

Cyphocoleus Chaudoir (Coleoptera, Carabidae, Odacanthini): descriptive taxonomy, phylogenetic relationships, and the Cenozoic history of New Caledonia

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Abstract

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The precinctive New Caledonian genus *Cyphocoleus* Chaudoir is revised with 22 species recognized, 12 newly described: *C. lissus* sp. n., *C. prolixus* sp. n., *C. parovicollis* sp. n., *C. burwelli* sp. n., *C. angustatus* sp. n., *C. monteithi* sp. n., *C. fasciatus* sp. n., *C. lescheni* Liebherr & Will, sp. n., *C. cordatus* sp. n., *C. bourailensis* sp. n., *C. subulatus* sp. n., and *C. iledespkinsensis* sp. n. *Atongolium* Park & Will is found to be a junior synonym of *Cyphocoleus*, with its two species recombined as *C. mirabilis* comb. n. and *C. moorei* comb. n. Results of a survey of Harpalinae Bonelli place *Cyphocoleus* as a member of Odacanthini based on synapomorphies of the eighth abdominal tergite and the female spermathecal assembly. *Cyphocoleus* shares with five other generic-level taxa – *Homethes* Newman, *Aeolodermus* Andrewes, *Stenocheila* Laporte, *Quammenis* Erwin and *Diplacanthogaster* Liebke – a single-segmented maxillary galea that is appressed to the outer margin of the maxillary lacinia. These six generic-level taxa are newly classified as members of subtribe Homethina **subtrib. n.** (type genus *Homethes*). Cladistic analysis including 79 taxa and utilizing 119 morphological characters supports division of Odacanthini into four monophyletic subtribes: **1**, Actenonycina (*Actenonyx* White); **2**, Homethina; **3**, Pentagonocina (*Pentagonica* Dana, *Parascopodes* Darlington, *Scopodes* Erichson); and **4**, Odacanthina (24 genera in this analysis monophyletically defined by *Lasiocera* Dejean and its adelphotaxon). These subtribes are phylogenetically arranged as: (Actenonycina (Homethina (Pentagonocina + Odacanthina). Area relationships defined within Homethina – (New Caledonia (Australia (South America + Central America))) – support the origin of New Caledonian *Cyphocoleus* prior to amphiantarctic vicariance between South America and Australia. Consistent with previous molecular dating of 100–105 Ma for the origin of Odacanthini, a general vicariance-based hypothesis proposes that New Zealandian *Actenonyx* and New Caledonian *Cyphocoleus* were emplaced on Zealandia prior to the completion of rifting between Zealandia and Australia during Late Cretaceous, and that both fragments of Zealandia remained subaerial throughout the Cenozoic. Alternatively, under a very specific time-constrained biogeographic hypothesis laden with an added assumption of dispersal, the ancestor of *Cyphocoleus* could have colonized New Caledonia during a 2–5 Ma period after its proposed subaerial reemergence at 37 Ma. A clade within *Cyphocoleus* synapomorphously exhibits an environmental patina: a varnish-like coating to the dorsal body surface that is hypothesized to enable crypsis of the adult beetle. Several specializations of elytral setae are also synapomorphies of this clade, suggesting evolutionary association of the patina and the setal specializations.

Introduction

When Baron Maximilien de Chaudoir (1877) described the genus *Cyphocoleus*, he wrote “Ce genre présente plusieurs particularités ... Sa place est assez difficile à préciser (p. 196).” He went on to suggest several tentative affinities: “il se rapproche des *Oxyglossus*; il ne rentre bien ni dans les Anchoméniides, ni dans les Thyréoptérides, et constitue une forme intermédiaire entre des deux groupes (genus osculans) (p. 196).” Thus he was conflicted as to whether the genus should be classified as Anchoméniides (tribe Platynini), or as Thyréoptérides (subtribe Pericalina of Lebiini of which *Oxyglossus* is a member) (Shpeley and Ball 2001). Given that Chaudoir described *Cyphocoleus* when he was 61 years old – after he had visited major insect collections at Oxford, London, Leiden, Brussels, Paris, Berlin, Genova, and Prague, had acquired specimens from collections developed by numerous authors, e.g. Bates, Dejean, La Ferté de Sénectère, Waterhouse, Wollaston, and had corresponded and discussed carabid beetles with many leading lights of his day (Basilevsky 1983, Ball and Erwin 1983) – his indecision regarding the placement of the new genus is remarkable. This indecision was partly based on lack of material, as he described his new genus and three new species from three specimens. He also acknowledged that New Caledonia, whence *Cyphocoleus* are precinctive, “fourni déjà tant de formes curieuses et spéciales [furnished already so many curious and special forms] (Chaudoir 1877, p. 196).” That *Cyphocoleus* beetles, with their bizarre physiognomy (Fig. 1) represent some of those “curious and special forms” may explain a connection that Chaudoir failed to make. In describing *Cyphocoleus* he noted the unsegmented galea, or outer lobe, of the maxilla. This observation is in keeping with his attention to the details of carabid beetle maxillae in this studies (Ball and Erwin 1983). He had previously also noted this condition in the Austral-Pacific genus *Homethes* Newman and the South American genus *Stenocheila* Laporte (Chaudoir 1872). But in 1877 he made no connection between *Cyphocoleus*, *Stenocheila*, and *Homethes*. Below it is shown that these taxa plus the genera *Aeolodermus* Andrewes (1929) [treated as *Homethes* in Chaudoir, 1872], *Diplacanthogaster* Liebke (1932) and *Quammenis* Erwin (2000), all of whom synapomorphously share an unsegmented maxillary galea, comprise a newly recognized monophyletic taxon.

Chaudoir’s first stated yet tentative placement of *Cyphocoleus* in tribe Platynini was summarily adopted by the only other species describer and reviser of the group (Fauvel 1882). These beetles remained rarely collected throughout the 19th and much of the 20th century. Prior to E. O. Wilson’s expedition to New Caledonia in 1955 (Fig. 1), 20th Century *Cyphocoleus* collections included 11 specimens (6 species, 2 newly described below) from the Sarasin and Roux (1911) Zoological Expedition (for other taxa see Sarasin and Roux 1913–1918), 7 specimens (2 species, 1 newly described) collected by P. D. Montague in 1914 (Turner 1919), and 9 specimens (3 species, 1 new-

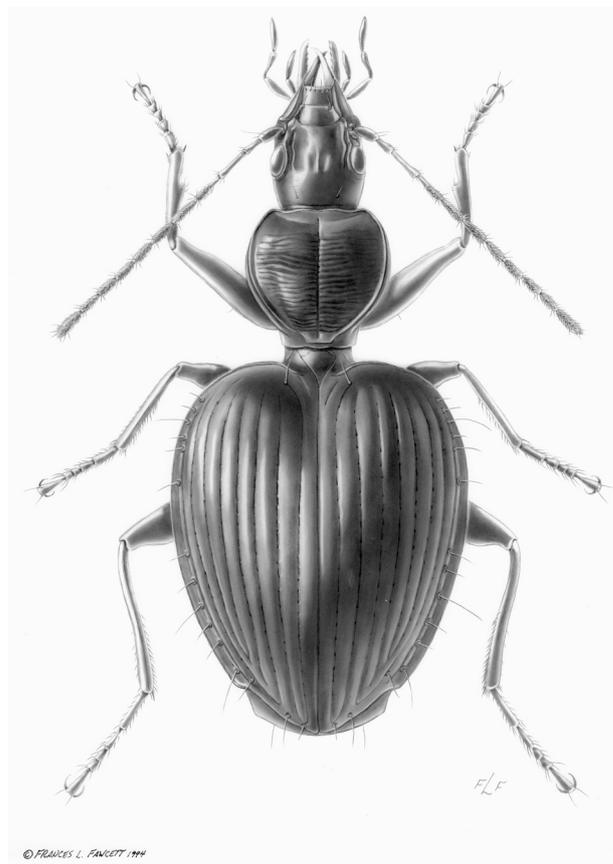


Figure 1. *Cyphocoleus subulatus* sp. n. male paratype dorsal view: NEW CALEDONIA, Ciu, near Mt. Canala, 300 m el., 1–3–i–1955, rainforest, E. O. Wilson (MCZ).

ly described) collected in 1944 by J. C. Herron during the Allied Forces’ occupation (Alexander 1948). Comprehensive taxonomic revision of *Cyphocoleus* is now possible based on field specimens collected by Dr. G. B. Monteith and his Queensland Museum colleagues over the past 30 years, with those samples taken from a wide range of localities visited over nearly 90 collecting days.

This revision aims primarily to delineate and describe the species that comprise *Cyphocoleus*. Taxonomic placement of the genus is based on cladistic analysis using morphological characters of the adult beetles. Comprehensive character analysis of *Cyphocoleus* shows clearly that these species are members of the tribe Odacanthini. Moreover, within Odacanthini, *Cyphocoleus* and five other genera form a monophyletic group defined in part by a remarkably salient character: a one-segmented maxillary galea that lies appressed to the outer margin of the maxillary lacinia. Its evolution may be an evolutionary specialization associated with elongation of the mandibles in these beetles, as a similar maxillary configuration – a one-segmented galea that is held free apically from the lacinia – is observed in the long-jawed bembidiine genus *Amerizus* Chaudoir (1868). However, a single segmented galea is also present in members of tribe Callistini (Chaudoir 1872), though these beetles exhibit only moderately elongated mouthparts: i.e. mandibles and maxillae. And a single-segmented galea is pres-

ent in *Monolobus* Solier of the tribe Migadopini, beetles of that genus exhibiting short mandibles (Jeannel 1938). Numerous other characters also support this newly recognized clade – classified as subtribe Homethina subtrib. n. – and place the lineage as an early offshoot within Odacanthini. Biogeographic relationships within Homethina are amphiantarctic, with other member genera occupying Australia, tropical South America, and Central America. It is proposed that these amphiantarctic biogeographic relationships are of Cretaceous age, and therefore associated with the fragmentation of Gondwana. This hypothesis necessitates that *Cyphocoleus* spp. have occupied a subaerial New Caledonia throughout the Cenozoic: i.e. over the past 60 Ma. The consequences of such a hypothesis are discussed in light of molecular dating studies of carabid beetles (Ober and Heider 2010) and the phylogenetic and biogeographic relationships among the various subtribal lineages that comprise Odacanthini.

