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Taxonomy, identification, and phylogeny of the African and Madagascan species of the tiger beetle genus *Chaetodera* Jeannel 1946 (Coleoptera: Cicindelidae)

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Abstract. The taxonomy of the African and Madagascan species of the tiger beetle genus *Chaetodera* Jeannel 1946 (Coleoptera: Cicindelidae) is reviewed based on studies of primary types and additional museum specimens. Six species are recognized: *C. andriana* (Alluaud 1900), *C. antatsima* (Alluaud 1902), *C. blanchardi* (Fairmaire 1882), *C. maheva* (Künckel d'Herculais 1887), *C. perrieri* (Fairmaire 1897), and *C. regalis* (Dejean 1831). All species are illustrated, including color variants, and a key to species and maps of species distributions are provided. A hypothesis of phylogenetic relationships is proposed for the nine worldwide species of the genus *Chaetodera* based on computerized parsimony analysis of a matrix containing data on 16 adult morphological characteristics.

Introduction

The tiger beetle genus *Chaetodera* Jeannel (Coleoptera: Cicindelidae) contains nine species (Wiesner 1992) that are found in sub-Saharan Africa, Madagascar, India, and eastern Asia. Adults and larvae of the African and Madagascan species of *Chaetodera* are found primarily in association with sandy areas near water, including riverine sandbars, sandy riverbanks, and sandy beaches (Olsoufieff 1934; Werner 2000; Mawdsley and Sithole 2009). Certain species of *Chaetodera*, particularly the sub-Saharan species *C. regalis* Dejean, can be abundant in riparian and riverine areas, especially at sites where there has been minimal human disturbance (Werner 2000; Mawdsley and Sithole 2009). Accordingly, Mawdsley and Sithole (2009) have suggested that *C. regalis* could potentially serve as an “indicator” (in the sense of Pearson and Cassola 1992 and Kremen et al. 1993) of the health and overall environmental quality of African riverine systems. It is possible that other species in this genus might also have value as indicators of environmental conditions in riparian and riverine systems.

This paper forms part of a series of studies on southern African Carabidae and Cicindelidae, with a focus on riverine taxa and species associated with the Kruger National Park in the Republic of South Africa. Previous contributions in this series include Mawdsley and Sithole (2008; 2009), Mawdsley (2009), and Mawdsley et al. (2011). The goal of this series of publications is to provide high-quality identification materials for ground beetles and tiger beetles which are of potential interest to conservation biologists, environmental scientists, and park and natural area managers.

Separation of the species of *Chaetodera* from taxa in allied genera is based primarily on characteristics of the internal sac of the male genitalia (Rivalier 1957; Acciavatti and Pearson 1989; Werner 2000). Few outward characteristics readily separate all species of *Chaetodera* from species in allied genera (Acciavatti and Pearson 1989), particularly the closely related genus *Lophyra* Motschulsky. There is confusion in the literature regarding the boundaries between these two groups: in particular, two Madagascan species included by Rivalier (1957) and Wiesner (1992) in *Chaetodera* (*C. antatsima* and *C. perrieri*) have been placed by other authors in *Lophyra* (Jeannel 1946; Moravec 2008).

Some recent authors (e.g. Kryzhanovskij et al. 1995) have even gone so far as to consider *Chaetodera* to be a synonym of *Lophyra*. However, the separation of *Chaetodera* from *Lophyra* has been generally accepted by most recent authors (e.g. Acciavatti and Pearson 1989; Werner 1991; 1992; 2000; Moravec 2008). As noted by Acciavatti and Pearson (1989), most *Chaetodera* species are considerably larger than species of *Lophyra*, have distinctly different elytral markings, and have important differences in the position and number of setae, particularly on the antennae.

Some species of the genus *Chaetodera* have been included in other recent taxonomic treatments. The two Indian species of *Chaetodera* were revised by Acciavatti and Pearson (1989) while the single east Asian species was included in a treatment of the Palearctic Cicindelidae by Werner (1991; 1992). Werner

(2000) illustrated the two species from sub-Saharan Africa and briefly discussed their relationships and natural history. The Madagascan species were included in a series of earlier papers on Madagascan Cicindelidae by Horn (1934), Olsoufieff (1934), and Jeannel (1946). The four Madagascan species show clear relationships to the continental African species, and thus I include these two groups of species together in this study. One of the Indian species, *C. vigintiguttata* Herbst (1806), appears to be a member of the same lineage as *C. regalis*, *C. maheva*, and *C. andriana*. However, the relationships between the other Afrotropical and the Indian and Asian taxa in the genus *Chaetodera* are much less clear. In the final section of this paper, I present a provisional hypothesis of phylogenetic relationships for the nine species of the genus *Chaetodera* based on computerized cladistic analysis of a data matrix containing 16 adult morphological characters.

Materials Examined

I examined specimens from the following institutional and personal collections: **AMNH** (American Museum of Natural History, New York City, USA); **CMNH** (Carnegie Museum of Natural History, Pittsburgh, USA); **DEIC** (Deutsche Entomologische Institut, Eberswalde, Germany); **DWBC** (David W. Brzoska, Naples, Florida, USA); **FMNH** (Field Museum of Natural History, Chicago, USA); **KNPC** (Kruger National Park Research Collection, Skukuza, South Africa); **NMNH** (National Museum of Natural History, Washington, DC, USA); **SANC** (National Collection of Insects, Pretoria, South Africa); and **TMSA** (Transvaal Museum, Pretoria, South Africa).

Primary types of the taxa *Cicindela andriana* Alluaud, *Cicindela antatsima* Alluaud, *Cicindela antatsima* var. *fotsy* Alluaud, *Cicindela blanchardi* Fairmaire, *Cicindela maheva* Künckel d'Herculais, and *Cicindela perrieri* Fairmaire were obtained on loan from DEIC. Paratypes of *Cicindela regalis bremeri* Mandl were examined from DEIC and TMSA.

