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Revision of the genus *Chalcasthenes* Arrow (Coleoptera: Scarabaeidae: Dynastinae: Oryctoderini) from the Solomon Islands

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Abstract

The genus *Chalcasthenes* Arrow (Dynastinae: Oryctoderini), a scarab beetle genus endemic to the Solomon Islands, is reviewed. Based on examination of type specimens, the genus *Strehlia* Frey (Rutelinae: Rutelini: Parastasiina) is a new junior synonym of *Chalcasthenes*. The historical classification of these genera (either in the subfamily Dynastinae or Rutelinae) and character-based criteria for assigning the taxa to the Dynastinae are provided. We discuss character states that support the monophyly of members of the genus *Chalcasthenes*, comment on the distribution and biogeography of species in the genus and provide a key to species. The genus includes four species: *Chalcasthenes divinus* Endrödi, *Chalcasthenes pulcher* Arrow, *Chalcasthenes squamigerus* Frey new combination and *Chalcasthenes styroceros* Jameson and Ratcliffe n. sp. Species hypotheses are corroborated based on evidence from Pleistocene geological reconstructions of the Solomon Islands, geographic variation of bird species in the region, and development in scarab beetles.

Keywords: allometry, biogeography, Rutelinae, Scarabaeoidea, *Chalcasthenes*, *Strehlia*

Introduction

During the course of our research on Rutelinae and Dynastinae (both Coleoptera: Scarabaeidae), we encountered examples of two rare and unusual scarab beetles, *Strehlia squamigera* Frey (Rutelinae: Rutelini: Parastasiina) and *Chalcasthenes divinus* Endrödi (Dynastinae: Oryctoderini). We discovered that these beetles are the same insect, each of which was placed in a different subfamily. The mistaken classification has gone undetected for decades. Classification errors such as this prevent retrieval of biodiversity data and cause measures of biodiversity to be overestimated.

In this work, we correct this problem and provide characters that support synonymy of the genus *Strehlia* Frey with *Chalcasthenes* Arrow, discuss the characters that warrant classification of the taxon in the subfamily Dynastinae and provide a revision of the four species in the genus, including a key, distributional data and descriptions. Representative specimens in the genus are rare, and variability in the genus could be linked to allometric characters. Thus, our morphology-based species hypotheses are corroborated based on three other sources of evidence: (1) the distribution of *Chalcasthenes* species is consistent with geological information on island formation; (2) the high degree of geographic variation in *Chalcasthenes* species correlates with the high degree of geographic variation in Solomon Island bird species; and (3) the observed interspecific variation in beetle characteristics is consistent with hypotheses for speciation based on developmental pathways of allometric characters in scarab beetles.

Materials and Methods

Specimens for this research are deposited at the BMNH (The Natural History Museum, London, UK), BPBM (Linsley Gressitt Center for Research Entomology, Bernice P. Bishop Museum, Honolulu, HI, USA), FSCA (Florida State Collection of Arthropods, Gainesville, FL, USA), MLJC (Mary Liz Jameson collection, Lincoln, NE, USA), NAGAI (Shinji Nagai Collection, Tokyo, Japan), NAIC (National Agricultural Insect Collection, Boroko, Papua New Guinea), NHMB (Naturhistorisches Museum Basel, Basel, Switzerland), UNSM (University of Nebraska State Museum, Lincoln, NE, USA) and USNM (United States National Museum, Washington, DC, USA; currently housed at UNSM).

Internal and external morphological characters formed the basis of this work. The broadest range of potentially phylogenetically informative morphological characters was used for morphological analyses and comparisons. Body measurements, puncture density, puncture size and density of setae are based on the following standards. Body length was measured from the apex of the clypeus to the apex of the pygidium. Body width was measured across the elytral humeri. Puncture density was considered “dense” if punctures were nearly confluent to less than two puncture diameters apart, “moderately dense” if punctures were from two to six puncture diameters apart and “sparse” if punctures were separated by more than six puncture diameters. Puncture size was defined as “small” if punctures were 0.02 mm in diameter or smaller, “moderate” if 0.02–0.07 mm, “moderately

large" if 0.07–0.12 mm and "large" if 0.12 mm or larger. Setae density was defined as "dense" if the surface was not visible through the setae, "moderately dense" if the surface was visible but with many setae and "sparse" if there were few setae. Types of setae were defined as "bristle-like" if slender and erect, "thickened" if slightly thick and erect or partially decumbent and "scale-like" if broad, flat and decumbent. It should be noted that setae are subject to wear and might be abraded away. The interocular width measures the number of transverse eye diameters that span the width on the frons between the eyes. This was measured by placing the ocular micrometer in a position such that it intersects the frons and eyes (dorsal view), focusing on the surface of the frons and then measuring the width of the frons and width of the eyes without adjusting the focus.

Characters and specimens were observed with 6.3–50.0× magnification and fiber-optic illumination. Digital images of specimens and structures were captured using the Auto-Montage imaging system by Syncroscopy (Synoptics Inc., Frederick, MD, USA). Images were edited in Adobe Photoshop CS2 (Adobe Systems Inc., San Jose, CA, USA) (background removed, contrast manipulated).

We use the phylogenetic species concept (Wheeler & Platnick 2000) in this work: "a species is the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states."

History of classification of *Strehlia* and *Chalcasthenes*

The genus *Chalcasthenes* Arrow (1937) was originally placed in the tribe Cyclocephalini (Dynastinae) which, at that time, included some genera that are currently considered members of the tribe Oryctoderini (e.g. *Oryctoderus* Boisduval, *Chalcocrates* Heller) as well as the tribe Cyclocephalini (e.g. *Cyclocephala* Dejean, *Chalepides* Casey, *Dyscinetus* Harold). Arrow named the genus for a single species, *Chalcasthenes pulcher* Arrow, and he commented that the taxon "is probably more nearly related to the very isolated genus *Chalcocrates* than to any other yet known" (Arrow 1937, p. 42). Arrow stated that the genera *Chalcocrates* and *Chalcasthenes* shared such features as metallic surface, prominent eyes, form of the clypeus (small and narrow), and form of the mouthparts and legs. In addition, he identified several characteristics that are unique to the new taxon: surface with scale-like setae, shape of the body (short, convex, broad), propygidium with a stidulatory file (which he compared with *Heteronychus* Burmeister), nine-segmented antenna, form of the fifth protarsomere (enlarged and with a wide cleft) and form of the protarsal claws of the male (deeply and widely cleft).

Frey (1969) described the genus *Strehlia* and included in it one species: *S. squamigera* Frey. Frey placed the genus in the subfamily Rutelinae, and he compared the taxon with *Ceroplophana* Gestro (Rutelini: Parastasiina), but he did not discuss character states shared among the genera and provided little commentary regarding classification. He did, however, include figures of the head (dorsal and lateral) showing the unusual horn-like process. Frey believed the species be-

longed to the subfamily Rutelinae, so apparently he did not investigate the literature for similar species in the Dynastinae. He might have relied on the form of the protarsal claws (widely cleft) and the labrum (weakly produced beyond the apex of the clypeus) to place the species in the subfamily Rutelinae. These characters, however, are not wholly reliable for circumscription of the subfamilies.

Endrödi (1971) described *C. divinus* and noted that his new species was closely related to *C. pulcher* based on the shared form of the male parameres and the unusual scale-like setae. He included the new taxon in the tribe Oryctoderini, a group that he had created by splitting the tribe Cyclocephalini into a New World component and a component that included taxa from Oceania, Indomalaysia and the Oriental region (Endrödi 1967, 1971). He also noted that the new species was the only member of the Oryctoderini with a well-developed head horn, unusual metallic sheen (shared only with *Chalcocrates*, also a member of the Oryctoderini) and peculiar form of the claws that are split and similar to some Rutelinae. Endrödi stated that the form of the claws is shared with some Rutelinae and Dynastinae and it is "proof" that the two subfamilies are "extraordinarily close," and this character overlap occasionally caused classification conflicts (Endrödi 1971, p. 208). His remarks were, in fact, quite prescient.

