pump much shorter than receptacle. Apex of spermathecal pump cylindrical or rounded. Spermathecal receptacle shortened, very widened and globose, not sinuate, in the form of a bomb that distinctly narrowed in the apical 1/4 part and very widened in the basal 3/4 part. Spermathecal pump attached to middle of receptacle top. Maximum width of receptacle situated at about middle. Basal part of receptacle distinctly wider than apical. Minimum width of receptacle situated distinctly apically. Spermathecal duct shorter than receptacle, but longish. Apex of spermathecal duct up to about 4/5 of receptacle, spermathecal gland at about 3/4 of receptacle. Basal part of spermathecal duct more or less straight. Apical part of spermathecal duct more or less corrugeted. Spermatheca bomb-shaped in general.

The subgenus is included only 1 species in Palaearctic region (see below) that was placed by Ruan et al. (2019) in the nominative subgenus (Table 3).

The subgenus is represented in all regions evaluated in this study.

Diagnosis. Spermathecal structure of this subgenus is unique.

Etymology. The name "confinoides", meaning confinis-like, is derivated after "*confinis*" the specific epithet of the type species.

Some external characters for the subgenus. Frontal ridge between antennal sockets narrow and convex. Frons with only relatively long setae on sides present. Vertex flat, situated about on same level as orbit. Surface of vertex sparsely and unevenly covered with several punctures (4-7) near eye. Punctures about as large as pronotal punctures. Pronotum with evenly but relatively sparsely punctures. Diameter of pronotal punctures 2–4 times smaller than distance between them. Pronotal punctures smaller than elytral punctures. Basal stria of punctures on pronotum absent. Base of pronotum without longitudinal impressions. Elytra with convex sided. Elytral punctures regular including periscutellar rows.

Table 3. Palaearctic species in this subgenus.

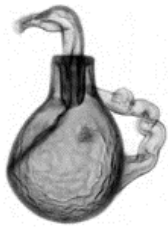
Palaearctic Species	Subgenus under the present study	Subgenus under the previous studies*
C. confinis Crotch, 1873	*Confinoides*	*Chaetocnema*

* Ruan et al. (2019).

This subgenus includes also the following 2 Oriental, 3 Afrotropical, 3 Madagascan, 1 Nearctic and 2 Australian species, of which spermathecal structures have been studied by cited references:

Oriental *C.* (*Confinoides*) species: *C. confinis* Crotch, 1873; *C. dapitanica* Ruan et al., 2019. **Afrotropical *C.* (*Confinoides*) species:** *C. cinctipennis* Laboissière, 1941; *C. confinis* Crotch, 1873 and *C. fuscipennis* Scherer, 1962. **Madagascan *C.* (*Confinoides*) species:** *C. confinis* Crotch, 1873; *C. coronilla*

Bechyné, 1964 and *C. fuscipennis* Scherer, 1962. **Nearctic *C.* (*Confinoides*) species:** *C. confinis* Crotch, 1873. **Australian *C.* (*Confinoides*) species:** *C. allardi* Perroud, 1864 and *C. arsipodoides* Samuelson, 1973.



1

Plate III. Spermathecal morphology of Palaearctic species of the subgenus *C.* (*Confinoides*) subgen. nov.: 1. *C. confinis* Crotch (taken from Ruan et al., 2019).

In addition, the following 2 Nearctic species of which spermathecal structures are unknown, it is possible that may be belonging to this subgenus based on their aedeagal structures and external morphological characters:

Possible Nearctic *C.* (*Confinoides*) species: *C. repens* McCrea, 1973 and *C. serpentina* White, 1996.

Subgenus *DALESSANDROIANA* subgen. nov. (Plate IV)

***Dalessandroiana* subgen. nov.** (type species: *Chaetocnema audisiana* Biondi, 2000).

Description. Spermathecal pump about as long as receptacle. Apex of spermathecal pump more or less cylindrical or rounded. Spermathecal receptacle relatively shortened, more or less widened in basal half, bottle-shaped, distinctly sinuate preapically on both ventral and dorsal surfaces. Spermathecal pump attached to middle of receptacle top. Maximum width of receptacle situated basally. Basal part of receptacle slightly wider than apical. Minimum width of receptacle situated preapically. Spermathecal duct as long as receptacle, longish. Apex of spermathecal duct up to about apical margin of receptacle, but spermathecal gland at about apical 4/5 or preapical part of receptacle. Basal part of spermathecal duct usually corrugated as once coiled. Apical part of spermathecal duct straight. Spermatheca bottle-shaped in general.

The subgenus is included only 1 species in Afrotropical region (see below) now (Table 4).

The subgenus is represented only in Afrotropical region evaluated in this study.

Diagnosis. Spermathecal structure of this subgenus is unique.

Etymology. The name is dedicated to Paola D'Alessandro who has made important contributions to the Afrotropical *Chaetocnema* species.

Some external characters for the subgenus. Frontal ridge between antennal sockets wide and flat. Frons evenly covered with relatively short, white setae. Vertex flat, situated about on same level as orbit. Surface of vertex with evenly and more or less densely punctures into a band of well impressed punctures placed between eyes. Pronotum with evenly and densely punctures.

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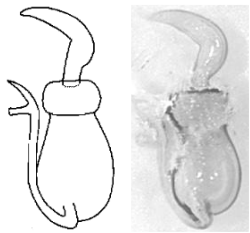
(January, 2021)

Pronotal punctures smaller than elytral punctures. Basal stria of punctures on pronotum absent. Base of pronotum without longitudinal impressions. Elytra with convex sided. Elytral punctures regular including periscutellar rows.

Table 4. Afrotropical species in this subgenus.

Afrotropical Species	Subgenus under the present study
C. audisiana Biondi, 2000	*Dalessandroiana*



1

Plate IV. Spermathecal morphology of Afrotropical species of the subgenus *C.* (*Dalessandroiana*) subgen. nov.: 1. *C. audisiana* Biondi (taken from Biondi, 2000; Biondi & D'Alessandro, 2006).

Subgenus *GAHANIOIDES* subgen. nov. (Plate V)

***Gahanioides* subgen. nov.** (type species: *Chaetocnema gahani* Jacoby, 1897).

Description. Spermathecal pump about as long as receptacle. Apex of spermathecal pump more or less cylindrical or rounded. Spermathecal receptacle relatively shortened, more or less widened, pyriform or cylindrical, not sinuate. Spermathecal pump attached to middle of receptacle top. Maximum width of receptacle situated basally. Basal part of receptacle wider than apical. Minimum width of receptacle usually situated apically. Spermathecal duct as long as receptacle, shorter or much shorter than receptacle, but relatively longish or shortened. Apex of spermathecal duct up to about apical margin or near of receptacle, or at least at about middle of receptacle, but spermathecal gland at about apical 3/4 or at basal half near middle of receptacle. Basal part of spermathecal duct usually corrugated as once coiled. Apical part of spermathecal duct straight. General shape of spermatheca more or less cylindrical or pyriform

The subgenus is included a total of 9 species in Afrotropical region (see below) now. It can be divided into 2 groups on the basis of their spermathecal morphology as Group A (spermathecal duct longer); Group B (spermathecal duct shorter) (Table 5).

The subgenus is represented only in Afrotropical region evaluated in this study.

Diagnosis. Spermathecal structure of this subgenus is more or less similar to that of the subgenera *Nitidoides* subgen. nov. and the nominative subgenus at first glance. It can be easily distinguished from *Nitidoides* subgen. nov. mainly by characters of spermathecal pump (relatively shorter, more or less cylindrical or rounded apex and relatively wider at the basal part). It clearly differs from the nominative subgenus mainly by longer spermathecal pump etc.

Etymology. The name "gahanioides", meaning gahani-like, is derivated after "*gahani*" the specific epithet of the type species.

Some external characters for the subgenus. Frontal ridge between antennal sockets narrow and convex. Frons evenly covered with relatively short, white setae. Vertex flat, situated about on same level as orbit. Surface of vertex with evenly and more or less densely punctures. Punctures about as large as pronotal punctures. Pronotum with evenly but relatively sparsely punctures. Diameter of pronotal punctures 2–4 times smaller than distance between them. Pronotal punctures distinctly smaller than elytral punctures. Basal stria of punctures present throughout but distinctly defined or not. Base of pronotum without longitudinal impressions. Elytra with more or less convex sided. Elytral punctures regular including periscutellar rows.

Table 5. Afrotropical species in this subgenus.

Afrotropical Species	Subgenus under the present study
Group A	
C. brincki (Bechyné, 1959)	*Gahanioides*
C. gahani Jacoby, 1897	*Gahanioides*
C. danielssoni Biondi & D'Alessandro, 2006	*Gahanioides*
C. sudafricana Biondi & D'Alessandro, 2006	*Gahanioides*
Group B	
C. adamastori Biondi & D'Alessandro, 2018	*Gahanioides*
C. capeneri Biondi & D'Alessandro, 2006	*Gahanioides*
C. capensis Bryant, 1928	*Gahanioides*
C. saldanhai Biondi & D'Alessandro, 2018	*Gahanioides*
C. tuckeri Biondi & D'Alessandro, 2006	*Gahanioides*

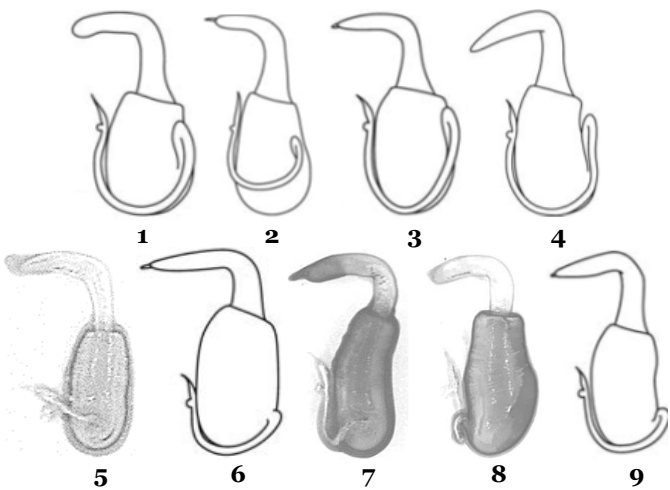


Plate V. Spermathecal morphology of Afrotropical species of the subgenus *Chaetocnema* (*Gahanioides*) subgen. nov.: **Group A 1-4:** 1. *C. brincki* (Bechyné), 2. *C. gahani* Jacoby, 3. *C. danielssoni* Biondi & D'Alessandro, 4. *C. sudafricana* Biondi & D'Alessandro, **Group B 5-9:** 5. *C. adamastori* Biondi & D'Alessandro, 6. *C. capeneri* Biondi & D'Alessandro, 7. *C. capensis* Bryant, 8. *C. saldanhai* Biondi & D'Alessandro, 9. *C. tuckeri* Biondi & D'Alessandro (taken from Biondi & D'Alessandro, 2006, 2018).

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Subgenus *HORTENSOIDES* subgen. nov. (Plates VI & VII)

***Hortensoides* subgen. nov.** (type species: *Altica hortensis* Geoffroy, 1785).

Description. Spermathecal pump much shorter than receptacle. Apex of spermathecal pump flattened or pointed. Spermathecal receptacle long, distinctly elongated, narrowed or slightly widened and sinuate medially on dorsal surface, larviform. Spermathecal pump attached to middle of receptacle top. Maximum width of receptacle situated basally, apically or at about middle. Basal part of receptacle about as wide as apical, wider than apical or narrower than apical. Minimum width of receptacle usually situated basally. Spermathecal duct much shorter than receptacle, but longish. Apex of spermathecal duct up to about beyond middle or at most about 2/3 of receptacle, spermathecal gland at about basal third or at most near middle of receptacle. Basal part of spermathecal duct more or less straight or corrugated. Apical part of spermathecal duct more or less straight or corrugated. Spermatheca larviform in general.

The subgenus is included a total of 38 species in Palaearctic region (see below) that most of them were placed by Warchalowski (2010) and Döberl (2010) in the nominative subgenus. It can be divided into 3 groups on the basis of their spermathecal morphology as Group A (spermathecal receptacle long, narrow and sinuate, basal part of spermathecal duct more or less corrugated, apical part of spermathecal duct more or less straight); Group B (spermathecal receptacle long, narrow and sinuate, basal part of spermathecal duct more or less straight, apical part of spermathecal duct more or less corrugated); Group C (spermathecal receptacle longish, widened and sinuate, basal and apical parts of spermathecal duct more or less straight) (Table 6).

The subgenus is represented in all regions evaluated in this study.

Diagnosis. Spermathecal structure of this subgenus is unique, but its closest subgenus is *Chaetocnema* (*Nigricoides*) subgen. nov..

Etymology. The name "hortensoides", meaning hortensis-like, is derivated after "*hortensis*" the specific epithet of the type species.

Some external characters for the subgenus. Frontal ridge between antennal sockets wide and flat. Frons evenly covered with relatively short, white setae. Vertex flat, situated about on same level as orbit. Surface of vertex with evenly and densely punctures. Punctures about as large as pronotal punctures. Pronotum with evenly and densely punctures. Diameter of pronotal punctures subequal to distance between them. Pronotal punctures usually about as large as elytral punctures. Basal stria of punctures on pronotum absent. Base of pronotum without longitudinal impressions. Elytra with convex sided. Elytral punctures confused including periscutellar rows at least in basally or entirely regular including periscutellar rows. Moreover, periscutellar row of punctures on elytron regular and single, confused or more than one (geminate) and second through sixth rows of punctures at base of elytron regular.

Table 6. Palaearctic species in this subgenus.

Palaearctic Species	Subgenus under the present study	Subgenus under the previous studies*
Group A		
C. afghana Gruev, 1988	*Hortensoides*	*Udorpes*
C. arida Foudras, 1860	*Hortensoides*	*Chaetocnema*
C. belka Konstantinov et al., 2011	*Hortensoides*	

C. costulata (Motschulsky, 1860)	*Hortensoides*	*Chaetocnema*
C. cylindrica (Baly, 1874)	*Hortensoides*	*Chaetocnema* or *Udorpes*
C. hortensis (Geoffroy, 1785)	*Hortensoides*	*Chaetocnema*
C. imitatrix Gruev, 1990	*Hortensoides*	*Chaetocnema*
Group B		
C. aerosa (Letzner, 1847)	*Hortensoides*	*Chaetocnema*
C. arenacea (Allard, 1860)	*Hortensoides*	*Chaetocnema*
C. aridula (Gyllenhal, 1827)	*Hortensoides*	*Chaetocnema*
C. bella (Baly, 1877)	*Hortensoides*	*Chaetocnema*
C. bretinghami Baly, 1877	*Hortensoides*	*Udorpes*
C. concinnicollis (Baly, 1874)	*Hortensoides*	*Chaetocnema*
C. concinnipennis Baly, 1877	*Hortensoides*	*Chaetocnema* or *Udorpes*
C. confusa (Boheman, 1851)	*Hortensoides*	*Chaetocnema*
C. eastafghanica Konstantinov et al., 2011	*Hortensoides*	*Udorpes*
C. ganganensis Bechyné, 1955	*Hortensoides*	*Chaetocnema*
C. gottwaldi Král, 1969	*Hortensoides*	*Chaetocnema*
C. grandis Pic, 1909	*Hortensoides*	*Chaetocnema*
C. igori Konstantinov et al., 2011	*Hortensoides*	
C. ingenua (Baly, 1877)	*Hortensoides*	*Chaetocnema*
C. klapperichi Lopatin, 1963	*Hortensoides*	*Chaetocnema*
C. leonhardi Heikertinger, 1951	*Hortensoides*	*Chaetocnema*
C. mannerheimii (Gyllenhal, 1827)	*Hortensoides*	*Chaetocnema*
C. modesta Gressitt & Kimoto, 1963	*Hortensoides*	*Chaetocnema*
C. montenegrina Heikertinger, 1912	*Hortensoides*	*Chaetocnema*
C. nocticolor Rapilly, 1978	*Hortensoides*	*Chaetocnema*
C. obesa (Boieldieu, 1859)	*Hortensoides*	*Chaetocnema*
C. oblonga Lopatin, 1990	*Hortensoides*	*Chaetocnema*
C. paganettii Heikertinger, 1913	*Hortensoides*	*Chaetocnema*
C. psylloides Pic, 1909	*Hortensoides*	*Chaetocnema*
C. rufofemorata Pic, 1915	*Hortensoides*	*Chaetocnema*
C. sahlbergii (Gyllenhal, 1827)	*Hortensoides*	*Chaetocnema*
C. subcoerulea (Kutschera, 1864)	*Hortensoides*	*Chaetocnema*
C. tarsalis Wollaston, 1860	*Hortensoides*	*Chaetocnema*
C. wollastoni Baly, 1877	*Hortensoides*	*Chaetocnema*
C. zangana Chen & Wang, 1981	*Hortensoides*	*Chaetocnema* or *Udorpes*
Group C		
C. shabalini Palij, 1968	*Hortensoides*	*Tlanoma* or *Udorpes*

* Warchalowski (2010), Döberl (2010), Ruan et al. (2019).

This subgenus includes also the following 26 Oriental, 4 Afrotropical, 6 Madagascan and 2 Australian species, of which spermathecal structures have been studied by cited references:

Oriental *C.* (*Hortensoides*) species: *C. afghana* Gruev, 1988; *C. angustifrons* Ruan et al., 2019; *C. bella* (Baly, 1877); *C. belli* Jacoby, 1904; *C. bretinghami* Baly, 1877; *C. cognata* Baly, 1877; *C. concinnicollis* (Baly, 1874); *C. concinnipennis* Baly, 1877; *C. cylindrica* (Baly, 1874); *C. eastafghanica* Konstantinov et al., 2011; *C. fusiformis* Chen & Wang, 1980; *C. glabra* Ruan et al., 2019; *C. greenica* Ruan et al., 2019; *C. ingenua* (Baly, 1877); *C. kumaonensis* Scherer, 1969; *C. malayana* Baly, 1877; *C. merguiensis* Bryant, 1941; *C. midimpunctata* Ruan et al., 2019; *C. modesta* Gressitt & Kimoto, 1963; *C. modiglianii* Jacoby, 1896; *C. paragreenica* Ruan et al., 2019; *C. psylloides* Pic, 1909; *C. pusaensis* Maulik, 1926; *C. reteimpunctata* Ruan et al., 2019; *C. sulcicollis* Chen & Wang, 1980 and *C. zangana* Chen & Wang, 1981.

Afrotropical *C.* (*Hortensoides*) species: *C. bamakoensis* Bechyné, 1955; *C. ganganensis* Bechyné, 1955; *C. hortensis* (Geoffroy, 1785) and *C. wollastoni* Baly, 1877. **Madagascan *C.* (*Hortensoides*) species:** *C. bamakoensis* Bechyné, 1955; *C. basipunctata* Bechyné, 1964; *C. consobrina* Weise, 1910; *C. ganganensis* Bechyné, 1955; *C. pauliani* Bechyné, 1964 and *C. wollastoni* Baly, 1877. **Nearctic *C.* (*Hortensoides*) species:** *C. hortensis* (Geoffroy, 1785). **Australian *C.* (*Hortensoides*) species:** *C. nesophila* Samuelson, 1967 and *C. paspalae* (Broun, 1923).

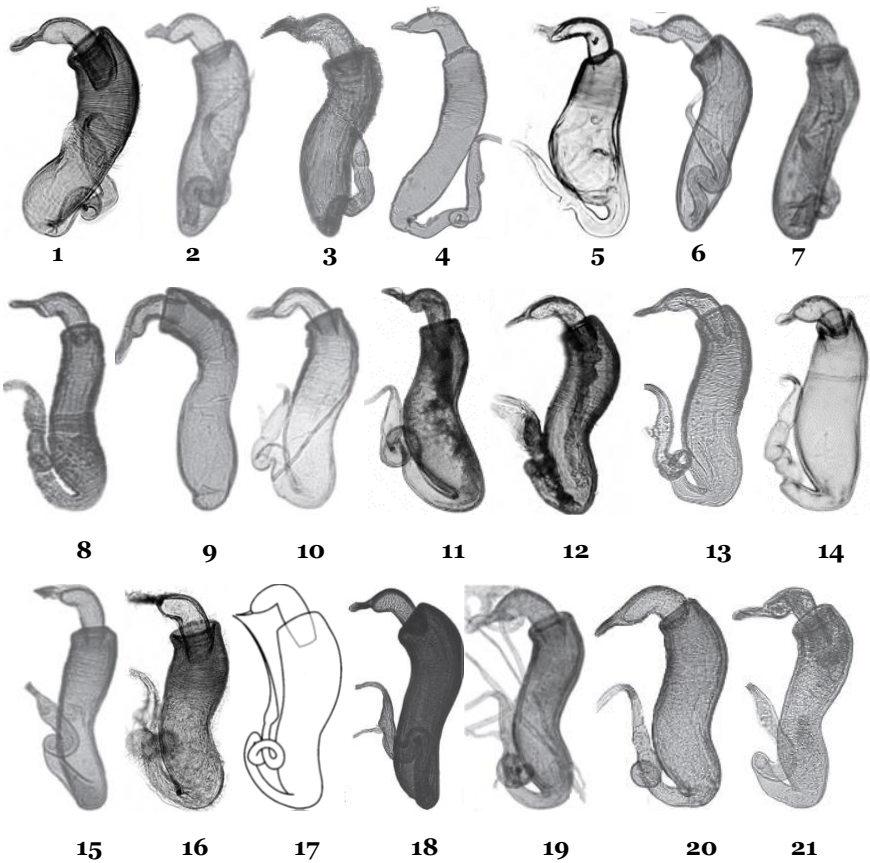

Plate VI. Spermathecal morphology of Palaearctic species of the subgenus *C.* (*Hortensoides*) subgen. nov.: **Group A 1-7:** 1. *C. afghana* Gruev, 2. *C. arida* Foudras, 3. *C. belka* Konstantinov et al., 4. *C. costulata* (Motschulsky), 5. *C. cylindrica* (Baly), 6. *C. hortensis* (Geoffroy), 7. *C. imitatrix* Gruev, **Group B 8-21:** 8. *C. aerosa* (Letzner), 9. *C. arenacea* (Allard), 10. *C. aridula* (Gyllenhal), 11. *C. bella* (Baly), 12. *C. bretinghami* Baly, 13. *C. concinnicollis* (Baly), 14. *C. concinnipennis* Baly, 15. *C. confusa* (Boheman), 16. *C. eastafghanica* Konstantinov et al., 17. *C. ganganensis* Bechyné (taken from Biondi, 2001), 18. *C. gottwaldi* Král, 19. *C. grandis* Pic, 20. *C. igori* Konstantinov et al., 21. *C. ingenua* (Baly) (taken from Konstantinov et al., 2011; Ruan et al., 2019).