Moravec and Gillett (2009) noted that some Madagascan Cicindelidae in the collections of The Natural History Museum, London, had been erroneously labeled as “type” or “co-type” specimens. The type material of Madagascan Cicindelidae examined for the present study consists of specimens identified and labeled as types by W. Horn (presumably as part of his own taxonomic studies; see Horn 1934) or subsequent authors (e.g. Mandl 1982). Most of these specimens are syntypes which were obtained by W. Horn in exchange from the original authors or from the Muséum National d'Histoire Naturelle, Paris. Jeannel (1946) noted the presence of additional syntype specimens of many of these species in the collection of the Muséum National d'Histoire Naturelle, Paris. Because these species are reasonably well known from a taxonomic perspective, I have generally refrained from designating lectotypes for the Afrotropical species of *Chaetodera*.

Genus *Chaetodera* Jeannel 1946

Cicindela (*Chaetodera*) Jeannel (1946: 151; proposed as subgenus under *Cicindela*).
Chaetodera Jeannel (Rivalier 1957: 314, 330; elevation to full generic status).

Type species. *Cicindela regalis* Dejean, by original designation.

Synonyms.

Pseudochaetodera Pajni and Bedi (1974: 940), type species *Cicindela albina* Wiedemann 1819, synonymy by Acciavatti and Pearson (1989: 139-140).

Rivaliera Pajni and Bedi (1974: 939), type species *Cicindela vigintiguttata* Herbst 1806, synonymy by Acciavatti and Pearson (1989: 139-140).

Tribonophora Rivalier (1950: 223, 240), type species *Cicindela laetescripta* Motschulsky 1860, synonymy by Schilder (1953: 555).

Diagnosis. Acciavatti and Pearson (1989) listed the following diagnostic characters for the Indian species of the genus *Chaetodera*; this list will also serve to separate the Madagascan and African species from species in related genera:

- 1) Male aedeagus with well-developed internal sac, with long, highly convoluted flagellum and membrane which forms a fold on the right dorsal aspect;
- 2) Medium to large body size (length 10.0-18.5 mm);
- 3) Elytra with full complement of markings (humeral and apical lunules, basal spot, median band, and sutural band) that may be fused together or expanded to form transverse or oblique bands;
- 4) Abundant decumbent white setae, particularly on the thoracic and abdominal sternites, but also on the coxae, tibiae, tarsi, and occasionally on dorsal surface;
- 5) Fourth antennomere with additional setae and with a fully-formed penicillum (in the sense of Cassola 1983) present on fourth antennomere of males of four species.

Key to African and Madagascan Species of *Chaetodera* Jeannel

1. Femora iridescent coppery, rarely coppery with green sheen 2
- Femora metallic bluish-black or violet-black, rarely entirely black 4
- 2(1). Elytra almost entirely yellow, with an oblique black mark at base and numerous round black punctures on disc; Somalia ***C. blanchardi* (Fairmaire 1882)**
- Elytra ivory-white with black or brownish-black fasciae (bands), lacking numerous black punctures on disc; Madagascar 3
- 3(2). Dark elytral markings extending to lateral margin at one and usually two points, forming large oblique bands or stripes ***C. perrieri* (Fairmaire 1897)**
- Dark elytral markings not extending to lateral margin, often reduced to a network of narrow lines on disc ***C. antatsima* (Alluaud 1902)**
- 4(1). Yellow elytral markings narrow, strongly oblique (angled) ***C. maheva* (Künckel d'Herculais 1887)**
- Yellow elytral markings broader and more transverse (running more directly across the width of the elytra), especially on apical half (the half closest to the tip) 5
- 5(4). Dark elytral markings usually iridescent blue; yellow stripe along suture of elytra very short, not extending more than 1/3 the length of the elytra starting from the base; sub-Saharan Africa .
..... ***C. regalis* (Dejean 1831)**
- Dark elytral markings usually black; yellow stripe along suture of elytra much longer, extending more than 1/3 the length of the elytra starting at the base; Madagascar ***C. andriana* (Alluaud 1900)**

Group 1 – *perrieri* group

Diagnosis. The two species in this group (both Madagascan) can be distinguished by the lack of setae (glabrous) on the gena, the presence of ivory and black (as opposed to yellow and black) elytral markings, a more strongly convex pronotal disc whose surface is strongly shining, and by their coppery iridescent legs.

Taxonomic history. These two species are similar in appearance to some species of the genus *Lophyra* Motschulsky, particularly the South African *L. candida* (Dejean), and were treated as species of *Lophyra* by Jeannel (1946) and Moravec (2008). In contrast, Rivalier (1948; 1957) argued strongly to transfer these two species from *Lophyra* to *Chaetodera* based on shared similarities in the male genitalia and especially in the structure of the internal sac. Based on the combination of adult characters shared by these species, either these two species are members of the genus *Lophyra* that happen to have genitalic structures convergent on those of species of *Chaetodera*, or these two species are relatively basal members of the genus *Chaetodera*, sharing a derived genitalic structure with other members of the genus but still retain-

ing many of the features present in a *Lophyra*-like ancestor. On the basis of the character analysis presented at the end of this paper, I include these two species here as basal members of the genus *Chaetodera*.

***Chaetodera antatsima* (Alluaud 1902)**

Figures 1, 2, 16

Cicindela antatsima Alluaud (1902: 639-640, figure 5).

Synonym. *Cicindela antatsima* var. *fotsy* Alluaud (1913: 495). Synonymy by Horn (1934: 19).

Type material. Syntype male of *C. antatsima*, labeled “Madagascar (Sud)/Bassin du Mandraré/Alluaud 1900 44” (DEIC, examined); Syntype female of *C. antatsima* var. *fotsy*, labeled “Mananpatra” (DEIC, examined).

Diagnosis. Length 10.5-12.5 mm. Dorsal coloration as shown in Figures 1, 2. The extensive white coloration on the elytra separates this species from sympatric species of *Chaetodera* and *Lophyra*. It is most closely related to the Madagascan *C. perrieri*, from which it may be distinguished by the elytral color characteristics mentioned in the key to species (the elytral white areas are broadly expanded in *C. antatsima*, covering much of the disc, whereas the white areas on the elytra of *C. perrieri* are less extensive and tend to form alternating bands with the dark ground coloration).

