SCIREA Journal of Biology

http://www.scirea.org/journal/Biology

November 6, 2023

Volume 8, Issue 6, December 2023

https://doi.org/10.54647/biology180320

Phylogenetic Systematics of *Chrysotus* (Diptera, Diaphorinae, Dolichopodidae)—On the Origin and Evelotion of *Chrysotus*

Wei LianMeng

Centre for Disease Prevention and Control of Anshun City, Anshun, Guizhou, China

Corresponding author: wlm510520@sina.com, https://orcid.org/0000-0002-2412-8119

Abstract

According to the concepts, methods and principles of cladistics, and through the discovery of many synapomorphy, patristic relationship, ancestral-descendant sequence transformation characters, (recency of common ancestor), in particular, the recurrence of the ancestral-descendant sequence transformation characters in monophyletic groups and subgroups at different levels, the phylogeny of *Chrysotus* is clarified, on which, the natural history of the origin and evolution of the genus was revealed.

Key words: Dolichopodidae, Diaphorinae, Chrysotini, *Chrysotus*, phylogeny, origin and evolution

Introduction

As small insects of about 2 mm, the genus *Chrysotus* belongs to the subfamily Diaphorinae in the family Dolichopodidae. At present, there are 548 species currently known worldwide (Liu et al. 2020). Previous studies have shown that *Chrysotus* is mainly distributed in the Western

Hemisphere and accounts for two-thirds of the known species in the world (Yang et al. 2006, 2011; Grichanov 2016). However, recent studies have reversed this distribution pattern. The discovery of a large number of species has confirmed that the Eastern Hemisphere, represented by southwestern China as part of the Oriental, is rich in species and actually accounts for over half of the world total (Liu et al. 2013, 2015, 2016a, 2016b, 2017, 2019, 2020, 2021; Wang and Yang 2006, 2008a,b, 2009; Wang et al. 2016; Wei 2012, 2018; Wei et Yang 2007, Wei et Zhang 2010, Wei et al. 2011, 2014; Zhou and Wei 2017). This indicates that the Oriental part of China may be the modern distribution centre of world *Chrysotus*, or one of the centres.

China is a vast country, longitudinally spanning Palaearctic and Oriental, with a long geological history, advantageous geographical conditions, a richness in biological resources and a complex species diversity. In particular, the Qinghai-Tibet Plateau, Hengduan Mountain area (Shangri-La) where three rivers run parallel, as well as the many nature reserves which are situated in the southwest of China, are the centre of the origin and differentiation of species and an important biological gene pool. Southwest China is one of the regions with the richest biological resources in the world, comparable to the Amazon region of South America (private correspondence between the author and Adrian Pont of the Natural History Museum, London in 1992).

MATERIAL AND METHOD

Direct observation of specimens：*Chrysotus* at least 600 spp., about half of 20,000 specimens (♂♀) mainly from SW China. The following abbreviations are used: ad–anterodorsal setae, Cx–Coxa, Cx_{1-3}–fore, mid and hind Coxa, pd–posterodorsal setae. (■)–apomorphy, (□)–plesimorphy.

Results

Taxonomy

Genus *Chrysotus* Meigen.

Chrysotus Meigen, 1824: 40.

Type species: *Dolichopus neglectus* Wiedemann, 1817, by subsequent designation Froriep 1826, 134 (Evenhuis, Pape 2019, 51) [invalid design. Westwood 1840, 134: *Musca nigripes*

Fabricius, 1794 (as understood by Meigen)].

Diagnosis: See Becker (1922a, 1922b), Bickel (2009), Capellari (2015), Capellari and Amorim (2010, 2012), Grichanov and Brooks (2017), Negrobov (1980), Robinson et Vockeroth (1981), Van Duzee (1924), Wei and Zhang (2010), Wei (2012a,b, 2018), Wei et al (2014), Wei et Luo (2023) and Yang et al. (2006, 2011).

Taxnomic System of *Chrysotus* Meigen, 1824

Chrysotus Meigen, 1824

non-*decipiens* group

angustus group *sensus* Wei, Oriental (Oriental, 1 sp)

fujianensis group *sensus* Wei, Oriental (Oriental, 10 spp)

laesus group *sensus* Wei et Zhang, 2010, Oriental, Palaearctic and Neotropical (24 spp)

adunatus subgroup *sensus* Wei et Zhang, 2010 (Oriental, 1sp)

brevicercus subgroup *sensus* Zhou et Wei, 2017(Oriental, Palaearctic, 12 spp)

laesus subgroup *sensus* Zhou et Wei, 2017 (Oriental, Holarctic, 4 spp)

nudisetus subgroup *sensus* Zhou et Wei, 2017 (Oriental, Palaearctic, 5 spp)

trapezinus subgroup *sensus* Zhou et Wei, 2017 (Oriental, 1sp)

longipalpus group *sensus* Van Duzee, 1924 (Neotropical, 12 spp)

leigongshanus group *sensus* Wei, 2018 (Oriental, 63 spp)

aperturus subgroup *sensus* Wei (Oriental, 1 sp)

apicibifidus subgroup *sensus* Wei, 2018 (Oriental, 22 spp)

apicirotundus subgroup *sensus* Wei, 2018 (Oriental, 9 spp)

apicisetosus subgroup *sensus* Wei (Oriental, 9 spp)

chishuiensis subgroup *sensus* Wei, 2018 (Oriental, 10 spp)

comminus subgroup *sensus* Wei, 2018 (Oriental, 1 sp)

daozhenus subgroup *sensus* Wei, 2018 (Oriental, 1 sp)

herterosus subgroup *sensus* Wei (Oriental, 2 spp)

lanciniatus subgroup *sensus* Wei (Oriental, Palaearctic, 4 spp)

suiyangus subgroup *sensus* Wei (Oriental, 1 sp)

triprojicienus subgroup *sensus* Wei (Oriental, 1 sp)

unumprojicienus subgroup *sensus* Wei (Oriental, 1 sp)

xishuangbannaensis subgroup *sensus* Wei (Oriental, 1 sp)

papuanus group *sensus* Wei, Zhang et Zhou, 2014 (Oriental, Australian, 109 spp)

abatus subgroup *sensus* Wei, Zhang et Zhou, 2014 (Oriental, 14 spp)

araeobasus subgroup *sensus* Wei, Zhang et Zhou, 2014 (Oriental, 3 spp)

abdominus subgroup *sensus* Wei, Zhang et Zhou, 2014 (Oriental, 90 spp)

papuanus subgroup *sensus* Wei, Zhang et Zhou, 2014 (Australia, 1 spp)

zhuae subgroup *sensus* Wei, Zhang et Zhou, 2014 (Oriental, 1 spp)

decipiens group *sensus* Wei (Oriental, Palaearctic, 5 old spp, 274 new spp)

Type I *sensus* Wei (Oriental, Palaearctic, 4 old spp, 237 new spp)

aberrantus subgroup *sensus* Wei (Oriental, 37 new spp)

acolus subgroup *sensus* Wei (Oriental, 16 new spp)

adelus subgroup *sensus* Wei (Oriental, 18 new spp)

aestus subgroup *sensus* Wei (Oriental, 19 new spp)

agastus subgroup *sensus* Wei (Oriental, 14 new spp)

albulus subgroup*sensus* Wei (Oriental, 6 new spp)

andrenus subgroup*sensus* Wei (Oriental, 8 new spp)

angustlus subgroup *sensus* Wei (Oriental, 5 new spp)

apicidentus subgroup *sensus* Wei (Oriental, 40 spp, 38 new spp)

blaesus subgroup *sensus* Wei (Oriental, 18 new spp)

bomus subgroup *sensus* Wei (Oriental, 14 new spp)

decipiens subgroup *sensus* Wei (Oriental, 35 spp, 33 new spp)

euagus subgroup *sensus* Wei (Oriental, 6 new spp)

guttus subgroup *sensus* Wei (Oriental, 5 new spp)

Type II *sensus* Wei (Oriental, Palaearctic, 1 old spp, 27 new spp)

baicalenensis subgroup *sensus* Wei (Oriental, 4 new spp)

largifolius subgroup *sensus* Wei (Oriental, 3 new spp)

baptosus subgroup *sensus* Wei (Oriental, Palaearctic, 10 new spp)

burrus subgroup *sensus* Wei (Oriental, 3 new spp)

liui subgroup *sensus* Wei (Oriental, Palaearctic, 2 spp, 1 new spp)

saigusai subgroup *sensus* Wei (Palaearctic, 3 new spp)

Remarks: Based on Becker's key, many species of *C. decipiens* group will run to *C. excretus* Becker, 1922 which lacks the description of male genitalia. The Afrotropical is not clear because all species in this area do not have the descriptions of male genitalia. In addition, a large number of old species, especially those from the Western Hemisphere, have no the descriptions of male genitalia.

In the keys to Chinese, Oriental, Palaearctic and Nearctic species of *Chrysotus* (Yang et al., 2011; Becker 1922a,b; Negrobov et al. 2000; Van Duzee 1924), none of the new species of the *decipiens* group will run clearly to any species.

The groups *sensus* Negrobov and Van Duzee

The 20 groups established by the North America Van Duzee, 1924 with taxonomic status remaining to be determined due to the lack of the description of male gentalia except *C. longipalpus* group. Negrobov and his colleagues established 3 groups of *C. cilipes*, *C. gramineus* and *C. laesus* based on Palaearctic species. However, it is regrettable that the authors did not explain why and how to establish these 3 groups at that time, but only mentioned the 2 groups of *C. cilipes* and *C. laesus* with Cx_1 having pale setae anteriorly, or even for *C. gramineus* group with only the names and the contained species but absent of the definition of specific species group. Among of them *C. laesus* group *sensus* Negrobov, 1980 (=*C. laesus* group *sensus* Wei et Zhang, 2010) and *C. cilipes* Meigen belonging to *C. decipiens* group, and *C. gramineus* (Fallén) belonging to *C.* non-*decipiens* group.