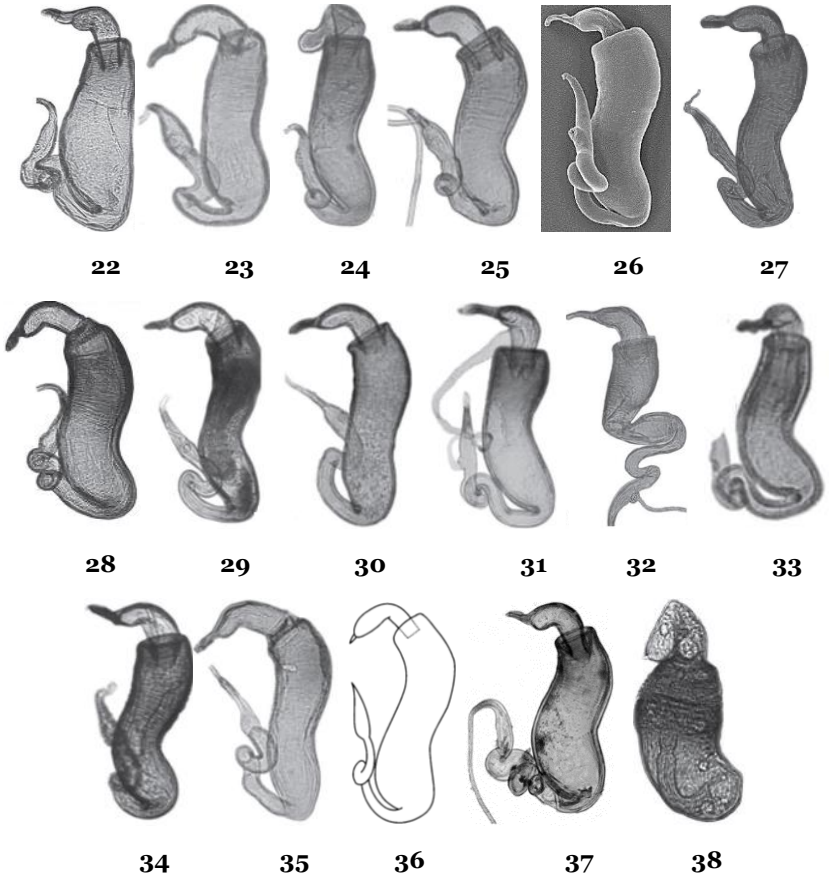

Plate VII. Spermathecal morphology of Palaearctic species of the subgenus *C.* (*Hortensoides*) subgen. nov.: **Group B 22-37:** 22. *C. klapperichi* Lopatin, 23. *C. leonhardi* Heikertinger, 24. *C. mannerheimii* (Gyllenhal), 25. *C. modesta* Gressitt & Kimoto, 26. *C. montenegrina* Heikertinger (original), 27. *C. nocticolor* Rapilly, 28. *C. obesa* (Boieldieu), 29. *C. oblonga* Lopatin, 30. *C. paganettii* Heikertinger, 31. *C. psylloides* Pic, 32. *C. rufofemorata* Pic, 33. *C. sahlbergii* (Gyllenhal), 34. *C. subcoerulea* (Kutschera), 35. *C. tarsalis* Wollaston, 36. *C. wollastoni* Baly (taken from Biondi, 2001), 37. *C. zangana* Chen & Wang; **Group C 38:** 38. *C. shabalini* Palij (taken from Konstantinov et al., 2011; Ruan et al., 2019).

In addition, the following 7 Palaearctic, 6 Oriental, 1 Madagascan and 26 Nearctic species of which spermathecal structures are unknown, it is possible that may be belonging to this subgenus based on their aedeagal structures and external morphological characters:

Possible Palaearctic *C.* (*Hortensoides*) species: *C. bergeali* Konstantinov et al., 2011; *C. franzi* Konstantinov et al., 2011; *C. jelineki* Lopatin, 1990; *C. kabakovi* Lopatin, 1995; *C. latipennis* Pic, 1911; *C. sinuata* Weise, 1889 and *C. tbilisiensis* Konstantinov et al., 2011. **Possible Oriental *C.* (*Hortensoides*) species:** *C. cupreata* Chen, 1934; *C. latapronota* Ruan et al.,

Munis Entomology & Zoology
https://www.munisentzool.org/
ISSN 1306-3022

Mun. Ent. Zool.
(January, 2021)

2019; *C. paraumesaoi* Ruan et al., 2019; *C. singala* Maulik, 1926; *C. umesaoi* Chûjô, 1961 and *C. westwoodi* Baly, 1877. **Possible Madagascan *C.* (*Hortensoides*) species:** *Chaetocnema hygrophila* Biondi, 2001. **Possible Nearctic *C.* (*Hortensoides*) species:** *C. acuminata* White, 1996; *C. acupunctata* White, 1996; *C. aequabilis* White, 1996; *C. albiventris* White, 1996; *C. borealis* White, 1996; *C. californica* White, 1996; *C. coacta* White, 1996; *C. costata* Fall, 1907; *C. cribrata* LeConte, 1878; *C. cribrifrons* LeConte, 1879; *C. denticulata* (Illiger, 1807); *C. difficilis* White, 1996; *C. floridana* Blatchley, 1923; *C. fuscata* White, 1996; *C. irregularis* LeConte, 1857; *C. megachora* White, 1996; *C. megasticta* White, 1996; *C. minitrunctata* White, 1996; *C. ordinata* White, 1996; *C. perturbata* Horn, 1889; *C. pinguis* LeConte, 1878; *C. producta* White, 1996; *C. prolata* White, 1996; *C. protensa* LeConte, 1878; *C. texana* Crotch, 1873 and *C. truncata* White, 1996.

Subgenus *LONGICORNOIDES* subgen. nov. (Plate VIII)

***Longicornoides* subgen. nov.** (type species: *Chaetocnema longicornis* Jacoby, 1895).

Description. Spermathecal pump much shorter than receptacle. Apex of spermathecal pump more or less cylindrical or rounded. Spermathecal receptacle longish, more or less widened, distinctly curved ventrad in approximately entire basal half and distinctly sinuate ventro-medially, like a worm or larva. Spermathecal pump attached to middle of receptacle top. Maximum width of receptacle situated basally. Basal part of receptacle wider than apical. Minimum width of receptacle situated apically. Spermathecal duct shorter than receptacle, but relatively longish or slightly shortened. Apex of spermathecal duct up to about apical 3/4 or 4/5 of receptacle, spermathecal gland at about apical 3/4 or beyond middle of receptacle. Basal and apical parts of spermathecal duct straight. Spermatheca larviform in general.

The subgenus is included only 3 species in Afrotropical region (see below) now (Table 7).

The subgenus is represented only in Afrotropical region evaluated in this study.

Diagnosis. Spermathecal structure of this subgenus is unique.

Etymology. The name "longicornoides", meaning longicornis-like, is derivated after "*longicornis*" the specific epithet of the type species.

Some external characters for the subgenus. Frontal ridge between antennal sockets narrow and convex. Frons partly covered with relatively short, white setae. Surface of vertex with evenly and more or less densely punctures into a band of well impressed punctures placed between eyes or at least with some weakly impressed punctures near upper ocular margins. Punctures about as large as pronotal punctures. Pronotum with evenly but relatively sparsely punctures. Diameter of pronotal punctures 2–4 times smaller than distance between them. Pronotal punctures smaller than elytral punctures. Basal stria of punctures on pronotum absent. Base of pronotum without longitudinal impressions. Elytra with convex sided. Elytral punctures regular including periscutellar rows.

Table 7. Afrotropical species in this subgenus.

Afrotropical Species	Subgenus under the present study
C. kapirensis Biondi & Nardis, 2000	*Longicornoides*
C. longicornis Jacoby, 1895	*Longicornoides*
C. reprehensa Bechyné, 1960	*Longicornoides*

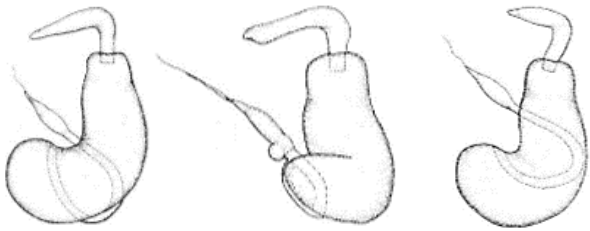

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Plate VIII. Spermathecal morphology of Afrotropical species of the subgenus *C.* (*Longicornoides*) subgen. nov.: 1. *C. kapirensis* Biondi & Nardis, 2. *C. longicornis* Jacoby, 3. *C. reprehensa* Bechyné (taken from Biondi & Nardis, 2000).

In addition, the following 1 Afrotropical species of which spermathecal structure is unknown, it is possible that may be belonging to this subgenus based on their aedeagal structure and external morphological characters:

Possible Afrotropical *C.* (*Biondiana*) species: *C. phuhthaditjhabensis* Biondi & Nardis, 2000.

Subgenus *MAJOROIDES* subgen. nov. (Plate IX)

***Majoroides* subgen. nov.** (type species: *Plectroscelis major* Jacquelin du Val, 1852).

Description. Spermathecal pump about as long as receptacle. Apex of spermathecal pump cylindrical or rounded. Spermathecal receptacle shortened, widened, more or less pyriform and sinuate ventro-medially. Spermathecal pump attached to middle of receptacle top. Maximum width of receptacle situated basally. Basal part of receptacle wider than apical. Minimum width of receptacle situated apically. Spermathecal duct shorter than receptacle, shortened. But apex of spermathecal duct up to about 4/5 of receptacle, spermathecal gland at about middle of receptacle. Basal and apical parts of spermathecal duct more or less straight. General shape of spermatheca more or less cylindrical or pyriform

The subgenus is included a total of 3 species in Palaearctic region (see below) that all of them were placed by Warchalowski (2010) and Döberl (2010) in the subgenus *Tlanoma* Motschulsky, 1845 (Table 8).

The subgenus is represented only in Palaearctic region evaluated in this study.

Diagnosis. Spermathecal structure of this subgenus is unique.

Etymology. The name "majoroides", meaning major-like, is derivated after "*major*" the specific epithet of the type species.

Some external characters for the subgenus. Frontal ridge between antennal sockets narrow and convex. Frons with only relatively long setae on sides present. Vertex flat, situated about on same level as orbit. Surface of vertex sparsely and unevenly covered with punctures, usually only near eye. Punctures

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https://www.munisentzool.org/
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Mun. Ent. Zool.
(January, 2021)

about as large as pronotal punctures. Pronotum with evenly but relatively sparsely punctures. Diameter of pronotal punctures 2–4 times smaller than distance between them. Pronotal punctures smaller than elytral punctures. Basal stria of punctures on pronotum usually absent throughout, if present only between two longitudinal depressions. Base of pronotum with two well-developed longitudinal impressions, both near basal margin and further anteriorly. Elytra with parallel sided. Periscutellar row of punctures on elytron regular and single, confused or more than one. Second through sixth rows of punctures at base of elytron regular.

Table 8. Palaearctic species in this subgenus.

Palaearctic Species	**Subgenus under the present study**	**Subgenus under the previous studies***
C. major (Jacquelin du Val, 1852)	*Majoroides*	*Tlanoma*
C. mandschurica Heikertinger, 1951	*Majoroides*	*Tlanoma*
C. schlaeflii (Stierlin, 1866)	*Majoroides*	*Tlanoma*

* Warchalowski (2010), Döberl (2010).

1 **2** **3**

Plate IX. Spermathecal morphology of Palaearctic species of the subgenus *Chaetocnema* (*Majoroides*) subgen. nov.: 1. *C. major* (Jacquelin du Val), 2. *C. mandschurica* Heikertinger, 3. *C. schlaeflii* (Stierlin) (taken from Konstantinov et al., 2011).

Subgenus *NIGRICOIDES* subgen. nov. (Plate X)

***Nigricoides* subgen. nov.** (type species: *Chaetocnema nigrica* Motschulsky, 1858).

Description. Spermathecal pump much shorter than receptacle. Apex of spermathecal pump flattened or pointed. Spermathecal receptacle relatively elongated, slightly widened, distinctly sinuate preapically on dorsal surface. Spermathecal pump attached to middle of receptacle top. Maximum width of receptacle situated preapically. Basal part of receptacle narrower than apical. Minimum width of receptacle situated basally. Spermathecal duct much shorter than receptacle, but long. Apex of spermathecal duct up to about middle or a little beyond middle of receptacle, spermathecal gland at about basal fourth of receptacle. Basal part of spermathecal duct straight. Apical part of spermathecal duct more or less corrugated. Spermatheca more or less larviform in general.

The subgenus is included only 1 species (see below) that was placed by Döbrl (2010) and Ruan et al. (2019) in the subgenus *Tlanoma* Motschulsky, 1845 and the nominative subgenus respectively (Table 9).

The subgenus is represented in all regions evaluated in this study.

Diagnosis. Spermathecal structure of this subgenus is unique, but its closest subgenus seems to be *Chaetocnema* (*Hortensoides*) subgen. nov..

Etymology. The name "nigricoides", meaning nigrica-like, is derivated after "*nigrica*" the specific epithet of the type species.

Some external characters for the subgenus. Frontal ridge between antennal sockets narrow and convex. Frons with only relatively long setae on sides present. Vertex flat, situated about on same level as orbit. Surface of vertex without punctures, except 2-3 on each side near eye. Punctures larger than pronotal punctures, except about as large as deep row of large punctures at base of pronotum. Pronotum with evenly but relatively sparsely punctures. Diameter of pronotal punctures 6-10 times smaller than distance between them. Pronotal punctures smaller than elytral punctures, except about as large as deep row of large punctures at base of pronotum. Basal stria of deep punctures on pronotum present throughout. Base of pronotum without longitudinal impressions. Elytra with convex sided. Elytral punctures regular including periscutellar rows.

Table 9. Palaearctic species in this subgenus.

Palaearctic Species	Subgenus under the present study	Subgenus under the previous studies*
C. nigrica Motschulsky, 1853	*Nigricoides*	*Tlanoma* or *Chaetocnema*

* Döberl (2010), Ruan et al. (2019).

This subgenus includes also the following 4 Oriental, 4 Afrotropical 1 Madagascan and 1 Australian species, of which spermathecal structures have been studied by cited references:

Oriental *C.* (*Nigricoides*) species: *C. nigrica* (Motschulsky, 1858); *C. resplendens* Warchalowski, 1973; *C. warchalowskii* Döberl, 2009 and *C. yaosanica* Chen, 1939. **Afrotropical *C.* (*Nigricoides*) species:** *C. nigrica* (Motschulsky, 1858); *C. pulla* Chapuis, 1879; *C. subquadrata* Jacoby, 1897 and *C. vanschuytbroecki* Biondi & D'Alessandro, 2008. **Madagascan *C.* (*Nigricoides*) species:** *C. pulla* Chapuis, 1879. **Australian *C.* (*Nigricoides*) species:** *C. nigrica* (Motschulsky, 1858).

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Plate X. Spermathecal morphology of Palaearctic species of the subgenus *C.* (*Nigricoides*) subgen. nov.: 1. *C. nigrica* Motschulsky (taken from Ruan et al., 2019).

In addition, the following 1 Oriental species of which spermathecal structure is unknown, it is possible that may be belonging to this subgenus based on their aedeagal structure and external morphological characters:

Possible Oriental *C.* (*Nigricoides*) species: *C. fallaciosa* Heikertinger, 1951.

Munis Entomology & Zoology
https://www.munisentzool.org/
ISSN 1306-3022

Mun. Ent. Zool.
(January, 2021)

Subgenus *NITIDOIDES* subgen. nov. (Plate XI)

***Nitidoides* subgen. nov.** (type species: *Phyllotreta nitida* Broun, 1880).

Description. Spermathecal pump longer than receptacle. Apex of spermathecal pump more or less flattened or pointed. Spermathecal receptacle distinctly shortened, more or less cylindrical, not sinuate. Spermathecal pump attached to middle of receptacle top. Maximum width of receptacle situated about at middle. Basal part of receptacle about as wide as apical. Minimum width of receptacle usually situated basally and apically. Spermathecal duct as long as receptacle or slightly shorter than receptacle. Apex of spermathecal duct up to about apical margin or near of receptacle, but spermathecal gland at about middle or at basal half near middle of receptacle. Basal and apical parts of spermathecal duct straight. Spermatheca long-necked water bird-shaped in general.

The subgenus is included 2 species in Australian region (see below) now (Table 10).

The subgenus is represented only in Australian region evaluated in this study.

Diagnosis. Spermathecal structure of this subgenus is more or less similar to that of the subgenera *Gahanioides* subgen. nov. and the nominative subgenus at first glance. It can be easily distinguished from *Gahanioides* subgen. nov. mainly by characters of spermathecal pump (relatively longer, apex more or less flattened or pointed and relatively narrower at the basal part). It clearly differs from the nominative subgenus mainly by much longer spermathecal pump etc.

Etymology. The name "nitidoides", meaning nitida-like, is derivated after "*nitida*" the specific epithet of the type species.

Some external characters for the subgenus. Frontal ridge between antennal sockets wide or narrow but always convex. Surface of vertex without punctures, except 3-5 on each side near eye. Pronotum with evenly and densely punctures, uniformly or not. Basal stria of punctures absent throughout. Base of pronotum without longitudinal impressions. Elytra with more or less convex sided. Elytral punctures regular including periscutellar rows.

Table 10. Australian species in this subgenus.

Australian Species	Subgenus under the present study
C. moriori Samuelson, 1973	*Nitidoides*
C. nitida (Broun, 1880)	*Nitidoides*

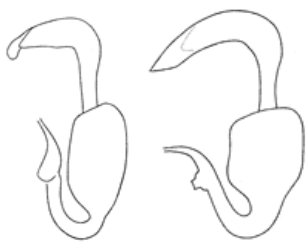

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Plate XI. Spermathecal morphology of Australian species of the subgenus *C.* (*Nitidoides*) subgen. nov.: 1. *C. moriori* Samuelson, 2. *C. nitida* (Broun) (taken from Samuelson, 1973).

Subgenus *PLECTROSCELIS* Dejean, status restored (Plate XII)

***Plectroscelis* Dejean, 1836: 393** (type species: *Haltica dentipes* sensu Oliver, 1808 [= *Altica chlorophana* Duftschmid, 1825, fixed by Konstantinov et al., 2011: 18 under Article 70.3; not *Haltica dentipes* Koch, 1803 = *Chrysomela concinna* Marsham, 1802], misidentified in the first subsequent designation by Chevrolat, 1845: 6).

Exorhina Weise, 1886: 750 (Type species: *Altica chlorophana* Duftschmid, 1825, subsequent designation by Döberl, 2010: 508).

Description. Spermathecal pump about as long as receptacle. Apex of spermathecal pump cylindrical or rounded. Spermathecal receptacle shortened, very widened and more or less vesicular or globose, slightly sinuate preapically on dorsal surface. Spermathecal pump attached to side of receptacle top. Maximum width of receptacle situated at about middle or basally. Basal part of receptacle wider than apical. Minimum width of receptacle situated apically. Spermathecal duct shorter than receptacle, shortened. But apex of spermathecal duct up to about 4/5 of receptacle, spermathecal gland at about 2/3 of receptacle. Basal and apical parts of spermathecal duct more or less straight or not clearly corrugated. Spermatheca globose, fat duck-shaped in general.

The subgenus is included a total of 4 species in Palaearctic region (see below) that most of them were placed by Warchalowski (2010) and Döberl (2010) in the subgenus *Tlanoma* Motschulsky, 1845. It can be divided into 2 groups on the basis of their spermathecal morphology as Group A (maximum width of receptacle situated at about middle); Group B (maximum width of receptacle situated basally) (Table 11).

The subgenus is represented only in Palaearctic region evaluated in this study.

Diagnosis. Spermathecal structure of this subgenus is unique.

Some external characters for the subgenus. Frontal ridge between antennal sockets narrow and convex. Frons with only relatively long setae on sides present. Vertex flat, situated about on same level as orbit. Surface of vertex sparsely and unevenly covered with punctures, not only near eye. Punctures about as large as pronotal punctures. Pronotum with evenly but relatively sparsely punctures. Diameter of pronotal punctures 2–4 times smaller than distance between them or at most subequal. Pronotal punctures smaller than elytral punctures. Basal stria of punctures on pronotum absent. Base of pronotum with two well-developed longitudinal impressions, both near basal margin and further anteriorly or without longitudinal impressions. Elytra with parallel sided. Elytral punctures regular including periscutellar rows.

Table 11. Palaearctic species in this subgenus.

Palaearctic Species	Subgenus under the present study	Subgenus under the previous studies*
Group A		
C. chlorophana (Duftschmid, 1825)	*Plectroscelis*	*Tlanoma*
C. coyei (Allard, 1864)	*Plectroscelis*	*Tlanoma*
C. pelagica Caillol, 1924	*Plectroscelis*	*Chaetocnema*
Group B		
C. punctifrons (Abeille, 1907)	*Plectroscelis*	*Tlanoma*

* Warchalowski (2010), Döberl (2010).