Materials and methods

Taxonomic material. The taxonomic revision of *Cyphocoleus* is based on 826 specimens borrowed from 19 institutions (see Acknowledgements). All type specimens were examined for 20 of the 22 species. For two species – *Cyphocoleus mirabilis* (Park & Will) and *C. moorei* (Park & Will) – a paratype specimen (QMB) was compared to recently collected material to verify the identifications. Specimens representing outgroups of *Cyphocoleus* represented in the cladistic analysis were obtained from other institutions listed in the Acknowledgements (see Suppl. material 1). Holotypes for all newly described species are deposited in MNHN, Paris. Lectotypes are designated for those species described from a syntype series. Information on primary type labels is reported verbatim from the specimen labels, with separate lines of text on a label demarked by a single slash (/), and separate labels by a double slash (//). All label text is presented as non-italics, as per the printed or handwritten labels themselves.

Laboratory techniques. Standard light microscopy, dissection and staining protocols used in this study are described in Liebherr (2015: 18–20). The major exception involves dissection of male genitalia, where both abdominal segments VIII and IX were removed, along with the male aedeagus, from the male abdomen during this study. This procedure allowed examination of mediotergite VIII and the position of the associated spiracles in beetles of the studied taxa. These segments are routinely removed together in female dissections, along with the female reproductive tract, and in some instances the female tergites and ventrites of abdominal segment VIII were slide mounted in glycerine for microscopic examination. The vast majority of beetles studied were prepared in dry-mounted condition on pins or points. A small minority of specimens are maintained in 100% ethanol; these specimens were determined and labeled just as the dry material.

Descriptive conventions. All ingroup *Cyphocoleus* specimens were determined to species through comprehensive examination, including both external characteristics and male genitalia. In order to assess the latter in a comprehensive manner, males of most collecting series, and in some instances numerous males, were dissected. The dissected males were labeled in succession as “male 1, male 2, ...”, with these working labels retained on the specimens along with the genitalia stored in polyethylene genitalia vials. Once specimens had been sorted to species, five specimens (or as many as possible for more rarely collected species) were chosen for mensural analysis. The five specimens included the largest and smallest beetle for the species, plus a representation of males and females. These specimens were labeled as “measured specimen 1 ...” and subjected to intensive examination of external characters. Based on the sample specimens, body size range, and variation among various body ratios were estimated. Also, qualitative characters were assessed among the five to ensure consistency among the specimens sorted to species. All data were entered into multiple Excel® spreadsheet pages, with these data serving as the basis for the dichotomous key, diagnoses, and descriptions.

Several measurements proved useful for diagnosing species. Eye development was quantified by the ocular ratio: MHW/mFW, or maximum head width across eyes divided by the minimum frons width between eyes. Dimensions of the pronotum were routinely used to diagnose several of the species, with four measurements made: **1**, MPW, maximum pronotal (or prothoracic) width, measured either across the pronotum, or across the externally bulging proepisterna if visible in dorsal view; **2**, APW, apical pronotal width, measured between the two most anterior points along the front of the pronotum; **3**, BPW, basal pronotal width, measured across the base of the pronotum along the lateral marginal bead; and **4**, PL, pronotal length, or the distance from the apex of the pronotum to the basal margin measured along the midline. These measurements were variously combined into the ratios APW/BPW, MPW/BPW, and MPW/PL, in order to describe prothoracic configuration. The ranges of these ratios are used for descriptive purposes only without any statistical connotations.

Three measurements of the elytra were also used to describe body shape: **1**, MEW, maximal elytral width; **2**, HuW, humeral width, or the distance between the anterior-most points along the basal elytral margin on both sides of the scutellum; and **3**, EL, elytral length, or the distance from the base of the scutellum to the elytral apex, measured parallel to the fused suture, and to the farther of the two apices if they are separated by a median invagination at the suture. These measurements were combined into two ratios, MEW/EL, and MEW/HuW. The former describes the relative elytral breadth, whereas the latter ratio describes the relative width at the front of the elytra, i.e. the humeral development, versus the maximal elytral width near the elytral midlength.

Variation among individuals for counts and relative positions of the lateral elytral setae – i.e. those setae present in the broadened eight elytral interval – is presented using the convention of a(b) + c + d(e). In this sequence, “a” represents the modal number of setae in the anterior series of lateral elytral setae commencing just laterad the humerus, and “(b)” represents the number of setae in the minority of specimens, assuming there is variation observed. The value “c” is used if a seta is isolated between the anterior and posterior series of lateral setae. And “d” represents the modal number of setae in the posterior series of lateral elytral setae situated just anterad the elytral subapical situation, with “(e)” representing the number of setae in the minority of specimens for this setal series, assuming variation is observed.

Standardized body length used to describe body size is the sum of three measurements: **1**, head length measured from the labral medioapical margin to the cervical ridge at the head-pronotal juncture; **2**, pronotal length as measured above; **3**, elytral length as measured above. As this sum of measurements ignores the apical portion of the elongate mandibles (always in variable positions specimen to specimen) and any distended portions of the abdomen (also variable dependent on specimen condition when prepared), the standardized body length measure will be smaller than the size perceived by eye.

Results

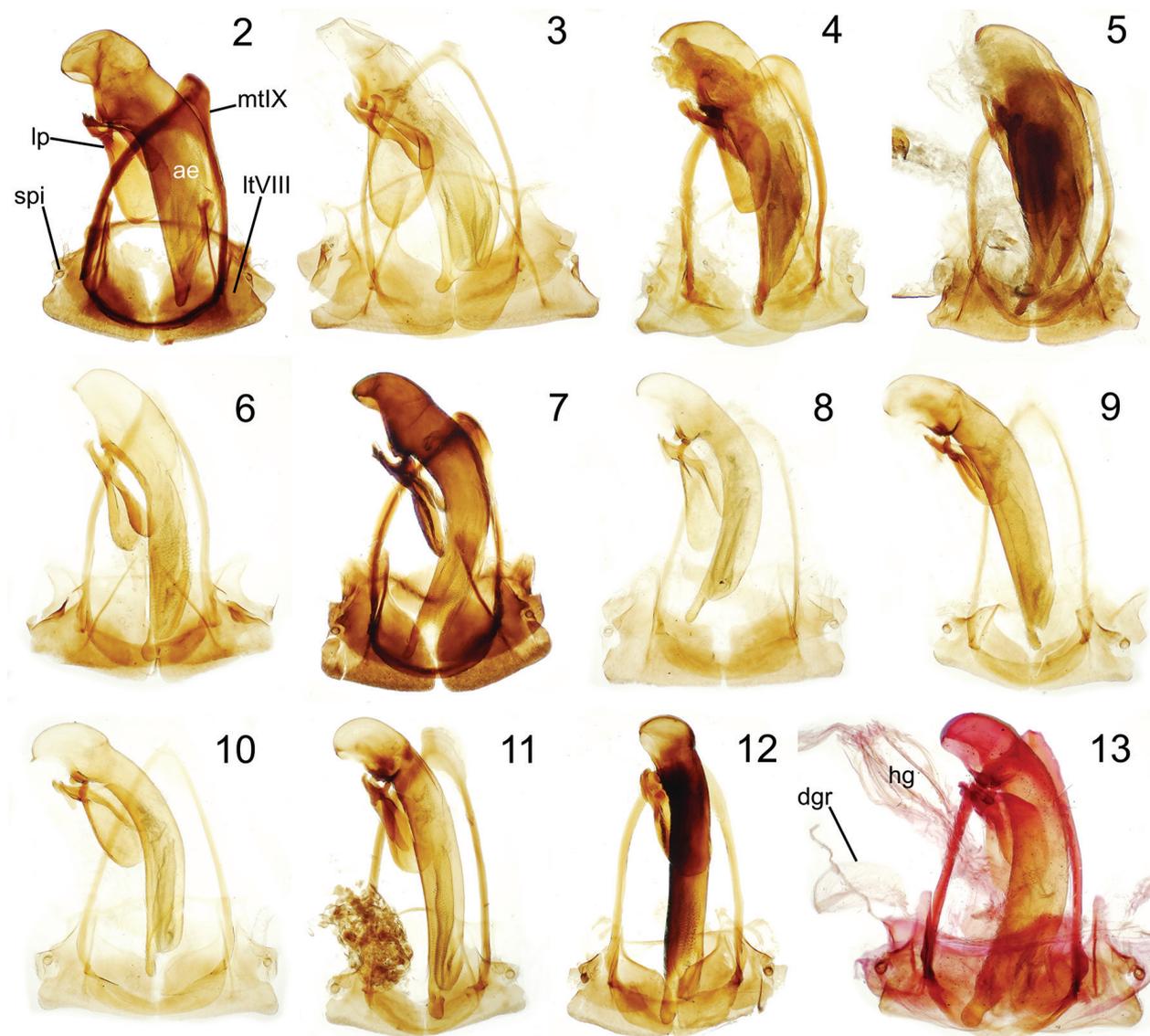
Ingroup circumscription. The principal intents of this study are to revise the species-level taxa assigned to *Cyphocoleus*, and to deduce the phylogenetic relationships of those taxa. The latter goal requires robust definition of outgroup taxa to be included in the phylogenetic analysis of *Cyphocoleus*. This task was complicated by the variety of published proposals regarding taxa found in this study to be related to *Cyphocoleus*. The female reproductive tract of *Cyphocoleus* supports inclusion of the genus in Odacanthini, as the spermathecal assembly exhibits a unique configuration (Figs 35–43, 60–65), wherein the spermatheca is composed of two parts, an apical and basal bulb, that attach to a spermathecal basal sclerite. This sclerite arcuately joins the common oviduct (Fig. 39). Liebherr (1990) found that this configuration characterizes the genera *Homethes* Newman and *Aeolodermus* Andrewes, necessitating transfer of those genera from Tribe Platynini Bonelli to Odacanthini Laporte. Based on a simplified cladistic analysis, Liebherr (1990) also transferred the genera *Pentagonica* Dana and *Scopodes* Erichson to Odacanthini, thereby synonymizing Tribe Pentagonicipini Bates. This proposal was not unanimously accepted, with the pentagonicipines either maintained as a subtribal entity (Lorenz 2005), or as a distinct tribe (Bousquet 2012). Previously Liebherr (1988) proposed the superfamily Odacanthitae to include the tribes Odacanthini and Lachnophorini, the member taxa of these taxa characterized by a bipartite spermatheca. Liebherr