STUDY ON THE PHYLOGENETIC THEORIES RELATED TO CLADISTICS

The origin and evolution of sister group

A sister group is a pair of taxa with a vertical and horizontal relationship. The sister group with vertical relationship is a heterolevel taxa, which with homology homomorphism or homology heteromorphism feature, and they are the longitudinal development of the system, the tree of systems thus can grow upward. The sister group with horizontal relationship is the homolevel of taxon, which with homology heteromorphism feature, and they are the horizontal development of the system, the tree of systems thus can grow horizontally. Tracing to its source, the sister group arises from a binary split of characters. In this process, a pair of features derived from the split is amoporphy and plesamoporphy, respectively, and each of them represents an amoporphic or a plesamorphic branch in the sister group, in which the plesamorphic branch indicates the origin of the sister group. Although both are derived from the common parent species, the former has undergone a completely different change, viz, so-called homology heteromorphism belonging to direct homology. The morphology of the latter did not change or changed little, viz., so-called homology homomorphism belonging to so-called parallel homology. This should be the general rule of phylogeny. For example, both *Acridomyia* and *Chelisia* of Anthomyidae lack the family synapomorphy, viz., cu_1+an_1 reaching to wing margin and scutellum with pale erected hairs apicoventrall (Fan 1988). Similarly, both *Graphomya* and *Hebecnema* (Muscidae, Mydaeyinae) lack the subfamily synapomorphy viz., radial node absent of small setae ventrally (Vockeroth 1972).

Also, the longitudinally developed sister groups is not a true sisterhood, but a pair of taxa with mother-daughter relationships (Brudin 1968), which is also called "pseudo-sister group" (Zhao 1995) or "heterolevel sister group" (Wei and Luo 2023). Otherwise, a pair of sister groups developed horizontally is indeed a true sisterhood, with a parallel relationship. The homolevel feature of a pair of homology heteromorphism shareed by them are also synapomorphy—a pair of ancestral-descendant character that simeble or unresemble the characters of the parent species. This causes them to become a pair of sisters that is similar or unsimilar to parent.

The origin and evolution of synapomorphy

In a clade, the virtual mother species and a pair of sister group together form a monophyletic group, the synapomorphy of which arise from the mother species derives a pair of

ancestral-descendant character shared by 2 daughters and is the heterolevel feature of homology homomorphism and homology heteromorphism. This is the first possible origin way of the synapomorphy. For example, Diaphorinae derives Diaphorini and Chrysotini by epandrium with apical projetion bifurcated or unbifurcated—a pair of ancestral-descendant character (synapomorphy). The second way, the synapomorphy arise from the single feature of the homolevel feature of homology homomorphism. For example, *C. laesus* group with epandrium bearing an apomorphic angular projection posteriorly. The third way, the synapomorphy arise from a series transformation characters of ancestral-descendant (recency of common ancestor). For example, *Dubius* with fr/fa ratio being regular change and *C. papuana* group with epandrium ventral projector bearing regular change.

All three modes of origin result from binary splitting of features, the first being the longitudinal or step development of the systems. The last two are the lateral development of the system. In the first mode, we tend to see only one the synapomorphy, and the corresponding representative species of the symplesiomorphy (in fact, it is also synapomorphy) is either not being found or actually extinct. The third way is actually a continuous evolution of the second way.

On ancestral extinction in phylogeny

The cladistic school does not recognize ancestors. However strictly speaking, the cladistic school simply does not recognize ancestor as a terminal taxon, but considers ancestor to be virtual (my ancestors live in my heart). In one branch, the parent species is lost by the split of characters, but the characters of the parent species are not lost, they are preserved (in a changed or unchanged form) in a pair of daughter species as sisters. The characters derived from the split is the synapomorphy of each sister, or the false synapomorphy (form fale sister group, Zhao 1995), and the synapomorphy of two sisters together constitute a pair of symplesiomorphy, which stores in the virtual parent species. Or say, the characters of the mother species split in two (plesimorphy and apomorphy) and remain in the two daughter species. This is the whole possible process of the formation and evolution of a branch. Each branch of the sister group can further break into new clade. In this way the whole system develops accompany the mother species dies and clades are formed continually and the whole system constantly formes and developes accompanied by the mother species continues to die, branches continue to form. In other words, the whole process of phylogeny is that the ancestors are constantly dying out and new sister groups are constantly being created. The result is the "imprint of history" that we can, and only can, see in living things that have been

handed down from generation to generation. In any living organism, we can see from the most primitive DNA to the characters of kingdoms, phyla, class, order, family, genus, and species. DNA is the synapomorphy of all being. From these features, we can reasonably infer the ancestors of all levels of any living thing. In this way the whole biological world developed monophyletically and historically (Darwen). From this we can safely say that the features of living organisms also have the dimension of time same as a paleontological fossil, and that historical conclusions can be drawn from them.

The dynamics of phylogeny

Why does the phylogeny grow from nothing, from small to large, and still continue to develop?

It is reasonable to speculate that the basic driving force of its development should be the attribute of genes - variability. And natural selection plays the role of director, has been playing the role of mentor for eons of years, "guiding" the vivid and magnificent life from nothing to existence, from small to large, and constantly developing and expanding the historical process.

THE PHYLOGENY OF CHRYSOTUS (MALE)

The synapomorphy of *Chrysotus:* Tg6 without strong and long setae apically, abdomen not yellow basally. **Palpus:** The active changes in varying degrees of enlargement and extension, light color mainly be found in the groups of *C. albipalpus*, *C. fujianensis*, *C. longipalpus*, *C. philtrum*, *C. largifolius* subgroup and *C. chukotkensis*, etc, which are convergence features origined independently in above groups. In addition, a large number of other convergent or parallel features are also found in the *decipiens* group: Such as body bronze, scutum with golden longitudinal strip, Cx_1 with color changing from light to dark, the dark patches on all femora regular evolution, etc. It is worth mentioning that, above convergent or parallel features always are the synapomorphy of each monophyletic subgroup in the decipiens group. The yellow leg widely found in the *decipiens* and *fujianensis* groups, but the former with spot and the latter without spot. In addition leg yellow also often found in Dolichopodidae. Therefore, leg yellow should be plesimorphy and black (including dark spotted) is apomorphy. Body color also has such a similar situation, light is plesimorphy, dark is apomorphy. **Coxae:** The *decipiens* group with coxae in color from light to dark, yellow to black, through a series of light to dark color changes. The non-*decipiens* group with Cx often darkish and leg with no

spots. **Trochanter:** The non-*decipiens* group with trochanter dark but yellow in the *decipiens* group. **Tibia:** The non-*decipiens* group with tibia not entirely yellow but the *decipiens* group with fore and mid tibiae are certainly yellow, hind tibia yellow to black or even pitch-dark. The *decipiens* group with hind tibia normal or thickened and basal piles long and dense anteriorly. The *leigongshanus* and *papuanus* groups with mid tibia bearing 1 ad near basal 1/4 and usually without pd, which are symplesiomorphy in these 2 groups and may be parallel characters, a pair of sister group. Also, fore tibia with 1 short and weak ad, mid tibia with 2 strong ad and 2 short small pd in the *decipiens* group. On the contrary, the non-*decipiens* group abent of such a set of tibia setae, which is symplesiomorphy in these 2 groups. **Femur:** The non-*decipiens* group with femur black to brownish black and usually absent of yellow at two apexes. But the *decipiens* group with femur yellow at two apexes and femoral spots in regular changes. Namely, all femora entirely yellow to black in colour. If with only one dark spot, it always occurs on the hind femur and on the preapex of the hind femur. If with 2 dark spots, they always occur on each of mid and hind femora, viz., it never happens that each of the fore and hind femora is with a dark spot but the mid femur lacks a dark spot or that the fore and mid femora are with a dark spot but the hind femur lacks a dark spot. If there are 3 dark spots, they always occur on each of the fore, mid and hind femora, viz., it never happens that each of the femora has 2 dark spots. If the dark spot on the hind femur is less than 2/5 of the hind femoral length, the fore and mid femur is certain to be unspotted or at most spotted incompletely on mid femur. If hind femur with preapical dark spot being about half as long as hind femoral length, the mid femur is certain to be spotted and fore femur usually is unspotted or spotted incompletely. If the dark spot on the hind femur almost occupy the whole hind femoral length, the fore and mid femur is certain to be spotted and almost occupy the whole femoral length as that of hind femur. The evolutionary rule of the dark patches on fore, mid and hind femora: from non-existence to existence, expanding from small to large, the colour changing from light to dark and from an incomplete in form (in longitudinal cracked, always occur in fore and mid femora) to a complete in form. However, when the dark spots on mid and hind femora almost occupy the whole femoral length, the hind femur with basal yellow spot may occur following situations: from almost invisible to nearly half of femoral length. Usually, the yellow apical spots on mid femur never longer than that of fore femur and at least equal to that of hind femur, however, hind femur with yellow apical spot small, never longer than the apical width of femur. In other words, it never happens that the dark spot on fore femur larger or deeper in colour than that of mid and hind femora or that of mid femur larger or deeper in colour than in hind femur. Finally, there is a possibility that when the dark spots