Munis Entomology & Zoology
https://www.munisentzool.org/
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Mun. Ent. Zool.
(January, 2021)

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Plate XII. Spermathecal morphology of Palaearctic species of the subgenus *C.* (*Plectroscelis*) Weise, stat. rest.: **Group A 1-3:** 1. *C. chlorophana* (Duftschmid), 2. *C. coyei* (Allard), 3. *C. pelagica* Caillol, **Group B 4:** 4. *C. punctifrons* (Abeille) (taken from Konstantinov et al., 2011).

In addition, the following 1 Palaearctic species of which spermathecal structure is unknown, it is possible that may be belonging to this subgenus based on their external morphological characters:

Possible Palaearctic *C.* (*Plectroscelis*) species: *C. kerimi* (Fairmaire, 1875).

Subgenus *PSEUDOCHAETOCNEMA* subgen. nov. (Plate XIII)

***Pseudochaetocnema* subgen. nov.** (type species: *Haltica conducta* Motschulsky, 1838).

Description. Spermathecal pump much shorter than receptacle. Apex of spermathecal pump flattened or pointed. Spermathecal receptacle relatively shortened, more or less widened or narrowed, pyriform or cylindrical, but not sinuate. Spermathecal pump attached to middle of receptacle top. Maximum width of receptacle situated basally. Basal part of receptacle wider than apical. Minimum width of receptacle usually situated apically. Spermathecal duct shorter or much shorter than receptacle, but relatively long or shortened. Apex of spermathecal duct up to about 2/3 of receptacle or at about middle of receptacle, but spermathecal gland at basal half near middle or basal third of receptacle. Basal part of spermathecal duct straight or corrugated. Apical part of spermathecal duct more or less straight or corrugated. General shape of spermatheca more or less cylindrical or pyriform.

The subgenus is included a total of 5 species (see below) that most of them were placed by Warchalowski (2010) and Döberl (2010) in the subgenera *Tlanoma* Motschulsky, 1845. It can be divided into 2 groups on the basis of their spermathecal morphology as Group A (basal part of spermathecal duct straight, apical part of spermathecal duct more or less corrugated); Group B (basal part of spermathecal duct more or less corrugated, apical part of spermathecal duct more or less straight) (Table 12).

The subgenus is represented in all regions evaluated in this study.

Diagnosis. Spermathecal structure of this subgenus is very similar to that of the nominative subgenus at first glance, but can be easily distinguished from it mainly by the flattened or pointed apex of spermathecal pump.

Etymology. This name is derivated by adding the prefix "pseudo-" in Latin (meaning fake or false in English) to the nominative subgeneric name.

Some external characters for the subgenus. Frontal ridge between antennal sockets narrow and convex or wide and flat. Frons with only relatively long setae on sides present. Vertex flat, situated about on same level as orbit. Surface of vertex sparsely and unevenly covered with punctures, near eye or not. Punctures about as large as pronotal punctures. Pronotum with evenly but relatively sparsely punctures. Diameter of pronotal punctures 2–4 to 6–10 times smaller than distance between them. Pronotal punctures smaller than elytral punctures. Basal stria of punctures on pronotum present, throughout or only absent on middle. Base of pronotum without longitudinal impressions. Elytra with convex sided. Elytral punctures regular including periscutellar rows.

Table 12. Palaearctic species in this subgenus.

Palaearctic Species	Subgenus under the present study	Subgenus under the previous studies*
Group A		
C. conducta (Motschulsky, 1838)	*Pseudochaetocnema*	*Tlanoma*
C. hongkongensis Ruan et al., 2019	*Pseudochaetocnema*	*Chaetocnema*
C. tristis Allard, 1889	*Pseudochaetocnema*	*Tlanoma* or *Chaetocnema*
Group B		
C. kanmiyai Kimoto, 1974	*Pseudochaetocnema*	*Tlanoma*
C. orientalis (Bauduér, 1874)	*Pseudochaetocnema*	*Tlanoma*

* Warchalowski (2010), Döberl (2010), Ruan et al. (2019).

This subgenus includes also the following 12 Oriental, 5 Afrotropical and 1 Madagascan species, of which spermathecal structures have been studied by cited references:

Oriental *C.* (*Pseudocaetocnema*) species: *C. excavata* Medvedev, 1997; *C. gracilis* Motschulsky, 1858; *C. granulicollis* Jacoby, 1896; *C. hainanensis* Chen, 1933; *C. hongkongensis* Ruan et al., 2019; *C. jinxiuensis* Ruan et al., 2019; *C. nigrilata* Ruan et al., 2019; *C. parafusiformis* Ruan et al., 2019; *C. philippina* Medvedev, 1996; *C. sabahensis* Ruan et al., 2019; *C. tristis* Allard, 1889 and *C. yiei* Kimoto, 1970. **Afrotropical *C.* (*Pseudocaetocnema*) species:** *C. conducta* (Motschulsky, 1838); *C. lopatini* Biondi & D'Alessandro, 2005; *C. nkolentangana* Bechyné, 1959; *C. orientalis* (Bauduér, 1874) and *C. suturalis* Bryant, 1948. **Madagascan *C.* (*Pseudocaetocnema*) species:** *C. similis* Weise, 1910.

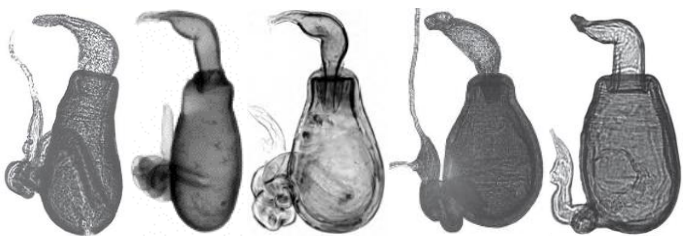

Plate XIII. Spermathecal morphology of Palaearctic species of the subgenus *Chaetocnema* (*Pseudochaetocnema*) subgen. nov.: **Group A 1-3:** 1. *C. conducta* (Motschulsky), 2. *C. hongkongensis* Ruan et al., 3. *C. tristis* Allard; **Group B4-5:** 4. *C. kanmiyai* Kimoto, 5. *C. orientalis* (Bauduér) (taken from Konstantinov et al., 2011; Ruan et al., 2019).

Munis Entomology & Zoology
https://www.munisentzool.org/
ISSN 1306-3022
Mun. Ent. Zool.
(January, 2021)

In addition, the following 1 Palaearctic, 7 Oriental and 8 Nearctic species of which spermathecal structures are unknown, it is possible that may be belonging to this subgenus based on their aedeagal structures and external morphological characters:

Possible Palaearctic *C.* (*Pseudocaetocnema*) species: *C. tonkinensis* Chen, 1934. **Possible Oriental *C.* (*Pseudocaetocnema*) species:** *C. appendiculata* Ruan et al., 2019; *C. babai* Kimoto, 1991; *C. longipunctata* Maulik, 1926; *C. subbasalis* Ruan et al., 2019; *C. taiwanensis* Chûjô, 1965; *C. tonkinensis* Chen, 1934 and *C. trapezoida* Ruan et al., 2019. **Possible Nearctic *C.* (*Pseudocaetocnema*) species:** *C. anisota* White, 1996; *C. brunnescens* Horn, 1889; *C. minuta* Melsheimer, 1847; *C. obesula* LeConte, 1878; *C. opacula* LeConte, 1878; *C. pulicaria* Melsheimer, 1847; *C. quadricollis* Schwarz, 1878 and *C. subviridis* LeConte, 1859.

Subgenus *UDORPES* Motschulsky, status restored (Plate XIV)

***Udorpes* Motschulsky, 1845a: 107** (type species: *Udorpes splendens* Motschulsky, 1845, by monotypy).

Ydorpes Motschulsky, 1845b: [549] (unjustified emendation of *Udorpes* Motschulsky, 1845a).
Udorpus; Agassiz (1846:167), *lapsus calami* for *Udorpes*.
Hydropus Motschulsky, 1860: 235 (unjustified emendation of *Udorpes* Motschulsky, 1845a).
Hydorpes; Motschulsky (1860:257), *lapsus calami* for *Hydropus*.

Description. Spermathecal pump about as long as receptacle. Apex of spermathecal pump flattened or pointed. Spermathecal receptacle shortened, more or less widened or narrowed, more or less cylindrical or pyriform and slightly sinuate dorso-medially or not. Spermathecal pump attached to middle of receptacle top. Maximum width of receptacle situated usually at about middle or sometimes basally. Basal part of receptacle about wider than apical, as wide as apical or narrower than apical. Minimum width of receptacle usually situated apically or basally. Spermathecal duct much shorter than receptacle, shortened. Apex of spermathecal duct up to about middle of receptacle, spermathecal gland at about basal third of receptacle. Basal and apical parts of spermathecal duct straight. Spermatheca long-billed bird-shaped in general.

The subgenus is included a total of 7 species (see below) that all of them were placed by Warchalowski (2010) and Döberl (2010) in the nominative subgenus. It can be divided into 2 groups on the basis of their spermathecal morphology as Group A (spermathecal receptacle more or less widened); Group B (spermathecal receptacle more or less narrowed) (Table 13).

The subgenus is represented only in Palaearctic region evaluated in this study.

Diagnosis. Spermathecal structure of this subgenus is unique.

Some external characters for the subgenus. Frontal ridge between antennal sockets wide and flat. Frons evenly covered with relatively short, white setae. Vertex flat, situated about on same level as orbit. Surface of vertex densely and evenly covered with punctures. Punctures about as large as pronotal punctures. Pronotum with evenly but relatively sparsely punctures or with evenly and densely punctures. Diameter of pronotal punctures 2–4 or 6-10 times smaller than distance between them or subequal. Pronotal punctures distinctly smaller

than elytral punctures. Basal stria of punctures on pronotum absent. Base of pronotum without longitudinal impressions. Elytra with more or less convex sided. Periscutellar row of punctures on elytron regular and single, confused or more than one. Second through sixth rows of punctures at base of elytron regular.

Table 13. Palaearctic species in this subgenus.

Palaearctic Species	Subgenus under the present study	Subgenus under the previous studies*
Group A		
C. balanomorpha (Boieldieu, 1859)	*Udorpes*	*Chaetocnema*
C. ljudmilae Lopatin, 1961	*Udorpes*	*Chaetocnema*
C. splendens (Motschulsky, 1845)	*Udorpes*	*Chaetocnema*
C. ussuriensis Heikertinger, 1951	*Udorpes*	*Chaetocnema*
Group B		
C. angustula (Rosenhauer, 1847)	*Udorpes*	*Chaetocnema*
C. compressa (Letzner, 1847)	*Udorpes*	*Chaetocnema*
C. procerula (Rosenhauer, 1856)	*Udorpes*	*Chaetocnema*

* Warchalowski (2010), Döberl (2010).

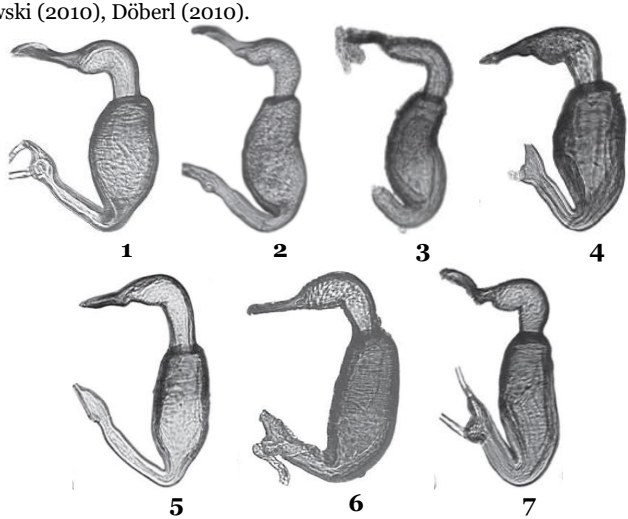

Plate XIV. Spermathecal morphology of Palaearctic species of the subgenus *C.* (*Udorpes*) Motschulsky, stat. rest.: **Group A 1-4:** 1. *C. balanomorpha* (Boieldieu), 2. *C. ljudmilae* Lopatin, 3. *C. splendens* (Motschulsky), 4. *C. ussuriensis* Heikertinger, **Group B 5-7:** 5. *C. angustula* (Rosenhauer), 6. *C. compressa* (Letzner), 7. *C. procerula* (Rosenhauer) (taken from Konstantinov et al., 2011).

In addition, the following 3 Palaearctic and 3 Oriental species of which spermathecal structures are unknown, it is possible that may be belonging to this subgenus based on their aedeagal structures and external morphological characters:

Possible Palaearctic *C.* (*Udorpes*) species: *C. alticola* Maulik, 1926; *C. polita* (Abeille, 1907) and *C. shanxiensis* Chen &Wang, 1980. **Possible Oriental *C.* (*Udorpes*) species:** *C. alticola* Maulik, 1926; *C. rahlensis* Shukla, 1960 and *C. shanxiensis* Chen &Wang, 1980.

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Mun. Ent. Zool.
(January, 2021)

Spermathecal pump much longer, longer, about as long as or much shorter than receptacle. Apex of spermathecal pump more or less cylindrical / rounded or flattened / pointed. Spermathecal receptacle variable in shape, sinuate or not. Spermathecal pump attached to middle or side of receptacle top. Maximum width of receptacle situated basally, medially or apically. Basal part of receptacle about wider than apical, as wide as apical or narrower than apical. Minimum width of receptacle usually situated basally, apically or preapically. Spermathecal duct long, longish or shortened in various ways; much shorter, shorter, slightly shorter than receptacle or as long as receptacle. Apex of spermathecal duct up to about middle to apical margin of receptacle. Spermathecal gland at about basal fourth to apical 4/5 or preapical part of receptacle. Basal and apical parts of spermathecal duct straight or corrugated.

Relationships among the subgenera described above according to spermathecal structures

Two groups can be distinguished on the basis of attachment point with spermathecal receptacle of spermathecal pump. Only in PLE, spermathecal pump is attached to side of receptacle top, while to middle in all other subgenera (Fig. 2).

Figure 2. Spermathecal morphology of (**1**) *C. coyei* (Allard), (**2**) *C. major* (Jacquelin du Val) (taken from Konstantinov et al., 2011).

Also the subgenera of *Chaetocnema* Stephens based on the shape of apex of spermathecal pump can be divided into 2 groups which are Group I with apex of spermathecal pump more or less cylindrical or rounded (CHA BIO CON DAL GAH LON MAJ PLE) and Group II with apex of spermathecal pump more or less flattened or pointed (HOR NIG NIT PSE UDO) (Fig. 3).

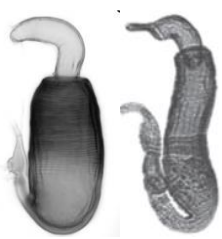

Figure 3. Spermathecal morphology of (**1**) *C. constricta* Ruan et al. (taken from Ruan et al., 2019), (**2**) *C. aerosa* (Letzner) (taken from Konstantinov et al., 2011).

In addition, on the basis of the comparision according to length of spermathecal pump and spermathecal receptacle, the subgenera can also be divided into 4 groups which are Group I with spermathecal pump much longer than receptacle (BIO), Group II with spermathecal pump longer than receptacle (NIT), Group III with spermathecal pump about as long as receptacle (DAL GAH MAJ PLE UDO) and Group IV with spermathecal pump much shorter than receptacle (CHA CON HOR LON NIG PSE) (Fig. 4).

Figure 4. Spermathecal morphology of (**1**) *C. zulu* Biondi & Nardis (taken from Biondi & Nardis, 2000), (**2**) *C. nitida* (Broun) () (taken from Samuelson, 1973), (**3**) *C. gahani* Jacoby (taken from Biondi & D'Alessandro, 2006), (**4**) *C. nebulosa* Weise (taken from Konstantinov et al., 2011).

Moreover, on the basis of sinuation of spermathecal receptacle, the subgenera can be divided into 2 main supergroups which are Supergroup I with spermathecal receptacle not sinuate (CHA BIO CON GAH NIT PSE) and Supergroup II with spermathecal receptacle sinuate (DAL HOR LON MAJ NIG PLE UDO) (Fig. 5).

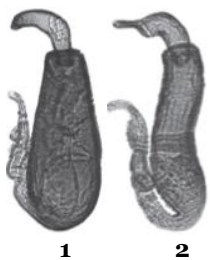

Figure 5. Spermathecal morphology of (**1**) *C. nebulosa* Weise, (**2**) *C. aerosa* (Letzner) (taken from Konstantinov et al., 2011).

Accordingly, the subgenera in Supergroup II can also be divided into 7 Groups which are Group I with spermathecal receptacle distinctly sinuate preapically on both ventral and dorsal surfaces (DAL), Group II with sinuate medially on dorsal surface (HOR), Group III with distinctly sinuate ventro-medially (LON), Group IV with sinuate ventro-medially (MAJ), Group V with distinctly sinuate preapically on dorsal surface (NIG), Group VI with slightly sinuate preapically on dorsal surface (PLE) and Group VII with slightly sinuate dorso-medially or not (UDO) (Fig. 6).

Munis Entomology & Zoology
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(January, 2021)

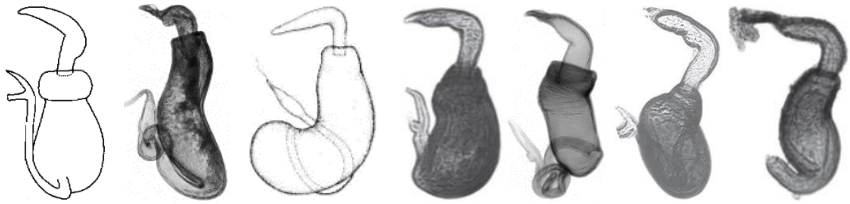

Figure 6. Spermathecal morphology of (**1**) *C. audisiana* Biondi (taken from Biondi, 2000), (**2**) *C. bella* (Baly) (taken from Ruan et al., 2019), (**3**) *C. kapirensis* Biondi & Nardis (taken from Biondi & Nardis, 2000), (**4**) *C. major* (Jacquelin du Val) (taken from Konstantinov et al., 2011), (**5**) *C. nigrica* Motschulsky (taken from Ruan et al., 2019), (**6**) *C. coyei* (Allard) (taken from Konstantinov et al., 2011), (**7**) *C. splendens* (Motschulsky) (taken from Konstantinov et al., 2011).

Whereas the subgenera with spermathecal receptacle not sinuate in Supergroup I, based on the shape of apex of spermathecal pump (see above, Fig. 3), can also be divided into 2 groups which are Group I with apex of spermathecal pump more or less cylindrical or rounded (CHA BIO CON GAH) and Group II with apex of spermathecal pump more or less flattened or pointed (NIT PSE).

Firstly, on the other side, the subgenera in the Group I on the basis of the comparision according to length of spermathecal pump and spermathecal receptacle (see above, Fig. 4), can also be divided into 3 subgroups which are Subgroup I with spermathecal pump much longer than receptacle (BIO), Subgroup II with spermathecal pump about as long as receptacle (GAH) and Subgroup III with spermathecal pump much shorter than receptacle (CHA CON). The subgenera in the Subgroup III can easily be distinguished from each other by at least shape of their spermathecal receptacle: Spermathecal receptacle cylindrical or pyriform, narrowed apically or not (CHA) and globose, much narrowed apically (CON) (Fig. 7).

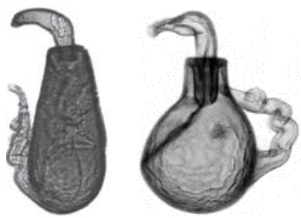

Figure 7. Spermathecal morphology of (**1**) *C. nebulosa* Weise (taken from Konstantinov et al., 2011), (**2**) *C. confinis* Crotch (taken from Ruan et al., 2019).

Secondly, the subgenera in the Group II can easily be distinguished from each other by at least the length of spermathecal pump and spermathecal receptacle: Spermathecal pump longer than receptacle (NIT) and much shorter than receptacle (PSE) (Fig. 8).

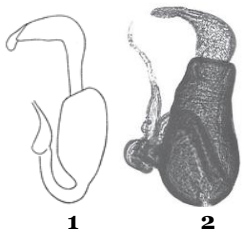

Figure 8. Spermathecal morphology of (**1**) *C. moriori* Samuelson (taken from Samuelson, 1973), (**2**) *C. conducta* (Motschulsky) (taken from Konstantinov et al., 2011).

Finally, on the basis of the general shape of spermathecae, the subgenera can also be divided into 8 groups which are Group I with spermathecae more or less cylindrical or pyriform (CHA GAH MAJ PSE), Group II with spermathecae more or less like a worm or larviform (HOR LON NIG), Group III with spermathecae long-handled gourd-shaped (BIO), Group IV with spermathecae widened basally and distinctly narrowed apically, like a bomb (CON), Group V with spermathecae more or less widened basally and sinuated preapically, bottle-shaped (DAL), Group VI with spermathecae long-necked water bird-shaped (NIT), Group VII with spermathecae globose, fat duck-shaped (PLE) and Group VIII with spermathecae long-billed bird-shaped (UDO) (Fig. 9).