and Will (1998) provided an expanded taxonomic survey of female reproductive tract characters, proposing 11 genera – including *Pentagonica*, *Scopodes*, and *Cyphocoleus* – as members of Odacanthini. They also proposed that the bipartite spermathecal configuration observed in Odacanthini was homologous to that observed in Lachnophorini, indicating a sister-group relationship between these tribes. This phylogenetic scheme was followed by Erwin and Zamorano (2014), who proposed three lineages to comprise the supertribe Odacanthitae: Odacanthini, Lachnophorini LeConte, and Calophaenini Jeannel. Within their classification, five genera were placed *incertae sedis* within Lachnophorina: *Homethes*, *Aeolodermus*, *Stenocheila*, *Diplacanthogaster* Liebke, and *Selina* Motschulsky.

Based on DNA molecular sequence data, Ober and Maddison (2008) presented a starkly different hypothesis for the phylogenetic relationships of these taxa. In their maximum likelihood 28Sbe + wg dataset (Ober and Maddison 2008, fig. 2), Odacanthini comprise the sister group to Peleciini, whereas the distantly related Lachnophorini are the adelphotaxon to the various panagaeite lineages (Chlaeniini Brullé, Oodini La Ferté-Sénectère, Panagaeini Bonelli, and Licinini Bonelli). Dating the molecular divergences of these various lineages puts the incongruity in temporal terms, with divergence of the two tribes, plus the tribe Platynini Bonelli, at well over 100 Ma (Oder and Heider 2010). The molecular data agree with the previous synonymy of Pentagonicipini and Odacanthini as the pentagonicipine exemplar taxa (*Pentagonica*, *Scopodes*, and *Actenonyx* White) and odacanthine representatives were found to be reciprocally paraphyletic (Ober and Maddison 2008: fig. 2).

These starkly different sets of results suggest the need for reevaluation of the previously proposed relationship of Lachnophorini and Odacanthini based principally on spermathecal configuration. Whether to include lachnophorine taxa as outgroups for the phylogenetic analysis of *Cyphocoleus* formed the proximate question in this endeavor. More broadly, an anatomical survey of taxa placed in Lachnophorini and Odacanthini was undertaken to allow a robust circumscription of taxa to be assigned to Odacanthini. By necessity, such circumscription must precede cladistic analysis of the constituent taxa.

In a seminal morphological analysis of the abdominal terminalia of Carabidae, Deuve (1993) studied the mediotergite VIII of a variety of taxa across Harpalinae. He found that the eighth mediotergite was plesiomorphically continuous medially, with several taxa exhibiting a derived membranous median division of the sclerite. Lachnophorini share the continuous, plesiomorphic mediotergite with taxa in Platynini, Chlaeniini, Abacetini Chaudoir, Hexagoniini G. Horn, and various zuphiite tribes (Dryptini Bonelli, Zuphiini Bonelli, and Galeritini Kirby) (Deuve 1993: 95). Conversely, *Pentagonica* shares with various lebiite genera (*Peliocypas* Schmidt-Göbel, *Pseudomasoreus* Desbrocher des Loges, and *Eurydera* Laporte) the derived, mediotergite condition wherein it is divided into two laterotergites.

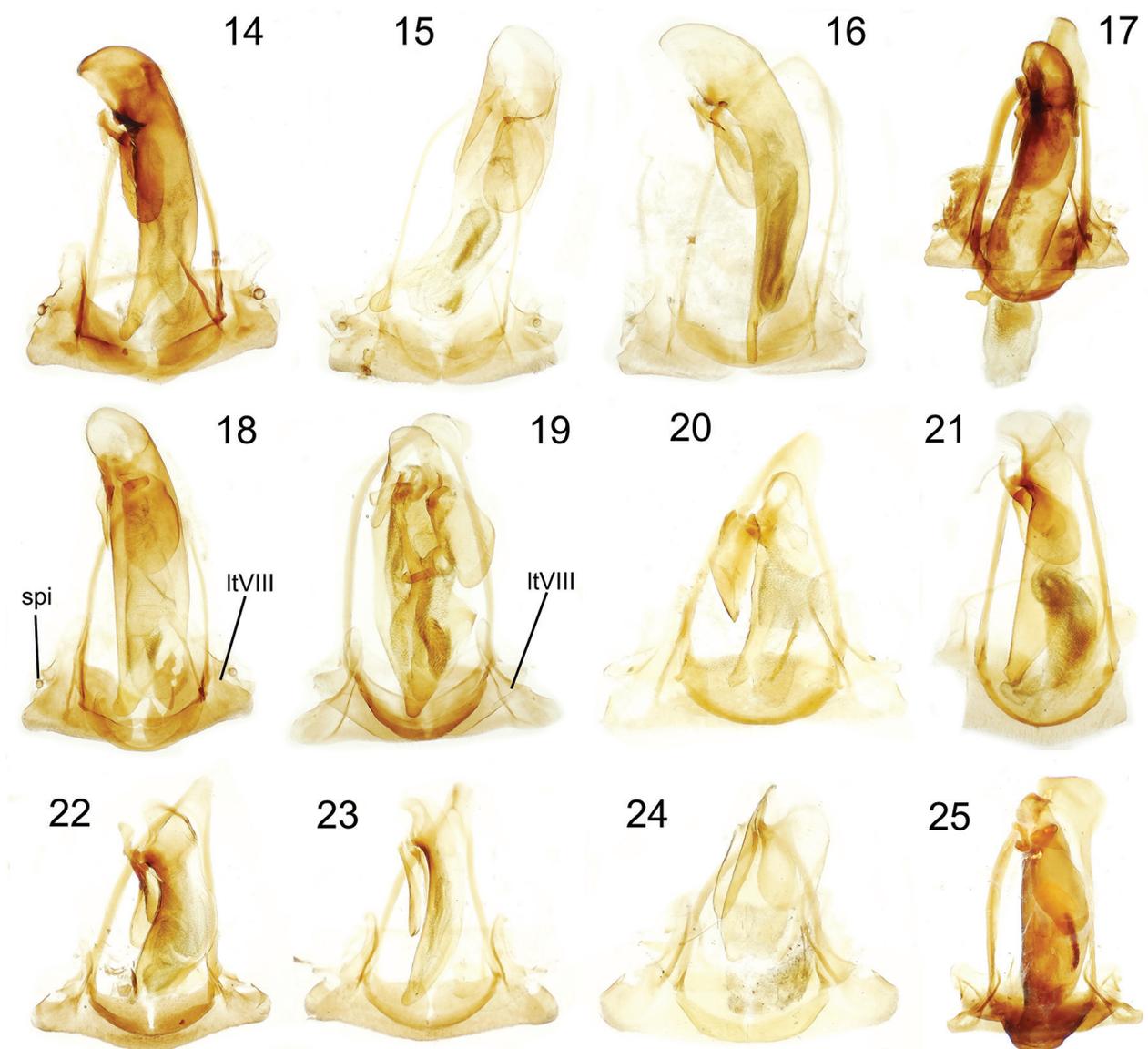


Figures 2–13. Male aedeagus with associated abdominal segments VIII and IX, dorsal view, for taxa assigned to Odacanthini (see Suppl. material 1): **2**, *Actenonyx bembidioides*; **3**, *Homethes guttifer*; **4**, *Quammenis spectabilis*; **5**, *Stenocheila lacordairei*; **6**, *Pentagonica daimella*; **7**, *Scopodes edwardsii*; **8**, *Lasiocera orientalis*; **9**, *Eucolliuris fuscipennis*; **10**, *Renneria kamouni*; **11**, *Arame macra*; **12**, *Odacantha melanura*; **13**, *Deipyrodes palustris*. For abbreviations see Table 1.