on fore and mid femora occupy almost the entire femoral length (basal yellow spot is very small and almost invisible). However, the basal yellow spot on hind femur may appear obviously larger than width of femur, namely larger than in fore and mid femora, and gradually shrink until it is almost invisible. The reasonable explanation of this situation is that the basal yellow spots on hind femora go through the evolution process from big to small. Why did not expand from small to big? Because we have never seen a case where the hind femur spot occupies almost the entire length of femur meanwhile both fore and mid femur are yellow. On the contrary, had happened everywhere the hind femur with the basal yellow spot larger, when the fore and mid femur with the basal yellow spot nearly invisible. Therefore, the evolution process of the basal macula should be from large to small. **Body colour** *Chrysotus* usually with body metallic green except the groups of *C. leigongshanus* and the *C. papuanus* blackish brown to brownish black. **Epandrium** more or less recurvated backwards; lateral lobe usually tongue shaped and more or less recurvated backwards in each group of *C. laesus* and *C. leigongshanus*. **Cercus** with the implications of cercus for system evolution mainly seen in the *papuanus* group, namely, the transition of the U-shaped incision of cercus basally might be from none, or small, to large (or from shallow to deep) and from irregular to regular. **Surstylus** with or without an apical inner angle being the synapomorphies of each *C. decipiens* and *C.* non-*decipiens* group. In *C. leigongshanus* group, surstylus with anterior margin always uniform smooth curved but sometimes waved and often with its basiventral process arced but sometimes rectangular or nearly so. The *leigongshanus* and *C. decipiens* groups with the included angle between axises of surstylus and epandrium usually approaching or exceeding 45° but occasionally at small or very small angle, as usually seen in the members of *Chrysotus*. **St8** with a pair of strong spines posteriorly in *C. leigongshanus* group. **Phallus** usually simple except for *C. papuanus* and *C. decipiens* denticulate dorsoventrally. **Phallus sheath** usually with structure complex, which sometimes distinctly divided into dorsal and ventral lobes in the *leigongshanus* group, with or without dorsal, laterodorsal or ventral projections, respectively. In the *decipiens* group, phallus sheath distally with the apical margin of apicoventral projection developed in various forms of protuberance which are the morphological base of many subgroups origin. However, phallus sheath distally with apex simple is the primitive type.Ventral projection of epandrium normally with its apex never gradually shrinking into slender conical but expanding into an arrowhead in *decipiens* group. However, the *papuanus* group with ventral projection having its apex gradually shrinking into slender conical until remarkably elongate, widely or narrowly separated from or touching to or even overlapping with lateral lobe, from outside to inside, gradually in-depth,

its end more or less near to or contacted with or even protruding from surstylus. The regular evolution of ventral projection of epandrium recurring in a few monophyletic subgroups with many species. **Ejaculatory apodeme** usually is stick-like in the *papuanus* group and usually nail-like or nearly so, folded strongly from basally in the *leigongsanus* group.

The synapomorphy of *C. decipiens* group: Surstylus with an apical inner angle (■); fore tibia with 1 small ad near basal 1/4 (■), mid tibia with 2 strong ad (■) and 2 short and weak pd (■).

The synapomorphy of *C.* non-*decipiens* group: Surstylus without an apical inner angle (□); fore tibia with 1 small ad near basal 1/4 , mid tibia without 2 strong ad (□) and 2 short and weak pd (□).

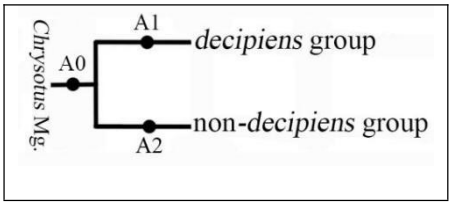


Figure 1 The pylogenetic tree of two natural groups in *Chrysotus* Meigen (male)

A0: Tg6 without strong and long setae apically (■). Abdomen black basally (■). **A1**: Surstylus with an apical inner angle (■); fore tibia with 1 small ad near basal 1/4 (■), mid tibia with 2 strong ad (■) and 2 short and weak pd (■). **A2**: Surstylus without an apical inner angle (□); fore tibia with 1 small ad near basal 1/4 , mid tibia without 2 strong ad (□) and 2 short and weak pd (□).

The synapomorphy of *C. angustus* group *sensus* Wei: All Cx yellow. All femora more or less black. Postgonite with anterior process undeveloped, bifurcate. Antenna unforked apically.

The synapomorphy of *C. fujianensis* group *sensus* Wei: Only Cx_1 yellow. All femora usually pale yellow. Postgonite with anterior process developed, not bifurcate. Antenna forked or unforked apically.

Key to the groups of *Chrysotus* (Male)

1. Pale species. Surstylus with an apical inner angle, with no exception; ventral projection of epandrium with its apex usually expanded into an arrowheaded. Fore tibia with 1 ad at basal 1/4, mid tibia usually with 2 strong ad, 2 short and weak pd. Hind tibia usually thickened, with dense and long basal piles anteriorly. Femur usually with yellow spot at two ends. Squama and haltere usually pale…….....***C. decipiens* group**

−. Pale or dark species. Surstylus without an apical inner angle. Ventral projection of epandrium with its apex not expanded into an arrowheaded. Fore tibia usually with 0 ad. Mid tibia usually with 1 ad, 0 pd. Hind tibia normal or abnormal, with normal or abnormal basal pile anteriorly. Femur usually without yellow spot at two apexes. Squama and haltere dark to pale (***C*. non-*decipiens* group**).....……..…….....2

2. More or less dark species. Legs usually brownish black or black, at most individual species with femora yellowish at tip, with Cx dark but tibiae always more or less yellow.....3

−. Pale species. Legs yellow, $Cx_{2\text{-}3}$ yellow or yellowish brown.....5

3. Darker species. Epandrium with an apomorphic angular projection posteriorly. Black metallic green species. Postocular and occiput with setae usually black. Mid tibia usually with 2 ad. Hind tibia with normal basal pile anteriorly.....***C*. *laesus* group**

−. More or less dark species. Epandrium without the apomorphic angular projection posteriorly. Mid tibia with 1 ad near basal 1/4 and usually lack pd. Hind tibia with normal or abnormal basal pile anteriorly.....4

4. Dark species. Ventral projection of epandrium remarkably elongated, with apex conical. St8 without a pair of strong apomorphic spines apically. Epandrium straight, never recurved backwards. Ejaculatory apodeme usually stick-like. The transition of the U-shaped incision of cercus basally might be from none, or small, to large (or from shallow to deep) and from irregular to regular. Phallus sheath usually without a developed projection apically. Hind tibia with long and dense basal pile.....***C*. *papuanus* group**

−. Darker species. Ventral projection of epandrium short, with apex usaually arrowheaded. St8 with a pair of strong apomorphic spines apically. Epandrium more or less recurved backwards. Ejaculatory apodeme usually nail-like, strongly flexed basally. Cercus without U-shaped incision basally in transition from irregular to regular. Phallus sheath usually with a developed projection apically. Hind tibia usually with normal pile

anteriorly.....

.....***C. leigongshanus* group**

5. Palpus variously enlarged and ornamented. Fore tarsomere I with ventroapical swelling. Mid femur with 2 rows of ventral setae on basal half. Hind tibia with row of anterior to anterodorsal setae. Phallus with small projection at apex.....***C. longipalpus* group**

−. Palpus usually neither enlarged nor ornamented. Fore tarsomere I without ventroapical swelling. Mid femur without ventral setae on basal half. Hind tibia without row of anterior to anterodorsal setae. Phallus without small projection at apex.....6

6. All Cx yellow. All femora more or less black. Postgonite with anterior process undeveloped, bifurcate. Antenna unforked apically.....***C. angustus* group**

−. Only Cx_1 yellow. All femora usually pale yellow. Postgonite with anterior process developed, not bifurcate. Antenna forked or unforked apically.....***C. fujianensis* group**

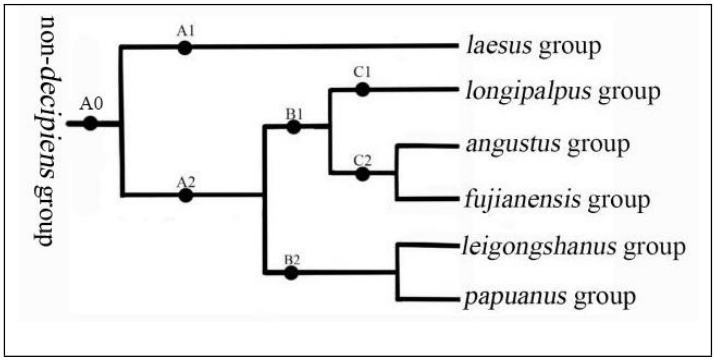


Figure 2 The phylogenetic tree of *C.* non-*decipiens* group (male)

A0: Surstylus without an apical inner angle (■); fore tibia without 1 small ad near basal 1/4 (■), mid tibia without 2 strong ad and 2 short and weak pd (■). **A1**: Epandrium with characterstic angular projection posteriorly (■). **A2** Epandrium without characterstic angular projection posteriorly (□). **B1**: Legs yellow (□), Cx_1 yellow (□), Cx_{2-3} yellow or yellowish brown (□); mid tibiae without ad (□). **B2**: Legs bownish black (■), Coxae not yellow (■), Cx_{2-3} dark (■); mid tibiae with 1 ad (■). **C1**: Male palpus variously enlarged and ornamented (■); fore tarsomere I with ventroapical swelling (■), mid femur with 2 rows of ventral setae on basal half (■); hind tibia with row of anterior to anterodorsal setae (■); phallus with small projection at

apex (■). **C2**: Male palpus usually not enlarged and ornamented (□); fore tarsomere I without ventroapical swelling (□), mid femur without ventral setae on basal half (□); hind tibia without row of anterior to anterodorsal setae (□); phallus without small projection at apex (□). The ancestral-descendant characters of the groups of *angustus*, *fujianensis*, *papuanus* and *leigongshanus* see the description of the key.