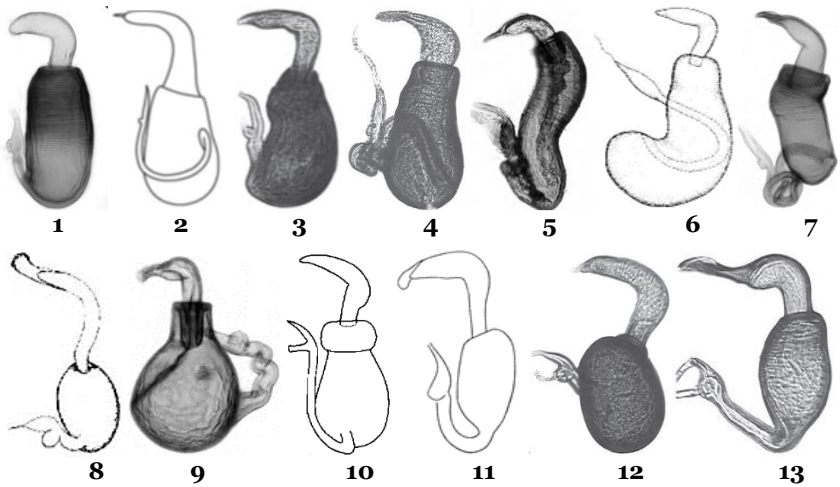

Figure 9. Spermathecal morphology of (**1**) *C. constricta* Ruan et al. (taken from Ruan et al., 2019), (**2**) *C. gahani* Jacoby (taken from Biondi & D'Alessandro, 2006), (**3**) *C. major* (Jacquelin du Val) (taken from Konstantinov et al., 2011), (**4**) *C. conducta* (Motschulsky) (taken from Konstantinov et al., 2011), (**5**) *C. bretinghami* Baly (taken from Ruan et al., 2019), (**6**) *C. reprehensa* Bechyné (taken from Biondi & Nardis, 2000), (**7**) *C. nigrica* Motschulsky (taken from Ruan et al., 2019), (**8**) *C. mapumalangaensis* Biondi & Nardis (taken from Biondi & Nardis, 2000), (**9**) *C. confinis* Crotch (taken from Ruan et al., 2019), (**10**) *C. audisiana* Biondi (taken from Biondi, 2000), (**11**) *C. moriori* Samuelson (taken from Samuelson, 1973), (**12**) *C. chlorophana* (Duftschmid) (taken from Konstantinov et al., 2011), (**13**) *C. balanomorpha* (Boieldieu) (taken from Konstantinov et al., 2011).

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(January, 2021)

Key to subgenera of the genus *Chaetocnema* Stephens, 1831 on the basis of especially spermathecal morphology

1. Spermathecal pump much longer or longer than receptacle.....**2**
-. Spermathecal pump much shorter than receptacle or about as long as receptacle.....**3**

2. Spermathecal pump much longer than receptacle. Apex of spermathecal pump more or less cylindrical or rounded. Frontal ridge between antennal sockets narrow and convex. Surface of vertex sparsely and unevenly covered with some weakly impressed punctures (3-5) near upper ocular margins. Pronotum with evenly but relatively sparsely punctures. Diameter of pronotal punctures at least 2-4 times smaller than distance between them. Base of pronotum without longitudinal impressions. Elytra with convex sided. Elytral punctures regular including periscutellar rows. Average body length 2.08-2.29 mm.....
.....***Biondiana* subgen. nov.**
-. Spermathecal pump longer than receptacle. Apex of spermathecal pump more or less flattened or pointed. Frontal ridge between antennal sockets wide or narrow and always convex. Surface of vertex without punctures, except 3-5 on each side near eye. Pronotum with evenly and densely punctures, uniformly or not. Basal stria of punctures absent throughout. Base of pronotum without longitudinal impressions. Elytra with more or less convex sided. Elytral punctures regular including periscutellar rows. Average body length 2.2-2.4 mm.....***Nitidoides* subgen. nov.**

3. Spermathecal pump much shorter than receptacle.....**4**
-. Spermathecal pump about as long as receptacle.....**9**

4. Apex of spermathecal pump cylindrical or rounded.....**5**
-. Apex of spermathecal pump flattened or pointed.....**7**

5. Spermathecal receptacle longish, more or less widened, distinctly curved ventrad in approximately entire basal half and distinctly sinuate ventro-medially, like a worm or larva. Frons partly covered with relatively short, white setae. Surface of vertex with evenly and densely punctures into a band of well impressed punctures placed between eyes or at least with some weakly impressed punctures near upper ocular margins. Punctures about as large as pronotal punctures. Base of pronotum without longitudinal impressions. Relatively larger, average body length: 2.71-3.36 mm.....***Longicornoides* subgen. nov.**
-. Spermathecal receptacle relatively shortened, not sinuate. Frons with only relatively long setae on sides present. Surface of vertex sparsely and unevenly covered with varying number of punctures near eye only. Punctures about as large as or slightly larger than pronotal punctures. Base of pronotum without longitudinal impressions or with two well-developed longitudinal impressions, both near basal margin and further anteriorly. Relatively smaller, body length under 2.70 mm.....**6**

6. Spermathecal receptacle shortened, very widened and globose, not sinuate, in the form of a bomb that distinctly narrowed in the apical 1/4 part and very widened in the basal 3/4 part. Minimum width of receptacle situated distinctly apically. Apex of spermathecal duct up to about 4/5 of receptacle, spermathecal gland at about 3/4 of receptacle. Base of pronotum without longitudinal impressions. Average body length: 1.50-2.50 mm.....
.....***Confinoides* subgen. nov.**
-. Spermathecal receptacle relatively shortened, more or less narrowed or widened, cylindrical or pyriform, but not sinuate. Minimum width of receptacle usually situated apically, but relatively not distinct. Apex of spermathecal duct up to about 2/3 or 3/4 of receptacle, but spermathecal gland at about middle of receptacle Base of pronotum without longitudinal impressions or with two well-developed longitudinal impressions, both near basal margin and further anteriorly. Average body length usually under 2.40 mm (1.54-2.34), exceptionally at most to 2.70 mm.....***Chaetocnema* Stephens**

7. Spermathecal receptacle relatively shortened, not elongated, pyriform or cylindrical, but not sinuate. Basal part of receptacle wider than apical. Minimum width of receptacle usually situated apically. Surface of vertex sparsely and unevenly covered with punctures, near eye or not. Pronotum with evenly but relatively sparsely punctures. Diameter of pronotal punctures never subequal and 2–4 to 6–10 times smaller than distance between them. Basal stria of punctures on pronotum present, throughout or only absent on middle. Elytral punctures regular including periscutellar rows. Average body length 1.43-2.10 mm, rarely 3.50–4.00 mm.....***Pseudochaetocnema* subgen. nov.**

-. Spermathecal receptacle long or longish, more or less elongated and sinuate medially or preapically. Basal part of receptacle about as wide as apical or narrower than apical. Minimum width of receptacle usually situated basally. Surface of vertex with evenly and densely punctures or without punctures, except 2-3 on each side near eye. Pronotum with evenly and densely punctures or with evenly but relatively sparsely punctures. Diameter of pronotal punctures subequal to or 6-10 times smaller than distance between them. Basal stria of punctures on pronotum absent or if present, throughout or absent on middle. Elytral punctures confused including periscutellar rows, at least in basally or regular including periscutellar rows. Average body length 1.30-2.76 mm.....**8**

8. Spermathecal receptacle long, distinctly elongated, narrowed or slightly widened and sinuate medially on dorsal surface, larviform. Maximum width of receptacle situated basally, apically or at about middle. Spermathecal gland at about basal third or at most near middle of receptacle. Frontal ridge between antennal sockets wide and flat. Frons evenly covered with relatively short, white setae. Surface of vertex with evenly and densely punctures. Pronotum with evenly and densely punctures. Diameter of pronotal punctures subequal to distance between them. Pronotal punctures usually about as large as elytral punctures. Basal stria of punctures on pronotum absent. Relatively larger, average body length 1.59-2.76 mm.....***Hortensoides* subgen. nov.**

-. Spermathecal receptacle less elongated, slightly widened, distinctly sinuate preapically. Maximum width of receptacle always situated preapically on dorsal surface. Spermathecal gland at about basal fourth of receptacle. Frontal ridge between antennal sockets narrow and convex. Frons with only relatively long setae on sides present. Surface of vertex without punctures, except 2-3 on each side near eye. Pronotum with evenly but relatively sparsely punctures. Diameter of pronotal punctures 6-10 times smaller than distance between them. Pronotal punctures smaller than elytral punctures, except about as large as deep row of large punctures at base of pronotum. Basal stria of deep punctures on pronotum present throughout. Relatively smaller, average body length 1.30–1.60 mm.....
.....***Nigricoides* subgen. nov.**

9. Apex of spermathecal pump flattened or pointed. Apex of spermathecal duct up to about middle of receptacle, spermathecal gland at about basal third of receptacle. Spermathecal receptacle shortened, more or less widened or narrowed, more or less pyriform and slightly sinuate dorso-medially or not. Frontal ridge between antennal sockets wide and flat. Frons evenly covered with relatively short, white setae. Surface of vertex densely and evenly covered with punctures. Basal stria of punctures on pronotum absent. Base of pronotum without longitudinal impressions. Elytra with more or less convex sided. Relatively smaller, average body length 1.83-2.75 mm.....***Udorpes* Motschulsky**

-. Apex of spermathecal pump cylindrical or rounded. Apex of spermathecal duct up to about 4/5 of receptacle, about apical margin or near of receptacle, or at least at about middle of receptacle, spermathecal gland at about middle, about apical 2/3 or 3/4 of receptacle. Frontal ridge between antennal sockets narrow and convex or wide and flat. Frons with only relatively long setae on sides present or covered with relatively short, white setae. Surface of vertex sparsely and unevenly covered with punctures or with evenly and more or less densely punctures. Basal stria of punctures on pronotum absent or present. Base of pronotum with two well-developed longitudinal impressions, both near basal margin and further anteriorly or without longitudinal impressions. Elytra with more or less parallel or convex sided. Relatively larger, average body length 2.44-3.79 mm.....**10**

Munis Entomology & Zoology
https://www.munisentzool.org/
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(January, 2021)

10. Spermathecal pump attached to side of receptacle top. Spermathecal receptacle more or less vesicular or globose, slightly sinuate preapically on dorsal surface. Frontal ridge between antennal sockets narrow and convex. Frons with only relatively long setae on sides present. Surface of vertex sparsely and unevenly covered with punctures, not only near eye. Elytra with parallel sided. Average body length 2.44-3.32 mm.....***Plectroscelis* Dejean -.** Spermathecal pump attached to middle of receptacle top. Spermathecal receptacle not globose, more or less pyriform or cylindirical and sinuate or not. Frontal ridge between antennal sockets narrow and convex or wide and flat. Frons evenly covered with relatively short, white setae or with only relatively long setae on sides present. Surface of vertex with evenly and more or less densely punctures, into a band of well impressed punctures placed between eyes or usually only near eye. Elytra with more or less convex or parallel sided.....**11**

11. Spermathecal receptacle not sinuate. Spermathecal duct as long as receptacle, shorter or much shorter than receptacle, but relatively longish or shortened. Apex of spermathecal duct up to about apical margin or near of receptacle, or at least at about middle of receptacle. Spermathecal gland at about apical 3/4 or at basal half near middle of receptacle. Basal part of spermathecal duct usually corrugated as once coiled. Surface of vertex with evenly and densely punctures. Basal stria of punctures present throughout but distinctly defined or not. Average body length 2.33–3.96 mm.....***Gahanioides* subgen. nov. -.** Spermathecal receptacle sinuate. Surface of vertex with evenly and more or less densely punctures into a band of well impressed punctures placed between eyes or with sparsely and unevenly punctures, usually only near eye. Basal stria of punctures on pronotum absent throughout or rarely if present only between two longitudinal basal depressions.....**12**

12. Spermathecal receptacle relatively shortened, more or less widened in basal half, bottle-shaped, distinctly sinuate preapically on both ventral and dorsal surfaces. Minimum width of receptacle situated preapically. Spermathecal duct as long as receptacle. Frontal ridge between antennal sockets wide and flat. Frons evenly covered with relatively short, white setae. Surface of vertex with evenly and more or less densely punctures into a band of well impressed punctures placed between eyes. Pronotum with evenly and densely punctures. Basal stria of punctures on pronotum absent. Base of pronotum without longitudinal impressions. Elytra with convex sided. Elytral punctures regular including periscutellar rows. Relatively smaller, body length: 2.21 mm.....***Dalessandroiana* subgen. nov. -.** Spermathecal receptacle shortened, widened, more or less pyriform and sinuate ventro-medially. Minimum width of receptacle situated apically. Spermathecal duct shorter than receptacle. Frontal ridge between antennal sockets narrow and convex. Frons with only relatively long setae on sides present. Surface of vertex sparsely and unevenly covered with punctures, usually only near eye. Pronotum with evenly but relatively sparsely punctures. Basal stria of punctures on pronotum usually absent throughout, if present only between two longitudinal depressions. Base of pronotum with two well-developed longitudinal impressions, both near basal margin and further anteriorly. Elytra with parallel sided. Periscutellar row of punctures on elytron regular and single, confused or more than one. Second through sixth rows of punctures at base of elytron regular. Relatively larger, body length: 2.71-3.79 mm... .....***Majoroides* subgen. nov.**

ANALYSIS I (on spermathecal characteristics).

Finally, herein presented an analysis based on description of spermathecal structures of subgenera given above. This analysis includes 30 characters in total. The character states and coding used in this analysis are:

AA. Spermathecal pump much shorter than receptacle; (0) Yes (1) No
AB. Spermathecal pump about as long as receptacle; (0) Yes (1) No
AC. Spermathecal pump much longer or longer than receptacle; (0) Yes (1) No
AD. Shape of apex of spermathecal pump; (0) more or less cylindrical or rounded (1) more or less flattened or pointed
AE. Attachment point of spermathecal pump to receptacle top; (0) attached to middle (1) attached to side

AF. Relative comparison of spermathecal receptacle to subgenera; (0) more or less shortened (1) more or less longened, elongated
AG. General shape of spermathecal receptacle more or less cylindrical or pyriform; (0) Yes (1) No
AH. General shape of spermathecal receptacle more or less globose; (0) Yes (1) No
AI. General shape of spermathecal receptacle more or less larviform; (0) Yes (1) No
AK. General shape of spermathecal receptacle more or less widened basally and distinctly narrowed apically, like a bomb; (0) Yes (1) No
AL. General shape of spermathecal receptacle more or less widened basally and sinuated preapically, bottle-shaped; (0) Yes (1) No
AM. Sinuation on spermathecal receptacle; (0) absent (1) present
AN. Maximum width of spermathecal receptacle situated basally; (0) Yes (1) No
AO. Maximum width of spermathecal receptacle situated medially; (0) Yes (1) No
AP. Maximum width of spermathecal receptacle situated apically; (0) Yes (1) No
AQ. Maximum width of spermathecal receptacle situated preapically; (0) Yes (1) No
AR. Basal part of receptacle narrower than apical; (0) Yes (1) No
AS. Basal part of receptacle about as wide as apical; (0) Yes (1) No
AT. Basal part of receptacle wider than apical; (0) Yes (1) No
AU. Minimum width of spermathecal receptacle situated basally; (0) Yes (1) No
AV. Minimum width of spermathecal receptacle situated apically; (0) Yes (1) No
AW. Minimum width of spermathecal receptacle situated preapically; (0) Yes (1) No
AY. Spermathecal duct much shorter than receptacle; (0) Yes (1) No
AZ. Spermathecal duct shorter than receptacle; (0) Yes (1) No
BA. Spermathecal duct slightly shorter than receptacle; (0) Yes (1) No
BB. Spermathecal duct about as long as or longer than receptacle; (0) Yes (1) No
BC. Basal part of spermathecal duct more or less straight; (0) Yes (1) No
BD. Basal part of spermathecal duct more or less corrugated; (0) Yes (1) No
BE. Apical part of spermathecal duct more or less straight; (0) Yes (1) No
BF. Apical part of spermathecal duct more or less corrugated; (0) Yes (1) No

Table 14. Matrix of the character-states considered in the analysis (see above) (the names of subgenera are abbreviated with the first three letters).

	S	U	B	G	E	N	E	R	A			
	BIO	CHA	CON	DAL	GAH	HOR	LON	MAJ	NIG	NIT	PLE	PSE	UDO
AA	1	0	0	1	1	0	0	1	0	1	1	0	1
AB	1	1	1	0	0	1	1	0	1	1	0	1	0
AC	0	1	1	1	1	1	1	1	1	0	1	1	1
AD	0	0	0	0	0	1	0	0	1	1	0	1	1
AE	0	0	0	0	0	0	0	0	0	0	1	0	0
AF	0	0	0	0	0	1	1	0	1	0	0	0	0
AG	1	0	1	1	0	1	1	0	1	0	1	0	0
AH	0	1	1	1	1	1	1	1	1	1	0	1	1
AI	1	1	1	1	1	0	0	1	0	1	1	1	1
AK	1	1	0	1	1	1	1	1	1	1	1	1	1
AL	1	1	1	0	1	1	1	1	1	1	1	1	1
AM	0	0	0	1	0	1	1	1	1	0	1	0	1
AN	1	0	1	0	0	0	0	0	1	1	0	0	0
AO	0	0	0	1	1	0	1	1	1	0	0	1	0
AP	1	1	1	1	1	0	1	1	1	1	1	1	1
AQ	1	1	1	1	1	1	1	1	0	1	1	1	1
AR	1	0	1	0	1	0	1	1	0	1	1	1	0
AS	0	0	1	1	1	0	1	1	1	0	1	1	0
AT	1	0	0	1	0	0	0	0	1	1	0	0	0
AU	0	1	1	1	1	0	1	1	0	0	1	1	0
AV	0	0	0	1	0	1	0	0	1	0	0	0	0
AW	1	1	1	0	1	1	1	1	1	1	1	1	1
AY	0	1	1	1	0	0	1	1	0	1	1	0	0
AZ	1	0	1	1	0	0	0	1	0	1	1	0	1
BA	1	1	0	1	1	1	0	0	1	0	0	1	1
BB	1	1	1	0	0	1	1	1	1	0	1	1	1
BC	0	0	0	1	1	0	0	0	0	0	0	0	0
BD	1	0	1	0	0	0	1	1	1	1	1	0	1
BE	0	0	1	0	0	0	0	0	1	0	0	0	0
BF	1	1	0	1	1	0	1	1	0	1	1	0	1

Munis Entomology & Zoology
https://www.munisentzool.org/
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Mun. Ent. Zool.
(January, 2021)

According to matrix given above, subgenera that were found different or similar based on the character-states are shown below (Table 15).

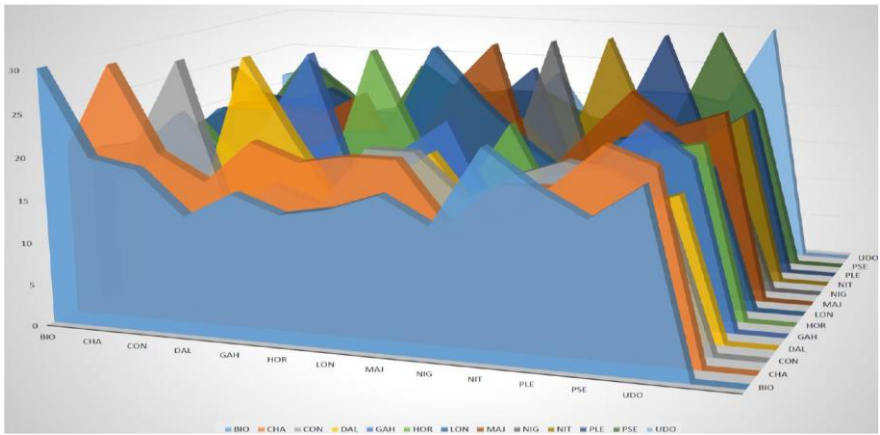
Table 15. Subgenera according to each character-state.

	SUBGENERA	
AA	BIO DAL GAH MAJ NIT PLE UDO	CHA CON HOR LON NIG PSE
AB	BIO CHA CON HOR LON NIG NIT PSE	DAL GAH MAJ PLE UDO
AC	CHA CON DAL GAH HOR LON MAJ NIG PLE PSE UDO	BIO NIT
AD	BIO CHA CON DAL GAH LON MAJ PLE	HOR NIG NIT PSE UDO
AE	BIO CHA CON DAL GAH HOR LON MAJ NIG NIT PSE UDO	PLE
AF	BIO CHA CON DAL GAH MAJ NIT PLE PSE UDO	HOR LON NIG
AG	BIO CON DAL HOR LON NIG PLE	CHA GAH MAJ NIT PSE UDO
AH	CHA CON DAL GAH HOR LON MAJ NIG NIT PSE UDO	BIO PLE
AI	BIO CHA CON DAL GAH MAJ NIT PLE PSE UDO	HOR LON NIG
AK	BIO CHA DAL GAH HOR LON MAJ NIG NIT PLE PSE UDO	CON
AL	BIO CHA CON GAH HOR LON MAJ NIG NIT PLE PSE UDO	DAL
AM	DAL HOR LON MAJ NIG PLE UDO	BIO CHA CON GAH NIT PSE
AN	CHA DAL GAH HOR LON MAJ PLE PSE UDO	BIO CON NIG NIT
AO	BIO CHA CON HOR NIT PLE UDO	DAL GAH LON MAJ NIG PSE
AP	BIO CHA CON DAL GAH LON MAJ NIG NIT PLE PSE UDO	HOR
AQ	BIO CHA CON DAL GAH HOR LON MAJ NIT PLE PSE UDO	NIG
AR	BIO CON GAH LON MAJ NIT PLE PSE	CHA DAL HOR NIG UDO
AS	CON DAL GAH LON MAJ NIG PLE PSE	BIO CHA HOR NIT UDO
AT	CHA CON GAH HOR LON MAJ PLE PSE UDO	BIO DAL NIG NIT
AU	CHA CON DAL GAH LON MAJ PLE PSE	BIO HOR NIG NIT UDO
AV	BIO CHA CON GAH LON MAJ NIT PLE PSE UDO	DAL HOR NIG
AW	BIO CHA CON GAH HOR LON MAJ NIG NIT PLE PSE UDO	DAL
AY	BIO GAH HOR NIG PSE UDO	CHA CON DAL LON MAJ NIT PLE
AZ	BIO CON DAL MAJ NIT PLE UDO	CHA GAH HOR LON NIG PSE
BA	BIO CHA DAL GAH HOR NIG PSE UDO	CON LON MAJ NIT PLE
BB	BIO CHA CON HOR LON MAJ NIG PLE PSE UDO	DAL GAH NIT
BC	BIO CHA CON HOR LON MAJ NIG NIT PLE PSE UDO	DAL GAH
BD	BIO CON LON MAJ NIG NIT PLE UDO	CHA DAL GAH HOR PSE
BE	BIO CHA DAL GAH HOR LON MAJ NIT PLE PSE UDO	CON NIG
BF	BIO CHA DAL GAH LON MAJ NIT PLE UDO	CON HOR NIG PSE

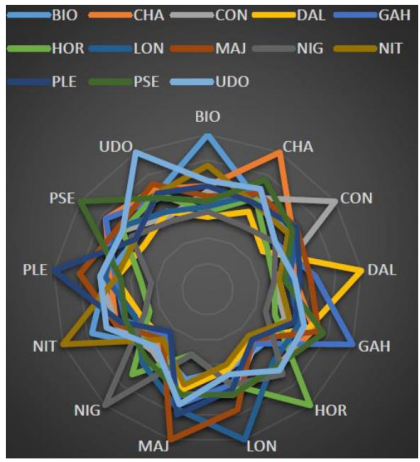
As seen from the table, no character was found uniform among the subgenera defined and thus the subgenera were found to differ more or less each other. Total numbers of characters that are similar among the subgenera defined according to the 30 characters, are presented below (Table 16). The graph created according to the values given in table 16 is also presented after the table (Graph 1).