Given this distinctive difference in abdominal configuration, abdominal segments VIII and IX and associated male genitalia were dissected from a variety of taxa previously assigned to Odacanthini and Lachnophorini (Figs 2–25). Based on the molecular results placing *Actenonyx* with pentagonicine taxa, as well as earlier suggestions of affinities between *Actenonyx* and Odacanthini (Britton 1941, Lieberr 1988), *A. bembidioides* White was included and found to exhibit the derived, mediotergite divided into paired laterotergites VIII (Fig. 2). Moreover, the spiracle of abdominal VIII was found to be incorporated into the lateral portion of the laterotergite, where it is surrounded by a narrow membranous lunule (Fig. 2). The genera *Pentagonica* and *Scopodes* (Figs 6, 7) also exhibit this condition, as do other taxa consistently included within Odacanthini (Figs 8–18). Three other

genera – *Homethes*, *Quammenis* Erwin, and *Stenocheila* (Figs 3–5) – also exhibit the derived, divided tergite VIII, as do females of *Aeolodermus* (not figured).

Conversely, males of taxa consistently assigned to Lachnophorini do not exhibit a divided mediotergite VIII (Figs 19–25). These include the American genera *Eucaerus* LeConte, *Anchonoderus* Reiche, *Euphorticus* G. Horn, *Lachnophorus* Dejean, *Calybe* Laporte, and *Calophaena* Klug, and the widespread Old World *Selina* Motschulsky. The spiracle of segment VIII is not associated with the lateral margin of the tergite in these taxa, instead being situated more ventrally in the intersegmental membrane. Therefore the abdominal configuration of taxa assigned to either Odacanthini or Lachnophorini based on abdominal configuration are consistent with results of the DNA-sequence data.



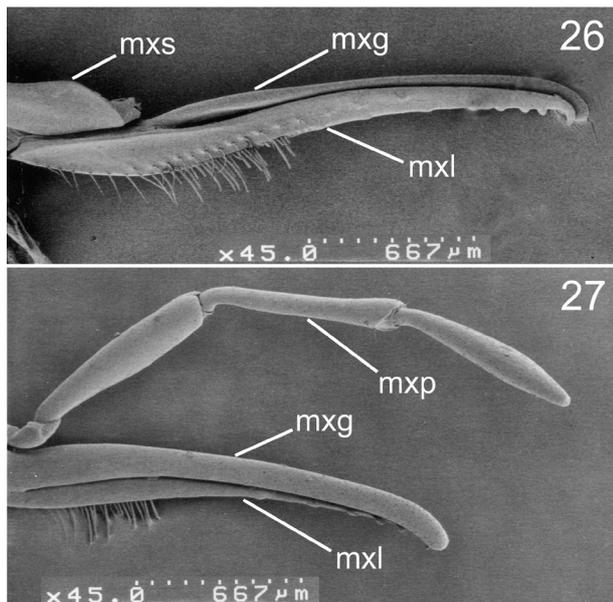
Figures 14–25. 14–18 Male aedeagus with associated abdominal segments VIII and IX, dorsal view for taxa assigned to Odacanthini (see Suppl. material 1): 14, *Colliuris oglobini*; 15, *Erectocolliuris fairmairei*; 16, *Basistichus micans*; 17, *Archicolliuris papua*; 18, *Colliuris ludoviciana*; 19–24 Male aedeagus with associated abdominal segments VIII and IX, dorsal view, for taxa assigned to Lachnophorini (Erwin and Zamorano 2014; repository indicated in parentheses): 19, *Selina westermanni* Motschulsky (BMUL); 20, *Eucaerus* sp. (Trinidad, Simla; CUIC); 21, *Anchonoderus subtilis* Bates (CUIC); 22, *Euphorticus pubescens* (Dejean) (CUIC); 23, *Lachnophorus leucopterus* Chevrolat (CUIC); 24, *Calybe argentina* Brèthes (CUIC). 25. Male aedeagus with associated abdominal segments VIII and IX, dorsal view, for taxon assigned to Calophaenini (Erwin and Zamorano 2014; repository indicated in parentheses): *Calophaena cruciata* Bates (CUIC). For abbreviations see Table 1.

Pertinent to the goal of this survey, *Cyphocoleus* males demonstrate the odacanthine abdominal segment VIII condition, with the mediotergite broadly divided into two laterotergites, and the spiracles incorporated into the lateral portion of the tergites (Figs 28–32).

Based on these results, a reexamination of the homology of the bipartite spermatheca observed in lachnophorine and odacanthine taxa is in order. Within Odacanthini, the spermathecal assembly is based on a well-sclerotized spermathecal basal sclerite (sbs) which attaches the spermathecal assembly to the common oviduct (Fig. 39). The spermatheca itself includes a bulb

that extends from the apex of the spermathecal basal sclerite (termed the spermathecal basal bulb by Liebherr and Will 1998), with the duct of the spermathecal gland entering at the apex of this bulb. In many Odacanthini, there is also a balloon-like spermathecal apical bulb which joins the spermathecal basal sclerite near the base of the basal bulb (Liebherr and Will 1998). This bulb has no associated ductules or ducts (e.g. Fig. 39) and is connected to the spermathecal basal sclerite by a narrow duct.

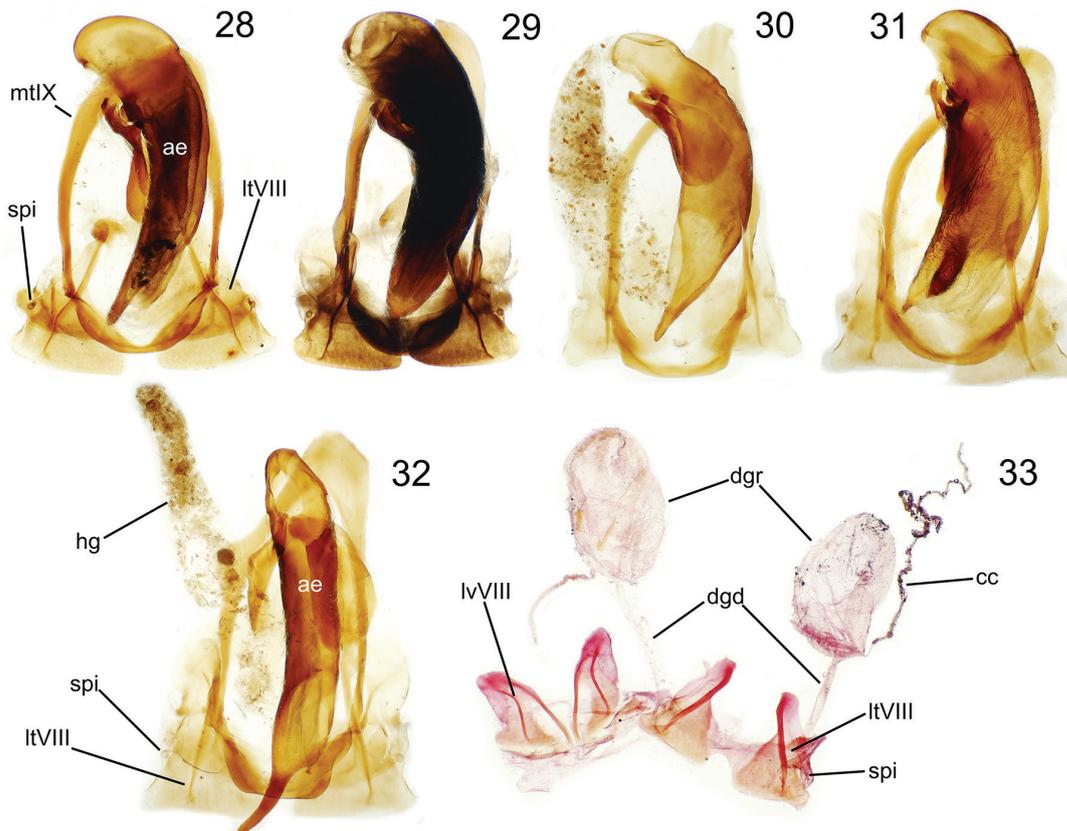
The spermatheca of Lachnophorini does not share this configuration because the spermathecal gland duct joins