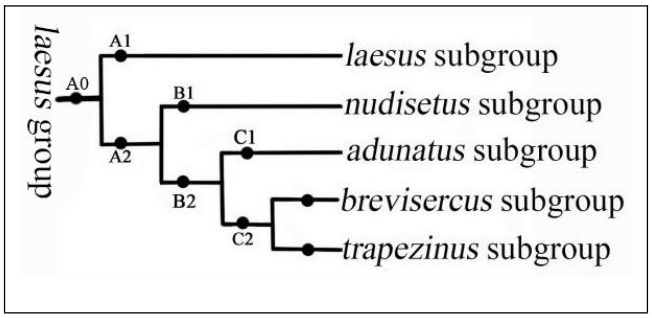


Figure 3 The phylogenetic tree of *C. laesus* group

A0: Epandrium with an apomorphic angular projection posteriorly (■). **A1**: Postocular and occiput with setae pale (■). Cx_1 with pale setulae and setae anteriorly (■). Phallus sheath distally with apex globular expanded (■), without lateral or ventral projection (□). **A2**: Postocular and occiput usually with setae black (□). Cx_1 with black setulae and setae anteriorly (□). Phallus sheath distally with apex not globular expanded (□), with lateral or ventral projection (■). **B1**: Phallus sheath distally with a pair of projections (■). **B2**: Phallus sheath distally with a projection only. **C1**: Phallus sheath distally with a lateral projection (■), without a ventral projection (□). **C2**: Phallus sheath distally with a ventral projection (■), without a lateral projections (□). ***C. brevicercus* subgroup**: Phallus sheath distally without ventral projection strip-like having apex widened and ridged marginly (□), with ventral projection strip-like having apex fingerlike and usually pointed apically (■). ***C. trapezinus* subgroup**: Phallus sheath distally with ventral projection strip-like being widened apically and ridged marginly (■), without ventral projection strip-like having apex fingerlike and usually pointed apically (□)**.**

Key to the subgroups of *C. laesus* group (Male)

1. Phallus sheath distally with apex globular expanded, without projection .....

   .....***C. laesus* subgroup**

–. Phallus sheath distally with apex not globular expanded, with projection.....2

2. Phallus sheath distally divided apically, with a pair of apical projections, at least one of which located dorsally or laterally.....***C. nudisetus* subgroup**

–. Phallus sheath distally undivided apically, without projection.....3

3. Phallus sheath distally with lateral banana-shaped projection .....***C. adunatus* subgroup**

–. Phallus sheath without lateral projection but with ventral one.....4

4. Phallus sheath distally with ventral projection strip-like being widened apically and ridged marginly.....***C. trapezinus* subgroup**

–. Phallus sheath distally with ventral projection strip-like being fingerlike and usually pointed apically.....***C. brevicercus* subgroup**

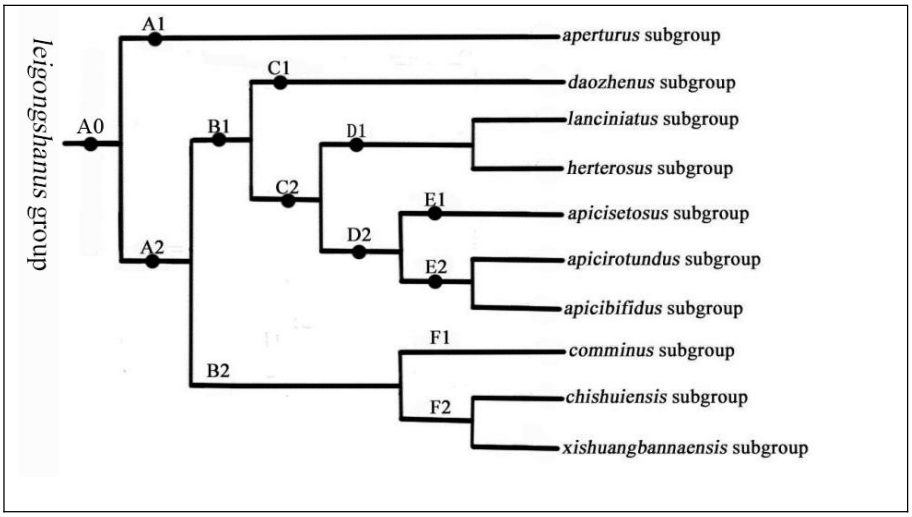


Figure 4 The phylogenetic tree of *C. leigongshanus* group

A0(■): Ventral projection of epandrium short, usaually arrowheaded. St8 with a pair of strong apomorphic spines apically. Epandrium more or less recurved backwards. Ejaculatory apodeme usually nail-like, strongly flexed basally. Cercus without U-shaped incision basally in transition from irregular to regular. Phallus sheath usually with a developed projection apically. Hind tibia usually with normal pile anteriorly. **A1**: Epandrium straight (□). The included angle between axises of surstylus and epandrium about 0º (□). **A2**: Epandrium more or less recurvated backwards (■). The included angle between axises of surstylus and epandrium more than 0º (■). **B1**: Phallus sheath distally without apicodorsal projection (□), with an apicoventral projection only (■). **B2**: Phallus sheath distally with an apicodorsal projection only (■), without apicoventral projection (□). **C1**: Phallus sheath distally with a pair of apicoventral projections (■). **C2**: Phallus sheath distally with an apicoventral projection only (□). **D1:** Phallus sheath distally without a triangular apicoventral projection (□) but with a clubbed or conical apicoventral projection (■). **D2:** Phallus

sheath distally with a triangular apicoventral projection (■) but without a clubbed or conical apicoventral projection (□). **E1**: Phallus sheath distally with 2 triangular apical ventral processes that are decumbent B-shaped or nearly so (■). **E2**: Phallus sheath distally with a triangular apical ventral process only (□). **F1**: Phallus sheath distally with apical dorsal projection undeveloped, narrow conical (□). **F2**: Phallus sheath distally with apicodorsal projection more or less developed, erect, trapezoidal or near triangular (■). ***C. lanciniatus*** **subgroup**: Phallus sheath distally with a long and developed clubbed apicoventral projection (■). ***C. herterosus*** **subgroup**: Phallus sheath distally with a short and undeveloped conical apicoventral projection (□). ***C. apicirotundus*** **subgroup**: Distal portion of phallus sheath: apical ventral process of ventral lobe without striplike, folded downwards preapical projection, at most with short, digitiform or triangular apicodorsal angle (□). ***C. apicibifidus*** **subgroup**: Distal portion of phallus sheath: apical ventral process of ventral lobe with striplike, folded downwards preapical projection, even if it is only very slightly curved downward (■). ***C. chishuiensis*** **subgroup**: Phallus sheath distally with apicodorsal projection very large, erect, usually triangular but sometimes platelike; sometimes with subapical dorsal projection; laterodorsal projection present (■). ***C. xishuangbannaensis***: Phallus sheath distally with apicodorsal projection undeveloped, trapezoidal, weakly sclerotised, sloped apically (□).

2.4.1. Key to subgroups of *C. leigongshanus* group (Male)

1. Phallus sheath distally with dorsal and ventral projections apically ....***C. aperturus*** **subgroup**

– Phallus sheath distally with a ventral or dorsal projection apically.....2

2. Phallus sheath distally with an apicoventral projection only, without apicodorsal projection...

.....3

– Phallus sheath distally with an apicodorsal projection only, without apicoventral projection....

.....8

3. Phallus sheath distally with a pair of apicoventral projections .....***C. daozhenus*** **subgroup**

– Phallus sheath distally with an apicoventral projection only.....4

4. Phallus sheath distally with a clubbed apicoventral projection.....5

– Phallus sheath distally with a triangular apicoventral projection.....6

5. Phallus sheath distally with a very long and developed apicoventral projection.....

.....***C. lanciniatus* subgroup**

– Phallus sheath distally with a short and narrow conical apicoventral projection.....

..... ***C. herterosus* subgroup**

6. Phallus sheath distally with 2 triangular apical ventral processes that are decumbent B-shaped or nearly so .....***C. apicisetosus* subgroup**

– Phallus sheath distally with a triangular apical ventral process only.....7

7. Phallus sheath distally with apical ventral process very large, triangular, membranous, which with strip-like, folded downwards preapical projection; usually with subapical ventral process long conical, well-sclerotised, with slender apical portion which fused to apical ventral process and forming its dorsal spine .....***C. apicibifidus* subgroup**

– Phallus sheath distally with apical ventral process very large, triangular, usually membranous, which without strip-like, folded downwards preapical projection instead of apicodorsal angle .....***C. apicirotundus* subgroup**

8. Phallus sheath distally with apical dorsal projection undeveloped, narrow conical.....

.....***C. comminus* subgroup**

– Phallus sheath distally with apicodorsal projection more or less developed, erect, trapezoidal or near triangular.....9

9 Phallus sheath distally with apicodorsal projection very large, erect, usually triangular but sometimes platelike; sometimes with subapical dorsal projection; laterodorsal projection present .....***C. chishuiensis* subgroup**

– Phallus sheath distally with apicodorsal projection undeveloped, trapezoidal, weakly sclerotised, sloped apically.....***C. xishuangbannaensis* subgroup**

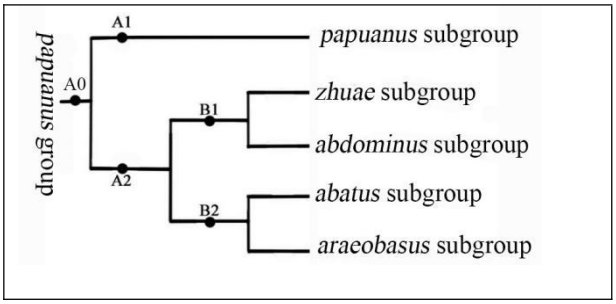


Figure 5 The phylogenetic tree of *C. papuanus* group

A0(■): Ventral projection of epandrium abnormal, remarkably elongated. St8 without a pair of strong apomorphic spines apically. Epandrium straight, never recurved backwards. Ejaculatory apodeme usually stick-like. The transition of the U-shaped incision of cercus basally might be from none, or small, to large (or from shallow to deep) and from irregular to regular. Phallus sheath usually without a developed projection apically. Hind tibia with long and dense basal pile. **A1**: Phallus with an odontoid projection apicoventrally (■). Mid tibia with tip somewhat enlarged (■). **A2**: Phallus without an odontoid projection apicoventrally (□). Mid tibia with tip normal (□). **B1**: Phallus sheath distally with dorsal projection apically or far from apex (■), unexpanded apically (□). **B2**: Phallus sheath distally without dorsal projection (□), more or less expanded apically (■). ***C. zhuae* subgroup**: Phallus sheath distally with a small, spherical, dorsal projection far from end (■), without dorsal projection apically (□). Cercus developed (■). ***C. abdominus* subgroup**: Phallus sheath distally without a small, spherical, dorsal projection far from end (□), with a small dorsal projection apically (■). Cercus undeveloped (□). ***C. abatus* subgroup**: Phallus sheath proximally with a well-developed projection (■). Cercus usually deeply with an U-shaped incision basally and with developed apex, which evidently shrinks into a finger-like projection or in acute triangle (■). ***C. araeobasus* subgroup**: Phallus sheath proximally without a well-developed projection (□). Cercus without an U-shaped incision basally, developed apex, which evidently shrinks into a finger-like projection or in acute triangle (□).