Table 16. Total numbers of characters that are similar among the subgenera defined according to the all specified characters of spermathecal structures.

	BIO	CHA	CON	DAL	GAH	HOR	LON	MAJ	NIG	NIT	PLE	PSE	UDO
BIO	30	20	19	14	17	15	16	18	15	24	20	17	21
CHA	20	30	20	17	22	20	21	21	14	19	19	24	22
CON	19	20	30	13	16	14	21	21	16	19	21	20	16
DAL	14	17	13	30	21	13	16	20	13	14	18	15	17
GAH	17	22	16	21	30	14	19	23	12	17	18	24	20
HOR	15	20	14	13	14	30	19	13	22	12	13	20	21
LON	16	21	21	16	19	19	30	24	19	15	20	21	17
MAJ	18	21	21	20	23	13	24	30	13	19	25	21	23
NIG	15	14	16	13	12	22	19	13	30	13	11	18	15
NIT	24	19	19	14	17	12	15	19	13	30	18	17	21
PLE	20	19	21	18	18	13	20	25	11	18	30	17	21
PSE	17	24	20	15	24	20	21	21	18	17	17	30	20
UDO	21	22	16	17	20	21	17	23	15	21	21	20	30



A



B

Graph 1. Relationship among the subgenera defined on the base of total numbers of similar characters of spermathecae, A. Area graph, B. Radar trail graph.

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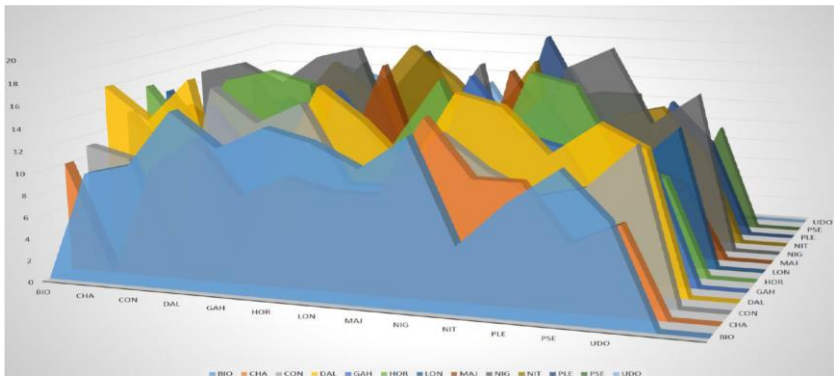
Mun. Ent. Zool.
(January, 2021)

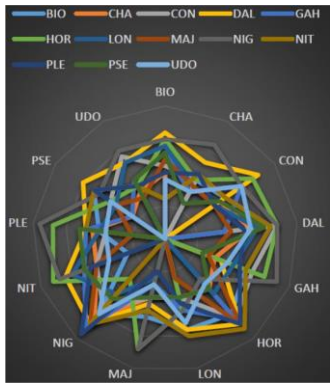
Also, total numbers of characters that are different among the subgenera defined according to the 30 characters, are presented below (Table 17). The graph created according to the values given in table 17 is also presented after the table (Graph 2).

Table 17. Total numbers of characters that are different among the subgenera defined according to the all specified characters of spermathecal structures.

	BIO	CHA	CON	DAL	GAH	HOR	LON	MAJ	NIG	NIT	PLE	PSE	UDO
BIO	0	10	11	16	13	15	14	12	15	6	10	13	9
CHA	10	0	10	13	8	10	9	9	16	11	11	6	8
CON	11	10	0	17	14	16	9	9	14	11	9	10	14
DAL	16	13	17	0	9	17	14	10	17	16	12	15	13
GAH	13	8	14	9	0	16	11	7	18	13	12	6	10
HOR	15	10	16	17	16	0	11	17	8	18	17	10	9
LON	14	9	9	14	11	11	0	6	11	15	10	9	13
MAJ	12	9	9	10	7	17	6	0	17	11	5	9	7
NIG	15	16	14	17	18	8	11	17	0	17	19	12	15
NIT	6	11	11	16	13	18	15	11	17	0	12	13	9
PLE	10	11	9	12	12	17	10	5	19	12	0	13	9
PSE	13	6	10	15	6	10	9	9	12	13	13	0	10
UDO	9	8	14	13	10	9	13	7	15	9	9	10	0



A



B

Graph 2. Relationship among the subgenera defined on the base of total numbers of different characters of spermathecae, A. Area graph, B. Radar trail graph.

ANALYSIS II (on some external characteristics).

Herein also presented an analysis based on some external structures of subgenera given above. This analysis includes 19 characters in total. The character states and coding used in this analysis are:

A. Frontal ridge between antennal sockets narrow and convex; (0) Yes (1) No
B. Frons with only relatively long setae on sides present; (0) Yes (1) No
C. Frons evenly covered with relatively short, white setae; (0) Yes (1) No
D. Frons partly covered with relatively short, white setae; (0) Yes (1) No
E. Surface of vertex sparsely and unevenly covered only with varying number of punctures near eye; (0) Yes (1) No
F. Surface of vertex sparsely and unevenly covered with punctures, not only near eye; (0) Yes (1) No
G. Surface of vertex with evenly and more or less densely punctures; (0) Yes (1) No
H. Surface of vertex with evenly and densely punctures into a band of well impressed punctures placed between eyes; (0) Yes (1) No
I. Pronotum; (0) with evenly but relatively sparsely punctures, diameter of punctures 2–4 to 6-10 times smaller than distance between them (1) with evenly and densely punctures, diameter of punctures about subequal to distance between them
K. Basal stria of punctures on pronotum present throughout but distinctly or hardly defined or only absent on middle; (0) Yes (1) No
L. Basal stria of punctures on pronotum absent throughout; (0) Yes (1) No
M. Basal stria of punctures on pronotum usually absent throughout, if present only between two longitudinal depressions; (0) Yes (1) No
N. Pronotal punctures; (0) smaller than elytral punctures (1) usually about as large as elytral punctures
O. Base of pronotum without longitudinal impressions; (0) Yes (1) No
P. Base of pronotum with two well-developed longitudinal impressions, both near basal margin and further anteriorly; (0) Yes (1) No
Q. Elytra; (0) with more or less convex sided (1) with more or less parallel sided
R. Periscutellar row of punctures on elytron always regular and single; (0) Yes (1) No
S. Periscutellar row of punctures on elytron confused or at least geminate; (0) Yes (1) No
T. Second through sixth rows of punctures at base of elytron; (0) regular (1) confused

Table 18. Matrix of the character-states considered in the analysis (see above) (the names of subgenera are abbreviated with the first three letters).

	S	U	B	G	E	N	E	R	A			
	BIO	CHA	CON	DAL	GAH	HOR	LON	MAJ	NIG	NIT	PLE	PSE	UDO
A	0	0	0	1	0	1	0	0	0	0	0	0	1
B	0	0	0	1	1	1	1	0	0	0	0	0	1
C	1	1	1	0	0	0	1	1	1	1	1	1	0
D	1	1	1	1	1	1	0	1	1	1	1	1	1
E	0	0	0	1	1	1	1	0	0	0	1	1	1
F	1	1	1	1	1	1	1	1	1	1	0	0	1
G	1	1	1	1	0	0	1	1	1	1	1	1	0
H	1	1	1	0	1	1	0	1	1	1	1	1	1
I	0	0	0	1	0	1	0	0	0	1	0	0	0
K	1	1	1	1	0	1	1	1	0	1	1	0	1
L	0	0	0	0	1	0	0	0	1	0	0	0	0
M	1	1	1	1	1	1	1	0	1	1	1	1	1
N	0	0	0	0	0	1	0	0	0	0	0	0	0
O	0	0	0	0	0	0	0	1	0	0	0	0	0
P	1	0	1	1	1	1	1	0	1	1	0	1	1
Q	0	0	0	0	0	0	0	1	0	0	1	0	0
R	0	0	0	0	0	1	0	1	0	0	0	0	1
S	1	1	1	1	1	0	1	0	1	1	1	1	0
T	0	0	0	0	0	1	0	0	0	0	0	0	0

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According to matrix given above, subgenera that were found different or similar based on the character-states are shown below (Table 19).

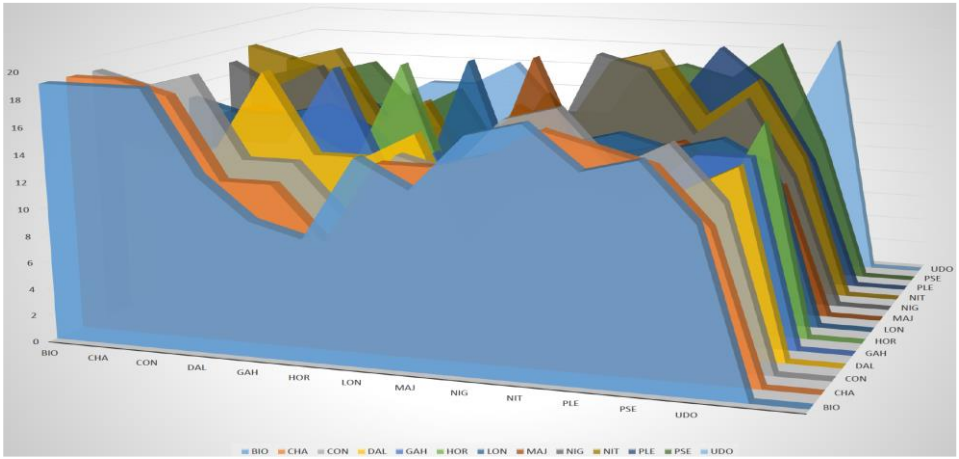
Table 19. Subgenera according to each character-state.

	S U B G E N E R A	
A	BIO CHA CON GAH LON MAJ NIG NIT PLE PSE	DAL HOR UDO
B	BIO CHA CON MAJ NIG NIT PLE PSE	DAL GAH HOR LON UDO
C	BIO CHA CON LON MAJ NIG NIT PLE PSE	DAL GAH HOR UDO
D	BIO CHA CON DAL GAH HOR MAJ NIG NIT PLE PSE UDO	LON
E	DAL GAH HOR LON PLE PSE UDO	BIO CHA CON MAJ NIG NIT
F	BIO CHA CON DAL GAH HOR LON MAJ NIG NIT UDO	PLE PSE
G	BIO CHA CON DAL LON MAJ NIG NIT PLE PSE	GAH HOR UDO
H	BIO CHA CON GAH HOR MAJ NIG NIT PLE PSE UDO	DAL LON
I	BIO CHA CON GAH LON MAJ NIG NIT PLE PSE UDO	DAL HOR
K	BIO CHA CON DAL HOR LON MAJ PLE UDO	GAH NIG NIT PSE
L	BIO CHA CON DAL HOR LON MAJ NIT PLE PSE UDO	GAH NIG
M	BIO CHA CON DAL GAH HOR LON NIG NIT PLE PSE UDO	MAJ
N	BIO CHA CON DAL GAH LON MAJ NIG NIT PLE PSE UDO	HOR
O	BIO CHA CON DAL GAH HOR LON NIG NIT PLE PSE UDO	MAJ
P	BIO CON DAL GAH HOR LON NIG NIT PSE UDO	CHA MAJ PLE
Q	BIO CHA CON DAL GAH HOR LON NIG NIT PSE UDO	MAJ PLE
R	BIO CHA CON DAL GAH LON NIG NIT PLE PSE	HOR MAJ UDO
S	BIO CHA CON DAL GAH LON NIG NIT PLE PSE	HOR MAJ UDO
T	BIO CHA CON DAL GAH LON MAJ NIG NIT PLE PSE UDO	HOR

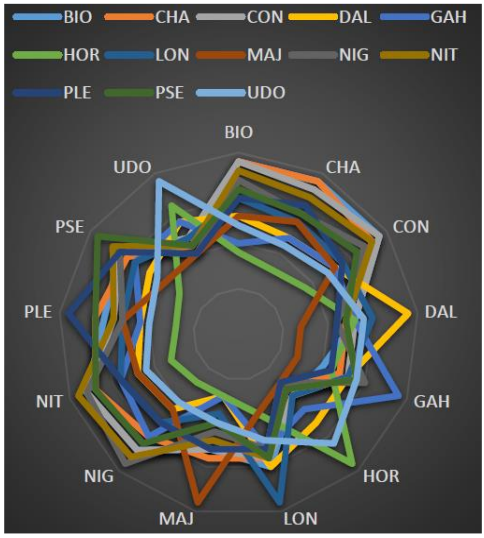
Total numbers of characters that are similar among the subgenera defined according to the 19 characters, are presented below (Table 20). The graph created according to the values given in table 20 is also presented after the table (Graph 3).

Table 20. Total numbers of characters that are similar among the subgenera defined according to the all specified characters of some external structures.

	BIO	**CHA**	**CON**	**DAL**	**GAH**	**HOR**	**LON**	**MAJ**	**NIG**	**NIT**	**PLE**	**PSE**	**UDO**
BIO	19	19	19	13	10	9	15	13	17	18	15	16	12
CHA	19	19	18	12	12	8	14	14	15	17	16	15	11
CON	19	18	19	13	13	9	14	13	17	18	14	16	12
DAL	13	12	13	19	13	13	15	7	11	12	11	12	14
GAH	10	12	13	13	19	11	13	7	15	14	11	14	14
HOR	9	8	9	13	11	19	9	7	7	8	7	8	16
LON	15	14	14	15	13	9	19	9	13	14	13	14	12
MAJ	13	14	13	7	7	7	9	19	11	12	13	10	10
NIG	17	15	17	11	15	7	13	11	19	18	13	16	10
NIT	18	17	18	12	14	8	14	12	18	19	14	17	11
PLE	15	16	14	11	11	7	13	13	13	14	19	16	10
PSE	16	15	16	12	14	8	14	10	16	17	16	19	11
UDO	12	11	12	14	14	16	12	10	10	11	10	11	19



A



B

Graph 3. Relationship among the subgenera defined on the base of total numbers of similar characters of some external structures, A. Area graph, B. Radar trail graph.

In addition, total numbers of characters that are different among the subgenera defined according to the 19 characters, are presented below (Table 21). The graph created according to the values given in table 21 is also presented after the table (Graph 4).

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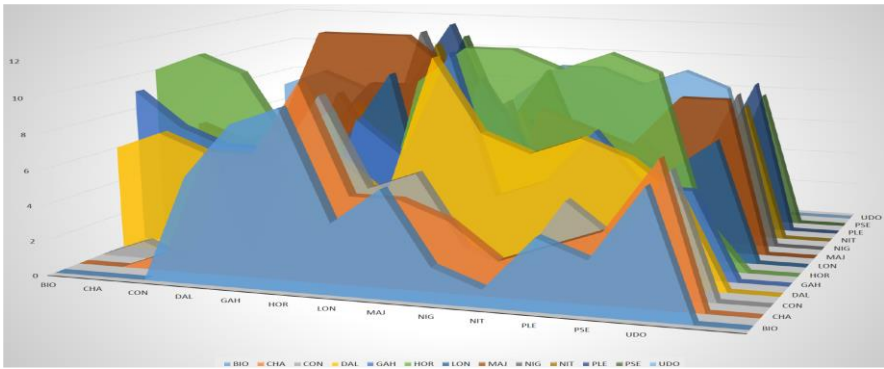
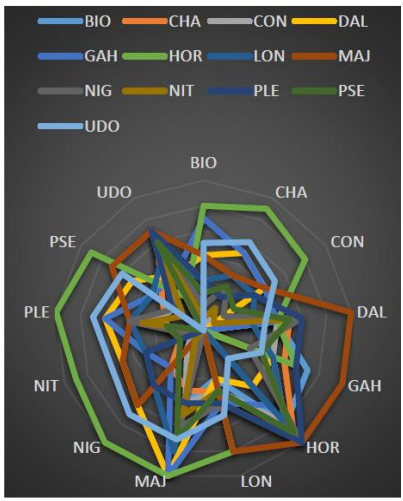
Table 21. Total numbers of characters that are different among the subgenera defined according to the all specified characters of some external structures.

	BIO	CHA	CON	DAL	GAH	HOR	LON	MAJ	NIG	NIT	PLE	PSE	UDO
BIO	0	0	0	6	9	10	4	6	2	1	4	3	7
CHA	0	0	1	7	7	11	5	5	4	2	3	4	8
CON	0	1	0	6	6	10	5	6	2	1	5	3	7
DAL	6	7	6	0	6	6	4	12	8	7	8	7	5
GAH	9	7	6	6	0	8	6	12	4	5	8	5	5
HOR	10	11	10	6	8	0	10	12	12	11	12	11	3
LON	4	5	5	4	6	10	0	10	6	5	6	5	7
MAJ	6	5	6	12	12	12	10	0	8	7	6	9	9
NIG	2	4	2	8	4	12	6	8	0	1	6	3	9
NIT	1	2	1	7	5	11	5	7	1	0	5	2	8
PLE	4	3	5	8	8	12	6	6	6	5	0	3	9
PSE	3	4	3	7	5	11	5	9	3	2	3	0	8
UDO	7	8	7	5	5	3	7	9	9	8	9	8	0



A



B

Graph 4. Relationship among the subgenera defined on the base of total numbers of different characters of some external structures, A. Area graph, B. Radar trail graph.

DISCUSSIONS AND CONCLUSIONS

First of all, both analyzes performed above reveal different results from each other. According to the tables and graphics given in Analysis I based on spermathecal structures and Analysis II based on some external structures, the results obtained in Analysis I for a subgeneric arrangement such as in this study seem much more convenient and usable than those from Analysis II. This situation supports the subgeneric arrangement to be made using spermathecal structures, which is our purpose of study. On the other hand, an arrangement to be made according to the results obtained in Analysis II which is based on external structures, will not be sufficient and realistic (since not all species can be placed in the appropriate subgenera for various reasons). This fact or assumption is in line also with the acceptance given at the beginning of the study that some authors proposed not use any subgenus until a comprehensive phylogenetic study was conducted for the genus *Chaetocnema*.

Döberl (2010) included 118 species with some Oriental species in his catalogic work because of the boundaries of Palaearctic region were kept a little wider than the traditional sense, and some cities and countries that we did not actually think were included in this region were added to the Palaearctic realm. On the other side, there were a total of 75 species in Konstantinov et al. (2011), 7 of which are new species described. Because contrary to Döberl (2010), the boundaries of Palaearctic region were used narrower than traditional sense in this study. The revision only covers the Palaearctic species in the traditional sense in which, for example, species from North Africa, Tibet and Central & Southern China have been excluded. Unfortunately, the revision provides no results of an analysis that validates this assumption for *Chaetocnema* species in Palaearctic realm. This delimitation of the Palaearctic region seems to be no problem because the geographic realm is clearly defined. Problematic, however, is the exclusion of some species that do occur in this realm. For example, the species in the North Africa, Tibet and also some other provinces of China that are in Palaearctic region, have not been included.

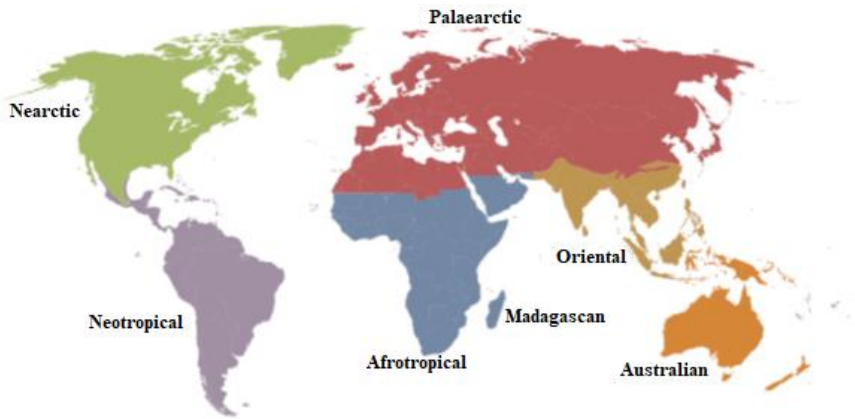


Figure 10. World map showing the seven major biogeographic regions according to WWF (taken from https://en.wikipedia.org/wiki/Biogeographic_realm).

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Similarly, Ruan et al. (2019) considered Tibet and some other Chinese provinces that are in the Palaearctic region, in the Oriental region. As understood herein, we accept Palaearctic region in the traditional sense which includes also Tibet and some other Chinese provinces that are accepted in Oriental region by Ruan et al. (2019) (Fig. 10).

As a solution to the problem in China, we accept and approve the map proposed by Fellowes (2006) for the borders of Palaearctic and Oriental regions. Accordingly, from West to East most part of Yunan, most part of Guizhou, Guangxi, most part of Hunan, Guangdong, Hainan, most part of Jiangxi, Fujian, most part of Zhejiang and Taiwan in China were evaluated in the Oriental region. The remaning parts of China with Tibet were evaluated in Palaearctic region (Fig. 11).