Since this time, little attention has been paid to the genera *Strehlia* and *Chalcasthenes*. Images of the taxon were published in Endrödi (1985) as *Chalcasthenes* and in Nagai (2001) as *Chalcasthenes*. However, the similarity of these two disparately classified beetle genera has gone unnoticed.

Dynastinae vs. Rutelinae

The problem in classifying *Chalcasthenes* and *Strehlia* originates from the difficulty in diagnosing the subfamilies Dynastinae and Rutelinae. The lack of circumscription of higher-level taxa based on shared, derived character states has created a disconnect that has resulted in classification problems and does not allow for predictions based on evolutionary relationships. It is our hope that ongoing research on the higher-level phylogenetics of phytophagous scarabs will establish a solid foundation for addressing the evolution, biogeography, and classification of this diverse group of scarab beetles.

The subfamilies Rutelinae and Dynastinae belong to the phytophagous scarab clade (Melolonthinae, Cetoniinae, Dynastinae, Rutelinae, and minor subfamilies) (Smith et al. 2006), also referred to as the "pleurostict" scarabs (Erichson 1847). Monophyly of this clade is well supported (e.g. Howden 1982; Browne & Scholtz 1998; Smith et al. 2006), but relationships within the clade are poorly studied and not resolved (Smith et al. 2006). Within the phytophagous scarab clade, there is evidence that the subfamilies Dynastinae and Rutelinae form a clade (Howden 1982; Browne & Scholtz 1998; Jameson 1998; Smith et al. 2006). However, based on morphological (Jameson 1998) and molecular data (Smith et al. 2006), some higher-level groups (genera, subtribes, tribes) within the Dynastinae and Rutelinae

Table 1. Diagnostic characters and character states for Rutelinae and Dynastinae (Scarabaeidae)

Character	State in Dynastinae	State in Rutelinae
Fifth mesotarsomeres and metatarsomeres	Apices entire (not split) claws not independently movable	Apices with a medial, longitudinal slit that allows the claws to move independently
Unguitractor plate	Cylindrical (at least at the base)	Laterally flattened
Inner apex of the metatarsomeres	Truncate (not posteriorly produced)	Posteriorly produced

are hypothesized to be paraphyletic. For example, molecular data support a clade comprised of the ruteline tribes Anomalini and Adoretini plus the Dynastinae (Anomalini + (Adoretini + Dynastinae)) as sister to the remaining Rutelinae, thus rendering the Rutelinae paraphyletic. Many systematists have discussed shared morphological character states of the Rutelinae and Dynastinae (e.g. Arrow 1908; Endrödi 1971; Howden 1982; Browne & Scholtz 1998; Jameson 1998; Smith et al. 2006), thus raising questions of paraphyly in several tribes of Rutelinae and Dynastinae. These data speak to the historic difficulties in classifying such genera as *Strehlia*, *Chalcasthenes*, *Peltonotus* Burmeister, *Melanhyphus* Fairmaire, *Neohyphus* Heller, *Acrobolbia* Ohaus, and others. In particular, classification problems have involved members of the dynastine tribes Oryctoderini and Cyclocephalini as well as the ruteline tribes and/or subtribes Peltonotini, Pelidnotina, Acrobolbiina, and Parastasiina. For example, members of the Indomalayan genera *Melanhyphus*, *Neohyphus*, and *Peltonotus* have vacillated between the Dynastinae (being placed either in the tribe Oryctoderini or Cyclocephalini) and Rutelinae (being placed in the tribe Rutelini or Peltonotini) (e.g. Burmeister 1847; Arrow 1917; Endrödi 1971, 1985; Machatschke 1972; Kuijten 1994; Jameson 1998; Jameson & Wada 2004).

As currently constituted, we distinguish the subfamilies Dynastinae and Rutelinae based on the general characteristics in Table 1 (Jameson 1998; Jameson et al. 2002).

Synonymy of Strehlia with Chalcasthenes

Based on examination of the type species for the genera *Strehlia* and *Chalcasthenes*, we synonymize the genus *Strehlia*. The type species of *Strehlia*, *S. squamigera*, and the type species of *Chalcasthenes*, *C. pulcher*, are congeneric based on the diagnostic character states (see “Diagnosis” of the genus *Chalcasthenes*) and additional shared character states such as maxilla with six teeth in two parallel rows (Figure 7), lacinia with inner apex produced, tooth-like (Figure 7), form of the hind wing (Figure 13), form of the male genitalia (Figure 12a,b), prosternal keel bridged to sternum, male protibia tridentate with basal tooth removed and less laterally produced than other teeth (Figures 19–22). Based on these shared features, we consider the genus *Strehlia* to be a new junior synonym of *Chalcasthenes*.

The genus *Chalcasthenes* is a member of the subfamily Dynastinae based on the following character states: the fifth mesotarsomeres and metatarsomeres with apices not split, claws not independently movable, unguitractor plate cylindrical, inner apex of the metatarsomeres not produced posteriorly.

Biogeography and endemism in the Solomon Islands

Species of *Chalcasthenes* are endemic to the Solomon Islands, a region that hosts high levels of endemism. A number of factors have worked in concert to produce high endemism in this region: remoteness of the islands from continental areas, fragmentation of species’ ranges caused by insularity of the islands, post-Pleistocene colonization and diversification across islands, and habitat diversity created by diverse geography, volcanism, and climatic conditions. Within the Solomon Islands, 40% of the orchids are endemic (Hunt 1969), 44% of the land birds are endemic (Smith & Filardi 2007), and 38% of the birds occur elsewhere but are represented by distinct races and subspecies (Mayr 1945; Mayr & Diamond 2001). The exceptional endemism and patterns of speciation in the Solomon Islands inspired formation of the biological species concept (Mayr 1942, 1963), the theory of island biogeography (MacArthur & Wilson 1967), and theories on dispersal, competition, and gene flow (Diamond 1970, 1974).

In order to understand the evolution of biodiversity in the region, one must understand the composition of the Solomon Islands. The Solomons and Bougainville are part of the East Melanesia region in the southwest Pacific and are a biodiversity hotspot (Mittermeier et al. 2004). The islands are located in the Pacific “ring of fire,” a string of active volcanoes that erupt periodically. The distance between the westernmost and easternmost islands is approximately 1500 km. Buka and Bougainville Islands are at the northern end of the Solomon Islands, but they are politically part of Papua New Guinea. Bougainville is the largest of the Solomon Island chain and is home to several high massifs, some of which are volcanic (including Mount Balbi at 2,685 m). Southeast of Bougainville and Buka are the remainder of the Solomon Islands which are formed by two parallel chains of islands. The northern chain includes Choiseul, Santa Isabel, Malaita, and Ulawa, while the southern chain includes Vella Lavella, Kolombangara, New Georgia Islands and Rendova, the Russell Islands, the Florida Islands, Guadalcanal, and Makira.

The Solomon Island insect fauna is influenced by the ocean-equatorial climate that produces an annual rainfall of approximately 3,050 mm, mean temperatures of 27°C and high humidity. Seasonality is slight, but high rainfall and occasional squalls or cyclones are more likely from April to November when trade winds blow from the southeast (Mittermeier et al. 2004). On exposed islands, seasonal cyclones cause mosaics of secondary successional forests. Islands that are less exposed to cyclones are home to tall gallery forests.

Diversification of species within the Solomon Islands is poorly understood. The islands have never been in direct contact with New Guinea, and it is generally thought that the biota is a mix of long-distance dispersers and older indigenous taxa that are derived from Pacific-Gondwana lineages (Mittermeier et al. 2004). Biota of the Solomon Islands region is distinctively Melanesian and is thought to have been part of the migrating Solomon arc terrane in the Oligocene (Polhemus & Polhemus 1998). Distribution patterns of aquatic Heteroptera suggest that fauna were derived from westward extensions of the Solomons arc or due to dispersal following accretion of the arc with Papua New Guinea (Polhemus & Polhemus 1998). Reconstructions of the biotic history in Southeast Asia support a pattern of relationship between the Solomon Islands to Papua New Guinea and Australia (Turner et al. 2001).