Notes. Horn (1934) and Olsoufieff (1934) considered this species to be a regional variant or subspecies of *C. perrieri*, while Jeannel (1946) treated these two taxa as separate species. Based on the specimens examined for this study, I concur with Jeannel’s assessment. The differences in color pattern between *C. antatsima* (Figure 1-2) and *C. perrieri* (Figure 3-4), although subtle, appear to be consistent among the specimens available for study. I was unable to find any specimens that represented intermediate forms that might be expected if subspecific variation was involved. I confirm that *C. antatsima* var. *fotsy* is conspecific with *C. antatsima* based on examination of the relevant type specimens. Specimens identified as *C. antatsima* var. *fotsy* in collections are individuals of *C. antatsima* in which the dark markings of the elytra are especially reduced.

Material examined. MADAGASCAR: Ambositra (1 female, DEIC); Ampandrandava (1 male, 1 female, DEIC); Beroroha (1 male, DEIC); Mananpatra (1 male, 1 female, DEIC); Mandrare, I.1933 (1 female, DEIC), 1933 (1 female, DEIC); Morondava, III.1931 (1 female, DEIC); Plateau de l’Andray – Reg. d’Ambovombe (1 male, DEIC); Tamatave, 9.IV.1920 (1 female, DEIC); Tananarive (1 male, DEIC), XII.1919 (2 males, CMNH).

***Chaetodera perrieri* (Fairmaire 1897)**

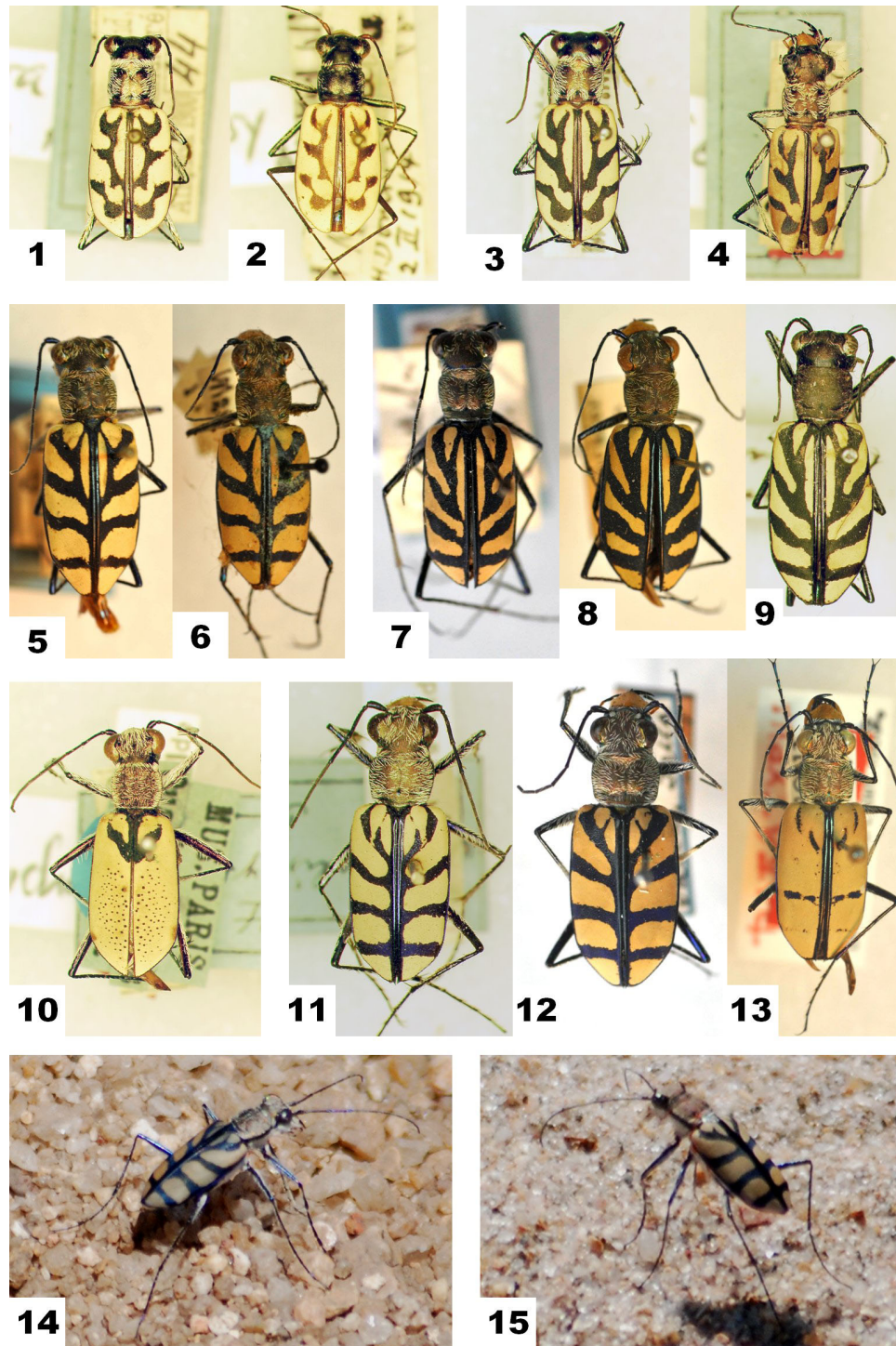
Figures 3, 4, 16

Cicindela perrieri Fairmaire (1897: 364)