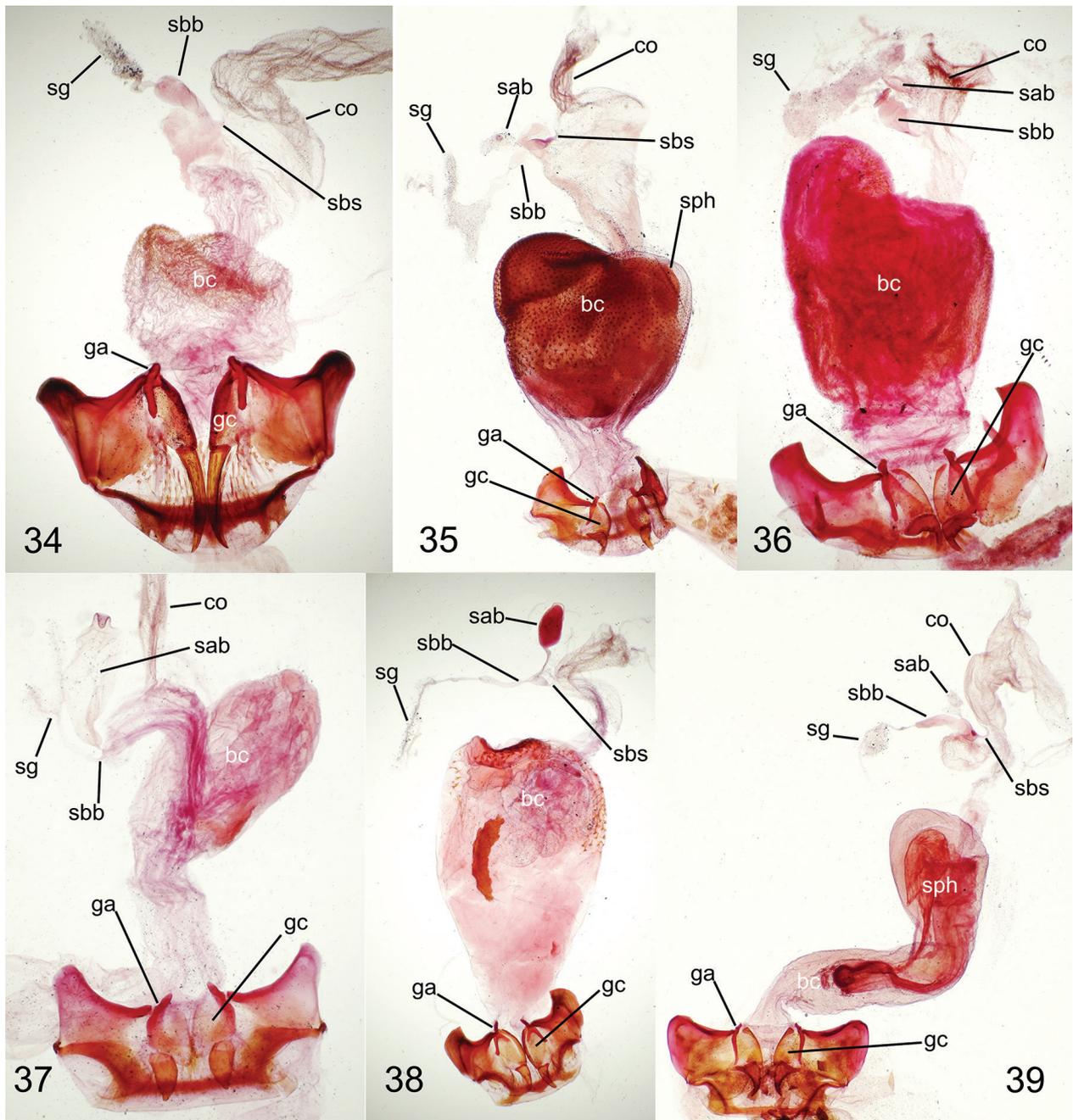
Figures 26–27. Right maxillary stipes, lacinia, galea, and palp, *Cyphocoleus subulatus*: **26**, dorsal view; **27**, ventral view. Single-segmented galea of *Cyphocoleus* and other Homethina lies laterad the lacinia, with a rabbeted groove on the dorsomedial surface of the galea accommodating the lateral margin of the lacinia, thereby supporting lacinia during alternating, rotary movements of the maxillae. For abbreviations see Table 1.

Table 1. Key to abbreviations for morphological structures indicated in figures.

Abbreviation	Structure
ae	male aedeagal median lobe
bc	female bursa copulatrix
cc	collecting canal of defensive gland
co	female common oviduct
dgd	defensive gland duct
dgr	defensive gland reservoir
ga	female gonocoxal apodeme
gc	female gonocoxa
hg	hindgut
lp	left paramere of male aedeagus
ltVIII	laterotergite of abdominal segment VIII
lvVIII	lateroventrite of abdominal segment VIII
mtIX	mediotergite of abdominal segment IX
mxg	maxillary galea
mxl	maxillary lacinia
mxp	maxillary palp
mxs	maxillary stipes
sab	apical bulb of female spermatheca
sbb	basal bulb of female spermatheca
sbs	female spermathecal basal sclerite
sg	female spermathecal gland
sp	female spermatheca
sph	spermatophore
spi	spiracle



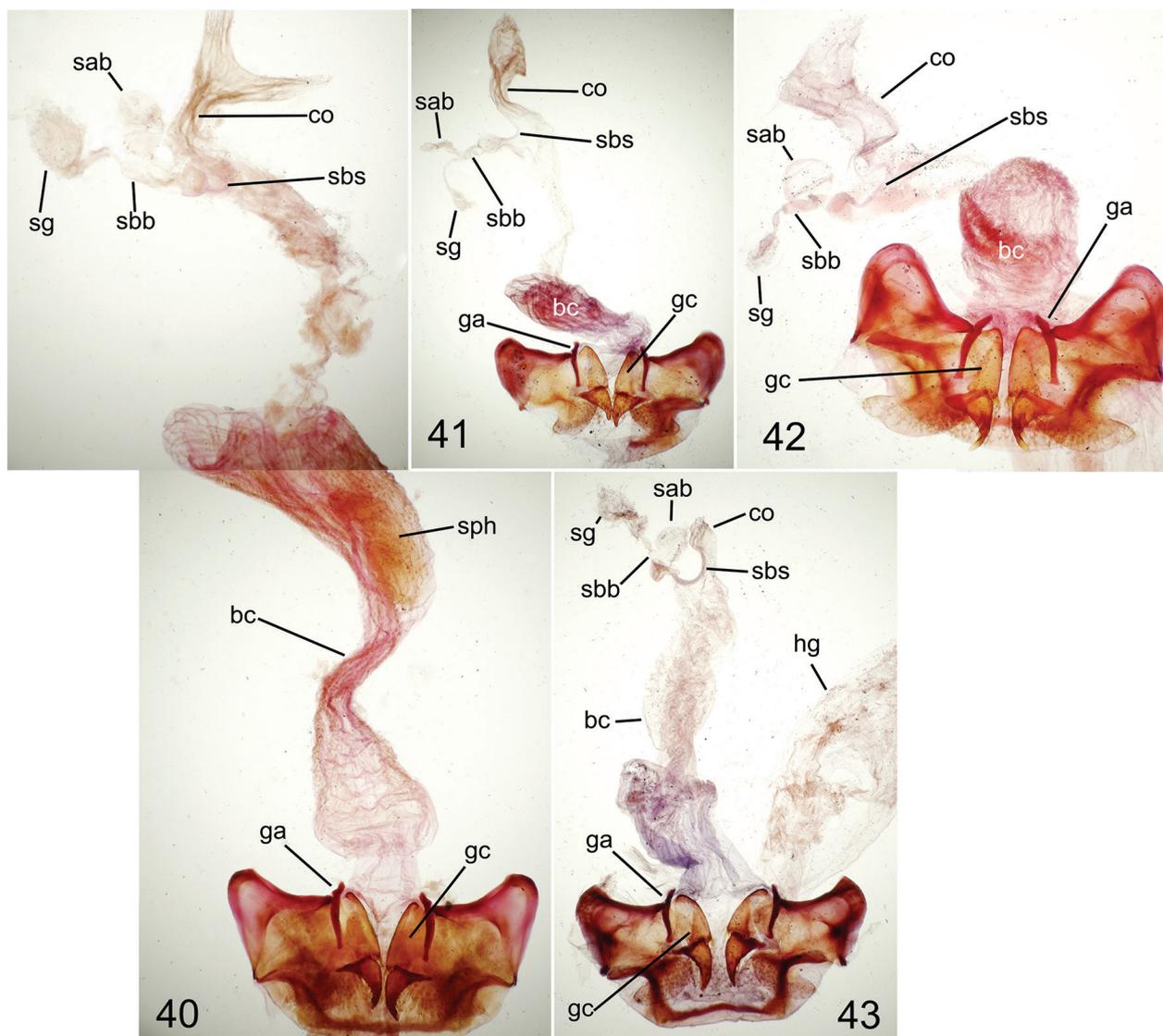
Figures 28–33. **28–32** Male aedeagus with associated abdominal segments VIII and IX, dorsal view, *Cyphocoleus* spp.: **28**, *C. heterogenus*; **29**, *C. angustatus*; **30**, *C. mirabilis*; **31**, *C. cordatus*.; **32**, *C. subulatus*. **33.** Abdominal lateroventrites VIII (left) and laterotergites VIII (right), showing membranous division of laterotergites, male *C. latipennis*. Dorsal gland reservoir is globose without dorsal lobe. For abbreviations see Table 1.



Figures 34–39. Female gonocoxal ovipositor and female reproductive tract, ventral view for taxa assigned to Odacanthini (see Suppl. material 1): **34**, *Actenonyx bembidioides*; **35**, *Homethes gracilis*; **36**, *Stenocheila lacordairei*; **37**, *Pentagonica daimella*; **38**, *Scopodes edwardsii*; **39**, *Eudalia atrata*. For abbreviations see Table 1.

the spermatheca near the base of the basal bulb, not at the apex (Liebherr and Will 1998: fig. 55). This fundamentally different entry point for the spermathecal gland duct argues against homology of the basal bulb in Odacanthini versus Lachnophorini. Upsetting that homology undermines the homology of the bipartite spermathecal condition in the two tribes, suggesting the possibility that the bipartite condition evolved twice. This possibility is congruent with both the molecular phylogenetic data (Ober and Maddison 2008) and the results of the survey of abdominal tergite VIII presented above.