Key to subgroups of *C. papuanus* group (Male)

1. Phallus with an odontoid projection apicoventrally. Mid tibia with tip somewhat enlarged.....

.....***C. papuanus* group**

– Phallus without an odontoid projection apicoventrally. Mid tibia with tip normal.....2

2. Phallus sheath distally with dorsal projection apically or far from apex, unexpanded apically.....

....3

– Phallus sheath distally without dorsal projection, more or less expanded apically.....4

3. Phallus sheath distally with a small, spherical, dorsal projection far from end, without dorsal projection apically. Cercus developed.....***C. zhuae* subgroup**

– Phallus sheath distally without a small, spherical, dorsal projection far from end, with a small dorsal projection apically. Cercus undeveloped.....***C. abdominus* subgroup**

4 Phallus sheath proximally without a well-developed projection. Cercus without an U-shaped incision basally, developed apex, which evidently shrinks into a finger-like projection or in acute triangle…….....***C. araeobasus* subgroup**

– Phallus sheath proximally with a well-developed projection. Cercus usually deeply with an U-shaped incision basally and with developed apex, which evidently shrinks into a finger-like projection or in acute triangle.....…….....***C. abatus* subgroup**

The diagnostic characters of *C. decipiens* group (males)

This newly-defined *decipiens* group possesses the following characters shared by all members of the group, by which all of them can be easily distinguished from other *Chrysotus* species groups, species subgroups or species.

1. Legs yellow, Cx_1 with yellow color grandually bcomeing deep, until it turn completely black; all femora or mid and hind femora or only hind femur with a dark spot of different degrees of black; trochanters, fore and mid tibiae always yellow; mid and hind coxae usually dark; hind tibia, yellow to entirely black or even pitch black; fore and mid tarsi usually brownish-yellow to brown or yellowish-brown from tip of tarsomere 1 onwards, hind tarsus yellow to entirely black or even occasionally pitch black but tarsomere 1 often pale on basal 1/3 or half or mainly or even entirely black, sometimes all tarsi entirely yellow or nearly so (only hind tarsus somewhat darkened apically).

2. Fore tibia with 1 short and weak ad basally (at about basal 1/4), mid tibia usually with 2 strong ad and 2 short and weak pd, hind tibia always conspicuously or sometimes slightly to inconspicuously thickened, individually normal, densely and long pilose anteriorly but individually with hind tibia normal but also with normal or abnormal pilosity.

3. Surstylus with an apical inner angle, with no exceptions.

4. Phallus sheath distally with the apical structure rather complex, dispite without a remarkably developed projection, on which it can be divided into 4 types, 20 monophyletic subgroups and a few temporarily unplaced species.

Remarks: In the keys to Chinese, Oriental, Palaearctic and Nearctic species of *Chrysotus* (Yang et al. 2011; Becker 1922a,b; Negrobov et al. 2000; Van Duzee 1924), none of the new species of *C. decipiens* group will run clearly to any species.

Key to the subgroups of *C. decipiens* group (male)

1. Phallus sheath distally with the apical margin of apicoventral projection developed in various forms of protuberance **(Type-I)**.....2

–. Phallus sheath distally with various forms of protuberance apically **(Type II)** 15

2. Phallus sheath distally with the apical margin of apicoventral projection in a line or raised in a figure 7 shape, apex of which straight, never bends to backwards but sometimes bends forwards, without a small pale conical projection ventrally.....3

–. Phallus sheath distally with apicoventral margin raised in various

arcs.....4

3. Phallus sheath distally with the apical margin of apicoventral projection in a line.....

..... ***C. guttus*** **subgroup**

–. Phallus sheath distally with the apical margin of apicoventral projection raised in a figure 7 shape, never bends to backwards but sometimes bends forwards.....***C. acolus*** **subgroup**

4. Phallus sheath distally with the apical margin of apioventral projection uplifted in the various shape as an arc and a bow, apex of which points backwards or downwards, never bent
forwards.....5

–. Phallus sheath distally with the apical margin of apioventral projection uplifted in the various shape, such as semi-elliptical in shape, a long and wide oval shape, a S-shape, a S-shape with an apical ring, a fan-shape ring, a straight hook, a round hook, a hemispheric shape, a n-shape, a loop in n-shape, etc., the apexes of which more or less bend forwards, never points to backwards and downwards.....6

5. Phallus sheath distally with the apical margin of the apicoventral projection raised in a bow shape.....***C. decipiens*** **subgroup**

–. Phallus sheath distally with the apical margin of the apicoventral projection shape as an arc..... ***C. andrenus*** **subgroup**

6. Phallus sheath distally with the apical margin of apicoventral projection in a S-shape or a S-shape with an apical ring.....7

–. Phallus sheath distally with the apical margin of apicoventral projection not as above.....8

7. Phallus sheath distally with the apical margin of apicoventral projection in a

S-shape.....

.....***C. apicidentus*** **subgroup**

–. Phallus sheath distally with the apical margin of the apicoventral projection raised in a S-shape with an apical ring.....***C. agastus*** **subgroup**

8. Phallus sheath distally with the apical margin of the apicoventral projection raised in a open or closed n-shape..... 9

–. Phallus sheath distally with the apical margin of apicoventral projection not as above.....10

9. Phallus sheath distally with the apical margin of the apicoventral projection raised in a n-shape, the apex of which bends forwards, never points backwards and downwards.....

.....***C. bomus*** **subgroup**

–. Phallus sheath distally with the apical margin of the apicoventral projection developed as a

loop in n-shape, the apex of which bends forwards, forming a loop.....***C. euagus*** **subgroup**

10. Phallus sheath distally with the apical margin of the apicoventral projection developed in a long and wide oval shape, the apex of which bends forwards, never points backwards and downwards.....***C. albulus*** **subgroup**

–. Phallus sheath distally with the apical margin of the apicoventral projection not as above..... 11

11. Phallus sheath distally with the apical margin of the apicoventral projection raised in a fan-shape ring, the two ends of which are connected or nearly so.....***C. aestus***

subgroup

–. Phallus sheath distally with the apical margin of the apicoventral projection not raised in a fan-shape ring.....12

12. Phallus sheath distally with the apical margin of the apicoventral projection shape as a straight or round hook, the apex of which bends forwards, never points backwards and downwards.....13

–. Phallus sheath distally with the apical margin of the apicoventral projection not shape as above.....14

13. Phallus sheath distally with the apical margin of the apicoventral projection shape as a round hook.....***C. aberrantus* subgroup**

–. Phallus sheath distally with the apical margin of the apicoventral projection shape as a straight hook.....***C. blaesus* subgroup**

14. Phallus sheath distally with the apical margin of the apicoventral projection semi-elliptical in shape, the apex of which bends forwards, never points backwards and downwards.....

.....***C. adelus* subgroup**

–. Phallus sheath distally with the apical margin of the apicoventral projection raised in a hemispheric shape, the apex of which bends forwards, never points backwards and downwards.....***C. angustlus* subgroup**

15. Phallus sheath distally with apex simple, which neither raised in various forms nor expanded apically.....***C. baicalensis* subgroup**

–. Phallus sheath distally with the apex raised in various form or expanded

apically.....16

16. Phallus sheath distally with the apex expanded into globula, being absent of the differentiation of dorsal and ventral projectiones.....**C. *largifolius* subgroup**

–. Phallus sheath distally with the apex not expanded into globular, bearing the differentiation of dorsal and (or) ventral projection.....17

17. Phallus sheath distally with the apicoventral projection in flakiness, apex of which pointed or blunt.....18

–. Phallus sheath distally with the apicoventral projection conical or hooked.....19

18. Phallus sheath distally with the apicoventral projection rectangular....***C. baptosus* subgroup**

–. Phallus sheath distally with the apicoventral projection knife-shape, pointed and snubby apically.....***C. liui* subgroup**

19. Phallus sheath distally with the apicoventral projection conical, pointed apically.....

.....***C. saigusai* subgroup**

–. Phallus sheath distally with the apicoventral projection hooked, denticulate ventrally and snubby apically.....***C. burrus* subgroup**

Remarks: The points that require special emphasis are as follows:

1. The femur is usually not entirely black, but is at least more or less yellow at the base and even hardly visible. This feature helps distinguish *C. decipiens* group from *C. laesus* group, *C. leigongshanus* and *C. papuanus* groups, etc.

2. Every subgroup of *C. decipiens* group with a dark spot on a leg follows the above rules. It

gives a reasonable explanation as to why different species have the same shape spot on their leg. Fore example, there are many species with femur yellow, which belong to different monophyletic subgroups. This is heterologous similarity (non-homologous similarity) because each of them originates from a different monophyletic subgroup.