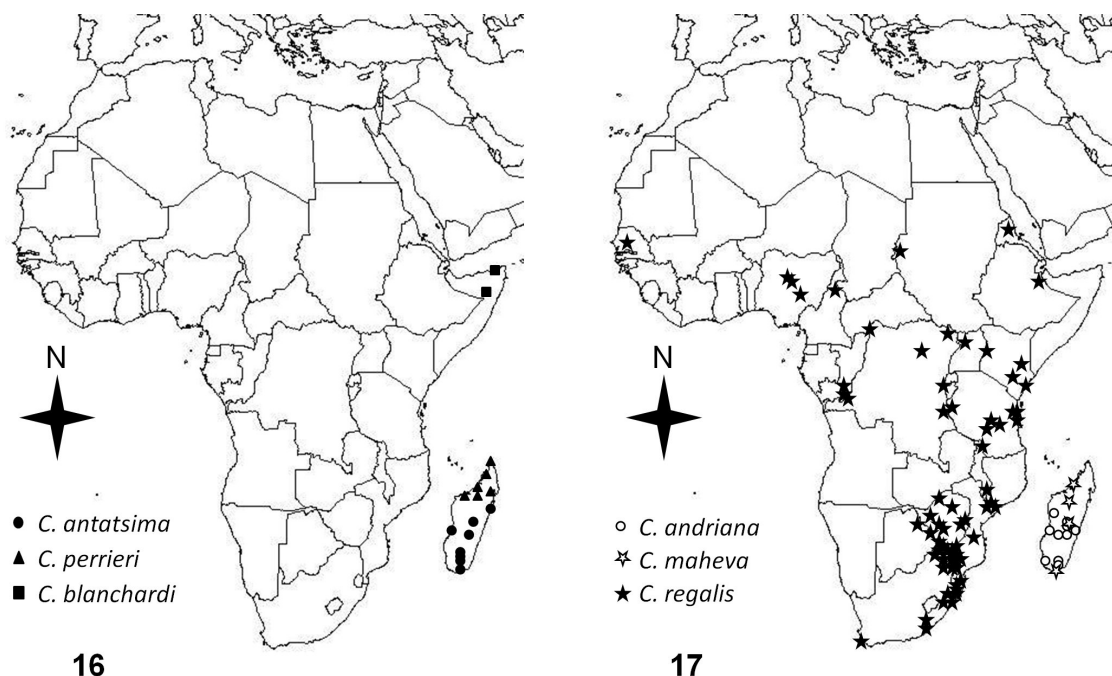
Type material. Syntype male of *C. perrieri*, labeled “Fairmaire/Madagascar” (DEIC, examined); Syntype female of *C. perrieri* labeled “Cicindela/perrieri/Madag.” and “Fairmaire/Perrier” (DEIC, examined).

Diagnosis. Length 10.0-13.0 mm. Dorsal coloration as shown in Figures 3, 4. This species is distinguished by its obliquely banded ivory-white and black elytral coloration. The other Madagascan species of *Chaetodera* with strongly oblique elytral markings is *C. maheva*, which has blue or violet tibiae and is much larger (15.0-18.5 mm in length vs. 10.0-13.0 mm) than *C. perrieri*.

Material examined. MADAGASCAR: Ambobaka, V (2 males, 1 female, DEIC); Analalava (1 male, DEIC); Ile de Berafia (1 female, CMNH); Majunga (1 male, 1 female, DEIC); Mt. d’Ambre, I.1929 (1 male, DEIC); Suberb Ile (1 male, DEIC).



Figures 1-15. Dorsal habitus images of Afrotropical *Chaetodera* species. 1) *C. antatsima*, syntype male, Madagascar Sud, Bassin du Mandraré. 2) *C. antatsima*, syntype female of *C. antatsima* var. *fotsy*, Mananpatra, Madagascar. 3) *C. perrieri*, male, Analaleva, Madagascar. 4) *C. perrieri*, syntype male, Madagascar. 5) *C. andriana*, syntype female, Madagascar (Sud), Bassin du Mandraré. 6) *C. andriana*, female, Ambositra, Madagascar. 7) *C. maheva*, syntype male, without locality label. 8) *C. maheva*, female, Majunga, Madagascar. 9) *C. maheva*, female, Maevatanana, Madagascar. 10) *C. blanchardi*, syntype male, Ouarsanguelis, Somalia. 11) *C. regalis*, male, Senegal. 12) *C. regalis*, female, Tana-Galla, Kenya. 13) *C. regalis*, paratype male of *C. regalis bremeri* Mandl, El Geneina, Darfur, Sudan. 14-15) Adult males of *C. regalis* photographed on sandbars of the Sabie River, Kruger National Park, South Africa.



Figures 16-17. Distribution of *Chaetodera* species in Africa and Madagascar. **16)** Distribution of *C. antatsima* (dark circles), *C. perrieri* (dark triangles), and *C. blanchardi* (dark squares). **17)** Distribution of *C. andriana* (open circles), *C. maheva* (open stars), and *C. regalis* (dark stars).

Group 2 – blanchardi group

Diagnosis. This group contains a single anomalous species from Somalia that appears to be intermediate in many of its characters between the species in Group 1 and the species in Group 3. The elytra are yellow and black, the pronotum is rectangular with the disc rugosely granulate, and the legs are iridescent coppery, occasionally coppery with a greenish sheen. The gena has a few setae that, however, are often rubbed off in specimens so that the gena appears glabrous.

Chaetodera blanchardi (Fairmaire 1882)

Figures 10, 16

Cicindela blanchardi Fairmaire (1882: 4)

Type material. Syntype male, labeled “Ouarsanguelis” and “Mus. Paris/Somali/Révoil.-1881” (DEIC, examined).

Diagnosis. Length 12.0-14.0 mm. Dorsal coloration as shown in Figure 10. This species is easily distinguished from all other species of *Chaetodera* by its unique elytral color pattern and the presence of large, black punctures on the elytral disc (Figure 10).

Material examined. SOMALIA: (1 male, 1 female, CMNH); 4 km SW of Garoowe, 23.V.1979 (1 male, 1 female, NMNH).

Group 3 – regalis group

Diagnosis. Originally recognized by Rivalier (1957), this group contains three large, stout-bodied species from Africa and Madagascar with similar color patterns and banded elytral markings. The elytra are yellow and black or blue, the legs are metallic blue-black or violet-black, and the gena is densely covered

with hair-like setae. The fourth antennomere of the males in this group has a true “penicillum” or flag-like cluster of erect sensory setae (in the sense of Cassola 1983). I tentatively assign *C. vigintiguttata* Herbst from India to this group, based on similarities in body size, antennal setae (including the presence of a penicillum on the fourth antennomere in males), and elytral markings.