In conclusion, the outgroups considered appropriate to include with *Cyphocoleus* in a cladistic analysis include those assigned to Odacanthini and Pentagonicini (Liebherr and Will 1998), plus the additional taxa found to share the divided mediotergite VIII and the odacanthine female reproductive tract with spermathecal gland duct entering the apex of the spermathecal basal bulb (Figs 34–43, Suppl. material 1). Those taxa previously assigned to Lachnophorini (or Lachnophorina and Calophaenina *sensu* Erwin and Zamorano 2014: Figs 19–25) are not included, as they do not form a natural group with Odacanthini as defined



Figures 40–43. Female gonocoxal ovipositor and female reproductive tract, ventral view for taxa assigned to Odacanthini (see Suppl. material 1): **40**, *Neoeudalia nigra*; **41**, *Odacantha melanura*; **42**, *Colliuris ludoviciana*; **43**, *Colliuris subdistincta*. For abbreviations see Table 1.

here. It follows that the hypothesis pairing Odacanthini and Lachnophorini as sister groups comprising a supertribe Odacanthitae (Liebherr 1988) must be discarded.

Ingroup phylogenetic analysis. The 79 taxa included in the analysis (Suppl. material 1, Figs 44, 45) were assessed for 119 morphological characters: 112 synapomorphies, 4 symplesiomorphies of the outgroup root taxon, 1 autapomorphy among the ingroup taxa for female characters, with some taxa not codable for females due to absence in the study set, and 2 autapomorphies included for future assessment against additional taxa (Suppl. material 2). The 78-taxon odacanthine ingroup was rooted at *Celaenephes linearis* (Walker) based on inclusion of that taxon in the “Pentagonicini + Odacanthini clade g” (Ober and Maddison 2008: fig. 2). An additional 120th character coding for geographic distributions of the taxa was also included to allow visualization of area relationships among the odacanthine taxa, although this character was not active in the analysis.

Characters. Characters are numbered sequentially starting at the anterior of the head, posterad to the abdomen and then legs for external characters, then to internal anatomical, male genitalic, and female reproductive tract characters. The distribution of character states among taxa can be viewed under the “Diagnoser” toggle of WinClada (Nixon 2002), using the data file provided as Suppl. material 2.

Character 0. Labrum: truncate to slightly emarginate apically (0); broadly convex apically (1).

Character 1. Mandibular length: short, \leq to $\sim 1.5\times$ distance antenna base-labral margin (0); moderately elongate, $1.5\text{--}1.75\times$ distance (1); elongate, $>1.8\text{--}2.25\times$ distance (2) (Fig. 47); very elongate, $>2.3\times$ distance (3) (Fig. 48).

Character 2. Maxillary galea comprising: two subequal segments (0); a single elongate segment (1) (Figs 26,

- 27). The united, single-segmented galea was observed in individuals of the *Cyphocolaus* spp. described by Chaudoir (1877). He also noted this condition in the genera *Homethes* and *Stenocheila* (Chaudoir 1872).
- Character 3. Maxillary galea: free of the lacinia (0); appressed to the outer surface of lacinia (1) (Fig. 26).
- Character 4. Apical maxillary palpomeres: apparently glabrous (0); covered with short, sparsely distributed setae (1); covered with long, dense setae (2).
- Character 5. Antennal scape: moderately long, length 2.0–2.3× breadth (0); elongate, length 2.4–3.2× breadth (1) (Fig. 46); very elongate, length 3.5–4.9× breadth (2) (Fig. 48).
- Character 6. Antennal scape: gracile to moderately broad, anterior surface at most slightly bowed (0); bowed, swollen, anterior surface distinctly convex (1) (Figs 99–103).
- Character 7. Antennomeres 2–3: glabrous except for apical setae (ring setae on 3) (0); with short setae sparsely distributed along shaft (1); with short setae densely distributed along shaft (2).
- Character 8. Antennomeres: concolorous or basal antennomeres paler (0); apical 3–4 antennomeres distinctly paler, testaceous (1); antennomeres 7–8 or 8–9 paler (2); antennomeres 7–10 paler (3).
- Character 9. Frons: broadly convex (0) (Fig. 47); with broad median convexity and two adjacent paralaral grooves (1) (Fig. 104); with cristate median convexity and paralaral grooves (2) (Fig. 1).
- Character 10. Frons: smooth or irregularly upraised (0); distinctly punctate (1).
- Character 11. Supraorbital setae: two, both anterior and posterior seta present (0); posterior seta present, anterior absent (1); neither anterior nor posterior seta present (2).
- Character 12. Eyes: moderate large, greatly projected (0); hypertrophied, convexly projected (1).
- Character 13. Eye size: moderate (0) (Fig. 82); very small (1) (Fig. 49).
- Character 14. Number of ommatidia across horizontal diameter of eye: 10 or more (0); 8 (1).
- Character 15. Eye convexity: moderately convex (0) (Fig. 50); very convex, pop-eyed (1) (Fig. 47).
- Character 16. Eye convexity: moderately convex (0) (Fig. 99); nearly flat (1) (Fig. 101).
- Character 17. Neck: without any constriction behind vertex, sides not constricted (0) (Fig. 47); with moderate constriction behind vertex, sides constricted (1) (Fig. 48); with very distinct neck constriction, head pedunculate (1) (Fig. 99).
- Character 18. Neck defined by: elongate gena, head stalked (0) (Fig. 47); short gena, head truncate behind (1) (Fig. 99).
- Character 19. Submentum: with two setae each side (0); with single seta (inner) each side (1).
- Character 20. Ventral surface of gena: glabrous (0); with seta each side (1).
- Character 21. Mentum: without median tooth (0); with shallow bidentate tooth (1); with obtuse median tooth, apex rounded (2); with acute median tooth, apex pointed (3).
- Character 22. Suture between mentum and gula/submentum straight and complete (0); reduced to an indistinct impression, straight or not (1).
- Character 23. Suture between mentum and gula/submentum: complete across width, distinct or not (0); absent medially, mentum and gula fused (1).
- Character 24. Pronotum: orbicular (0) (Fig. 47); parallel-sided or basal margins straight and divergent (1) (Figs 48, 49).
- Character 25. Pronotal length: subequal or less than width (0) (Fig. 47); greater than width (1) (Figs 48–49).
- Character 26. Pronotal length: less than to twice pronotal width (0); twice or more than twice pronotal width (1) (Fig. 48).
- Character 27. Front angles: rounded (0) (Fig. 48); briefly protruded (1) (Fig. 47); extensively protruded, acute (2) (Fig. 49); extensively protruded, horn-like or digitiform process (3) (Figs 101–103).
- Character 28. Pronotal hind angles: flat, not upraised (0) (Fig. 47); with slightly upraised tubercle (1) (Fig. 48); with elongate, spinose projection (2) (Fig. 104); with very elongate, horn-like or digitiform process (3) (Figs 101–103).
- Character 29. Median base: bordered by evenly convex marginal bead (0) (Fig. 47); bordered laterally by sinuate bead, basally by straight margin (1) (Figs 48–50).
- Character 30. Pronotal basal margin: straight between pronotal hind angles (0); with median lobe extended posteriorly (1).
- Character 31. Pronotal disc: smooth or punctate laterally (0) (Fig. 47); with shallow transverse wrinkles (1) (Fig. 123); with moderate transverse wrinkles (2) (Fig. 121); with deep transverse wrinkles (3) (Figs 122, 125).
- Character 32. Pronotal disc: smooth or transversely wrinkled overall (0); punctate overall (1).
- Character 33. Pronotal disc: without parasagittal impressions (0) (Fig. 121); with shallow parasagittal impressions (1) (Fig. 122); with deep parasagittal impressions (2) (Fig. 125).
- Character 34. Prothoracic episternum: not expanded nor visible in dorsal view (0) (Fig. 47); expanded, outer surface visible in dorsal view (1) (Fig. 99).
- Character 35. Proepisternum: smooth, impunctate (0); punctured in posterior half (1); distinctly punctured or wrinkled over entire surface (2).
- Character 36 (unordered). Pronotal lateral seta: present (0); absent (1); more than one seta present (2).
- Character 37 (unordered). Pronotal basal seta: present (0); absent (1); more than one seta present each side (2).
- Character 38. Pronotal base: smooth, wrinkled or punctate as anterior portion (0); punctate (1).
- Character 39. Pronotal lateral margin: straight to convexly curved (0); angulate at lateral seta (1).
- Character 40. Pronotal lateral margin: ridge-like, lateral depression present (0); absent, lateral seta if present not in groove (1).
- Character 41. Elytral humerus: sinuously rounded laterad parascutellar striole (0) (Fig. 164); tightly rounded to angulate near or laterad base of fifth interval (1) (Fig.