Pleistocene sea level fluctuations greatly affected the distribution of flora and fauna on the islands. At the height of the last glaciation, sea level was 170–200 m lower than present day (Ollier 1985; Lambeck & Chappell 2001). Lower sea levels during Pleistocene glacial episodes created the Pleistocene Island referred to as “Greater Bukida,” a region that included present-day Buka in the north to the Florida Islands in the south (Diamond et al. 1976). It is possible that Greater Bukida also included Guadalcanal Island (Diamond et al. 1976; Smith & Filardi 2007). The islands of Malaita and Makira in the southern Solomon Island chain were not part of Greater Bukida. Post-Pleistocene sea level rise subsequently isolated regions of Greater Bukida, resulting in the present island chain. Alternating fusion (during glacial episodes) and fission (during inter-glacial episodes) of closely related lineages complicates reconstruction of evolutionary events.

Patterns of diversification in the Solomon Islands region are controversial. Some research provides evidence that diversification followed a “stepping stone” pattern from continental to remote islands (Wilson 1959). However, molecular phylogenetic research on the monarch flycatchers with emphasis on endemic Solomon Island species (*Monarch* spp.; Monarchidae; Aves) inferred that diversification was centered in the tropical Pacific region (Filardi & Moyle 2005). This tropical Pacific lineage diverged into two clades: one that includes Micronesia and insular Melanesia, and another that includes central and eastern Polynesia. These two clades appear to meet (but not overlap) in the eastern Solomon Islands (Filardi & Moyle 2005).

As a biodiversity hotspot, conservation is an issue on the islands. The islands are still largely forested because of a modest human population density and an extremely wet climate that prevents burning of forest habitat. The Solomon Islands crowned pigeon (*Microgoura meeki* Rothschild: Columbidae) and an endemic race of grey teal (*Anas gibberifrons* Muller: Anatidae) are extinct from the islands, largely because of the introduction of cats. Nine other birds that are resident endemics of the Solomon Islands are hypothesized to be extinct. According to Diamond (1987), Solomon Islands birds are less at risk of extinction compared with other oceanic islands because human population pressures are not as

high and the Solomon Islands have native rats that, in effect, “immunize” the native bird species from the arrival of introduced rats. Rarity of *Chalcasthenes* specimens in collections suggests rarity in nature. We think the species are probably restricted to a narrow range of habitats in the Solomon Islands; thus, populations are at risk of endangerment because of human alteration of habitat.

In addition to members of the genus *Chalcasthenes*, other dynastine scarabs endemic to or present in the Solomon Islands include: *Papuana cheesmanae* Arrow, *Dipelicus oryctooides* Fairmaire (both Pentodontini), *Xylotrupes gideon szekessyi* Endrödi (Dynastini) (Endrödi 1967), *Coenoryctoderus candezei* (Lansberge), *C. robustus* Prell, *Oryctoderus godeffroyi anguliceps* Prell, *Melanhyphus platygenioides* Fairmaire, *Melanhyphus kleinschmidti* Fairmaire (all Oryctoderini) (Endrödi 1985), *Scapanes australis salomonensis* Sternberg (Oryctini) (Rowland et al. 2005) and *Xylotrupes ulysses clinias* Schaufuss (Dynastini) (Rowland 2003).

Variability and allometry in species of *Chalcasthenes*

High intraspecific variability is a hallmark of Solomon Island bird species (Diamond et al. 1976), and we noted a great deal of variation in members of *Chalcasthenes*, including a forward-projecting clypeal horn or no horn, small- or long-antennal club, arcuate or not arcuate protibia, twisted or not twisted metatibial spurs and small or large eyes. These characteristics could be associated with allometry, which could confound our species hypotheses. To address whether *Chalcasthenes* morphotypes were the equivalent of lineages (species) or whether they were representative of intraspecific variation, we examined developmental evidence in dynastine scarabs. We possess only one female specimen, thus we must rely on characters of males.

Research has demonstrated that modifications in development might drive morphological divergence and beetle diversification (Moczek & Nijhout 2003; Rowland 2003; Emlen et al. 2005). For example, it is hypothesized that the developmental system that controls male horn dimorphism in *Xylotrupes* Hope (Dynastinae) is regulated by an environmentally cued threshold response that is sensitive to larval size (Moczek 1998; Emlen & Nijhout 1999; Moczek & Emlen 1999). Male larvae smaller than a certain threshold body size develop only rudimentary horns, whereas male larvae larger than the threshold size express well-developed horns (Moczek 1998; Emlen & Nijhout 1999; Moczek & Emlen 1999; Moczek et al. 2004). This response is subject to rapid evolutionary modification that leads to diversification in populations (Rowland 2003).

There is, however, a cost to horn development because of longer larval development and increased risk to pathogens in the soil (Hunt & Simmons 1997) as well as developmental trade-offs that result in stunted relative growth of adjacent structures including eyes, wings, antennae, mouthparts, genitalia, and testes (Emlen 2001; Moczek & Nijhout 2004; Emlen et al. 2005; Emlen & Philips 2006). For example, horns that develop on the clypeus or frons are likely to reduce the relative size of the antennae, mouthparts, and eyes, thus possibly im-

1. *Chalcasthenes divinus*, male 2. *Chalcasthenes divinus*, female 3. *Chalcasthenes pulcher*, male 4. *Chalcasthenes squamigerus*, male 5. *Chalcasthenes styracoceros*, male

Figures 1–5. Habitus images of *Chalcasthenes* species. (1) *C. divinus*, male (paratype); (2) *C. divinus*, female (allotype); (3) *C. pulcher*, male (paralectotype); (4) *C. squamigerus*, male (holotype); (5) *C. styracoceros*, male (holotype). Scale line = 1.0 mm.

pacting olfactory capabilities, feeding, and vision, respectively (Emlen et al. 2005). Horns that develop on the thorax are likely to reduce the relative size of wings, thus affecting flight capabilities (Kawano 1995, 1997; Emlen 2000). According to Emlen et al. (2005), if the relative cost of horn growth differs across selective habitats and regimes, selection to minimize the cost of horn expression could lead to diversification in horn morphology. Thus, colonization of new habitat might result in a shift in horn morphology. In species of *Chalcasthenes*, developmental pressures could have influenced the various horn morphologies and associated allometric forms. Ancestral founder events on different islands might have affected developmental pathways for horns that led to fixation of traits. These mechanisms might have influenced diversification of populations of *Chalcasthenes* on the Solomon Islands.

Rowland et al. (2005) developed a numerical model for differentiating horn morphology (minor vs. major horn morphology) and detecting polymorphisms in populations. Because of the limited number of individuals in our sample for this research, we could not use Rowland's methods for examining male polymorphism in *Chalcasthenes*. It is our hope that this research will lead to additional material that will allow for more robust hypotheses.

Genus *Chalcasthenes* Arrow (1937) (Figures 1–24)

Chalcasthenes Arrow (1937, p. 42). Type species *C. pulcher* Arrow (1937, pp. 42–43) (by monotypy).

Strehlia Frey (1969, p. 480, f. 2). Type species *S. squamigera* Frey (1969, p. 481, f. 2) by monotypy. **New synonymy.**

Description. Scarabaeidae: Dynastinae. Length 12.0–21.0 mm; width 6.0–10.0 mm. **FORM** (Figures 1–5): subovate, sides subparallel, propygidium exposed or not beyond apex of elytra, pygidium exposed, apex of elytra broadly rounded. Surface shining, weakly metallic green, punctate and setose or not; setae (male) dense or moderately dense, scale-like or thickened; setae (female) sparse, scale-like or thickened. **HEAD** (Figures 14–18): frons weakly convex or flat, surface punctate, setose or not; setae moderately dense or sparse, scale-like or thickened, decumbent. Clypeus with (males) or without (males and/or females) forward-projecting horn; apex broadly parabolic (Figure 18a), trapezoidal (Figure 17a), angularly attenuated near mid-shaft with subrectangular apex (Figure 16a) or quadridentate (Figures 14a, 15a); surface punctate, with or without setae; lateral surface impunctate, punctate or rugopunctate.