3. “In a given taxa, the more complex the mosaic of heterologous features we have, the more reliable the phylogenetic relationships we can infer from them.” (Hennig 1965). Thus, with a thorough and in-depth study of *C. decipiens* group, we seem to be able to establish a history that reflects the origin and evolution of this specific group.

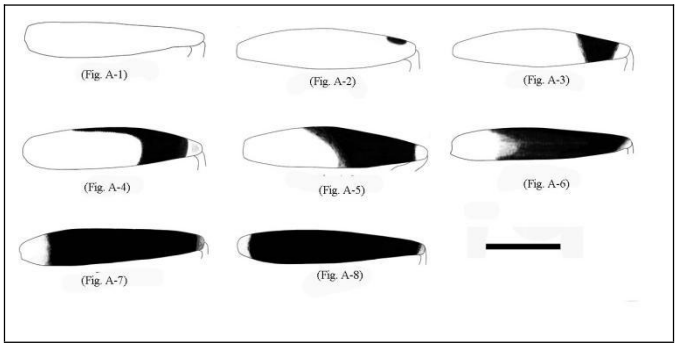


Figure 6 The patches on the hind femora of *C. aestus* subgroup, which show the monophyletic series

Fig. A−1,2 Conjectured types, Fig. A−3 *C. umbrinus* sp. nov., Fig. A−4 *C. diplacus* sp. nov., Fig. A−5 *C. crunus* sp. nov., Fig. A−6 *C. acolus* sp. nov., Fig. A−7 *C. binanfranctus* sp. nov. and Fig. A−8 *C. carpus* sp. nov. Scale bar = 0.3mm.

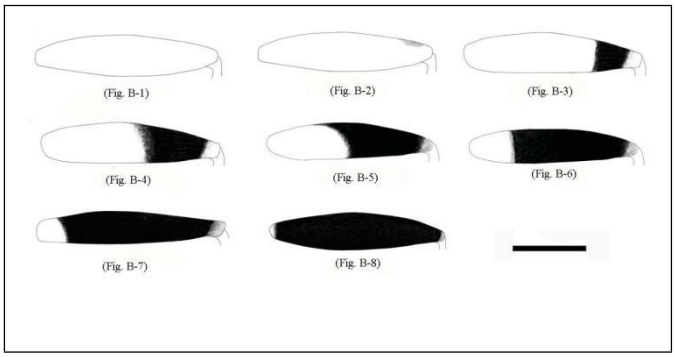


Figure 7 The patches on the hind femora of *C. apicidentus* subgroup, which show the monophyletic series

Fig. B−1,8,3 Conjectured types, Fig. B−2 *C. thysanus* sp. nov., Fig. B−4 *C. pleurus* sp. nov., Fig. B−5 *C. excertus* sp. nov., Fig. B−6 *C. apicidentus* Wei and Yang, 2007, Fig. B−7 *C. lustrabilus* sp. nov. Scale bar = 0.3 mm.

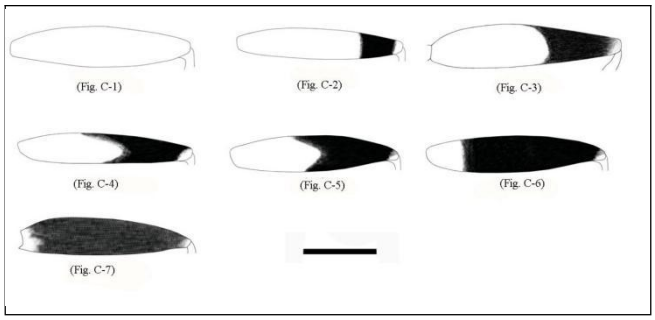


Figure 8 The patches on the hind femora of *C. decipiens* subgroup, which show the monophyletic series

Fig. C−1,6 Conjectured type, Fig. C−2 *C. metallus* sp. nov., Fig. C−3 *C. ancylus* sp. nov., Fig. C−4 *C. barbus* sp. nov., Fig. C−5 *C. minghuensis* sp. nov. and Fig. C−7 *C. hylus* sp. nov. Scale bar = 0.3 mm.

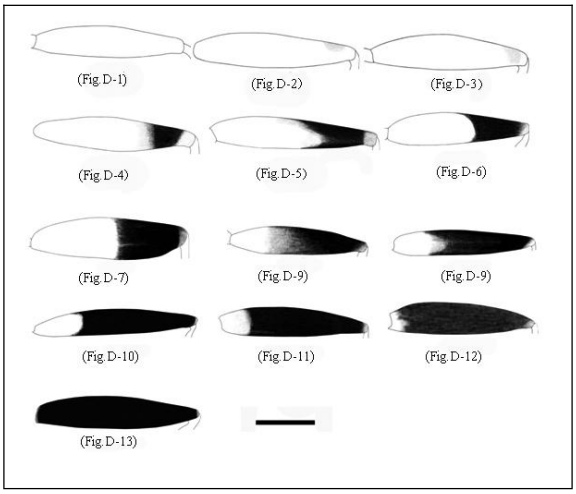


Figure 9 The patches on the hind femora of *C. decipiens* group, which show the heterologous series from various monophyletic subgroups

Fig. D−1 *C. baptosus* sp. nov. (*C. baptosus* subgroup), Fig. D−2 *C. majusus* sp. nov. (*C. baptosus* subgroup), Fig. D−3 *C. guiyangensis* sp. nov. (*C. liui* subgroup), Fig. D−4 *C. fecundus* sp. nov. (*C. agastus* subgroup), Fig. D−5 *C. tongrenensis* sp. nov. (*C. aestus* subgroup), Fig. D−6 *C. ancylus* sp. nov. (*C. decipiens* subgroup), Fig. D−7 *C. bitumineus* sp. nov. (*C. decipiens* subgroup), Fig. D−8 *C. fistulus* sp. nov. (*C. blaesus* subgroup), Fig. D−9 *C. scytus* sp. nov. (*C. euagus* subgroup), Fig. D−10 *C. culmenus* sp. nov. (*C. adelus* subgroup), Fig. D−11 *C. fastigus* sp. nov. (temporarily unplaced species), Fig. D−12 *C. hylus* sp. nov. (*C. decipiens* subgroup) and Fig. D−13 *C. largifolius* sp. nov. (*C. largifolius* subgroup). Scale bar = 0.3 mm.

Illustration: The patches on the hind femora of *C. decipiens* group, which show the monophyletic or heterologous series. Fig. A1-8, B1−8 and C1−7 show the monophyletic series. Fig. D1−13 show the heterologous series (convergence and parallellism) from various monophyletic subgroups. Fig. A−1, B−1, C−1 and D−1; C−2 and D−4 etc. show heterologous similarity. The rest may be analogous. For the monophyletic similarity, see the discussion in the text.

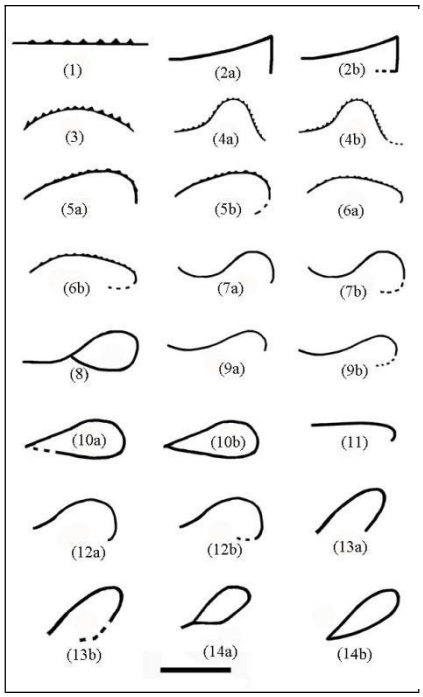


Figure 10 The apical margin of the apicoventral projection of the phallus sheath belonging to the second type of *C. decipiens* group Scale bar = 0.025mm.

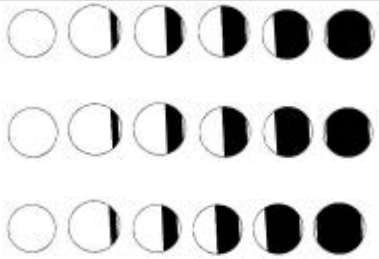
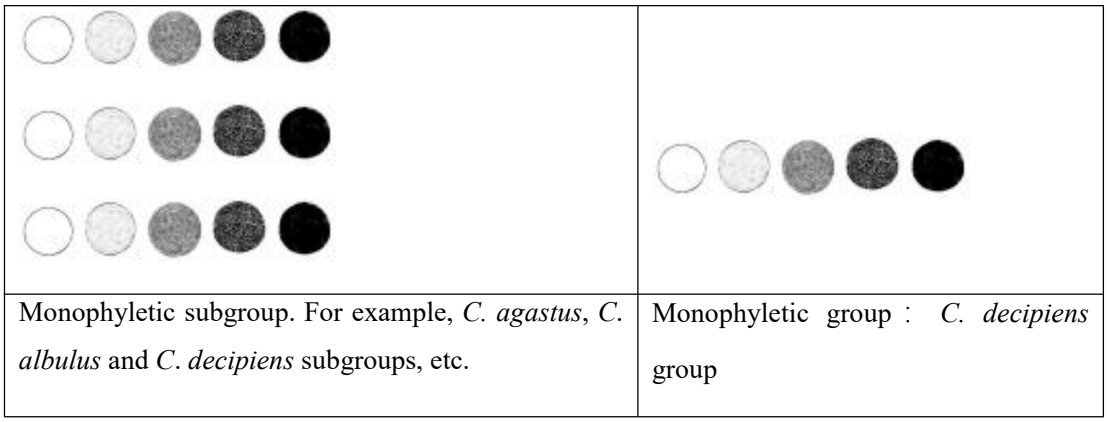
	
Monophyletic subgroup. For example, *C. agastus* *C. albulus* and *C. decipiens* subgroup, etc.	Monophyletic group：*C. decipiens* group

Figure 11 Showing the mosaic evolution of the spots on femora of *C. decipiens* group

The repetition of the same series transformation features of the spots on femora at different levels, which is shown to be repeated in the lower-level monophyletic subgroups (left) and the higher-level monophyletic groups (right).