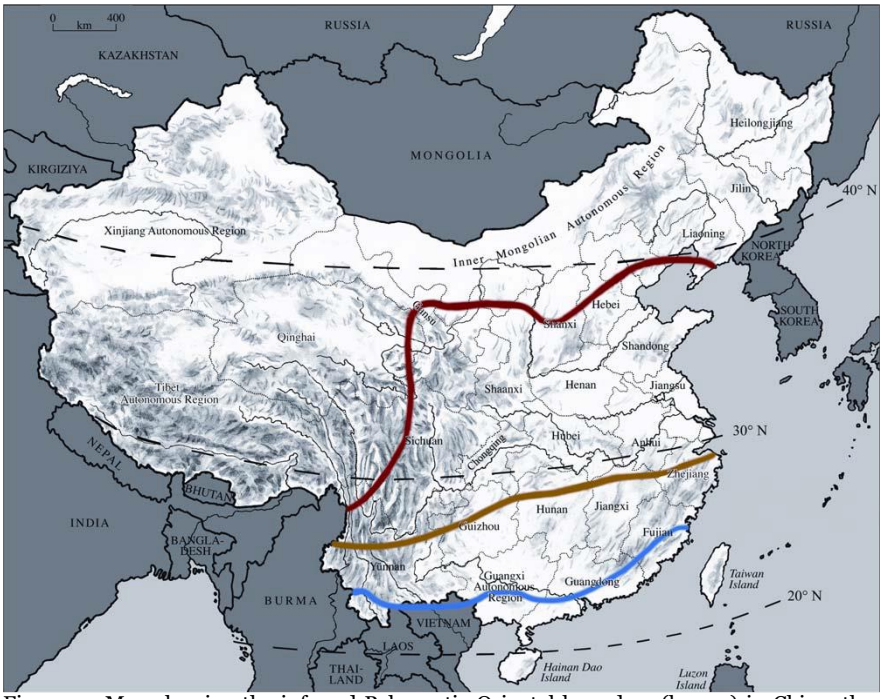

Figure 11. Map showing the inferred Palaearctic-Oriental boundary (brown) in China, the upper red line approximates the extreme northern limit of Oriental species and the lower blue line the extreme southern limit of Palaearctic species (taken from Fellowes, 2006).

In addition, spermathecal morphology of 16 Palaearctic species is unknown. Therefore, the subgenera of these species according to their spermathecal morphology could not be determined precisely. However, the subgenera to which these species belong can be given as follows based on their aedeagal morphology and known external morphological characters. It should not be forgotten that the exact determination of the subgenus to which these species belong is only possible by examining their spermathecal morphology.

Accordingly, 4 species as *C. bicolorata* Kimoto, *C. granulosa* (Baly), *C. melonae* Chen and *C. septentrionalis* Kimoto were found to be compatible with the nominative subgenus *Chaetocnema* Stephens and these species can be considered in this subgenus. Also 3 species as *C. alticola* Maulik, *C. polita* (Abeille) and *C. shanxiensis* Chen &Wang were found to be compatible with *Udorpes* Motschulsky and it can be accepted that these species may belong to this subgenus. 1 species as *C. kerimi* (Fairmaire) was found to be compatible with *Plectroscelis* Dejean and it can be accepted that the species may also belong to this subgenus. In addition, 1 species as *C. tonkinensis* Chen was found to be compatible with *Pseudochaetocnema* subgen. nov. and it can be considered in this subgenus. The remaining 7 species as *C. bergeali* Konstantinov et al., *C. franzi* Konstantinov et al., *C. jelineki* Lopatin, *C. kabakovi* Lopatin, *C. latipennis* Pic, *C. sinuata* Weise and *C. tbilisiensis* Konstantinov et al. were found to be compatible with *Hortensoides* subgen. nov. and also these species can be considered in this subgenus (Table 22).

Table 22. Possible subgenera to which Palaearctic species with unknown spermathecal morphology may belong.

Palaearctic Species	Possible Subgenera
C. bicolorata Kimoto, 1971	*Chaetocnema* Stephens, 1831
C. granulosa (Baly, 1874)	*Chaetocnema* Stephens, 1831
C. melonae Chen, 1934	*Chaetocnema* Stephens, 1831
C. septentrionalis Kimoto, 1963	*Chaetocnema* Stephens, 1831
C. bergeali Konstantinov et al., 2011	*Hortensoides* subgen. nov.
C. franzi Konstantinov et al., 2011	*Hortensoides* subgen. nov.
C. jelineki Lopatin, 1990	*Hortensoides* subgen. nov.
C. kabakovi Lopatin, 1995	*Hortensoides* subgen. nov.
C. latipennis Pic, 1911	*Hortensoides* subgen. nov.
C. sinuata Weise, 1889	*Hortensoides* subgen. nov.
C. tbilisiensis Konstantinov et al., 2011	*Hortensoides* subgen. nov.
C. kerimi (Fairmaire, 1875)	*Plectroscelis* Dejean, 1836
C. tonkinensis Chen, 1934	*Pseudochaetocnema* subgen. nov.
C. alticola Maulik, 1926	*Udorpes* Motschulsky, 1845
C. polita (Abeille, 1907)	*Udorpes* Motschulsky, 1845
C. shanxiensis Chen &Wang, 1980	*Udorpes* Motschulsky, 1845

Based on our traditional Palaearctic region acceptance, in fact, the genus *Chaetocnema* Stephens is represented by a total of 99 species with 24 species added to Konstantinov et al. (2011) including 3 newly described species [*C. cheni* Ruan et al. from Sichuan in China, *C. constricta* Ruan et al. from Anhui, Sichuan, Chongqing, Jiangsu in China, Korea, Japan and *C. salixis* Ruan et al. from Shannxi, Gansu, Sichuan in China] and 2 new records [*C. alticola* Maulik from Tibet and Xinjiang in China and *C. bretinghami* Baly from Israel] with 1 species from Israel [*C. wollastoni* Baly], 6 species from North Africa [*C. batophiloides* Abeille from Algeria, Israel, Jordan, *C. bilunulata* Demaison from Egypt, *C. ganganensis* Bechyné from Algeria, *C. kerimi* (Fairmaire) from Morocco, Algeria, Tunisia, Libya, *C. latipennis* Pic from Egypt, *C. polita* (Abeille) from Algeria], 5 species from Tibet [*C. duvivieri* Jacoby, *C. melonae* Chen, *C. simplicifrons* (Baly) from Tibet and Xinjiang in China, *C. tristis* Allard and *C. zangana* Chen & Wang], 6 species from other Palaearctic Chineese provinces [*C. confinis* Crotch from Jiangsu, *C. fortecostata* Chen from Shaanxi, Hubei, Chongqing, Sichuan and Japan, *C. hongkongensis* Ruan et al. from Nanking, *C. shanxiensis* Chen &Wang

from Shaanxi, *C. sticta* Maulik from Gansu and *C. tonkinensis* Chen, 1934 from Jiangsu], and 1 species from Japan [*C. concinnipennis* Baly]. All Palaearctic *Chaetocnema* species determined in this study and their subgenera are given below (Table 23).

The fact that this result (as a total of 99 Palaearctic species) is less than the number of species given in Döberl (2010) that was considered the borders of the Palaearctic region as wide, and is more than the number of species given in Konstantinov et al. (2011) that were considered the borders of the Palaearctic region as narrow, it is quite natural. In our opinion, our results are more acceptable for the Palaearctic region.

Finally, *Chaetocnema rhombea* Weise, 1886 that is a Nearctic species, currently listed among Palaearctic Alticini, was removed from Palaearctic region by Döberl (2010) and following Konstantinov et al. (2011), and therefore in this study.

Consequently, 28 Palaearctic species were found to belong to *Chaetocnema* (s. str.) Stephens, while 1 Palaearctic species belong to *C.* (*Confinoides*) subgen. nov.. Also, 45 Palaearctic species were found to belong to *C.* (*Hortensoides*) subgen. nov., while 3 Palaearctic species belong to *C.* (*Majoroides*) subgen. nov.. In addition, 1 Palaearctic species were found to belong to *C.* (*Nigricoides*) subgen. nov., while 5 Palaearctic species belong to *C.* (*Plectroscelis*) Dejean. Moreover, 6 Palaearctic species were found to belong to *C.* (*Pseudocaetocnema*) subgen. nov., while 10 Palaearctic species belong to *C.* (*Udorpes*) Motschulsky.

Table 23. All Palaearctic *Chaetocnema* species determined in this study and their subgenera.

Palaearctic Species	**Subgenera under the present study**
***Chaetocnema* (s. str.) Stephens, 1831**	
C. batophiloides Abeille, 1909	*Chaetocnema* Stephens, 1831
C. bicolorata Kimoto, 1971	*Chaetocnema* Stephens, 1831
C. bilunulata Demaison, 1902	*Chaetocnema* Stephens, 1831
C. breviuscula (Faldermann, 1837)	*Chaetocnema* Stephens, 1831
C. cheni Ruan, Konstantinov & Yang, 2014	*Chaetocnema* Stephens, 1831
C. concinna (Marsham, 1802)	*Chaetocnema* Stephens, 1831
C. constricta Ruan, Konstantinov & Yang, 2014	*Chaetocnema* Stephens, 1831
C. delarouzeei (Brisout, 1884)	*Chaetocnema* Stephens, 1831
C. depressa (Boieldieu, 1859)	*Chaetocnema* Stephens, 1831
C. duvivieri Jacoby, 1892	*Chaetocnema* Stephens, 1831
C. fortecostata Chen, 1939	*Chaetocnema* Stephens, 1831
C. granulosa (Baly, 1874)	*Chaetocnema* Stephens, 1831
C. heptapotamica Lubischev, 1963	*Chaetocnema* Stephens, 1831
C. kimotoi Gruev, 1980	*Chaetocnema* Stephens, 1831
C. koreana Chûjô, 1942	*Chaetocnema* Stephens, 1831
C. lubischevi Konstantinov et al., 2011	*Chaetocnema* Stephens, 1831
C. melonae Chen, 1934	*Chaetocnema* Stephens, 1831
C. nebulosa Weise, 1886	*Chaetocnema* Stephens, 1831
C. picipes Stephens, 1831	*Chaetocnema* Stephens, 1831
C. puncticollis (Motschulsky, 1858)	*Chaetocnema* Stephens, 1831
C. salixis Ruan, Konstantinov & Yang, 2014	*Chaetocnema* Stephens, 1831
C. scheffleri (Kutschera, 1864)	*Chaetocnema* Stephens, 1831
C. semicoerulea (Koch, 1803)	*Chaetocnema* Stephens, 1831
C. septentrionalis Kimoto, 1963	*Chaetocnema* Stephens, 1831
C. simplicifrons (Baly, 1876)	*Chaetocnema* Stephens, 1831

C. sticta Maulik, 1926	*Chaetocnema* Stephens, 1831
C. tibialis (Illiger, 1807)	*Chaetocnema* Stephens, 1831
C. transbaicalica Heikertinger, 1951	*Chaetocnema* Stephens, 1831
***C.* (*Confinoides*) subgen. nov.**	
C. confinis Crotch, 1873	*Confinoides* subgen. nov.
***C.* (*Hortensoides*) subgen. nov.**	
C. aerosa (Letzner, 1847)	*Hortensoides* subgen. nov.
C. afghana Gruev, 1988	*Hortensoides* subgen. nov.
C. arenacea (Allard, 1860)	*Hortensoides* subgen. nov.
C. arida Foudras, 1860	*Hortensoides* subgen. nov.
C. aridula (Gyllenhal, 1827)	*Hortensoides* subgen. nov.
C. belka Konstantinov et al., 2011	*Hortensoides* subgen. nov.
C. bella (Baly, 1877)	*Hortensoides* subgen. nov.
C. bergeali Konstantinov et al., 2011	*Hortensoides* subgen. nov.
C. bretinghami Baly, 1877	*Hortensoides* subgen. nov.
C. concinnicollis (Baly, 1874)	*Hortensoides* subgen. nov.
C. concinnipennis Baly, 1877	*Hortensoides* subgen. nov.
C. confusa (Boheman, 1851)	*Hortensoides* subgen. nov.
C. costulata (Motschulsky, 1860)	*Hortensoides* subgen. nov.
C. cylindrica (Baly, 1874)	*Hortensoides* subgen. nov.
C. eastafghanica Konstantinov et al., 2011	*Hortensoides* subgen. nov.
C. franzi Konstantinov et al., 2011	*Hortensoides* subgen. nov.
C. ganganensis Bechyné, 1955	*Hortensoides* subgen. nov.
C. gottwaldi Král, 1969	*Hortensoides* subgen. nov.
C. grandis Pic, 1909	*Hortensoides* subgen. nov.
C. hortensis (Geoffroy, 1785)	*Hortensoides* subgen. nov.
C. igori Konstantinov et al., 2011	*Hortensoides* subgen. nov.
C. imitatrix Gruev, 1990	*Hortensoides* subgen. nov.
C. ingenua (Baly, 1877)	*Hortensoides* subgen. nov.
C. jelineki Lopatin, 1990	*Hortensoides* subgen. nov.
C. kabakovi Lopatin, 1995	*Hortensoides* subgen. nov.
C. klapperichi Lopatin, 1963	*Hortensoides* subgen. nov.
C. latipennis Pic, 1911	*Hortensoides* subgen. nov.
C. leonhardi Heikertinger, 1951	*Hortensoides* subgen. nov.
C. mannerheimii (Gyllenhal, 1827)	*Hortensoides* subgen. nov.
C. modesta Gressitt & Kimoto, 1963	*Hortensoides* subgen. nov.
C. montenegrina Heikertinger, 1912	*Hortensoides* subgen. nov.
C. nocticolor Rapilly, 1978	*Hortensoides* subgen. nov.
C. obesa (Boieldieu, 1859)	*Hortensoides* subgen. nov.
C. oblonga Lopatin, 1990	*Hortensoides* subgen. nov.
C. paganettii Heikertinger, 1913	*Hortensoides* subgen. nov.
C. psylloides Pic, 1909	*Hortensoides* subgen. nov.
C. rufofemorata Pic, 1915	*Hortensoides* subgen. nov.
C. sahlbergii (Gyllenhal, 1827)	*Hortensoides* subgen. nov.
C. shabalini Palij, 1968	*Hortensoides* subgen. nov.
C. sinuata Weise, 1889	*Hortensoides* subgen. nov.
C. subcoerulea (Kutschera, 1864)	*Hortensoides* subgen. nov.
C. tarsalis Wollaston, 1860	*Hortensoides* subgen. nov.
C. tbilisiensis Konstantinov et al., 2011	*Hortensoides* subgen. nov.
C. wollastoni Baly, 1877	*Hortensoides* subgen. nov.
C. zangana Chen & Wang, 1981	*Hortensoides* subgen. nov.
***C.* (*Majoroides*) subgen. nov.**	
C. major (Jacquelin du Val, 1852)	*Majoroides* subgen. nov.
C. mandschurica Heikertinger, 1951	*Majoroides* subgen. nov.

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C. schlaeflii (Stierlin, 1866)	*Majoroides* subgen. nov.
***C.* (*Nigricoides*) subgen. nov.**	
C. nigrica Motschulsky, 1853	*Nigricoides* subgen. nov.
***C.* (*Plectroscelis*) Dejean, 1836**	
C. chlorophana (Duftschmid, 1825)	*Plectroscelis* Dejean, 1836
C. coyei (Allard, 1864)	*Plectroscelis* Dejean, 1836
C. kerimi (Fairmaire, 1875)	*Plectroscelis* Dejean, 1836
C. pelagica Caillol, 1924	*Plectroscelis* Dejean, 1836
C. punctifrons (Abeille, 1907)	*Plectroscelis* Dejean, 1836
***C.* (*Pseudochaetocnema*) subgen. nov.**	
C. conducta (Motschulsky, 1838)	*Pseudochaetocnema* subgen. nov.
C. hongkongensis Ruan et al., 2019	*Pseudochaetocnema* subgen. nov.
C. kanmiyai Kimoto, 1974	*Pseudochaetocnema* subgen. nov.
C. orientalis (Bauduér, 1874)	*Pseudochaetocnema* subgen. nov.
C. tonkinensis Chen, 1934	*Pseudochaetocnema* subgen. nov.
C. tristis Allard, 1889	*Pseudochaetocnema* subgen. nov.
***C.* (*Udorpes*) Motschulsky, 1845**	
C. alticola Maulik, 1926	*Udorpes* Motschulsky, 1845
C. angustula (Rosenhauer, 1847)	*Udorpes* Motschulsky, 1845
C. balanomorpha (Boieldieu, 1859)	*Udorpes* Motschulsky, 1845
C. compressa (Letzner, 1847)	*Udorpes* Motschulsky, 1845
C. ljudmilae Lopatin, 1961	*Udorpes* Motschulsky, 1845
C. polita (Abeille, 1907)	*Udorpes* Motschulsky, 1845
C. procerula (Rosenhauer, 1856)	*Udorpes* Motschulsky, 1845
C. shanxiensis Chen &Wang, 1980	*Udorpes* Motschulsky, 1845
C. splendens (Motschulsky, 1845)	*Udorpes* Motschulsky, 1845
C. ussuriensis Heikertinger, 1951	*Udorpes* Motschulsky, 1845

As can be understood from the table given above, 28.28% of 99 Palaearctic *Chaetocnema* species belongs to *Chaetocnema* (s. str.), 1.01% to *C.* (*Confinoides*) subgen. nov., 5.06% to *C.* (*Plectroscelis*), 45.45% to *C.* (*Hortensoides*) subgen. nov., 3.03% to *C.* (*Majoroides*) subgen. nov., 1.01% to *C.* (*Nigricoides*) subgen. nov., 6.06% to *C.* (*Pseudochaetocnema*) subgen. nov. and 10.10% to *C.* (*Udorpes*) (Table 24).

Table 24. All Palaearctic *Chaetocnema* species determined in this study and their percentage values according to subgenera.

Palaearctic subgenera	Percentage values
Chaetocnema (*Chaetocnema*) Stephens, 1831	28.28%
Chaetocnema (*Confinoides*) subgen. nov.	1.01%
Chaetocnema (*Hortensoides*) subgen. nov.	45.45%
Chaetocnema (*Majoroides*) subgen. nov.	3.03%
Chaetocnema (*Nigricoides*) subgen. nov.	1.01%
Chaetocnema (*Plectroscelis*) Dejean, 1836	5.06%
Chaetocnema (*Pseudochaetocnema*) subgen. nov.	6.06%
Chaetocnema (*Udorpes*) Motschulsky, 1845	10.10%

On the other side, Ruan et al. (2019) mentioned a total of 85 species for Oriental region. Among them, 59 Oriental species of which spermathecal structures are known were placed in the subgenera in this study. Also, as given above, 5 species [*C. alticola* Maulik, *C. granulosa* (Baly), *C. melonae* Chen, *C. shanxiensis* Chen &Wang, *C. tonkinensis* Chen], of which spermathecal structures

are unknown, which is also found in the Palaearctic region and mentioned for the Oriental region in Ruan et al. (2019), were placed in possible subgenera based on only their aedeagal structures and external morphological characters.

In addition, evaluation on the remaining 21 Oriental species of which spermathecal structures are unknown were done based on only their aedeagal structures and external morphological characters and they were placed in possible subgenera. In fact, it should not be forgotten that the exact determination of the subgenus to which these species belong is only possible by examining their spermathecal morphology.

Accordingly, 7 species as *C. furthi* Medvedev, *C. laotica* Medvedev, *C. malaisei* Bryant, *C. montivaga* Maulik, *C. nagpurensis* Duvivier, *C. sumatrana* Jacoby and *C. yonyonae* Chen were found to be compatible with the nominative subgenus *Chaetocnema* (s. str.) Stephens and these species can be considered in this subgenus. Also 6 species as *C. cupreata* Chen, *C. latapronota* Ruan et al., *C. paraumesaoi* Ruan et al., *C. singala* Maulik, *C. umesaoi* Chûjô and *C. westwoodi* Baly were found to be compatible with *C.* (*Hortensoides*) subgen. nov. and these species can be considered in this subgenus. 1 species as *C. fallaciosa* Heikertinger was found to be compatible with *C.* (*Nigricoides*) subgen. nov. and it can be accepted that the species may also belong to this subgenus. In addition, 6 species as *C. appendiculata* Ruan et al., *C. babai* Kimoto, *C. longipunctata* Maulik, *C. subbasalis* Ruan et al., *C. taiwanensis* Chûjô and *C. trapezoida* Ruan et al. were found to be compatible with *C.* (*Pseudochaetocnema*) subgen. nov. and these species can be considered in this subgenus. The remaining 1 species as *C. rahlensis* Shukla was found to be compatible with *C.* (*Udorpes*) Motschulsky and also these species can be considered in this subgenus (Table 25).

Showing the applicability of the subgeneric arrangement given in this study to Oriental species of which spermathecal structures are known is noteworthy as it is a proof that the arrangement made is feasible and acceptable. As a result, among the Oriental species mentioned in Ruan et al. (2019), there is no species that does not comply with the subgeneric arrangement given in this study.

Consequently, 24 Oriental species were found to belong to *Chaetocnema* (s. str.) Stephens, while 2 Oriental species belong to *C.* (*Confinoides*) subgen. nov.. Also, 32 Oriental species were found to belong to *C.* (*Hortensoides*) subgen. nov., while 5 Oriental species belong to *C.* (*Nigricoides*) subgen. nov.. In addition, 19 Oriental species were found to belong to *C.* (*Pseudocaetocnema*) subgen. nov., while 3 Oriental species belong to *C.* (*Udorpes*) Motschulsky.

Table 25. All Oriental *Chaetocnema* species mentioned in Ruan et al. (2019) and their subgenera.