Figures 6–13. Generic characters for members of the genus *Chalcasthenes*. (6) left mandible, dorsal view, of *C. divinus*; (7) right maxilla, ventral view, of *C. divinus*; (8) propygidium and pygidium, dorsal view, of *C. squamigerus*; (9) propygidium showing stridulatory rows of *C. squamigerus*; (10) protarsomeres 4–5 and protarsal claws, dorsal view, showing widely cleft claw of male in *C. divinus*; (11) metatibial apex showing twisted form of metatibial spur in *C. divinus* male; (12) male genitalia of *C. divinus* in dorsal (a) and lateral (b) views; (13) left hind wing, ventral view, of *C. squamigerus*.

Frontoclypeal suture weakly impressed, incomplete (approximately equal to length of ocular canthus), projecting posteriorly. Ocular canthus flat, not projecting anteriorly, not carinate. Labrum weakly produced anteriorly beyond apex of clypeus; apex broadly rounded, densely setose. Mandibles (Figure 6) weakly projecting anteriorly beyond apex of labrum, apex with two weakly recurved teeth, scissorial teeth lacking, molar area reduced and with poorly defined lamellae. Mentum broadest at base, length approximately 1.5 times width; surface flat; apex broadly rounded; labial palpus three-segmented. Maxilla (Figure 7) with six teeth in two parallel rows; four teeth from base to subapex parallel to two teeth from subapex to apex; lacinia with inner apex produced, tooth-like,

densely setose; palpus four-segmented. ANTENNA: nine- or 10-segmented, club shorter or longer than segments 2–7. PRONOTUM: form widest at middle, beaded laterally and anteriorly; anterior angles weakly acute or rounded; base weakly rounded, longest at mid-base, not beaded; basal angle (ventral view) with well-developed or poorly developed ridge; lateral margin rounded, weakly sinuate or sinuate (Figures 14b–18b). Surface punctate, with or without setae; vaulted (Figure 14b) or not (Figures 15b–18b) (lateral view). SCUTELLUM: shape parabolic, apex weakly acute, slightly wider than long, base declivous at pronotum. ELYTRA: elytral suture length subequal to width of both elytra. Surface with moderately dense to dense scale-like setae; setae cream-colored, elongate-oval or tear-drop-

Figures 14–18. Form of the head (a, dorsal view) and head, eye, antenna and thorax (b, lateral view) in members of *Chalcasthenes*. (14) *C. divinus*, male; (15) *C. styracoceros*, male; (16) *C. squamigerus*, male; (17) *C. pulcher*, male; (18) *C. divinus*, female.

shaped. Epipleuron of female simple (not expanded). Inner apex rounded. PROPYGIDIUM (Figures 8,9): surface armed with two rows of stridulatory pegs (Figure 9), each row with 6–16 pegs; rows separated at apex, weakly divergent at base; stridulatory pegs short, broadly cylindrical, with single seta on apex; seta stiff, tawny. PYGIDIUM (Figure 8): shape broadly ovate-triangular, evenly convex in lateral view, apex beaded. VENTER: prosternal keel produced to middle of procoxae, bridged to prosternum,

shape triangular; apex projecting anteriorly at approximately 80° with respect to ventral plane. Mesometasternal apex not produced or keel-like. Mesocoxae nearly contiguous. Sternum setigerously punctate; setae moderately dense or sparse, scale-like (decumbent, short, cream-colored) or bristle-like (not decumbent, moderately long, cream-colored or tawny). Sternites 1–4 subequal in length, sternite 5 approximately 1.25 times as long as sternite 4; sternite 1 deflexed slightly at apex. Last sternite with apex

Figures 19–23. Form of the protibia, protarsomeres and protarsal claws in members of *Chalcasthenes*. (19) *C. divinus*, male; (20) *C. pulcher*, male; (21) *C. squamigerus*, male; (22) *C. styracoceros*, male holotype; (23) *C. divinus*, female allotype.

weakly sinuate (male) or rounded (male or female). LEGS (Figures 10–11, 19–23): protibia with inner margin weakly arcuate or not, external margin tridentate, basal tooth removed and less produced laterally relative to other teeth (males; Figures 19–22) or not (females; Figure 23); apical spur decurved (males) or not (males and females). Protarsomeres of male longer than broad; tarsomeres 1 and 2 simple; 3 and 4 each with inner, apical tooth; 5 with inner ridge from base to apex, inner apical tooth well-developed or not; inner apex lacking longitudinal slit (claws not independently movable). Protarsomeres of female longer than broad; tarsomeres 1–4 simple; 5 lacking inner ridge and inner apical tooth; inner apex lacking longitudinal slit (claws not independently movable). Protarsal claws of male with dorsal claw widely toothed (Figures 10, 19–20, 22), ventral claw simple and approximately one-third size of dorsal claw. Protarsal claws of female simple, angled towards venter, ventral claw approximately two-thirds size of dorsal claw (Figure 23). Mesotarsal and metatarsal claws (males and females) simple, angled towards venter, ventral claw approximately two-thirds size of dorsal claw. Unguitractor plate extending beyond apex of fifth tarsomere, cylindrical, empodium bisetose. Mesotibia and metatibia of male with margins subparallel, with median carina, with apex truncate or with produced external tooth. Mesotibia and metatibia of female divergent from base, median carina and apex more divergent than male. Mesotibia

and metatibia with two apical spurs; spurs greatly curved (males; Figure 11) or not (males and females). Metatrochanter with apex simple (not produced). Metacoxa with apex subquadrate. HIND WING (Figure 13): precostal membrane with weakly developed hooks and thickened setae; hooks present from near base to near apex, moderately dense; setae present at apex, dense. Anterior edge from medial fold to apex of wing with dense, thickened setae. Vein AA1+2 short, approximately one-eighth length of vein AA3+4. MALE GENITALIA (Figure 12a,b): parameres hinged laterally, shape symmetrical, not diagnostic at species level.

Diagnosis. Within the Scarabaeoidea, the genus *Chalcasthenes* is readily distinguished based on the presence of thickened, scale-like setae on the body (e.g. Figures 1–5), the male protarsal claw with the dorsal claw widely toothed (Figure 10), the unusual form of the head horn in the male (Figures 1, 4–5, 14–16; absent in one species), the propygidium with two rows of stridulatory pegs (Figures 8, 9) and its distribution in the Solomon Islands and Bougainville (Figure 24). The form of the prosternal keel, which is bridged to the prosternum, is an unusual state that we have observed only in the New World species *Aegopsis curvicornis* Burmeister (Dynastinae: Agaocephalini). Segmentation of the antennae varies between species and within one species (nine-segmented, 10-segmented, nine- or 10-segmented).

Figure 24. Distribution of *Chalcasthenes* species.

Distribution (Figure 24). Solomon Islands and Bougainville Island in Papua New Guinea.

Natural history. Little is known of the natural history of species in the genus. Individuals have been collected from 150–700 m elevation. Habitat information is lacking.

Nomenclatural remarks. Endrödi (1985) characterized the genus *Chalcasthenes* based on the following characteristics: (1) dorsal surface with metallic luster and small, setose scales; (2) apex of clypeus with or without horn; (3) frons without horns or tubercles; (4) mandibles not produced beyond clypeus; (5) antennal club shorter than segments 2–7 combined; (6) prosternal process weakly produced; (7) propygidium with two rows of stridulatory grooves; (8) anterior tibia with three external teeth, apical and subapical teeth in male united; (9) apex of posterior tarsi truncate and with fine setae; and (10) inner protarsal claw in the male deeply incised. This description is erroneous in some facts and lacks sufficient details in others. It is erroneous in that the antennal club might be shorter or longer than segments 2–7 combined, that mandibles are produced beyond the clypeal apex and that the apex of the posterior tarsus is dilated or produced (rather than truncate) in some males. The description relies entirely on male characteristics (although Endrödi had one female specimen), and it lacks sufficient details such as form of the maxilla (Figure 7) and fifth protarsomere (Figure 10) that allow separation from other genera.