Monophyletic subgroup. For example, *C. agastus*, *C. albulus* and *C. decipiens* subgroups, etc.	Monophyletic group : *C. decipiens* group

Figure 12 Showing the mosaic evolution of the spots on Cx_1 of *C. decipiens* group

The repetition of the same series transformation features of the spots on Cx_1 at different levels, which is shown to be repeated in the lower-level monophyletic subgroups (left) and the higher-level monophyletic groups (right).

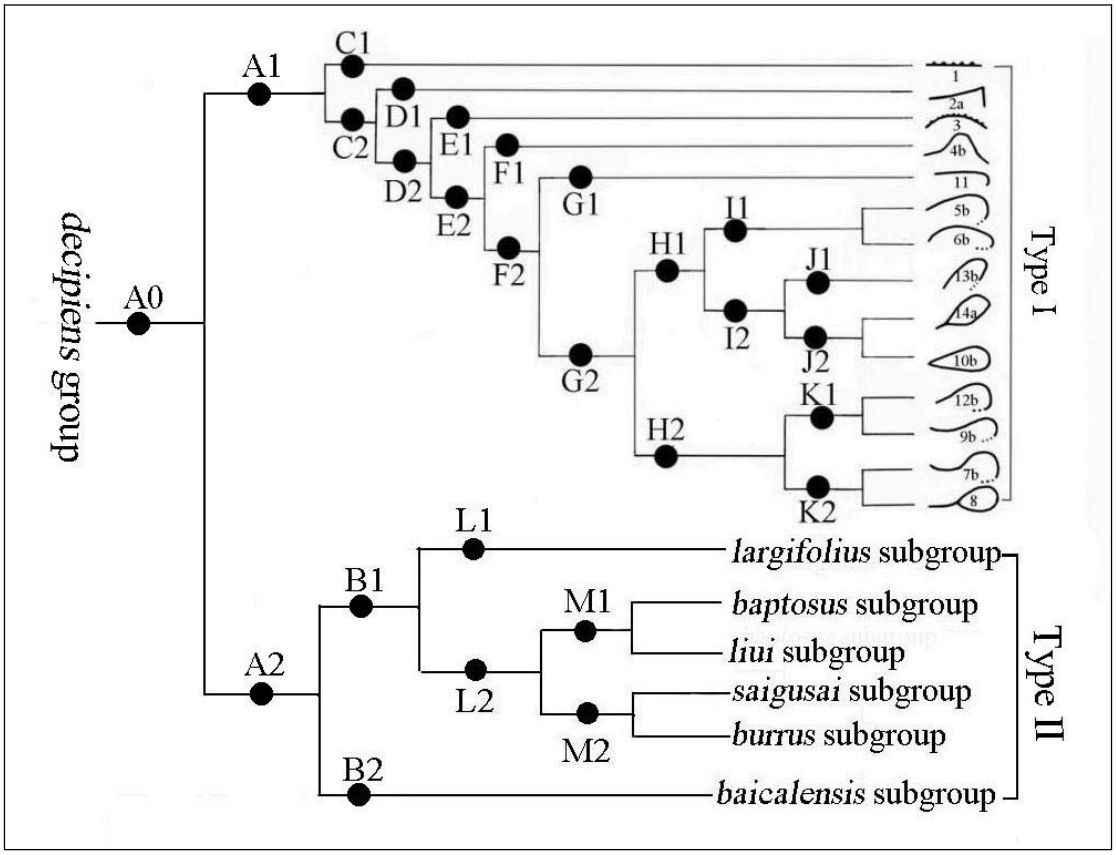


Figure 13 The phylogenetic tree of *C. decipiens* group

A0: Surstylus with an apical inner angle (■). Fore tibia with 1 small ad near basal 1/4 (■). Mid tibia with 2 strong ad (■) and 2 short and weak pd (■). **A1** (**Type I**): Phallus sheath distally with the apical margin of apicoventral projection developed in various forms of protuberance (■). **A2 (Type II)**: Phallus sheath distally with various forms of protuberance apically (■). **C1 (*C. guttus* subgroup)**: Phallus sheath distally with apicoventral margin in linear (□). **C2**: Phallus sheath distally with apicoventral margin in curved or folded processe (■). **D1 (*C. acolus* subgroup):** Phallus sheath distally with apicoventral margin raised in a

7-figure folded processe (■). **D2**: Phallus sheath distally with apicoventral margin raised in various arcs. (■). **E1 (*C. andrenus* subgroup):** Phallus distally with the apicomargin of the apicoventral projection shaped as an arc, the apex of which points backwards or downwards (□), never bent forwards (□). **E2**: Phallus sheath distally with the apicomargin of the apicoventral projection shaped as an arc, the apex of which points backwards (■) or forwards (■). **F1 (*C. decipiens* subgroup):** Phallus sheath distally with the apicomargin of the apicoventral projection shaped as an arc, the apex of which points backwards (■). **F2**: Phallus sheath distally with the apicomargin of the apicoventral projection shaped as an arc, the apex of which points backwards (■). **G1 (*C. blaesus* subgroup):** Phallus sheath distally with the apical margin of the apicoventral projection shaped as a straight hook (□). **G2**: Phallus sheath distally with the apical margin of the apicoventral projection raised in various remarkable expanded (■). **H1**：Phallus sheath distally with the apicomargin of the apicoventral projection shape as an oval, the dorsomedian of which not invaginated (□). **H2**：Phallus sheath distally with the apicomargin of the apicoventral projection shape as a S shape, the dorsomedian of which invaginated (■). **I1**：Phallus sheath distally with the apicomargin of the apicoventral projection raised in a semi-elliptical shape (■) or a wide and long oval shape (■). ***C. adelus*** **subgroup:** Phallus sheath distally with the apical margin of the apicoventral projection semi-elliptical in shape, the apex of which bends forwards, never points backwards and downwards. ***C. albulus*** **subgroup:** Phallus sheath distally with the apical margin of the

apicoventral projection developed in a long and wide oval shape, the apex of which bends forwards, never points backwards and downwards. **I2**: Phallus sheath distally with the apicomargin of the apicoventral projection raised in open (□) or closed (■) n-shape or fan-shaped (■). **J1** (***C. bomus*** **subgroup):** Phallus sheath distally with the apical margin of the apicoventral

projection raised in a n-shape, the apex of which bends forwards, never points backwards and downwards. **J2:** Phallus sheath distally with the apical margin of the apicoventral projection raised in a open or closed n-shape. ***C. euagus*** **subgroup:** Phallus sheath distally with the apical margin

Of the apicoventral projection developed as a loop in n-shape, the apex of which bends forwards,

forming a loop. ***C. aestus*** **subgroup:** Phallus sheath distally with the apical margin of the

apicoventral projection raised in a fan-shape ring, the two ends of which are connected or nearly so. **K1**：Phallus sheath distally with the apicomargin of the apicoventral projection raised in a hemispheric shape (□) or a round hook or a round hook (■). ***C. angustlus*** **subgroup**：Phallus sheath distally with the apical margin of the apicoventral projection raised in a hemispheric shape, the apex of which bends forwards, never points backwards and downwards. ***C. aberrantus*** **subgroup**：Phallus sheath distally with the apical margin of the apicoventral projection shape as a round hook **K2**: Phallus sheath distally with the apicomargin of the apicoventral projection raised in a S-shape (□) or S-shape apical ring (■). ***C. adelus*** **subgroup:** Phallus sheath distally with the apical margin of the apicoventral projection semi-elliptical in shape, the apex of which bends forwards, never points backwards and downwards.***C. angustlus*** **subgroup:** Phallus sheath distally with the apical margin of the apicoventral projection raised in

a hemispheric shape, the apex of which bends forwards, never points backwards and downwards. **B1 (*C. baicalensis* subgroup):** Phallus sheath distally with apex simple, which neither raised in various forms nor expanded apically. **B2:** Phallus sheath distally with the apex raised in various form or expanded apically. **L1 (*C. largifolius* subgroup):** Phallus sheath distally with the apex expanded into globula, being absent of the differentiation of dorsal and ventral projectiones. **L2:** Phallus sheath distally with the apex not expanded into globular, bearing the differentiation of dorsal and (or) ventral projection. **M1:** Phallus sheath distally with the apicoventral projection in flakiness, apex of which pointed or blunt**. M2:** Phallus sheath distally with the apicoventral projection conical or hooked. ***C. baptosus* subgroup:** Phallus sheath distally with the apicoventral projection rectangular. ***C. liui* subgroup:** Phallus sheath distally with the apicoventral projection knife-shape, pointed and snubby apically. ***C. saigusai* subgroup:** Phallus sheath distally with the apicoventral projection conical, pointed apically. ***C. burrus* subgroup:** Phallus sheath distally with the apicoventral projection hooked, denticulate ventrally and snubby apically.

Acknowledgements

Thanks to Professor Luo Qinghuai for discussing many taxonomic perspectives, theory and methods with the author, and put forward many useful opinions and suggestions.

REFERENCES

[1] Becker T. 1922a. Dipterologische Studien. Dolichopodidae. B. Nearktische und Neotropische Region [Diptera Study. Dolichopodidae I-III. B. Nearctic and Neotropical Regions]. Abhandlungen der Zoologisch-Botanischen Gesellschafin Wien 11 arifugus. 13: 1–394.