***Chaetodera andriana* (Alluaud 1900)**

Figures 5, 6, 17

Cicindela andriana Alluaud (1900: 18, figure 2)

Type material. Syntype female, labeled “Madagascar (Sud)/Bassin du Mandraré/Alluaud 1900 48” (DEIC, examined).

Diagnosis. Length 14.0-17.0 mm. Dorsal coloration as shown in Figures 5, 6. This species is easily distinguished from the Madagascan *C. maheva* by its broader yellow markings that run more directly across the width of the elytra (more transverse) than those of *C. maheva*, particularly on the back (apical) half of the elytra. From the continental African *C. regalis*, it differs in having the dark elytral markings black when viewed directly from above (these markings are typically metallic blue in *C. regalis*, but on rare occasions can be black) and in having a much longer yellow marking along the basal portion of the elytral suture. The black elytral markings of *C. andriana* occasionally will have a metallic blue sheen, especially when viewed obliquely (at an angle).

Material examined. MADAGASCAR: Ambositra (1 male, DEIC; 1 female, NMNH); Anakazoabo (1 male, AMNH); Analalava (1 female, AMNH); Ankazoabo (1 female, CMNH); Antsalova, I.1987 (1 male, TMSA); Befotaka (2 males, CMNH); Mandrare, I.1933 (1 male, DEIC); Morondava, III.1931 (1 female, DEIC); Plateau de l’Andray – Reg. d’Ambovombe (1 female, DEIC); Tananarive (1 female, CMNH; 1 male, 1 female, DEIC), 1924 (1 female, DEIC), V.1925 (1 male, CMNH); Tuléar, 1930 (3 males, 1 female, DEIC). “Madagascar” (1 male, DEIC).

***Chaetodera maheva* (Künckel d’Herculais 1887)**

Figures 7-9, 17

Cicindela maheva Künckel d’Herculais (1887: pl. 24 f. 3).

Type material. Syntype male, labeled “Cicindela/maheva/Fm” and “Fairmaire” (DEIC, examined). Syntype female, labeled “Cicindela/maheva/Fairm. Madg.” (DEIC, examined). Although labeled as type specimens by W. Horn, these may actually be material associated with the redescription of the species by Fairmaire (1897), rather than the original illustration by Künckel d’Herculais (Moravec and Gillett 2009).

Diagnosis. Length 15.0-18.5 mm. Dorsal coloration as shown in Figures 7-9. Easily separated from *C. andriana* and *C. regalis* by its much narrower and more strongly oblique (angled) black and yellow elytral markings. From *C. antatsima* and *C. perrieri* it can be separated by its larger size (body length 15.0 mm or more) and by its pale yellow elytral markings rather than ivory-white.

Material examined. MADAGASCAR: Maevatanana (1 male, 1 female, AMNH; 1 male, CMNH; 2 females, DEIC; 1 female, NMNH); Majunga (1 female, DEIC); Plateau de l’Andray – Reg. d’Ambovombe (1 female, DEIC); Tananarive (1 female, CMNH), XII.1919 (1 male, 1 female, FMNH).

Taxonomic Notes. The specific epithet has been attributed to Künckel d’Herculais (Jeannel 1946; Wiesner 1992; Moravec and Gillett 2009) and also to Fairmaire (Horn 1934; Olsoufieff 1934). The name “*Cicindela maheva*” was originally applied by Künckel d’Herculais (1887) to two figures in the “Atlas” volume of the “Histoire Naturelle des Coléoptères,” which in turn formed part of the monumental multi-volume “Histoire Physique, Naturelle, et Politique de Madagascar” edited by Alfred Grandidier. The first of the two figures (pl. 24 f. 3) labeled *C. maheva* by Künckel d’Herculais is the species now known as *C. maheva*, while the

second of the two figures (pl. 24 f. 4) labeled *C. maheva* by Künckel d'Herculais is the species now known as *C. andriana*. A full description of the species now known as *C. maheva* was not provided until Fairmaire (1897), leading other authors (Horn 1934; Olsoufieff 1934) to attribute the name to Fairmaire, rather than Künckel d'Herculais. According to the International Code of Zoological Nomenclature (ICZN 1999; see Article 12, Names published before 1931, and particularly section 12.2.7), the association of the name "*Cicindela maheva*" with the illustration in Künckel de Herculais (1887: pl. 24 f. 3) is sufficient "indication" to render the name *Cicindela maheva* available. Thus the name should be attributed to Künckel d'Herculais (1887) and not Fairmaire (1897).

***Chaetodera regalis* (Dejean 1831)**

Figures 11-15, 17

Cicindela regalis Dejean (1831: 251-252).

Synonyms. *Chaetodera regalis veneranda* Rivalier (1952: 213); *Chaetodera regalis bremeri* Mandl (1982: 70-71).

Type material. Of *Chaetodera regalis* (Dejean), type locality "dans les parties supérieures du Sénégal," type material in Muséum National d'Histoire Naturelle, Paris. Of *C. regalis veneranda* Rivalier, type locality "de l'Ouaddai (Iriba et environs d'Iriba, Bakauore, massif de Kapga)," type series in Muséum National d'Histoire Naturelle, Paris. Of *C. regalis bremeri* Mandl, 2 paratype males, labeled "Sudan, Prov. Darfur/ El Geneina/7.VIII.1977" and "ad lucem" (DEIC and TMSA, examined). Mandl (1982) misspelled the type locality of *C. regalis bremeri* as El Gemeina.

Diagnosis. Length 13.5-18.5 mm. Dorsal coloration as shown in Figures 11-15. The only species of *Chaetodera* found in most of sub-Saharan Africa, *C. regalis* can be easily recognized by its distinctive elytral color pattern and by the iridescent blue coloration on the elytra in most specimens (although individual specimens will occasionally have black elytral markings rather than iridescent blue markings).