Endrödi (1985) included the genus *Chalcasthenes* in the dynastine tribe Oryctoderini, a tribe that is poorly defined and lacks shared, derived character states. Endrödi (1985) characterized the tribe based on equivocal states: (1) mandibles in dorsal view hidden by clypeus or mandibles projecting beyond the clypeus (not hidden by clypeus); (2) prosternal process well-developed or poorly developed; (3) propygidium with stridulatory region or lacking stridulatory region; and (4) posterior tibia with apex truncate

or with one to four obtuse, triangular teeth. He also characterized the Oryctoderini as lacking incised inner claws, but male *Chalcasthenes* species clearly possess incised inner claws. We believe that classification and relationships in the Oryctoderini require revision and character-based analyses. Until this is completed, however, we maintain classification of the genus *Chalcasthenes* in this tribe.

Biogeography of Chalcasthenes species and justification for species delimitation

Discrete morphotypes in the genus *Chalcasthenes* are associated with different islands within the Solomon Island region: one on Bougainville Island, one on the Florida Islands and closely neighboring Guadalcanal Island, one on Malaita Island, and one on Ulawa Island. Interspecific variation in *Chalcasthenes* species could be attributed to isolation and fixation of genotypes, thus creating lineages and species. We hypothesize that the ancestral *Chalcasthenes* lineage might have colonized the Solomon Islands during Pleistocene periods of low sea level when the island region of Greater Bukida extended from Buka and Bougainville Islands in the north to the Florida Islands in the south (Diamond et al. 1976). It is possible that the neighboring Guadalcanal Island was also part of Greater Bukida (see “Biogeography and endemism in the Solomon Islands”). The presence of *Chalcasthenes styracoceros* on both the Florida Island and Guadalcanal Island supports the inference that Guadalcanal Island was part of Greater Bukida. When sea level rose, ancestral populations became isolated on islands. The high degree of geographic variation observed in Solomon Island birds is thought to have evolved in this manner (Diamond et al. 1976). Once isolated, differences in habitats and associated nutrition might have led to diversification in horn morphology (quadridentate horn with apices horizontal on the basal ramus on Bougainville Island (Figure 1); quadriden-

tate horn with apices acute and spine-like on the basal ramus on the Florida and Guadalcanal Islands (Figure 5); horn angularly attenuated horn mid-shaft with subrectangular apex on Malaita Island (Figure 4); a morphotype that lacks a horn on Ulawa Island (Figure 3)) as well as diversification in other allometric traits. Shifts in horn morphology resulted in trade-offs with adjacent characters such as size of antennal club and eyes. Thus, isolation on islands resulted in new, selective regimes for each population, affected developmental pathways and led to fixation of traits in these lineages. We interpret these lineages as species based on unique character states (Wheeler & Platnick 2000).

Key to the male species of *Chalcasthenes* Arrow

(Females are known for only *C. divinus* and are not included in the key)

- 1 Clypeus with forward-projecting horn (Figures 1, 4–5, 14–16). Protibia with inner margin arcuate (Figure 19) or weakly arcuate (Figures 21, 22)..... 2
- 1' Clypeus trapezoidal, lacking horn (Figures 3, 17). Protibia with inner margin straight, not arcuate (Figure 20) *C. pulcher* Arrow
- 2 Clypeus with forward-projecting, quadridentate horn; process with two external, basal teeth and two inner, apical teeth (Figures 1, 5, 14–15) 3
- 2' Clypeus with forward-projecting, horn-like process; process angularly attenuated near mid-shaft, apex subrectangular (Figures 4, 16) *Chalcasthenes squamigerus* Frey
- 3 Basal teeth of horn with apices acute, spine-like (Figures 5, 15). Metasternum clothed with moderately dense, bristle-like setae and with sparse scale-like setae *C. styracoceros* Jameson and Ratcliffe n. sp.
- 3' Basal teeth of horn with apices straight and horizontal (Figures 1, 14). Metasternum lacking bristle-like setae, instead clothed with moderately dense, scale-like setae *C. divinus* Endrödi

Chalcasthenes divinus Endrödi (1971) (Figures 1–2, 6–7, 10–12, 14, 18–19, 23–24)

Chalcasthenes divinus Endrödi (1971, pp. 235–236). Type material (holotype male, allotype female and 20 paratypes) at BPBM and BMNH. Allotype and 15 paratypes examined. Holotype male at BPBM (#9379) with labels: (a) "Bougainville: NE Mutahi, 700 m 18 km S.E. Tinputz" (typeface, white label); (b) "15–21.III.1968" (typeface, white label); (c) "& R. Straatman Collectors BISHOP MUSEUM" (typeface, white label); and (d) "Holotypus *Chalcasthenes divinus* Endr." (typeface and handwritten, white label with red border). Allotype female at BPBM with following labels: (a) "SOLOMON IS. BOUGAINVILLE Kugugai Vill. 150 m, XII. 1960" (typeface, white label); (b) "W.W. Brandt Collector BISHOP" (typeface, white label); and (c) "Allotype *Chalcasthenes divinus* Endr." (typeface and handwritten, white label with red border). Three male paratypes at BPBM with following labels: (a) "Bougainville: NE Mutahi, 700 m 18 km S.E. Tinputz" (type-

face, white label); (b) "15–21.III.1968" (typeface, white label); and (c) "& R. Straatman Collectors BISHOP MUSEUM" (typeface, white label). Two male paratypes at BPBM with labels a–b identical to previous paratypes but with (c) "Tawi Collector BISHOP" (typeface, white label). One male paratype at BPBM with label a and c identical to previous paratypes but with date "8–14.III.1968". Two male paratypes at BPBM with label a identical to previous paratype but with date "15–21.III.1968" and collector "& R. Straatman Collectors". Two male paratypes at BPBM with locality label and collector identical to previous paratype but one with date "8–14.III.1968" and the other with date "1–7.III.1968". Endrödi provided a lengthy description based on 22 type specimens. The location of five paratypes is not known. Two specimens in Endrödi's type series from Malaita Island represent individuals of *C. squamigerus* (one specimen at BPBM, one specimen at BMNH). Three specimens in Endrödi's type series from the Florida Islands and Guadalcanal Island represent individuals of *C. styracoceros* (two specimens at BPBM, one specimen at BMNH).

Description male ($n = 12$). Length 15.8–21.0 mm. Width 7.4–9.2 mm. HEAD (Figure 14a,b): frons flat, sparsely or moderately densely punctate; punctures small and moderate in size (mixed), setose; setae cream-colored, decumbent, scale-like, moderate in length. Interocular width 2.8–4.0. Clypeus with forward-projecting horn, apex quadridentate with two inner, apical teeth more produced than two external, basal teeth (Figure 14a); basal teeth with apices straight (Figure 14a); dorsal surface moderately densely punctate; punctures small and moderate in size (mixed), some rugopunctate at apices, setose; setae cream-colored, decumbent, scale-like, moderate in length; lateral surface from eye canthus to apex punctate; punctures small and moderate in size, sparse (base) to moderately dense (apex), some setose. ANTENNA: nine-segmented. Club 0.9 times as long as segments 2–7. PRONOTUM (Figure 14b): anterior angle right angled. Posterior angle (ventral view) with well-developed ridge. Lateral margin from middle to base sinuate (Figure 14b). Surface of mid-disc with minute and small or moderate, moderately dense punctures, some setose; setae sparse (at mid-disc) to moderately dense (near margins), scale-like, cream-colored; surface laterad of disc with small- and moderate-sized, moderately dense punctures, some contiguous and vermiform, some setose; setae dense or moderately dense, scale-like, cream-colored. PROPYGIDIUM: surface with 6–12 stridulatory pegs in each row. PYGIDIUM: surface with small, simple punctures and moderate to large, ocellate punctures, some with setae; setae moderately dense to dense, thickened and scale-like, cream-colored setae. VENTER: metasternum setigerously punctate with moderately dense, moderately long, bristle-like setae from apex to mid-disc and with moderately dense scale-like setae from apex to base, fewer setae at midline; setae creamy white. Sternites setigerously punctate with dense or moderately dense scale-like setae; setae creamy white. Last sternite with apex entire (not weakly sinuate or quadrate). LEGS (Figures 10–11, 19): protibia with inner margin arcuate, external margin tridentate; apical two teeth proximate with bases joined, gap be-

tween these two teeth and basal tooth much greater than bases of anterior two teeth; apical spur decurved. Protarsomere 5 (Figure 10) with inner, apical tooth well-developed, produced beyond apex of tarsomere 5. Metatibia at inner apex with produced projection. Mesotibial and metatibial apical spurs twisted (Figure 11).