[2] Becker T. 1922b. Dipterologische Studien. Dolichopodidae der Indo-Australischen Region [Diptera Study. Dolichopodidae of Indo-Australischen Region] Capita Zoologica. 1(4):1–247.

[3] Bickel DJ. 2009. Family Dolichopodidae, with annotated key to the New World genera. p.671–694. In: Brown BV, et al. Manual of Central American Diptera: Volume 1, Ottawa, Ontario, Canada: NRC Press. 714 pp.

[4] Brundin, L. 1968. Application of Phylogenetic Principles in Systematics and Evolutionary Theory. Current Froblems of Lower Vertebrate Phylogy, Φrvig, T.(ed.)1968: 473-495. In: Translated works of cladistic systematics Beijing: Science

Press.1983: 253pp. Zhou MZ et al translate.

[5] Capellari RS. 2015. Review of the longipalpus-group of Chrysotus Meigen (Diptera: Dolichopodidae), with description of four new species. Neotropical Entomology, 44: 47–58.

[6] Capellari RS, Amorim DS. 2010. Re-description and new combination of five New World species of Chrysotus Meigen, with comments on the Neotropical genus Lyroneurus Loew (Diptera: Dolichopodidae). Zootaxa, 2520: 49–65.

[7] Capellari RS, Amorim DS. 2012. Systematic position of the monotypic Azorean genus Falbouria Dyte with notes on the defnition of Chrysotus Meigen (Diptera: Dolichopodidae). Zootaxa, 3489: 81–88.

[8] Fan, ZD. et al. 1988. Diptera: Anthomyiidae. Economic insect fauna of China 37. xiv+396 pp., 10 pIs. (in Chinese, with English descriptions of new taxa).

[9] Grichanov IY. 2016. A check list of species of the family Dolichopodidae (Diptera) of the World arranged by alphabetic list of generic names [online database]. http://dolicho.narod.ru/Genera3.htm

[10] Grichanov IY, Brooks SE. 2017. Dolichopodidae (longlegged dance flies). In: Kirk-Spriggs AH. et Sinclair BJ. (Eds.). Manual of Afrotropical Diptera, Nematocerous Diptera and Lower Brachycera. Suricata 5. Pretoria: SANBI Graphics et Editing, pp. 1265–1320.

[11] Hennig W. 1965. Phylogenetic Systematics, Annual Review of Entomology, 10(1): 97–116.

[12] Hollis D. 1964. On the Diptera of Nepal (Stratiomyidae, Therevidae and Dolichopodidae). Bulletin of the British Museum (Natural History) Entomology, 15(4): 83–116.

[13] Liu RS, Liang XM, Yang D. 2017. Chrysotus Meigen (Diptera: Dolichopodidae) from Guangxi of China with Descriptions of Three New Species. Transactions American Entomological Society, 143(1): 179–188. http://taes. entomo logy-aes.org/.

[14] Liu RS, Wang MQ, Yang D. 2013. Chrysotus Meigen (Diptera: Dolichopodidae) from Tibet with descriptions of four new species. Zootaxa, 3717: 169–178.

[15] Liu RS, Wang MQ, Yang D. 2015a. Chrysotus Meigen (Diptera: Dolichopodidae) from Shanxi, China, with descriptions of two new species. Zoological Systematics, 40(1):

86–92.

[16] Liu RS, Wang MQ, Yang D. 2016a. Chrysotus Meigen (Diptera: Dolichopodidae) from Inner Mongolia with Descriptions of Two New Species. Transactions American Entomological Society, 142(2): 155–165.

[17] Liu RS, Bian Y, Wang MQ, Yang D. 2016b. Chrysotus Meigen (Diptera: Dolichopodidae) from Hainan Island with descriptions of four new species. Transactions American Entomological Society, 142(1): 23–34.

[18] Liu RS, Chang WC, Guo L, Yang D. 2021. The first enlarged-palpus species of Chrysotus (Diptera:Dolichopodidae) in China. Entomotaxonomia (2021) 43(4): 298–302. DOI: 10.11680/entomotax.2021039, ISSN 2095–8609.

[19] Liu RS, Huang SP, Wang MQ, Yang D. 2019. A review of Chrysotus Meigen (Diptera: Dolichopodidae) from Palaearctic China. Transactions of the American Entomological Society, 145: 75–85.

[20] Liu RS, Zhong Y, Zhang RF, Yang D. 2020. A study of Chrysotus (Diptera: Dolichopodidae) from Sichuan, China with one new species. Entomotaxonomia (2020) 42(2): 1–6. DOI: 10.11680/entomotax.2020016, ISSN 2095–8609.

[21] Meigen JW. 1824. Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten [Systimatic Description of known from Euroupean dipteral Insecta]. Vol. 4. Hamm, xii + 434 pp., pls. 67–74.

[22] Negrobov OP. 1980. A revision of Palaearctic species of the genus Chrysotus Meigen (Diptera, Dolichopodidae). I. C. cilipes Meigen and C. laesius Wied. species groups. Ento. Oboz., 59 (2): 415–420. https://doi.org/10.1134/s0013873brevipulvillus080033

[23] Negrobov OP, Tsurikov MN, Maslova OO. 2000. Revision of the Palaearctic species of the genus Chrysotus Mg. (Diptera, Dolichopodidae), III, Ento. Oboz., 79(1): 227–238 (in Russian). (In Russian, English summary).

[24] Robinson H, Vockeroth JR (1981) 48. Dolichopodidae.– In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR and Wood DM. 1981: Manual of Nearctic Diptera,Volume 1. – Agriculture Canada Monograph, Quebec. 674 pp.

[25] Runyon, JB. 2020. The Dolichopodidae (Diptera) of Montserrat, West Indies. ZooKeys, 966(1): 57–151.

[26] Van Duzee MC. 1924. A revision of the North American species of the dipterous genus Chrysotus. Bulletin of the Buffalo Society of Natural Sciences, 13(3): 3–53.

[27] Vockeroth, JR. 1972. A review of the world genera of Mydaeinae, with a revision of the species of New Guinea and Oceania (Diptera: Muscidae), Pacif. Ins. Mon., 29: 15–16.

[28] Wang MQ, Yang D. 2006. Species of Chrysotus Meigen from Beijing (Diptera: Dolichopodidae). Deutsche Entomologische Zeitschrif, 52: 249–255.

[29] Wang MQ, Yang D. 2008a. New Species of Chrysotus from China (Diptera: Dolichopodidae). In: Xiaocheng Shen, et al. editors, Classifcation and Distribution of Insects in China. 23–32 [in Chinese]. Beijing; China Agricultural Science and Technology Press. 583 pp.

[30] Wang MQ, Yang D. 2008b. Species of Chrysotus Meigen in Palaearctic China (Diptera: Dolichopodidae). Entomologica Fennica, 15: 232–240.

[31] Wang MQ, Liu RS, Przhiboro and, Yang D. 2016. New species of Dolichopodidae from eastern Mongolia (Diptera). Entomologica Fennica, 41(1): 102–108.

[32] Wei LM. 2012a. The evolutionary signifcance on fr/fa ritio of Chrysotus Meigen (Diptera, Dolichopodidae, Diaphorinae), with description of one new genus and fve new species. Acta Zootaxonomica Sinica, 37(3): 611–622.

[33] Wei LM. 2012b. Chrysotus Meigen (Diptera: Dolichopodidae) from China with description of new species. Oriental Insects, 46(1): 30–52. https://doi.org/10.1080/ 00305 316.2012.675659

[34] Wei LM. 2018. A review of the genus Chrysotus Meigen (Diptera: Dolichopodidae) from China with definition of the leigongshanus species group. Oriental Insects, 52(supplement): 1–158.

[35] Wei LM, Luo Qinhuai. 2023. the Origin and Evelotion of the Subfamily Diaphorinae (Diptera, Dolichopodidae). Journal of Anshun University, 25(3): 109–115.

[36] Wei LM, Yang ZH. 2007. Dolichopodidae. In: Li ZZ, Yang MF, Jin DC, editors. Insects from Leigongshan Landscape. 561–587. Guiyang: China: Guizhou Science and Technology Press. 759 pp.

[37] Wei LM, Zhang LL. 2010. A taxonomic study on Chrysotus Meigen (Diptera: Dolichopodidae) from Southwest China: description of eleven new species belonging to

the redefned C. laesus group. Zootaxa, 2683: 1–22. https://doi.org/10.1080/00305316.2012.675659

[38] Wei LM, Zhang LL, Yang ZH, Jiang SG, Li H. 2011. Diptera: Dolichopodidae. Insects from Mayanghe Landscape: 391–412. In: Chen XS, Li ZZ, Jin DC, editors. Guiyang: China: Guizhou Science and Technology Publishing House. 519 pp.

[39] Wei LM, Zhang L, Zhou ZX. 2014. A review of the genus Chrysotus Meigen (Diptera: Dolichopodidae) from China with defnition of papuanus species group. Oreintal Insects, 48(3–4): 187–298. https://doi.org/full/10.1080/00305316.2015.1005960

[40] Yang D, Zhu YJ, Wang MQ, Zhang LL. 2006. World catalog of Dolichopodidae (Insecta: Diptera). Beijing: China Agricultural University Press. 704 pp.

[41] Yang D, Zhang LL, Wang MQ, Zhu YJ. 2011. Fauna sinica. In: Insecta, Vol.53, Diptera, Dolichopodidae (I, II). Beijing: Science Press. 1912 pp.

[42] Zhao TQ. 1995. Concepts and methods of systems biology. Beijing: Science Press. 253pp.

[43] Zhou ZX, Wei LM. 2017. Chrysotus Meigen (Diptera: Dolichopodidae) from China with descriptions of fIve new species belonging to the C. laesus group. Oreintal Insects, 51(3): 227–245. https://doi.org/10.1080/00305316.2016.1276486