Notes on subspecific taxonomy. Specimens from portions of Niger, Chad and western Sudan have greatly expanded yellow markings on the elytra (Figure 13). Rivalier (1952) described specimens of this color form from Ouaddai, Chad, as *C. regalis veneranda*, while Mandl (1982) described specimens of this color form from El Geneina, Sudan as *C. regalis bremeri*. Rivalier (1952) noted the relative constancy in elytral coloration across the series of 28 specimens he examined from Chad. In contrast, Mandl (1982) noted a wide range of color forms in the El Geneina population, ranging from four specimens with the standard *C. regalis* elytral markings to a larger number of specimens with almost entirely yellow elytra, with a series of intermediate color forms also present. It is not clear from the limited information available whether the forms with expanded yellow markings are sufficiently abundant within enough populations to constitute a distinct geographical subspecies. Additional material from Chad and Sudan is needed in order to clarify the subspecific status of the populations with expanded markings. Should these populations form a valid subspecies, the name *C. regalis veneranda* has priority over *C. regalis bremeri*.

Material examined. BOTSWANA: 4 km E Francistown, Tati River, 29-30.XII.1987 (4 males, 7 females, CMNH); Nata, 13-15.I.1978 (4 males, 1 female, NMNH); 3 km W Nata, Nata River, 25.XII.1988 (19 males, 16 females, CMNH); 4 km W Nata, Nata River, 25.XII.1987 (16 males, 20 females, CMNH); 10 km E Nata, Nata River, 25.XII.1987 (1 male, CMNH); Tuli Lodge, Limpopo River, 1-3.IV.1988 (50 males, 41 females, CMNH). BURUNDI: Bujumbura, Lake Tanganyika, 26.I.1984 (3 males, 2 females, NMNH); 18.VI.1992 (1 male, 1 female, CMNH), same locality at 700 m, 24.VI.1992 (2 males, 2 females, CMNH), same locality at 750 m, 6.VII.1992 (3 males, 1 female, CMNH). CAMEROON: 10 km E Gouna, 3.IV.1972 (1 male, NMNH). CENTRAL AFRICAN REPUBLIC: Bangui-Bimbi, VIII.1978 (16 males, 16 females, CMNH). DEMOCRATIC REPUBLIC OF THE CONGO: Faradje, XI.1912 (1 female, AMNH); Kalemie, Lake Tanganyika, XII.1973 (1 male, CMNH); Kinchassa, 25.X.1896 (1 male, DEIC); Kisangani, XII.1979