- 161); distinctly angulate near or laterad base of fifth interval (2) (Fig. 49).
- Character 42. Elytral humerus: broadly extended laterally (0) (Fig. 47); narrowly extended laterally (1) (Fig. 48); very narrowly extended laterally (2) (Fig. 84).
- Character 43. Elytral basal margin: straight between humeri across scutellar base (0) (Fig. 49); inflexed at scutellar base, elytral base cordate (1) (Fig. 47).
- Character 44. Elytral basal groove: of uniform depth from scutellum to humerus (0); with deep pit at base of stria 3 (2).
- Character 45. Elytral lateral marginal depression: narrow outside anterior series of lateral elytral setae (0) (Fig. 47); broadly expanded outside anterior series of lateral elytral setae (1) (Fig. 49).
- Character 46. Elytral lateral margin: convex laterad anterior series of lateral elytral setae (0) (Fig. 47); invaginated laterad anterior series of lateral elytral setae (1) (Figs 48, 49).
- Character 47. Parascutellar seta: present, doubled or not (0); absent (1).
- Character 48. Parascutellar seta: in articulatory socket nearly to coplanar with interval 1 (0); in papillate articulatory socket elevated above interval 1 (1).
- Character 49. Parascutellar seta: single each elytron (0); double each elytron (1).
- Character 50. Dorsal elytral setae: 3–4 or more (0); 2 (anterior and medial setae present) (1); 1 (medial only) (2); 0 (3).
- Character 51. Dorsal elytral setae: 3–4 or less (0); more than 3–4, present along length of interval 3 (1).
- Character 52. Dorsal elytral setae: articulatory socket coplanar with elytral disc (0); set in foveate articulatory socket (1).
- Character 53. Dorsal elytral setae: not surrounded by differentially colored cuticular spot (0); surrounded by differentially colored cuticular spot (1).
- Character 54. Elytral macrosetae: present only on interval 3 (0); also present on interval 5 (1); also present on intervals 5 and 7 (2); also present in intervals 1, 5 and 7 (3); present on all intervals 1–7 (4).
- Character 55. Elytra: evenly convex from base to apex (0); with shallow lateral depression at basal 1/3 of length (1); with deep, distinct lateral depression at basal 1/3 of length (2); with deep lateral depressions in basal and apical halves (3).
- Character 56. Discal elytral intervals: flat to slightly convex (0); moderately convex (1); very convex (2) (Figs 47–50).
- Character 57. Elytral striae: present, shallow to deep (0); present basally and laterally, absent in apical half (1); absent (2).
- Character 58. Elytral intervals 3, 5, and 7: of equal convexity (or nearly equal) to others on disc (0) (Fig. 47); broader and more elevated than intervals 1, 2, 4, and 6 (1) (Fig. 48).
- Character 59. Elytral striae: impunctate to minutely punctate (0) (Fig. 47); regularly punctate (1) (Fig. 101); distinctly, broadly and deeply punctate (2) (Fig. 99).
- Character 60. Lateral elytral setae: with articulatory sockets not greatly raised (0); with papillate articulatory sockets (1).
- Character 61. Elytral apices: meeting at suture, margins evenly curved (0) (Figs 161–164); separately rounded with space between elytra (1) (Fig. 99); separately pointed, elytra bispinose apically (2) (Fig. 101); separately spinose, each elytron with apical spine (3).
- Character 62. Elytral subapical spine at apex of stria 3: absent (0); present (1).
- Character 63. Subapical sinuation: nearly obsolete, elytral apices obliquely truncate (0); evident (1); very distinct, angularly concave (2); very distinct, with subapical spine laterally (3).
- Character 64. Apical elytral setae: subapical and apical present (0); only subapical present (1).
- Character 65. Mesepisternal fovea: absent (0); present (1).
- Character 66. Metathoracic flight wings: present, functional with folded apex (1); vestigial (2).
- Character 67. Metepisternal length to width ratio: 2.5–4.0 (0); 2.0–2.4 (1); 1.3–1.6 (2); less than or equal to 1.0 (3).
- Character 68. Abdominal-metathoracic juncture: loosely articulated, membranous (0); tightly articulated, fused (1).
- Character 69. Elytral and abdominal ventrite cuticle: moderately sclerotized, somewhat flexible (0); extremely thick and brittle (1).
- Character 70. Surface of frons: apparently glabrous, micropunctures may be present (1); with short, sparse pelage (2); with dense pelage of visible setae (3).
- Character 71. Elytral intervals: glabrous except for primary setae (micropunctures possible) (0); with very short pelage of secondary setae (1); with moderately short pelage of secondary setae (2); with long dense pelage distributed over surface (3).
- Character 72. Dorsal pelage setae: fine, thin, pointed (0); thick, club-like (1) (Figs 101–103).
- Character 73. Head surface: glabrous except for macrosetae (0); with additional macrosetae posterad supraorbital setae (1).
- Character 74. Frons microsculpture: evident, isodiametric to transverse (0); reduced, not traceable except in spots (1); absent (2).
- Character 75. Frons: covered with distinct isodiametric sculpticells (0); covered with evident, stretched isodiametric sculpticells (1); covered with dense transverse microsculpture (1).
- Character 76. Frons surface: smooth (0); with longitudinal microreticulations (1).
- Character 77. Pronotal disc: with regular isodiametric mesh (0); with evident transverse microsculpture (1); with fine transverse lines (2); glossy, without evident microsculpture (3).
- Character 78. Pronotal discal surface: without microcuticular patterns (0); with swirling microcuticular ridges (1).
- Character 79. Elytral disc microsculpture: isodiametric mesh, may be in transverse rows (0); transverse mesh (1); evident transverse lines (2); not evident, surface glossy (3).

- Character 80. Elytral microsculpture sculpticells: moderately raised to not raised (0); extensively raised into granulate microsculpture (1).
- Character 81. Elytral disc: without window-like ivory spots (0); with apical window-like spot each elytron (1); with apical and basal window-like spot each elytron (2).
- Character 82. Environmental patina: absent (0) (Figs 47–50, 82–84); present (1) (Figs 85, 102).
- Character 83. Male abdominal apical setae: 2 (1 on each side) (0); 4 (2 (rarely 3) on each side) (1); 8 (4 on each side) (2).
- Character 84. Female apical abdominal setae: 4 or more (2 or more each side) (0); 2 (1 each side) (1).
- Character 85. Apical visible male abdominal ventrite medially: convex to slightly, broadly concave (0); with distinct, deeper notch-like invagination (1).
- Character 86. Metacoxae: trisetose (0); bisetose (1). A trisetose metacoxa has two lateral setae and one closer to body midline. The bisetose condition includes only the two lateral setae.
- Character 87. Femora: moderately elongate (0) (Fig. 47); extremely elongate (1) (Fig. 48).
- Character 88. Femora: concolorous from base to apex (0) (Fig. 47); with distinct, paler band in apical half, knees dark as base (1) (Fig. 104); with apex dark, basal 1/2 – 4/5 pale (2).
- Character 89. Fourth metatarsomere: truncate apically, without lateral lobes or with lobes short, obtuse (0) (Fig. 49); lobate, apical lobes half as long but shorter than mid-dorsal length (1) (Fig. 85); lobate, apical lobes longer than mid-dorsal length (2) (Fig. 99, 104).
- Character 90. Dorsal surface of tarsomeres: setose, setae long (0); sparsely covered with short setae (1); glabrous (2).
- Character 91. Metatarsomere 5: with 2 rows of 6–8 long ventrolateral setae (0); with 2 rows of 4–5 long ventrolateral setae (1); with 2 rows of 3–(2) long ventrolateral setae (3); with two rows of 3 short ventrolateral setae (4).
- Character 92. Abdominal tergite 8: complete, undivided medially by membranous cuticle (0); divided medially by narrowly membranous cuticle (1); divided medially by broadly membranous cuticle (2); divided medially by broad membrane, laterally extended as flaps (3).
- Character 93. Male tergite VIII apodemes: narrow, the laterotergite stalked (0); broadly triangular, therefore the laterotergite triangular (1).
- Character 94. Abdominal tergite 8 sclerotized margin: not incorporating spiracle (0); with spiracle incorporated (1).
- Character 95. Male tergite IX ring sclerite: angulate apically, wishbone-shaped (0); hemicircular apically, horseshoe shaped (1).
- Character 96. Male aedeagal median lobe: gracile (0) (Fig. 154); robust, broad dorsoventrally (1) (Fig. 153).
- Character 97. Aedeagal median lobe: short to elongate but broader basally than toward apex (0); elongate, dorsal and ventral surfaces parallel for much of length (1).
- Character 98. Aedeagal median lobe apex: gradually narrowed apicad ostium (0); parallel-sided, elongate apicad ostium (1); parallel-sided basally, curved into a hook apically (2).
- Character 99. Male aedeagal median lobe apex: evenly attenuated or expanded (0) (Fig. 154); sinuously curved ventrally, the apex offset to shaft (1) (Figs 91–98).
- Character 100. Male aedeagal median lobe apex: of moderate length, attenuate or spoon-shaped (0) (Figs 141–154); exceedingly elongate, porrect (1) (Figs 155–160).
- Character 101. Male aedeagal median lobe apex: attenuated, evenly or not, but tip acuminate (0) (Fig. 53); moderately broad, tip rounded (1) (Fig. 57); broadly rounded, spoon-shaped (2) (Fig. 55); broader apically with basal constriction, spatula-shaped (3) (Fig. 87).
- Character 102 (unordered). Male aedeagal internal sac: evenly spiculated (0) (Fig. 54); with ventral sclerotized field or tooth (1) (Figs 58, 59); with apical cockscomb of macrospicules (2) (Figs 56, 87); with apical tooth-like projection (3) (Fig. 86).
- Character 103. Female abdominal tergite IX: broadly convex (0); narrowly convex, apex tightly rounded (1).
- Character 104. Female abdominal tergum X: broad, broadly extended laterally beyond gonocoxites (0); narrow, little extended beyond gonocoxites (1).
- Character 105. Female bursa copulatrix: membranous (0) (Figs 60, 61); sclerotized across surface but translucent (1) (Fig. 64); heavily sclerotized, opaque (2) (Fig. 65).
- Character 106. Female bursa copulatrix: membranous, inner surface smooth (0); sparsely covered with spicules on inner surface (1); densely covered with thin or thick spicules on inner surface (2).
- Character 107. Female bursa copulatrix: vase-like, common oviduct short basad spermatheca (0); basally broad, with elongate oviduct basad spermatheca (1); basally broad, rectum-like, with very elongate extension to sp (2).
- Character 108. Female spermathecal assembly: without apical bulb basally adjoining basal bulb (0); with apical bulb entering basad basal bulb (1).
- Character 109. Spermathecal basal bulb: broadly joined to spermathecal sclerite (0); narrowly joined by a duct to spermathecal sclerite (1).
- Character 110. Spermathecal gland reservoir: globose or elongate, not divided apically (0); linear, divided or not apically, ductules on elongate strand (1).
- Character 111. Basal gonocoxite 1: with 1–3 apical fringe setae (0); with 5–12 apical fringe setae (1); with 14–16 apical fringe setae (2).
- Character 112. Basal gonocoxite 1: not extended medially mesad inner margin of gonocoxite 2 (0); convexly extended medially mesad inner margin of gonocoxite 2 (1).
- Character 113. Basal gonocoxite 1 basolateral apodeme: gradually thinned apically (0); very thick throughout length, bar-like (1).
- Character 114. Apical gonocoxite 2: with 2 (or 1) lateral ensiform setae (0) (Fig. 66); with 3 lateral ensiform setae (1) (Fig. 67); with 4–5 lateral ensiform setae (2).