Description female ($n = 1$). Female differs from the male in the following respects: Length 16.9 mm. Widest width 9.0 mm. HEAD (Figure 18a,b): frons moderately densely punctate, punctures small and moderate in size (mixed), not setose. Interocular width 3.5. Clypeus without forward-projecting horn, apex broadly parabolic (Figure 18a), lateral margins weakly reflexed, apex moderately reflexed; surface of disc weakly depressed, punctate or rugopunctate; punctures small to moderate in size (mixed); surface of margins rugopunctate. PRONOTUM (Figure 18b): anterior angle rounded. Posterior angle (ventral view) lacking well-developed ridge. Lateral margin from middle to base evenly rounded (Figure 18b). Surface of mid-disc with minute and small or moderate, moderately dense punctures; surface laterad of disc with small- and moderate-sized, moderately dense punctures, some setose at base; setae moderately dense (basolaterally) and sparse (mid-base), scale-like, cream-colored. PROPYGIDIUM: surface with seven stridulatory pegs in each row. PYGIDIUM: surface from base to mid-disc with moderate, ocellate punctures, some with setae; setae moderately dense, minute, tawny. Surface from mid-disc to apex with small to moderate, moderate dense to sparse punctures. VENTER: metasternum setigerously punctate with moderately dense, moderately long, bristle-like setae from apex to mid-disc and with moderately dense, elongate, scale-like setae from apex to base, fewer setae at midline; setae creamy white. Sternites punctate with moderately dense, elongate, scale-like setae at margins; setae creamy white. Last sternite with apex entire. LEGS (Figure 23): protibia with inner margin straight, external margin tridentate in apical half; teeth subequal in size. Apical spur straight. Protarsomere 5 simple (lacking inner, apical tooth). Mesotibia and metatibia more robust, inner apices without produced projection. Mesotibial and metatibial apical spurs not twisted. Metatarsomere 1 with external apex greatly attenuated.

Diagnosis. *Chalcasthenes divinus* is most similar to *C. styroceros*, but it is easily separated based on the following characteristics: (1) basal ramus of horn with apices horizontal and straight (Figures 1, 14a,b) (apices are spike-like in *C. styroceros* (Figures 5, 15a,b)); (2) metasternum densely clothed with moderately dense, scale-like setae (metasternum with bristle-like setae and sparse scale-like setae in *C. styroceros*); and (3) lateral surface of horn smooth or punctate (rugopunctate in *C. styroceros*).

In addition to these easily diagnosable character states, *C. divinus* differs from others in the genus by the following: (1) clypeal horn densely clothed with scale-like setae (less dense in *C. squamigerus*, *C. pulcher*, and *C. styroceros*); (2) lateral margin of pronotum from middle to base sinuate (weakly sinuate in *C. squamigerus* and *C. styroceros*, evenly rounded in *C. pulcher*); (3) protarsomere 5 with inner apical tooth well-developed (poorly developed in

C. pulcher, moderately developed in *C. squamigerus* and *C. styroceros*); and (4) mesotibial and metatibial apical spurs twisted (not twisted in *C. pulcher*, somewhat twisted in *C. squamigerus* and *C. styroceros*).

Distribution (Figure 24). Bougainville Island in Papua New Guinea in the Solomon Islands. Bougainville Island is immediately north of the Solomon Islands and part of the same geological island chain as the Solomon Islands.

Locality data. A total of 13 specimens examined from BMNH, BPBM, FSCA, MLJC, NAIC, NAGAI. Bougainville Island (Papua New Guinea) (13): Kukugai Village (150 m), Piva River, Tinputz (18 km SE; 700 m), no data.

Temporal data. January (1), March (10), September (1), December (1).

Natural history. *Chalcasthenes divinus* is recorded from 150–700 m elevation.

Remarks. Endrödi's type series for *C. divinus* was mixed with specimens that we consider members of *C. squamigerus* and *C. styroceros*. Specimens in the type series from Malaita Island at the southern end of the Solomon Islands chain are, in fact, *C. squamigerus*. Specimens from the Florida Islands and neighboring Guadalcanal Island represent *C. styroceros*.

Chalcasthenes pulcher Arrow (1937) (Figures 3, 17, 20, 24)

Chalcasthenes pulcher Arrow (1937, pp. 42–43). Lectotype male and paralectotype male at BMNH with label data: (1) "Type" (round label with red border, typeface); (2) mouthparts and male genitalia card mounted; (3) "SOLOMON IS. Ulawa 19.V.1934 R. A. Lever" (typeface and handwritten, white label); (4) "Pres. by Imp. Inst. Ent. B.M. 1934-6 44." (typeface and handwritten, white label); (5) "2824" (handwritten, white label); (6) "Ohaus determ. Subfam. Dynastin Tribe Cyclocephal." (handwritten and typeface, white label); (7) "*Chalcasthenes pulcher*, Arrow type" (handwritten, white label); and (8) "*Chalcasthenes pulcher* Arrow LECTOTYPE R.-P. Dechambre det 1976" (handwritten and typeface, white label, "lectotype" in red ink). Paralectotype male at BMNH with label data: (1) "Cotype" (round label with yellow border, typeface); (2) mouthparts, male genitalia and hind wing card mounted; (3) "SOLOMON IS. Ulawa 19.V.1934 R.A. Lever" (typeface and handwritten, white label); (4) "Pres. by Imp. Inst. Ent. B.M. 1934-6 44." (typeface and handwritten, white label); (5) "2824" (handwritten, white label); (6) "*Chalcasthenes pulcher*, Arrow co-type" (handwritten, white label); and (7) "*Chalcasthenes pulcher* Arrow PARALECTOTYPE R.-P. Dechambre det 1976" (handwritten and typeface, white label, "paralectotype" in red ink). Arrow (1937) did not state how many specimens comprised the type series, but he provided a length and width range for the species, thus indicating that at least two specimens were included in the original description.