(1 female, CMNH). ERITREA: Cheren (1 male, DEIC), XI (2 females, DEIC). ETHIOPIA: Harrar, Eren (2 males, DEIC). KENYA: Kacheliba, W Suk, IV.1961 (1 female, NMNH); 10 km N Malindi at Sabaki River, 25.IV.1978 (3 males, CMNH); Tana - Galla (1 male, 1 female, DEIC); Tana River, 1892-1893 (2 males, 1 female, NMNH; 1 female, AMNH); Yatta Ettui, XI.1960 (1 male, NMNH). MALAWI: Utale, Zomiza District, I.1903 (1 male, TMSA). MOZAMBIQUE: Boroma, Zambesi (1 male, FMNH); Luabo, 12.XII.1954 (1 female, TMSA); Massangana, 1-8.II.1964 (2 males, 2 females, NMNH); Senna, Zambezi River, 1904 (1 female, NMNH). NIGERIA: Benue State, 15 km E Makurdi, Abinsi, Benue River, 1.XI.1998 (16 males, 24 females, CMNH). Federal Capital Territory, at river near Abuja International Airport, 25.IX.1998 (5 males, 10 females, CMNH), 4 miles N Lapai, Guara Falls, 18.X.1998 (1 female, CMNH). REPUBLIC OF THE CONGO: Kintele, XI.1972 (14 males, 15 females, CMNH), 16.XII.1976 (1 male, 1 female, CMNH), 30.VIII.1977 (1 female, CMNH), 30.X.1977 (1 male, CMNH), 30.XI.1977 (1 female, CMNH), XI.1978 (1 male, CMNH); Odziba, XII.1978 (1 female, NMNH). SENEGAL: (2 males, DEIC). SOUTH AFRICA: Eastern Cape Province: Beacon Bay, 20.III.1981 (1 male, TMSA); Kei Cuttings, 13.I.1985 (2 females, TMSA). Gauteng Province: Pretoria (1 female, NMNH). Kruger National Park: Letaba, 8.III.1966 (1 female, KNPC), 1978 (2 males, 2 females, TMSA); Letaba Camp, 14-18.XI.1961 (1 male, NMNH); Letaba River, 25 km S Letaba Camp, 24.XI.1999 (3 males, 3 females, DWBC); Mahlengeni, on road, 29.XI.1996 (1 female, SANC); Olifants Camp, XI.1967 (2 males, 1 female, TMSA), 19.II.1968 (1 male, CMNH; 1 male, 1 female, KNPC; 6 males, 6 females, NMNH); Olifants River at Road S-90, 10 km S of Olifants Camp, 24.XI.1999 (3 males, 3 females, DWBC); Pafuri, 9.III.1966 (1 male, KNPC); Punda Maria, XI.1932 (2 males, 2 females, TMSA); Shingwedzi, 19-20.XI.1961 (1 female, NMNH; 1 male, 6 females, TMSA); Skukuza, 7-22.XII.1972 (1 male, SANC); Skukuza, malaise trap, 21.XI-5.XII.1972 (1 male, 1 female, SANC); Skukuza, 370 m, 5.XII.1977 (1 female, TMSA); Skukuza Research Camp, ultraviolet light and trap, 22.I.1995 (1 male, TMSA), 19.II.1995 (1 male, 1 female, TMSA). KwaZulu-Natal Province: Dukuduku Forest Station, lake shore, 4.IV.1974 (2 males, 3 females, TMSA); Empageni University, IX.1975 (1 male, TMSA); 80 miles N Empageni, XII.1927-I.1928 (1 female, NMNH); Greytown, XII.1897 (2 females, NMNH); Hluhluwe Game Reserve, Nzimane River (near Hippo Pool), 30.XI.1998 (3 males, 3 females, DWBC); Jozini Dam, Lebombo Mountains, 11-14.XII.1961 (1 female, TMSA); near Jozini, I.1985 (3 males, SANC); Mtunzini, at light at night, I.1998 (1 female, SANC); Natal (1 female, AMNH); Pongola, at river, 8.IV.1974 (1 male, 1 female, TMSA); Tugela, Mvoti, XI.1897 (1 male, NMNH); White Umfolozi, 2.I.1923 (1 male, 1 female, SANC); locality not specified (1 female, AMNH), 11.I.1955 (1 male, SANC). Limpopo or Northern Province: D'Nyala Nature Reserve, Ellisras District, 10-14.XI.1986 (1 male, SANC), 18-20.XII.1987 (1 male, SANC), 23-26.II.1987 (3 males, 2 females, SANC); Ellisras, 20.VII.1962 (1 female, TMSA), 16.XII.1964 (1 male, TMSA), 1.I.1971 (1 male, TMSA), 27.XII.1973 (1 male, TMSA); Farm Scrutton, 29.V.1976 (1 male, TMSA); Letaba Estates, I.1977 (1 male, SANC), 6.I.1978 (1 female, SANC), 10.I.1978 (1 male, SANC); Highway R36 – Makhutswi River (S Ofcolaco) (3 males, 3 females, DWBC); Mica, Olifants River, 3.I.1972 (1 male, CMNH); Mogol Nature Reserve, Ellisras, 19-23.XI.1979 (3 males, 3 females, SANC), 19.I.1983 (2 males, SANC), 27-29.II.1984 (1 male, 1 female, SANC), 28.II.1984 (1 male, 2 females, SANC); Nylsvlei, II.1903 (2 males, TMSA); Route 36 and Olifants River, 15.XII.2004 (2 males, 2 females, DWBC); Pont Drift, Limpopo River, 23.XII.1973 (1 female, CMNH); 63 km S Tzaneen, 29.XII.1977 (1 male, 1 female, TMSA); Vaalwater, IV.1963 (1 male, TMSA), 2.III.1980 (1 male, TMSA); Zomerkomst, Politzi, III.1964 (1 male, SANC); 20.III.1965 (1 male, SANC). Mpumalanga Province: 10 km E Hazyview, Sabie River, 18.IV.1992 (1 female, CMNH); Komatipoort, light trap, XII.1959 (1 female, SANC), I.1960 (1 female, SANC); Lydenburg District, 1896 (1 male, TMSA); Nelspruit, XII.1973 (1 male, NMNH); Strydam Tunnel, 31.V.1976 (1 male, 1 female, TMSA). Western Cape Province: Cape Town, Lions Head, III.1959 (1 male, 1 female, CMNH; 2 males, 2 females, TMSA). SUDAN: Prov. Darfur, El Geneina, 7.VIII.1977, at light (1 male, DEIC, and 1 male, TMSA, Paratypes of *Cicindela regalis bremeri* Mandl). TANZANIA: Dar es Salaam (1 male, NMNH; 1 female, CMNH); Kassanga (1 male, 1 female, NMNH); Lake Nyassa (1 female, NMNH); Madibira, XI.1908 (1 male, FMNH); Mhonda (1 male, 1 female, DEIC; 1 male, NMNH); Ruaha National Park, 18.I.1972 (1 male, CMNH); Ungoni (1 male, AMNH); Wiedhafen, 1906 (1 male, FMNH; 1 female, NMNH); Zanzibar (1 female, AMNH). UGANDA: Budonga Forest (1 male, NMNH). ZIMBABWE: Birchenough Bridge, 7.I.1947 (1 female, TMSA); Gwanda, 1906 (1 male, 1 female, SANC); Hot Springs, 7.XI.1973 (1 female, DEIC), 18.XI.1975 (1 male, TMSA); Kariba, 13.I.1973 (1 male, 2 females, TMSA), 14.I.1973 (1 male, TMSA), 5.II.1973 (1 female, TMSA); Highway A-8, Lukosi River, SE-Hwange, 1.XII.1999 (3 males, 3 females, DWBC); Lukosi Mission, 700 m, 30.XI-1.XII.1990 (3 males, 2

females, SANC); Mukumbata, 24.XII.1972 (1 male, TMSA); Sawmills, 17.XI.1917 (1 male, TMSA), 24.XI.1918 (1 female, SANC).

Cladistic Analysis

The following set of 16 adult morphological characters was identified through detailed study of pinned specimens of all known *Chaetodera* species. As in my previous phylogenetic studies of other lineages within Cicindelidae (Mawdsley 2009; 2010), surface sculpture and setal patterns provide a rich set of characters for use in phylogenetic reconstruction.

- 1) Frons mostly glabrous except for small clusters of white setae adjacent to eyes (0); more or less uniformly setose, sometimes with a glabrous patch at mid-frons (1).
- 2) Gena glabrous (0); with patch of dense white setae (1).
- 3) Antennomere 4 with 2-3 regular white setae (0); with a compact cluster of modified erect setae ("penicillum") (1).
- 4) Anterior margin of pronotum with a fringe of white, anteriorly-directed setae (0); fringe absent (1).
- 5) Pronotum lacking distinct setal tufts or clusters of white setae in apical corners (0); with tufts of white setae in apical corners (1).
- 6) Pronotum about as wide as long (0); distinctly longer than wide (1).
- 7) Pronotal disc convex, shape subcylindrical (0); planate, shape subquadrate (1).
- 8) Pronotal surface smooth (0); rugose (1).
- 9) Elytra stout, robust, lateral margin broadly rounded (0); elongate, slender, lateral margins more parallel-sided (1).
- 10) Elytral markings strongly oblique, including those on apical half of elytra (0); elytral markings more transverse, especially those on apical half (1).
- 11) Pale areas on elytral disc lacking large, conspicuous punctures at apex (0); with 3-4 large, conspicuous black punctures on apical fifth (1); not applicable because pale areas greatly reduced in size (?).
- 12) Elytral apices of female tapering to a single, shared point (0); elytral apices of female sinuate-truncate (1).
- 13) Elytral apex lacking a spine (0); with a distinct spine (1).
- 14) Legs metallic coppery (0); violet, blue, blue-green, or black (1); variable (?).
- 15) Metatarsal claws elongate, about as long as fifth metatarsomere (0); short, much shorter than fifth metatarsomere (1).
- 16) Internal sac of male genitalia small (0) large, elongate (1).