Oriental Species	**Subgenera under the present study**
***Chaetocnema* (s. str.) Stephens, 1831**	
C. baoshanica Ruan et al., 2019	*Chaetocnema* Stephens, 1831
C. cheni Ruan et al., 2014	*Chaetocnema* Stephens, 1831
C. constricta Ruan et al., 2014	*Chaetocnema* Stephens, 1831
C. deqinensis Ruan et al., 2014	*Chaetocnema* Stephens, 1831
C. duvivieri Jacoby, 1892	*Chaetocnema* Stephens, 1831
C. fortecostata Chen, 1939	*Chaetocnema* Stephens, 1831
C. furthi Medvedev, 1996	*Chaetocnema* Stephens, 1831
C. granulosa (Baly, 1874)	*Chaetocnema* Stephens, 1831
C. kingpinensis Ruan et al., 2014	*Chaetocnema* Stephens, 1831
C. laotica Medvedev, 2009	*Chaetocnema* Stephens, 1831

C. malaisei Bryant, 1939	*Chaetocnema* Stephens, 1831
C. melonae Chen, 1934	*Chaetocnema* Stephens, 1831
C. montivaga Maulik, 1926	*Chaetocnema* Stephens, 1831
C. nagpurensis Duvivier, 1892	*Chaetocnema* Stephens, 1831
C. puncticollis (Motschulsky, 1858)	*Chaetocnema* Stephens, 1831
C. purerulea Ruan et al., 2019	*Chaetocnema* Stephens, 1831
C. salixis Ruan et al., 2014	*Chaetocnema* Stephens, 1831
C. simplicifrons (Baly, 1876)	*Chaetocnema* Stephens, 1831
C. sticta Maulik, 1926	*Chaetocnema* Stephens, 1831
C. sumatrana Jacoby, 1896	*Chaetocnema* Stephens, 1831
C. wallacei Baly, 1877	*Chaetocnema* Stephens, 1831
C. yonyonae Chen, 1934	*Chaetocnema* Stephens, 1831
C. yulongensis Ruan et al., 2014	*Chaetocnema* Stephens, 1831
C. yunnanica Heikertinger, 1951	*Chaetocnema* Stephens, 1831
***C.* (*Confinoides*) subgen. nov.**	
C. confinis Crotch, 1873	*Confinoides* subgen. nov.
C. dapitanica Ruan et al., 2019	*Confinoides* subgen. nov.
***C.* (*Hortensoides*) subgen. nov.**	
C. afghana Gruev, 1988	*Hortensoides* subgen. nov.
C. angustifrons Ruan et al., 2019	*Hortensoides* subgen. nov.
C. bella (Baly, 1877)	*Hortensoides* subgen. nov.
C. belli Jacoby, 1904	*Hortensoides* subgen. nov.
C. bretinghami Baly, 1877	*Hortensoides* subgen. nov.
C. cognata Baly, 1877	*Hortensoides* subgen. nov.
C. concinnicollis (Baly, 1874)	*Hortensoides* subgen. nov.
C. concinnipennis Baly, 1877	*Hortensoides* subgen. nov.
C. cupreata Chen, 1934	*Hortensoides* subgen. nov.
C. cylindrica (Baly, 1874)	*Hortensoides* subgen. nov.
C. eastafghanica Konstantinov et al., 2011	*Hortensoides* subgen. nov.
C. fusiformis Chen & Wang, 1980	*Hortensoides* subgen. nov.
C. glabra Ruan et al., 2019	*Hortensoides* subgen. nov.
C. greenica Ruan et al., 2019	*Hortensoides* subgen. nov.
C. ingenua (Baly, 1877)	*Hortensoides* subgen. nov.
C. kumaonensis Scherer, 1969	*Hortensoides* subgen. nov.
C. latapronota Ruan et al., 2019	*Hortensoides* subgen. nov.
C. malayana Baly, 1877	*Hortensoides* subgen. nov.
C. merguiensis Bryant, 1941	*Hortensoides* subgen. nov.
C. midimpunctata Ruan et al., 2019	*Hortensoides* subgen. nov.
C. modesta Gressitt & Kimoto, 1963	*Hortensoides* subgen. nov.
C. modiglianii Jacoby, 1896	*Hortensoides* subgen. nov.
C. paragreenica Ruan et al., 2019	*Hortensoides* subgen. nov.
C. paraumesaoi Ruan et al., 2019	*Hortensoides* subgen. nov.
C. psylloides Pic, 1909	*Hortensoides* subgen. nov.
C. pusaensis Maulik, 1926	*Hortensoides* subgen. nov.
C. reteimpunctata Ruan et al., 2019	*Hortensoides* subgen. nov.
C. singala Maulik, 1926	*Hortensoides* subgen. nov.
C. sulcicollis Chen & Wang, 1980	*Hortensoides* subgen. nov.
C. umesaoi Chûjô, 1961	*Hortensoides* subgen. nov.
C. westwoodi Baly, 1877	*Hortensoides* subgen. nov.
C. zangana Chen & Wang, 1981	*Hortensoides* subgen. nov.
***C.* (*Nigricoides*) subgen. nov.**	
C. fallaciosa Heikertinger, 1951	*Nigricoides* subgen. nov.
C. nigrica Motschulsky, 1858	*Nigricoides* subgen. nov.
C. resplendens Warchalowski, 1973	*Nigricoides* subgen. nov.

C. warchalowskii Döberl, 2009	*Nigricoides* subgen. nov.
C. yaosanica Chen, 1939	*Nigricoides* subgen. nov.
***C.* (*Pseudochaetocnema*) subgen. nov.**	
C. appendiculata Ruan et al., 2019	*Pseudochaetocnema* subgen. nov.
C. babai Kimoto, 1991	*Pseudochaetocnema* subgen. nov.
C. excavata Medvedev, 1997	*Pseudochaetocnema* subgen. nov.
C. gracilis Motschulsky, 1858	*Pseudochaetocnema* subgen. nov.
C. granulicollis Jacoby, 1896	*Pseudochaetocnema* subgen. nov.
C. hainanensis Chen, 1933	*Pseudochaetocnema* subgen. nov.
C. hongkongensis Ruan et al., 2019	*Pseudochaetocnema* subgen. nov.
C. jinxiuensis Ruan et al., 2019	*Pseudochaetocnema* subgen. nov.
C. longipunctata Maulik, 1926	*Pseudochaetocnema* subgen. nov.
C. nigrilata Ruan et al., 2019	*Pseudochaetocnema* subgen. nov.
C. parafusiformis Ruan et al., 2019	*Pseudochaetocnema* subgen. nov.
C. philippina Medvedev, 1996	*Pseudochaetocnema* subgen. nov.
C. sabahensis Ruan et al., 2019	*Pseudochaetocnema* subgen. nov.
C. subbasalis Ruan et al., 2019	*Pseudochaetocnema* subgen. nov.
C. taiwanensis Chûjô, 1965	*Pseudochaetocnema* subgen. nov.
C. tonkinensis Chen, 1934	*Pseudochaetocnema* subgen. nov.
C. trapezoida Ruan et al., 2019	*Pseudochaetocnema* subgen. nov.
C. tristis Allard, 1889	*Pseudochaetocnema* subgen. nov.
C. yiei Kimoto, 1970	*Pseudochaetocnema* subgen. nov.
***C.* (*Udorpes*) Motschulsky, 1845**	
C. alticola Maulik, 1926	*Udorpes* Motschulsky, 1845
C. rahlensis Shukla, 1960	*Udorpes* Motschulsky, 1845
C. shanxiensis Chen &Wang, 1980	*Udorpes* Motschulsky, 1845

As can be understood from the table given above, 28.24% of 85 Oriental *Chaetocnema* species belongs to *Chaetocnema* (s. str.), 2.35% to *C.* (*Confinoides*) subgen. nov., 37.65% to *C.* (*Hortensoides*) subgen. nov., 5.88% to *C.* (*Nigricoides*) subgen. nov., 22.35% to *C.* (*Pseudochaetocnema*) subgen. nov. and 3.53% to *C.* (*Udorpes*) Motschulsky (Table 26).

Table 26. All Oriental *Chaetocnema* species determined in this study and their percentage values according to subgenera.

Oriental subgenera	Percentage values
Chaetocnema (*Chaetocnema*) Stephens, 1831	28.24%
Chaetocnema (*Confinoides*) subgen. nov.	2.35%
Chaetocnema (*Hortensoides*) subgen. nov.	37.65%
Chaetocnema (*Nigricoides*) subgen. nov.	5.88%
Chaetocnema (*Pseudochaetocnema*) subgen. nov.	22.35%
Chaetocnema (*Udorpes*) Motschulsky, 1845	3.53%

In addition to this, we believe that it would be appropriate to make evaluations on Afrotropical and Madagascan species with known spermatecal structures. The data required for this purpose are obtained from the previous works of Biondi & Nardis (2000), Biondi (2000, 2001, 2002a,b), Biondi & D'Alessandro (2005, 2006, 2018). Accordingly, a total of 40 Afrotropical and 20 Madagascan species from references were determined.

Biondi (2002a) included a total of 154 species for Afrotropical region with Madagascan species. However, he stated 41 names are synonyms and 2 names are homonyms. Also, according to Biondi (2002b), 4 species are in the separate genus

Munis Entomology & Zoology
https://www.munisentzool.org/
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Mun. Ent. Zool.
(January, 2021)

Carcharodis Weise, 1910 that was considered by some authors as a synonym of *Chaetocnema*. In addition, 11 species are known only from Madagascar and Comoro Islands. Thus, the number given for Afrotropical *Chaetocnema* species without Madagascan species in Biondi (2002a) is actually 96 in total.

On the other side, the total number of only Afrotropical *Chaetocnema* species is reached 104 with 8 newly described species as *C. lopatini* Biondi & D'Alessandro, 2005; *C. capeneri* Biondi & D'Alessandro, 2006; *C. danielssoni* Biondi & D'Alessandro, 2006; *C. sudafricana* Biondi & D'Alessandro, 2006; *C. tuckeri* Biondi & D'Alessandro, 2006; *C. vanschuytbroecki* Biondi & D'Alessandro, 2008; *C. adamastori* Biondi & D'Alessandro, 2018 and *C. saldanhai* Biondi & D'Alessandro, 2018.

Therefore, a total of 40 Afrotropical species that are about 39% of all known species and a total of 20 Madagascan species that are all known species were evaluated according to the subgeneric arrangement given in this study and were placed into subgenera are presented as follows (Tables 27, 29). Just like the Oriental species, showing the applicability of the subgeneric arrangement given in this study to Afrotropical and Madagascan species of which spermathecal structures are known is also noteworthy as it is another proof that the arrangement made is feasible and acceptable.

As a result, on the contrary the Oriental species, the subgenera identified in this study were not sufficient for all Afrotropical species and required also the description of four new subgenera are presented in the part of results.

Consequently, 2 Afrotropical species were found to belong to *C.* (*Biondiana*) subgen. nov., while 6 Afrotropical species belong to *Chaetocnema* (s. str.) Stephens. Also, 3 Afrotropical species were found to belong to *C.* (*Confinoides*) subgen. nov., while 1 Afrotropical species belong to *C.* (*Dalessandroiana*) subgen. nov. and 9 Afrotropical species belong to *C.* (*Gahanioides*) subgen. nov.. In addition, 4 Afrotropical species were found to belong to *C.* (*Hortensoides*) subgen. nov., while 3 Afrotropical species belong to *C.* (*Longicornoides*) subgen. nov.. Moreover, 4 Afrotropical species were found to belong to *C.* (*Nigricoides*) subgen. nov., while 5 Afrotropical species belong to *C.* (*Pseudocaetocnema*) subgen. nov..

Spermathecal structures of these 37 Afrotropical species are known. In addition, *C. mariobiondii* Biondi & Nardis, 2000 and *C. phuhthaditjhabensis* Biondi & Nardis, 2000 of which spermathecal structures are unknown were placed in possible subgenus *C.* (*Biondiana*) subgen. nov. and *C.* (*Longicornoides*) subgen. nov. respectively. *C. purpurea* Jacoby, 1906 of which spermathecal structure is unknown too was placed in possible subgenus *Chaetocnema* (s. str.) Stephens based on only their external morphological characters. Therefore, a total of 40 Afrotropical species were placed in the subgenera.

Table 27. The subgenera of 40 Afrotropical species of which spermathecal structures are known.

Afrotropical Species	**Subgenera under the present study**
***C.* (*Biondiana*) subgen. nov.**	
C. mariobiondii Biondi & Nardis, 2000	*Biondiana* subgen. nov.
C. mapumalangaensis Biondi & Nardis, 2000	*Biondiana* subgen. nov.
C. zulu Biondi & Nardis, 2000	*Biondiana* subgen. nov.
***Chaetocnema* (s. str.) Stephens, 1831**	
C. bilunulata Demaison, 1902	*Chaetocnema* Stephens, 1831
C. convexicollis (Boheman, 1859)	*Chaetocnema* Stephens, 1831

C. gregaria Weise, 1910	*Chaetocnema* Stephens, 1831
C. picipes Stephens, 1831	*Chaetocnema* Stephens, 1831
C. purpurea Jacoby, 1906	
C. rutovuensis Bechyné, 1955	*Chaetocnema* Stephens, 1831
C. tibialis (Illiger, 1807)	*Chaetocnema* Stephens, 1831
***C.* (*Confinoides*) subgen. nov.**	
C. cinctipennis Laboissière, 1941	*Confinoides* subgen. nov.
C. confinis Crotch, 1873	*Confinoides* subgen. nov.
C. fuscipennis Scherer, 1962	*Confinoides* subgen. nov.
***C.* (*Dalessandroiana*) subgen. nov.**	
C. audisiana Biondi, 2000	*Dalessandroiana* subgen. nov.
***C.* (*Gahanioides*) subgen. nov.**	
C. adamastori Biondi & D'Alessandro, 2018	*Gahanioides* subgen. nov.
C. brincki (Bechyne 1959)	*Gahanioides* subgen. nov.
C. capeneri Biondi & D'Alessandro, 2006	*Gahanioides* subgen. nov.
C. capensis Bryant, 1928	*Gahanioides* subgen. nov.
C. danielssoni Biondi & D'Alessandro, 2006	*Gahanioides* subgen. nov.
C. gahani Jacoby 1897	*Gahanioides* subgen. nov.
C. saldanhai Biondi & D'Alessandro, 2018	*Gahanioides* subgen. nov.
C. sudafricana Biondi & D'Alessandro, 2006	*Gahanioides* subgen. nov.
C. tuckeri Biondi & D'Alessandro, 2006	*Gahanioides* subgen. nov.
***C.* (*Hortensoides*) subgen. nov.**	
C. bamakoensis Bechyné, 1955	*Hortensoides* subgen. nov.
C. ganganensis Bechyné, 1955	*Hortensoides* subgen. nov.
C. hortensis (Geoffroy, 1785)	*Hortensoides* subgen. nov.
C. wollastoni Baly, 1877	*Hortensoides* subgen. nov.
***C.* (*Longicornoides*) subgen. nov.**	
C. kapirensis Biondi & Nardis, 2000	*Longiconoides* subgen. nov.
C. longicornis Jacoby, 1895	*Longiconoides* subgen. nov.
C. phuhthaditjhabensis Biondi & Nardis, 2000	*Longiconoides* subgen. nov.
C. reprehensa Bechyné, 1960	*Longiconoides* subgen. nov.
***C.* (*Nigricoides*) subgen. nov.**	
C. nigrica (Motschulsky, 1858)	*Nigricoides* subgen. nov.
C. pulla Chapuis, 1879	*Nigricoides* subgen. nov.
C. subquadrata Jacoby, 1897	*Nigricoides* subgen. nov.
C. vanschuytbroecki Biondi & D'Alessandro, 2008	*Nigricoides* subgen. nov.
***C.* (*Pseudochaetocnema*) subgen. nov.**	
C. conducta (Motschulsky, 1838)	*Pseudocaetocnema* subgen. nov.
C. lopatini Biondi & D'Alessandro, 2005	*Pseudocaetocnema* subgen. nov.
C. nkolentangana Bechyné, 1959	*Pseudocaetocnema* subgen. nov.
C. orientalis (Bauduér, 1874)	*Pseudocaetocnema* subgen. nov.
C. suturalis Bryant, 1948	*Pseudocaetocnema* subgen. nov.

As can be understood from the table given above, 7.50% of 40 Afrotropical *Chaetocnema* species belong to *C.* (*Biondiana*) subgen. nov., 17.50% to *Chaetocnema* (s. str.), 7.50% to *C.* (*Confinoides*) subgen. nov., 2.50% to *C.* (*Dalessandroiana*) subgen. nov., 22.50% to *C.* (*Gahanioides*) subgen. nov., 10.00% to *C.* (*Hortensoides*) subgen. nov., 10.00% to *C.* (*Longicornoides*) subgen. nov., 10.00% to *C.* (*Nigricoides*) subgen. nov. and 12.50% to *C.* (*Pseudochaetocnema*) subgen. nov. (Table 28).

Munis Entomology & Zoology
https://www.munisentzool.org/
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Mun. Ent. Zool.
(January, 2021)

Table 28. 40 Afrotropical *Chaetocnema* species determined in this study and their percentage values according to subgenera.

Afrotropical subgenera	Percentage values
Chaetocnema (*Biondiana*) subgen. nov.	7.50%
Chaetocnema (*Chaetocnema*) Stephens, 1831	17.50%
Chaetocnema (*Confinoides*) subgen. nov.	7.50%
Chaetocnema (*Dalessandroiana*) subgen. nov.	2.50%
Chaetocnema (*Gahanioides*) subgen. nov.	22.50%
Chaetocnema (*Hortensoides*) subgen. nov.	10.00%
Chaetocnema (*Longicornoides*) subgen. nov.	10.00%
Chaetocnema (*Nigricoides*) subgen. nov.	10.00%
Chaetocnema (*Pseudochaetocnema*) subgen. nov.	12.50%

Also, 8 Madagascan species were found to belong to *Chaetocnema* (s. str.) Stephens, while 3 Madagascan species belong to *C.* (*Confinoides*) subgen. nov. and 6 Madagascan species belong to *C.* (*Hortensoides*) subgen. nov.. In addition, 1 Madagascan species were found to belong to *C.* (*Nigricoides*) subgen. nov., while also 1 Madagascan species belong to *C.* (*Pseudocaetocnema*) subgen. nov..

Spermathecal structures of these 19 Madagascan species are known. In addition, *Chaetocnema hygrophila* Biondi, 2001 of which spermathecal structures is unknown and mentioned for Madagascan region in Biondi (2001), was placed in possible subgenus *C.* (*Hortensoides*) subgen. nov. based on only their aedeagal structure and external morphological characters.

Accordingly, 9 species among 20 Madagascan species are endemic to Madagascar Island, while 2 species are endemic to Madagascar and Comoro Islands. The remaining 9 species are known also from Afrotropical region.

Table 29. All Madagascan *Chaetocnema* species and their subgenera.

Madagascan Species	Subgenera under the present study
***Chaetocnema* (s. str.) Stephens, 1831**	
C. bilunulata Demaison, 1902	*Chaetocnema* Stephens, 1831
C. cachani Biondi, 2001	*Chaetocnema* Stephens, 1831
C. gregaria Weise, 1910	*Chaetocnema* Stephens, 1831
C. madagascariensis Baly, 1877	*Chaetocnema* Stephens, 1831
C. malgascia Biondi, 2001	*Chaetocnema* Stephens, 1831
C. orophila Biondi, 2001	*Chaetocnema* Stephens, 1831
C. picipes Stephens, 1831	*Chaetocnema* Stephens, 1831
C. vadoni Bechyné, 1948	*Chaetocnema* Stephens, 1831
C. (*Confinoides*) subgen. nov.	
C. confinis Crotch, 1873	*Confinoides* subgen. nov.
C. coronilla Bechyné, 1964	*Confinoides* subgen. nov.
C. fuscipennis Scherer, 1962	*Confinoides* subgen. nov.
C. (*Hortensoides*) subgen. nov.	
C. bamakoensis Bechyné, 1955	*Hortensoides* subgen. nov.
C. basipunctata Bechyné, 1964	*Hortensoides* subgen. nov.
C. consobrina Weise, 1910	*Hortensoides* subgen. nov.
C. ganganensis Bechyné, 1955	*Hortensoides* subgen. nov.
C. hygrophila Biondi, 2001	*Hortensoides* subgen. nov.
C. pauliani Bechyné, 1964	*Hortensoides* subgen. nov.
C. wollastoni Baly, 1877	*Hortensoides* subgen. nov.

***C.* (*Nigricoides*) subgen. nov.**	
C. pulla Chapuis, 1879	*Nigricoides* subgen. nov.
***C.* (*Pseudochaetocnema*) subgen. nov.**	
C. similis Weise, 1910	*Pseudocaetocnema* subgen. nov.

As can be understood from the table given above, 40.00% of 20 Madagascan *Chaetocnema* species belong to *Chaetocnema* (s. str.), 15.00% to *C.* (*Confinoides*) subgen. nov., 35.00% to *C.* (*Hortensoides*) subgen. nov., 5.00% to *C.* (*Nigricoides*) subgen. nov. and 5.00% to *C.* (*Pseudochaetocnema*) subgen. nov. (Table 30).

Table 30. All Madagascan *Chaetocnema* species and their percentage values according to subgenera.

Madagascan subgenera	Percentage values
Chaetocnema (*Chaetocnema*) Stephens, 1831	40.00%
Chaetocnema (*Confinoides*) subgen. nov.	15.00%
Chaetocnema (*Hortensoides*) subgen. nov.	35.00%
Chaetocnema (*Nigricoides*) subgen. nov.	5.00%
Chaetocnema (*Pseudochaetocnema*) subgen. nov.	5.00%

In addition, we believe that it would be appropriate to make evaluations also on Nearctic species of which spermathecal structures are unknown on the basis of only their aedeagal structures and external morphological characters in the revision of White (1996). It will be useful for generating an idea about the possible subgenera of Nearctic species. I would like to remind you again that in fact, it should not be forgotten that the exact determination of the subgenus to which these species belong is only possible by examining their spermathecal morphology.