Description male ($n = 2$). Length 12.9–13.0 mm. Width 6.8–7.4 mm. HEAD (Figure 17a,b): frons at base flat with weak, V-shaped depression at mid-disc; surface at base moder-

ately punctate, more densely punctate in depression, punctures minute and moderate in size (mixed), some setose; setae cream-colored, decumbent, scale-like and thickened, moderate in length; surface of disc densely punctate or rugopunctate; punctures small to moderate in size (mixed), sparsely setose; setae cream-colored, decumbent, scale-like, moderate in length. Interocular width 2.5–2.6. Clypeus without forward-projecting horn, apex broadly trapezoidal, weakly sinuate at middle (Figure 17a), lateral margins weakly reflexed, apex moderately reflexed; surface of disc weakly depressed, punctate or rugopunctate; punctures small to moderate in size (mixed); surface of margins rugopunctate. ANTENNA: 10-segmented. Club 1.5 times as long as segments 2–7. PRONOTUM (Figure 17b): anterior angle rounded. Posterior angle (ventral view) with poorly developed ridge. Lateral margin from middle to base evenly rounded (Figure 17b). Surface of mid-disc with minute and small, moderately dense punctures, some setose; setae sparse (at mid-line) and moderately dense, scale-like, cream-colored; surface laterad of disc with small and moderate, moderately dense punctures, some contiguous and vermiform, some setose; setae moderately dense, scale-like, cream-colored. PROPYGIDIUM: surface with 11–16 stridulatory pegs in each row. PYGIDIUM: surface with small, simple punctures and moderate to large, ocellate punctures, some with setae; ocellate punctures with minute and tawny setae (sparse), simple punctures with thickened, cream-colored setae (sparse). VENTER: metasternum setigerously punctate with moderately dense, moderately long, bristle-like setae (rarely with scale-like setae near margins), fewer setae at midline; setae creamy white. Sternites setigerously punctate with moderately dense, bristle-like and scale-like setae, setae creamy white. Last sternite with apex weakly sinuate or quadrate. LEGS (Figure 20): protibia with inner margin not arcuate, external margin tridentate; apical two teeth approximate with bases joined, gap between these two teeth and basal tooth subequal in width to bases of anterior two teeth; apical spur not decurved appreciably. Protarsomere 5 with inner, apical tooth not well-developed. Metatibia at inner apex lacking produced projection. Mesotibial and metatibial apical spurs simple, not twisted.

Female unknown.

Diagnosis. *Chalcasthenes pulcher* is easily separated from others in the genus based on the following characteristics: (1) clypeus of male without forward-projecting horn, instead the clypeal apex is broadly trapezoidal (Figure 17a) and the lateral margins are weakly reflexed (*C. divinus* and *C. styracoceros* possess forward-projecting quadridentate horns (Figures 14,15) and *C. squamigerus* possesses a quadrately stepped, horn-like process (Figure 16)); (2) antennal club of male is 1.5 times longer than segments 2–7 (club 0.9 times length of segments 2–7 in *C. divinus*, club 1.1–1.2 times longer than segments 2–7 in *C. squamigerus* and *C. styracoceros*); (3) metasternum with moderately dense, moderately long, bristle-like setae and only sparse scale-like setae (metasternum entirely clothed with moderately dense scale-like setae and lacking bristle-like setae in *C. divinus*; metasternum in *C.*

squamigerus is similar to *C. pulcher* and *C. styracoceros*); and (4) male with inner margin of protibia straight (Figure 20) (arcuate in *C. divinus* (Figure 19) and weakly arcuate in *C. styracoceros* and *C. squamigerus* (Figures 22,21, respectively)).

In addition to these easily diagnosable character states, *C. pulcher* differs from others in the genus by the following: (1) eyes larger than other species (interocular width 2.6–2.5) (interocular width is 2.8–4.0 in *C. divinus*; 3.1–3.7 in *C. squamigerus*); (2) lateral margin of pronotum from middle to base is evenly rounded (weakly sinuate in *C. squamigerus* and *C. styracoceros*, sinuate in *C. divinus*); (3) last sternite weakly sinuate at the apex (entire in *C. divinus*, weakly sinuate or quadrate in *C. squamigerus* and *C. styracoceros*); (4) protibial apical spur not decurved (decurved in *C. divinus*, *C. squamigerus*, and *C. styracoceros*); (5) protarsomere 5 with inner apical tooth poorly developed (moderately developed in *C. squamigerus* and *C. styracoceros*, well-developed in *C. divinus*); and (6) mesotibial and metatibial apical spurs not twisted (twisted in *C. divinus* and *C. squamigerus* and *C. styracoceros*).

Distribution (Figure 24). Known only from Ulawa Island in the southern portion of the Solomon Islands.

Locality Data. Two specimens examined from BMNH. Solomon Islands (2): Ulawa Island.

Temporal data. May (2).

Natural history. Nothing is known of the natural history of this species.

Remarks. Compared with other males in the genus, *C. pulcher* has very large eyes and lacks a head horn (Figure 17a,b). Endrödi (1971) used these features to separate *C. divinus* from *C. pulcher*.

Chalcasthenes squamigerus (Frey 1969),

New Combination (Figures 4, 8–9, 13, 16, 21, 24)

Strehlia squamigera Frey (1969, pp. 481–482, f. 2). Type material (holotype male, paratype male) at BPBM and NHMB. Holotype male at BPBM with following labels: (a) “SOLOMON IS. MALAITA: E. of Kwalo (E. of Auki) 350 m. Sept. 29, 1957” (typeface, white label); (b) male genitalia card mounted; (c) “TYPE” (typeface, red label); (d) illegible (verse, handwritten, in pencil); “+1” (obverse, handwritten in pencil); (e) “*Strehlia squamigera* Type m det. G. Frey 1967/1968 n. sp.” (handwritten in black ballpoint pen and type face); and (f) “*Chalcasthenes squamigera* Frey det. M.L. Jameson 1998”. Paratype male at NHMB with locality labels: (a) identical to holotype; (b) “P-TYPE” (typeface, red label); and (c) “*Strehlia squamigera* P-Type det. G. Frey 1967/1968 n. g. and n. spec.” (handwritten in black ballpoint pen and typeface). Frey stated that the description was based on two male specimens. Both specimens are from the same collecting event. **New Combination.**

Description male ($n = 5$). Length 13.8–16.8 mm. Width 7.0–8.5 mm. HEAD (Figure 16a,b): frons flat, sparsely or moderately densely punctate, punctures small and moderate in size (mixed), some setose; setae cream-colored, decumbent, scale-like and thickened, moderate in length. Interocular

width 3.5–3.7. Clypeus with forward-projecting horn-like process; horn angularly attenuated near mid-shaft, apex subrectangular (Figure 16a); surface of disc with weak, medial ridge from base or middle to near apex, punctate (at base) and rugopunctate (from base to apex and at margins); punctures small to moderate in size (mixed), sparse; lateral surface from eye canthus to subapex weakly rugopunctate; punctures small to moderate in size, sparse or moderately dense, lacking setae. ANTENNA: nine- or 10-segmented. Club 1.2 times as long as segments 2–7. PRONOTUM: anterior angle weakly acute, not rounded. Posterior angle (ventral view) with moderately developed ridge. Lateral margin from middle to base weakly sinuate (Figure 16b). Surface of mid-disc with minute and small, moderately dense punctures, some setose; setae sparse (at mid-line) and moderately dense, scale-like, cream-colored; surface laterad of disc with small- and moderate-sized, moderately dense punctures, some contiguous and vermiform, some setose; setae moderately dense, scale-like, cream-colored. PROPYGIDIUM (Figure 8,9): surface with 10–11 stridulatory pegs in each row. PYGIDIUM (Figure 8): surface with small, simple punctures and moderate to large, ocellate punctures, some with setae; setae moderately dense, thickened and scale-like, cream-colored. VENTER: metasternum setigerously punctate with moderately dense, moderately long, bristle-like setae (rarely with scale-like setae near margins), fewer setae at midline; setae creamy white. Sternites setigerously punctate, with moderately dense bristle-like and scale-like setae, setae cream-colored. Last sternite with apex weakly sinuate or quadrate. LEGS (Figure 21): protibia with inner margin weakly arcuate, external margin tridentate; apical two teeth approximate with bases joined, gap between these teeth and basal tooth subequal in width to base of anterior two teeth; apical spur decurved. Protarsomere 5 with inner apical tooth well-developed, produced slightly beyond apex of tarsomere 5. Metatibia at inner apex with weakly produced projection. Mesotibial and metatibial apical spurs moderately twisted.

Female unknown.