A taxon-character matrix was constructed in WinClada (Nixon 2002) by scoring each of these characters for each of the nine species of the genus *Chaetodera*, as listed by Wiesner (1992). *Lophyra candida* was selected as an outgroup species for the cladistic analysis, which appeared to be a logical choice given the strong similarities between *L. candida* and *C. antatsima* and *C. perrieri* that have already been noted earlier in this paper. All characters were scored for the outgroup taxon as well as the nine ingroup taxa.

Table 1. Taxon-character matrix for cladistic analysis of species of *Chaetodera* Jeannel. Characters are listed in numerical order from left (1) to right (16).

<i>Lophyra candida</i>	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0
<i>Chaetodera albina</i>	1	1	0	0	1	0	1	1	1	0	1	1	1	0	1
<i>Chaetodera andriana</i>	1	1	1	0	1	0	1	1	1	1	0	1	1	1	1
<i>Chaetodera antatsima</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1
<i>Chaetodera blanchardi</i>	1	1	0	0	1	0	1	1	1	0	1	1	1	?	1
<i>Chaetodera laetescripta</i>	0	1	0	0	1	1	0	0	1	0	1	1	1	1	1
<i>Chaetodera maheva</i>	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1
<i>Chaetodera perrieri</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1
<i>Chaetodera regalis</i>	1	1	1	0	1	0	1	1	1	1	0	1	1	1	1
<i>Chaetodera vigintiguttata</i>	1	1	1	1	1	0	1	1	1	0	?	1	1	1	1

Cladistic parsimony analysis of the resulting taxon-character matrix was conducted using the fast parsimony analysis program NONA (Goloboff 1993). The following settings were used in the NONA analysis: Hold (maximum number of trees to keep in memory) = 100; Number of replications = 5; Number of starting trees per rep = 5. Branch swapping was recommended and was performed on the resulting most parsimonious tree. A single tree with 18 steps, consistency index 88, and retention index 92 was recovered from the completed analysis. The tree was imported into the WinClada (Nixon 2002) software package and a “hard collapse” was performed to remove one node which was unsupported by character state transitions. The individual character state transitions were then mapped to this tree using the WinClada software package. Ambiguous state transformations were mapped using the “Fast” (accelerated transformation) command in WinClada (Nixon 2002). The resulting cladogram is shown as Figure 18.

The cladogram in Figure 18 indicates that the genus *Chaetodera* (in the sense of Wiesner 1992) is monophyletic, at least with respect to the South African outgroup taxon *Lophyra candida*. The two Madagascan species *C. antatsima* and *C. perrieri* are sister-taxa to the rest of the species currently recognized within *Chaetodera*. These two species are relatively isolated, both from the outgroup (from which they are separated by 5 steps) and from the remainder of the species in *Chaetodera* (from which they are separated by 7 or more steps). The possibility that these two species might represent an independent lineage within the genus *Lophyra* or within the broader *Lophyra* generic complex deserves further investigation. The node above the branching point of *C. antatsima* and *C. perrieri* is the most strongly supported node on the tree, with four non-homoplastic character state transitions. The one taxon that branches off at this node is *C. laetescripta*, an east Asian species which is isolated geographically from all other species of the genus and also exhibits significant differences in its body form and elytral markings from the other species in the genus. The next node is an unresolved trichotomy between two additional anomalous species (*C. albina* from India and *C. blanchardi* from Somalia) and the four closely related taxa in the *C. regalis* species group. As with *C. laetescripta*, *C. albina* and *C. blanchardi* have each evolved color patterns, surface sculpturing, and/or setal combinations which are not present in the other species of the genus. The species in the *C. regalis* group differ from each other mainly in details of the elytral markings; the cladogram in Figure 18 provides support for the hypothesis that these four species do in fact form a monophyletic group.

The relative positions of the taxa on the cladogram in Figure 18 suggest that much of the evolutionary history within the genus *Chaetodera* has taken place within sub-Saharan Africa and Madagascar. The most logical outgroup taxon for this group is South African, the basal clade is Madagascan, *C. blanchardi* is Somalian, and three of the four species in the *C. regalis* group are Afrotropical (two species are Madagascan and one species is widespread throughout sub-Saharan Africa). Figure 18 indicates that the three Asian species of *Chaetodera* are not most closely related to each other, suggesting that each of these species may represent a separate, independent past dispersal event during the evolutionary history of the genus *Chaetodera*.

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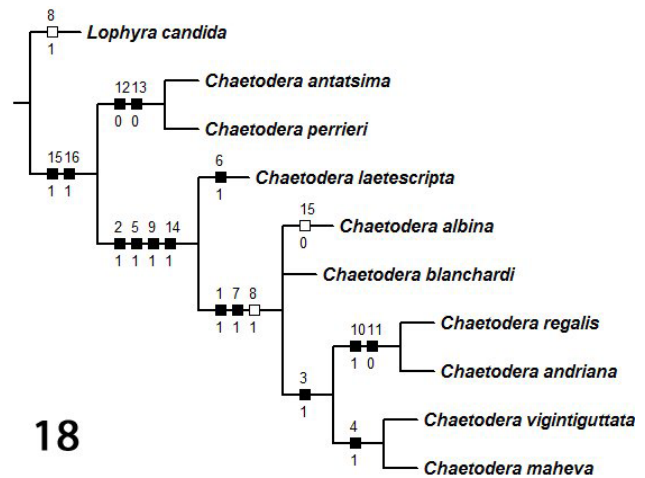


Figure 18. Most parsimonious tree resulting from cladistic analysis of the taxon-character matrix in Table 1, having length 18, consistency index 88, and retention index 92.

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