Gentner (1953) revised the North American species for his doctoral dissertation. His thesis included 36 species with 5 new. Unfortunately, he never published his revision. The whole North American fauna was revised by White (1996) which included a total of 59 *Chaetocnema* species for Nearctic region. In addition to this, recently also *C. hortensis* (Geoffroy, 1785) was discovered by Pentinsaari et al. (2019) in Nearctic region. Among them, spermathecal structures of only three species as *C. concinna* (Marsham, 1802), *C. confinis* Crotch, 1873 and *C. hortensis* (Geoffroy, 1785) are known.

Accordingly, the remaining 57 Nearctic *Chaetocnema species* were evaluated and they were placed in possible subgenera: except for the type species *C. concinna* (Marsham), 21 species as *C. aenigmatica* White, *C. alutacea* Crotch, *C. arizonica* White, *C. bicolor* Gentner, *C. blatchleyi* Csiki, *C. crenulata* Crotch, *C. densa* White, *C. dispar* Horn, *C. ectypa* Horn, *C. elongatula* Crotch, *C. extenuata* White, *C. fulvida* White, *C. gentneri* Cziki, *C. labiosa* White, *C. livida* White, *C. magnipunctata* Gentner, *C. obliterata* White, *C. opulenta* Horn, *C. rileyi* White, *C. subconvexa* White and *C. vesca* White were found to be compatible with the nominative subgenus *Chaetocnema* (s. str.) Stephens and these species can be considered in this subgenus. Also, except for the type species *C. confinis* Crotch, 2 species as *C. repens* McCrea and *C. serpentina* White were found to be compatible with *C.* (*Confinoides*) subgen. nov. and these species can be considered in this subgenus. In addition, except for the type species *C. hortensis* (Geoffroy), 26 species as *C. acuminata* White, *C. acupunctata* White, *C. aequabilis* White, *C.*

Munis Entomology & Zoology
https://www.munisentzool.org/
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Mun. Ent. Zool.
(January, 2021)

albiventris White, *C. borealis* White, *C. californica* White, *C. coacta* White, *C. costata* Fall, *C. cribrata* LeConte, *C. cribrifrons* LeConte, *C. denticulata* (Illiger), *C. difficilis* White, *C. floridana* Blatchley, *C. fuscata* White, *C. irregularis* LeConte, *C. megachora* White, *C. megasticta* White, *C. minitrunctata* White, *C. ordinata* White, *C. perturbata* Horn, *C. pinguis* LeConte, *C. producta* White, *C. prolata* White, *C. protensa* LeConte, *C. texana* Crotch and *C. truncata* White were found to be compatible with *C.* (*Hortensoides*) subgen. nov. and these species can be considered in this subgenus. Moreover, 8 species as *C. anisota* White, *C. brunnescens* Horn, *C. minuta* Melsheimer, *C. obesula* LeConte, *C. opacula* LeConte, *C. pulicaria* Melsheimer, *C. quadricollis* Schwarz and *C. subviridis* LeConte were found to be compatible with *C.* (*Pseudochaetocnema*) subgen. nov. and these species can be considered in this subgenus (Table 31).

Table 31. All Nearctic *Chaetocnema* species mentioned in White (1996) and their subgenera.

Nearctic Species	Possible subgenera
***Chaetocnema* (s. str.) Stephens, 1831**	
C. aenigmatica White, 1996	*Chaetocnema* Stephens, 1831
C. alutacea Crotch, 1873	*Chaetocnema* Stephens, 1831
C. arizonica White, 1996	*Chaetocnema* Stephens, 1831
C. bicolor Gentner, 1928	*Chaetocnema* Stephens, 1831
C. blatchleyi Csiki, 1940	*Chaetocnema* Stephens, 1831
C. concinna (Marsham, 1802)	*Chaetocnema* Stephens, 1831
C. crenulata Crotch, 1873	*Chaetocnema* Stephens, 1831
C. densa White, 1996	*Chaetocnema* Stephens, 1831
C. dispar Horn, 1889	*Chaetocnema* Stephens, 1831
C. ectypa Horn, 1889	*Chaetocnema* Stephens, 1831
C. elongatula Crotch, 1873	*Chaetocnema* Stephens, 1831
C. extenuata White, 1996	*Chaetocnema* Stephens, 1831
C. fulvida White, 1996	*Chaetocnema* Stephens, 1831
C. gentneri Cziki, 1940	*Chaetocnema* Stephens, 1831
C. labiosa White, 1996	*Chaetocnema* Stephens, 1831
C. livida White, 1996	*Chaetocnema* Stephens, 1831
C. magnipunctata Gentner, 1928	*Chaetocnema* Stephens, 1831
C. obliterata White, 1996	*Chaetocnema* Stephens, 1831
C. opulenta Horn, 1889	*Chaetocnema* Stephens, 1831
C. rileyi White, 1996	*Chaetocnema* Stephens, 1831
C. subconvexa White, 1996	*Chaetocnema* Stephens, 1831
C. vesca White, 1996	*Chaetocnema* Stephens, 1831
***C.* (*Confinoides*) subgen. nov.**	
C. confinis Crotch, 1873	*Confinoides* subgen. nov.
C. repens McCrea, 1973	*Confinoides* subgen. nov.
C. serpentina White, 1996	*Confinoides* subgen. nov.
C. (*Hortensoides*) subgen. nov.	
C. acuminata White, 1996	*Hortensoides* subgen. nov.
C. acupunctata White, 1996	*Hortensoides* subgen. nov.
C. aequabilis White, 1996	*Hortensoides* subgen. nov.
C. albiventris White, 1996	*Hortensoides* subgen. nov.
C. borealis White, 1996	*Hortensoides* subgen. nov.
C. californica White, 1996	*Hortensoides* subgen. nov.
C. coacta White, 1996	*Hortensoides* subgen. nov.
C. costata Fall, 1907	*Hortensoides* subgen. nov.
C. cribrata LeConte, 1878	*Hortensoides* subgen. nov.
C. cribrifrons LeConte, 1879	*Hortensoides* subgen. nov.

C. denticulata (Illiger, 1807)	*Hortensoides* subgen. nov.
C. difficilis White, 1996	*Hortensoides* subgen. nov.
C. floridana Blatchley, 1923	*Hortensoides* subgen. nov.
C. fuscata White, 1996	*Hortensoides* subgen. nov.
C. irregularis LeConte, 1857	*Hortensoides* subgen. nov.
C. hortensis (Geoffroy, 1785)	*Hortensoides* subgen. nov.
C. megachora White, 1996	*Hortensoides* subgen. nov.
C. megasticta White, 1996	*Hortensoides* subgen. nov.
C. minitrunctata White, 1996	*Hortensoides* subgen. nov.
C. ordinata White, 1996	*Hortensoides* subgen. nov.
C. perturbata Horn, 1889	*Hortensoides* subgen. nov.
C. pinguis LeConte, 1878	*Hortensoides* subgen. nov.
C. producta White, 1996	*Hortensoides* subgen. nov.
C. prolata White, 1996	*Hortensoides* subgen. nov.
C. protensa LeConte, 1878	*Hortensoides* subgen. nov.
C. texana Crotch, 1873	*Hortensoides* subgen. nov.
C. truncata White, 1996	*Hortensoides* subgen. nov.
***C.* (*Pseudochaetocnema*) subgen. nov.**	
C. anisota White, 1996	*Pseudocaetocnema* subgen. nov.
C. brunnescens Horn, 1889	*Pseudocaetocnema* subgen. nov.
C. minuta Melsheimer, 1847	*Pseudocaetocnema* subgen. nov.
C. obesula LeConte, 1878	*Pseudocaetocnema* subgen. nov.
C. opacula LeConte, 1878	*Pseudocaetocnema* subgen. nov.
C. pulicaria Melsheimer, 1847	*Pseudocaetocnema* subgen. nov.
C. quadricollis Schwarz, 1878	*Pseudocaetocnema* subgen. nov.
C. subviridis LeConte, 1859	*Pseudocaetocnema* subgen. nov.

As can be understood from the table given above, 36.67% of 60 Nearctic *Chaetocnema* species belong to *Chaetocnema* (s. str.), 5.00% to *C.* (*Confinoides*) subgen. nov., 45.00% to *C.* (*Hortensoides*) subgen. nov. and 13.33% to *C.* (*Pseudochaetocnema*) subgen. nov. (Table 32).

Table 32. All Nearctic *Chaetocnema* species and their percentage values according to subgenera.

Nearctic subgenera	Percentage values
Chaetocnema (*Chaetocnema*) Stephens, 1831	36.67%
Chaetocnema (*Confinoides*) subgen. nov.	5.00%
Chaetocnema (*Hortensoides*) subgen. nov.	45.00%
Chaetocnema (*Pseudochaetocnema*) subgen. nov.	13.33%

Although there is no precise data on fauna of Australian region, a total of 29 species have been determined for the region. Unfortunately, spermathecal structures of most species have not been studied up to now. Finally, we believe that it would be appropriate to make evaluations also at least on some Australian species of which spermathecal structures have been studied. The data required for this purpose are obtained from the previous works of Samuelson (1967, 1973). Accordingly, a total of 8 Australian species that are about 28% of all known species, from references were determined. The species, therefore, evaluated according to the subgeneric arrangement given in this study and were placed into subgenera are presented as follows (Table 33).

As a result, on the contrary the Oriental, Madagascan and Nearctic species, the subgenera identified in this study were not sufficient for the Australian species

Munis Entomology & Zoology
https://www.munisentzool.org/
ISSN 1306-3022
Mun. Ent. Zool.
(January, 2021)

and required also the description of a new subgenus is presented in the part of results.

Consequently, 1 Australian species was found to belong to *Chaetocnema* (s. str.) Stephens, while 2 Australian species belong to *C.* (*Confinoides*) subgen. nov.. Also, 2 Australian species were found to belong to *C.* (*Hortensoides*) subgen. nov., while 1 Australian species belong to *C.* (*Nigricoides*) subgen. nov.. In addition, 2 Australian species were found to belong to *C.* (*Nitidoides*) subgen. nov..

Table 33. The subgenera of 8 Australian species of which spermathecal structures are known.

Australian Species	Subgenera
***Chaetocnema* (s. str.) Stephens, 1831**	
C. littoralis (Broun, 1893)	*Chaetocnema* Stephens, 1831
***C.* (*Confinoides*) subgen. nov.**	
C. allardi Perroud, 1864	*Confinoides* subgen. nov.
C. arsipodoides Samuelson, 1973	*Confinoides* subgen. nov.
***C.* (*Hortensoides*) subgen. nov.**	
C. nesophila Samuelson, 1967	*Hortensoides* subgen. nov.
C. paspalae (Broun, 1923)	*Hortensoides* subgen. nov.
***C.* (*Nigricoides*) subgen. nov.**	
C. nigrica Motschulsky, 1858	*Nigricoides* subgen. nov.
***C.* (*Nitidoides*) subgen. nov.**	
C. moriori Samuelson, 1973	*Nitidoides* subgen. nov.
C. nitida (Broun, 1880)	*Nitidoides* subgen. nov.

On the other side, the remaining 21 Australian species of which spermathecal structures are unknown may be evaluated only based on their original descriptions. However, since the evaluations to be made without knowing the spermatecal structures of species (similarly for Neotropical species) are open to errors, therefore we avoid taking them into consideration and leave their exact evaluations to future studies since the data in their original descriptions are not sufficient for this purpose.

Anyway, to give you an idea on the fauna of Australian region only, possible subgenera for 19 of 21 Australian species mentioned above according to their original descriptions are presented herein (Table 34). Two species *C. frontosa* Csiki, 1940 and *C. thoracica* (Weise, 1923) are excluded.

Table 34. The possible subgenera of 19 Australian species of which spermathecal structures are unknown.

Australian Species	Possible subgenera
***Chaetocnema* (s. str.) Stephens, 1831**	
C. aenea (Waterhouse, 1838)	*Chaetocnema* Stephens, 1831
C. aeneonigra (Waterhouse, 1838)	*Chaetocnema* Stephens, 1831
C. albertisi Jacoby, 1885	*Chaetocnema* Stephens, 1831
C. graminicola (Broun, 1893)	*Chaetocnema* Stephens, 1831
C. olliffi (Blackburn, 1891)	*Chaetocnema* Stephens, 1831
C. propinqua Baly, 1877	*Chaetocnema* Stephens, 1831
C. wilsoni Baly, 1877	*Chaetocnema* Stephens, 1831
***C.* (*Hortensoides*) subgen. nov.**	
C. aciculata (Blackburn, 1896)	*Hortensoides* subgen. nov.
C. australica (Baly, 1876)	*Hortensoides* subgen. nov.
C. brevicornis Baly, 1877	*Hortensoides* subgen. nov.
C. calida (Blackburn, 1896)	*Hortensoides* subgen. nov.

C. crebra (Blackburn, 1896)	*Hortensoides* subgen. nov.
C. eyrensis (Blackburn, 1896)	*Hortensoides* subgen. nov.
C. impressipennis (Blackburn, 1896)	*Hortensoides* subgen. nov.
C. noxia (Blackburn, 1896)	*Hortensoides* subgen. nov.
C. minutalis (Blackburn, 1896)	*Hortensoides* subgen. nov.
C. subaenea (Waterhouse, 1838)	*Hortensoides* subgen. nov.
C. varipes (Blackburn, 1896)	*Hortensoides* subgen. nov.
C. (Pseudochaetocnema) subgen. nov.	
C. aotearoa Samuelson, 1973	*Pseudocaetocnema* subgen. nov.

As seen above, the genus *Chaetocnema* Stephens is represented with 6 subgenera in Australian region. Despite a small number of species in the region, the high number of subgenera is striking.

As can be understood from the tables given above, 29.63% of 27 Australian *Chaetocnema* species belong to *Chaetocnema* (s. str.), 7.41% to *C.* (*Confinoides*) subgen. nov., 48.15% to *C.* (*Hortensoides*) subgen. nov., 3.70% to *C.* (*Nigricoides*) subgen. nov., 7.41% to *C.* (*Nitidoides*) subgen. nov. and 3.70% to *C.* (*Pseudochaetocnema*) subgen. nov. (Table 35).

Table 35. 27 Australian *Chaetocnema* species and their percentage values according to subgenera.

Australian subgenera	Percentage values
Chaetocnema (*Chaetocnema*) Stephens, 1831	29.63%
Chaetocnema (*Confinoides*) subgen. nov.	7.41%
Chaetocnema (*Hortensoides*) subgen. nov.	48.15%
Chaetocnema (*Nigricoides*) subgen. nov.	3.70%
Chaetocnema (*Nitidoides*) subgen. nov.	7.41%
Chaetocnema (*Pseudochaetocnema*) subgen. nov.	3.70%

With this study, all known *Chaetocnema* species in Palaearctic, Oriental, Madagascan and Nearctic regions, about 39% of all known *Chaetocnema* species in Afrotropical region and about 28% of all known *Chaetocnema* species in Australian region were evaluated. According to the results of present study, the genus *Chaetocnema* Stephens is represented with 9 subgenera in Afrotropical region, while with 8 subgenera in Palaearctic region, 6 subgenera in Oriental and Australian regions, 5 subgenera in Madagascan region and 4 subgenera in Nearctic region. The 4 subgenera as *C.* (s. str.) Stephens, *C.* (*Confinoides*) subgen. nov., *C.* (*Hortensoides*) subgen. nov. and *C.* (*Pseudochaetocnema*) subgen. nov. are represented in all regions evaluated in this study. 2 subgenera as *C.* (*Majoroides*) subgen. nov. and *C.* (*Plectroscelis*) Dejean occur only in Palaearctic region, while 4 subgenera as *C.* (*Biondiana*) subgen. nov., *C.* (*Dalessandroiana*) subgen. nov., *C.* (*Gahanioides*) subgen. nov. and *C.* (*Longiconoides*) subgen. nov. present only in Afrotropical region and 1 subgenus *C.* (*Nitidoides*) subgen. nov. occurs only in Australian region (Table 36). Only Neotropical species are excluded in the present study and not evaluated at all.

Munis Entomology & Zoology
https://www.munisentzool.org/
ISSN 1306-3022
Mun. Ent. Zool.
(January, 2021)

Table 36. The subgenera determined of *Chaetocnema* in this study and their representing regions.

Subgenera	Pal. Reg.	Ori. Reg.	Afr. Reg.	Mad. Reg.	Nea. Reg.	Aus. Reg.
Biondiana	-	-	+	-	-	-
Chaetocnema	+	+	+	+	+	+
Confinoides	+	+	+	+	+	+
Dalessandroiana	-	-	+	-	-	-
Gahanioides	-	-	+	-	-	-
Hortensoides	+	+	+	+	+	+
Longicornoides	-	-	+	-	-	-
Majoroides	+	-	-	-	-	-
Nigricoides	+	+	+	+	-	+
Nitidoides	-	-	-	-	-	+
Plectroscelis	+	-	-	-	-	-
Pseudochaetocnema	+	+	+	+	+	?+
Udorpes	+	+	-	-	-	-

According to *Chaetocnema* species evaluated in this study and their percentage values to subgenera, the dominant subgenus is *C.* (*Hortensoides*) subgen. nov. with 45.45%, 37.65%, 45.00% and 48.15% in the Palaearctic, Oriental, Nearctic and Australian regions and *Chaetocnema* (s. str.) Stephens with 28.28%, 28.24%, 36.67% and 29.63% is followed it as subdominant subgenus respectively. However, the dominant subgenus is *C.* (*Gahanioides*) subgen. nov. with 22.50% in the Afrotropical region and the subdominant subgenus *Chaetocnema* (s. str.) Stephens with 17.50% is followed it. In Madagascan region, *Chaetocnema* (s. str.) Stephens is the dominant subgenus with 40.00% and *C.* (*Hortensoides*) subgen. nov. with 35.00% is followed it as subdominant subgenus (Table 37).

Table 37. Dominant (first and red colored) and subdominant (second and blue colored) subgenera in the Palaearctic, Oriental, Afrotropical, Madagascan, Nearctic and Australian regions according to percentage values of *Chaetocnema* species evaluated in this study.

Regions and subgenera	Percentage values
Palaearctic region	
Chaetocnema (*Hortensoides*) subgen. nov.	45.45%
Chaetocnema (*Chaetocnema*) Stephens, 1831	28.28%
Oriental region	
Chaetocnema (*Hortensoides*) subgen. nov.	37.65%
Chaetocnema (*Chaetocnema*) Stephens, 1831	28.24%
Afrotropical region	
Chaetocnema (*Gahanioides*) subgen. nov.	22.50%
Chaetocnema (*Chaetocnema*) Stephens, 1831	17.50%
Madagascan region	
Chaetocnema (*Chaetocnema*) Stephens, 1831	40.00%
Chaetocnema (*Hortensoides*) subgen. nov.	35.00%
Nearctic region	
Chaetocnema (*Hortensoides*) subgen. nov.	45.00%
Chaetocnema (*Chaetocnema*) Stephens, 1831	36.67%

Australian region	
Chaetocnema (*Hortensoides*) subgen. nov.	48.15%
Chaetocnema (*Chaetocnema*) Stephens, 1831	29.63%

Finally, the data obtained in a molecular study on DNA barcoding by Coral Şahin et al. (2019) also supports the subgeneric arrangement given in this study. COI sequences of 13 *Phyllotreta* species which constitutes approximately 30% of the Turkish fauna and 5 *Chaetocnema* species which constitutes approximately 20% of the Turkish fauna were examined in the study. The 5 *Chaetocnema* species studied are *C. arenacea* (Allard), *C. concinna* (Marsham), *C. conducta* (Motschulsky), *C. coyei* (Allard) and *C. tibialis* (Illiger). Turkish fauna of the genus *Chaetocnema* comprises of 26 species (Ekiz et al., 2013; Özdikmen, 2014). According to the subgeneric arrangement given in this study, *C. concinna* (Marsham) and *C. tibialis* (Illiger) belong to the subgenus *Chaetocnema* (s. str.), *C. arenacea* (Allard) belongs to the subgenus *C.* (*Hortensoides*), *C. coyei* (Allard) belongs to the subgenus *C.* (*Plectroscelis*) and *C. conducta* (Motschulsky) belongs to the subgenus *C.* (*Pseudochaetocnema*). Related part of a result obtained in Coral Şahin (2019) is presented below, without comment, as a small molecular evidence supporting the new subgeneric arrangement (Fig. 12).

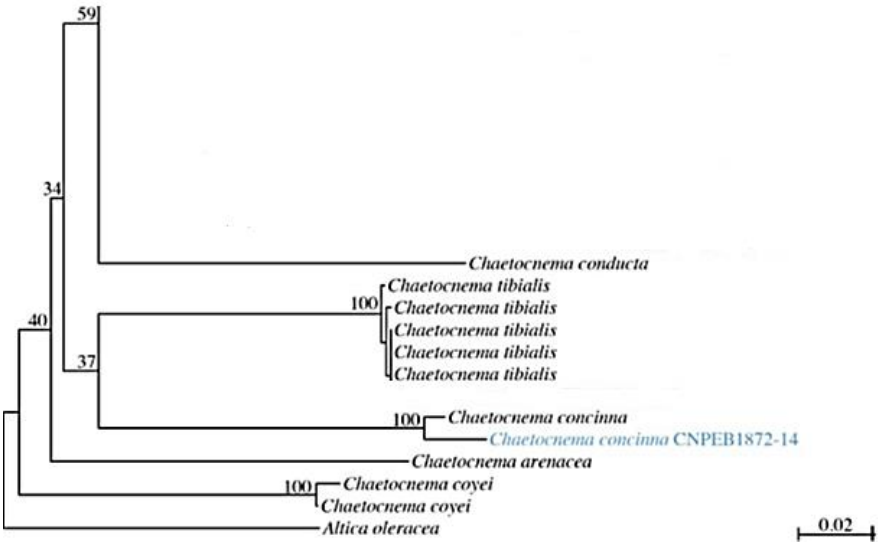

Figure 12. Neighbour-joining tree inferred on ds1 plus one representative sequence for each species. Bootstrap values are reported above the main lineages; the scale bar indicates the distance expressed in nucleotide substitutions per site; in light blue are reported the sequences from BOLD (taken from Coral Şahin, 2018).

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