Diagnosis. *Chalcasthenes squamigerus* is easily separated from others in the genus based on: (1) the unusual form of the male horn that is anteriorly attenuated near the mid-shaft with a subrectangular apex (Figure 16a,b); (2) antennal club of male that is subequal in length to segments 2–7 (antennal club is longer than segments 2–7 in *C. pulcher*, shorter than segments 2–7 in *C. divinus*, nearly subequal in *C. styracoceros*); (3) metasternum with moderately dense, moderately long, bristle-like setae and only sparse scale-like setae (metasternum entirely clothed with moderately dense scale-like setae and lacking bristle-like setae in *C. divinus*; metasternum in *C. squamigerus* is similar to *C. pulcher*); and (4) male with inner margin of protibia weakly arcuate (Figure 21) (straight in *C. pulcher* (Figure 20); arcuate in *C. divinus* (Figure 19); weakly arcuate in *C. styracoceros* (Figure 22)).

Distribution (Figure 24). Known from Malaita Island at the southern end of the Solomon Island chain.

Locality data. Five specimens examined from BPBM, BMNH, USNM, NHMB.

Solomon Islands (6): Malaita Island (5): Hulo, Kwalo (E. of Auki), near Kwalo.

Temporal data. June (1), September (2), October (1).

Natural history. *Chalcasthenes squamigerus* is recorded from 350 m elevation. Nothing is known of its biology.

Remarks. *Chalcasthenes squamigerus* and *C. styracoceros* share the following character states: lateral margin of pronotum from middle to base is weakly sinuate (evenly rounded in *C. pulcher*; sinuate in *C. divinus*); last sternite weakly sinuate or quadrate at the apex (entire in *C. divinus*; weakly sinuate in *C. pulcher*); protarsomere 5 with inner apical tooth moderately developed (poorly developed in *C. pulcher*; well-developed in *C. divinus*); mesotibial and metatibial apical spurs moderately twisted (twisted in *C. divinus*; not twisted in *C. pulcher*).

Chalcasthenes styracoceros Jameson and Ratcliffe n. sp. (Figures 5, 15, 22, 24)

Chalcasthenes styracoceros Jameson and Ratcliffe. Type material (holotype male, two male paratypes) at BPBM and BMNH. Holotype male at BPBM with labels: (a) male genitalia card mounted; (b) "SOLOMON IS. Florida Grp. Takopekope 12.IX.1960" (typeface, white label); (c) "C. W. O'Brien Collector" (typeface, white label); (d) "Paratypus *Chalcasthenes divinus* Endr." (typeface and handwritten, white label with red border); and (e) our holotype label. One male paratype at BPBM with following labels: (a) male genitalia card mounted; (b) "SOLOMON IS. Guadalcanal Lunga R. (bridge) 3.IX.1960" (typeface, white label); (c) "C. W. O'Brien Collector" (typeface, white label); (d) "Paratypus *Chalcasthenes divinus* Endr." (typeface and handwritten, white label with red border); and (e) our paratype label. Second male paratype at BMNH with following labels: (a) "SOLOMON IS. Florida Grp. Takopekope 12.IX.1960" (typeface, white label); (b) "C. W. O'Brien Collector" (typeface, white label); and (c) our paratype label.

Description holotype male. Length 16.9 mm. Width 8.4 mm.

HEAD (Figure 15a,b): frons flat, sparsely punctate; punctures small and moderate in size (mixed), setose; setae cream-colored, decumbent, scale-like, moderate in length. Interocular width 4.0. Clypeus with forward-projecting horn, apex quadridentate with two inner, apical teeth more produced than two external, basal teeth (Figure 15a); basal teeth with apices acute (Figure 15a); dorsal surface moderately densely punctate (base and disc) and punctostrigate (apex); punctures small and moderate in size (mixed), setose except at apex; lateral surface from eye canthus to apex rugopunctate; punctures moderate in size, dense, some setose; setae cream-colored, decumbent, scale-like, moderate in length. ANTENNA: nine-segmented. Club 1.1 times as long as segments 2–7. PRONOTUM (Figure 15b): anterior angle right angled. Posterior angle (ventral view) with moderately developed ridge. Lateral margin from middle to base weakly sinuate (Figure 15b). Surface of mid-disc with minute and small or moderate, moderately dense punctures, some setose; setae sparse (at mid-disc) to moderately dense (near margins), scale-like, cream-colored; surface laterad

of disc with small- and moderate-sized, moderately dense punctures, some setose; setae dense or moderately dense, scale-like, cream-colored. PROPYGIDIUM: surface with 6–12 stridulatory pegs in each row. PYGIDIUM: Surface with small, simple punctures and moderate to large, ocellate punctures, some with setae; setae sparse to moderately dense, thickened and scale-like, cream-colored setae. VENTER: metasternum setigerously punctate with moderately dense, moderately long, bristle-like setae and sparse, scale-like setae; setae lacking at mid-disc, creamy white. Sternites setigerously punctate with moderately dense, scale-like setae; setae creamy white. Last sternite with apex weakly sinuate. LEGS (Figure 22): protibia with inner margin arcuate, external margin tridentate; apical two teeth proximate with bases joined, gap between these two teeth and basal tooth much greater than bases of anterior two teeth; apical spur decurved. Protarsomere 5 with inner, apical tooth moderately developed, produced to apex of tarsomere 5. Metatibia at inner apex with weakly produced projection. Mesotibial and metatibial apical spurs twisted.

Description male paratypes ($n = 2$). Male paratypes differ from the holotype male in the following respects: Length 15.2–15.3 mm. Width 7.3–7.9 mm. HEAD: interocular width 3.1–3.4. ANTENNA: club 1.2 times as long as segments 2–7. PROPYGIDIUM: surface with nine stridulatory pegs in each row. VENTER: last sternite with apex entire weakly sinuate or quadrate.

Diagnosis. *Chalcasthenes styroceros* is most similar to *C. divinus*, but it is easily separated based on the following characteristics: (1) males with quadridentate horn, basal ramus with apices acute, spine-like (Figures 5,15a) (the anterior edge of the basal ramus is straight and horizontal in *C. divinus* (Figures 1,14a)); (2) metasternum clothed with moderately dense, bristle-like setae and sparse scale-like setae (metasternum with moderately dense scale-like setae and no bristle-like setae in *C. divinus*); (3) lateral surface of horn rugopunctate (lateral surface smooth or punctate in *C. divinus*); (4) antennal club of male 1.1–1.2 times longer than segments 2–7 (club 0.9 times length of segments 2–7 in *C. divinus*); and (5) last sternite of male with apex weakly sinuate (entire in *C. divinus*).

The form of the antenna and characterization of setae on the metasternum are shared with *C. squamigerus*; the forms of the horn (quadridentate), protibia (arcuate), metatibial spurs (twisted) and protarsomere 5 with well-developed inner apical tooth are all shared with *C. divinus*.

Distribution (Figure 24). Florida Islands and Guadalcanal Island in the Solomon Islands.

Locality data. Three specimens from BPBM (one deposited in BMNH).

Solomon Islands (3): Guadalcanal Island (1): Lunga River (bridge). Florida Islands (2): Takopekope.

Temporal data. September (3).

Natural history. Unknown.

Etymology. The specific epithet “*styroceros*” refers to the basal ramus of the horn that is pointed or spike-like. The

name is derived from the Greek *styrax* (genitive *styrakos*), meaning spike (as on the shaft of a spear) and from the Greek *ceros*, meaning horn. The species name is masculine to reflect the generic name, which is also masculine.

Remarks. Specimens of *C. styroceros* were part of Endrödi's type series for *C. divinus*, but they differ based on the less-developed clypeal horn (approximately half the length of typical horns in *C. divinus*), longer antennal club and metasternum with moderately dense, moderately long, bristle-like setae and sparse, scale-like setae. The forms of the antenna and characterization of setae on the metasternum are shared with *C. squamigerus*, while the forms of the horn (quadridentate), protibia (arcuate) and metatibial spurs (twisted) are all shared with *C. divinus*. Presence of *C. styroceros* on both the Florida Islands and Guadalcanal Island provides support for the hypothesis that these islands were part of Greater Bukida during the Pleistocene.

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