- Character 115. Lateral ensiform setae: arrayed along lateral margin of apical gonocoxite 2 (0); grouped near apex of apical gonocoxite 2 (1).
- Character 116. Apical gonocoxite 2: acuminate apically (0); triangular, rounded apically (2).
- Character 117. Gonocoxite 2: much narrower basally than length, falciform (0); narrower basally than width, acuminate to triangular (1).
- Character 118. Dorsal ensiform seta of gonocoxite 2: present (0); absent (1).
- Character 119 (inactive). Zoogeographic Region: New Caledonia, New Zealand, Australia, Asia, Africa incl. Madagascar, Palaearctic, Neotropical, Nearctic.

Cladistic analysis. The 79 taxon \times 119 character matrix was developed in WinClada (Nixon 2002) and analyzed under parsimony (Goloboff 1999) using the ratchet (Nixon 1999). An initial analysis using 200 ratchet runs followed by a boot based on 10,000 ratchet runs resulted in the same set of 29 equally parsimonious trees (step length 835, CI = 22, RI = 74). The strict consensus of the 29 trees collapsed eight nodes (Fig. 44), resulting in a consensus tree of 852-step length. The majority rule consensus tree collapsed the same eight nodes, leaving all remaining resolved nodes at 100% tree support (Fig. 45). The data set (Suppl. material 2) was submitted to TNT – Tree Analysis using New Technology (Goloboff and Catalano 2016) – using the New Technology search option, with 12 initial add-sequences, and 20 findings of minimum length, in order to confirm the 835-step minimum length cladogram. The TNT program examined 466,964,990 rearrangements, finding a minimum length 835-step tree 20 times.

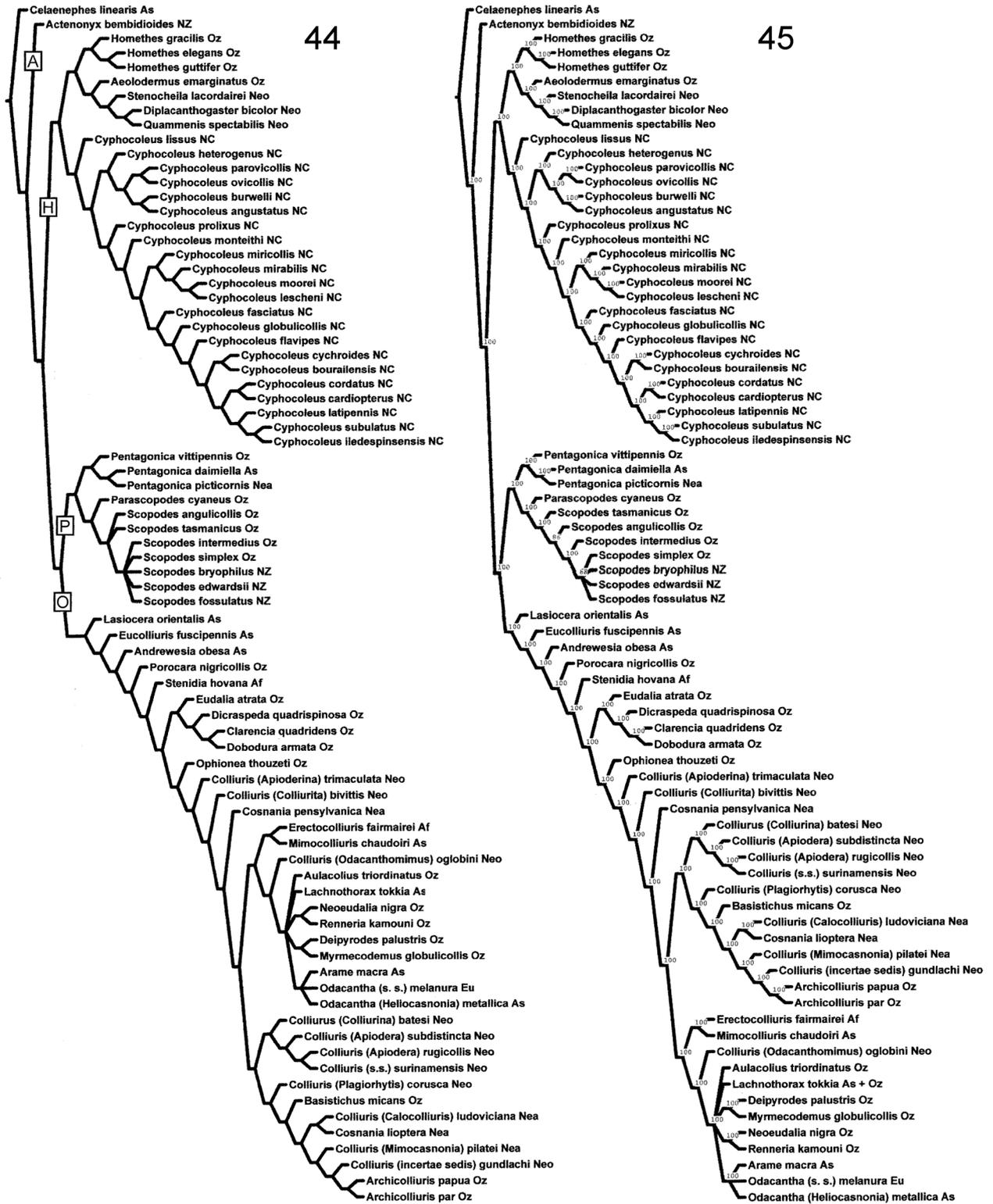
Classification of Odacanthini stat. n. The tribe Odacanthini is hereby proposed to consist of four monophyletic subtribes: **1**, Actenonycina; **2**, Homethina subtrib. n. (type genus *Homethes* Newman); **3**, Pentagonicina; and **4**, Odacanthina (Fig. 44, Suppl. material 1). Relative to the *Celaenephes linearis* outgroup, monophyly of Odacanthini is supported by nine characters. Three unreversed synapomorphies of the tribe are the medially membranous abdominal tergite VIII (character 92, state 1), the incorporation of the abdominal VIII spiracles into the lateral margin of the laterotergites (character 94, state 1: Figs 2–18, 28–33), and spermathecal basal bulb joined to common oviduct by narrow, sclerotized spermathecal basal sclerite (character 109, state 1). Other characters supporting the basal node defining Odacanthini are subordinately reversed on the tree. One such as the absence of the basal pronotal seta (character 37, state 1) is shared by most odacanthine taxa, however the character is reversed, i.e. seta present, among *Parascopodes* Darlington and most *Scopodes* in the analysis. Moreover some Odacanthina have more than one seta present near the pronotal hind angle (e.g., *Odacantha* and *Arame*). Also, the metacoxae are bisetose (character 86, state 1) in all odacanthines in the analysis with the exceptions of *Cyphocoleus angustatus*, *Dicraspeda quadrispinosa*, and species

of *Aulacolius*, *Lachnothorax*, *Arame*, and *Odacantha*. Odacanthines generally have moderately elongate to very elongate mandibles (character 1, states 1–3), but this is reversed to short mandibles in *Homethes*, *Aeolodermus*, the pentagonicines, and the species of *Ophionea* and *Myrmecodemus* in the Odacanthina. More numerous and complex patterns of reversals from the derived state occur in the final 3 characters supporting the basal odacanthine node: **1**, mentum with shallow bidentate tooth (character 21, state 1); **2**, subapical elytral situation evident (character 63, state 1); and **3**, male aedeagal median lobe broad dorsoventrally (character 96, state 1), so these characters cannot be used to diagnosis the tribe.

Actenonycina. The genus *Actenonyx* is included within Odacanthini based on the shared-derived abdominal configuration (Fig. 2), and the presence of a spermathecal basal sclerite (Fig. 34). However the absence of an apical bulb in the spermathecal assembly (character 108, state 1: e.g. Fig. 35) supports placement of *Actenonyx* as the adelphotaxon to the rest of the Odacanthini (Fig. 44, lineage A). This placement is supported also by the extremely narrow and stiletto-like gonocoxae (character 117, state 0: Fig. 34) compared to the broader gonocoxal configuration observed in females throughout the rest of the tribe (character 117, state 1: e.g. Figs 35–39). The genus can be diagnosed by the following combination: **1**, antennomeres 2–3 glabrous (character 7, state 0); **2**, gena with a ventral seta present (character 20, state 1); **3**, pronotal disc with shallow transverse wrinkles (character 31, state 1); **4**, pronotal lateral seta absent (character 36, state 1); **5** apical tarsomere with reduced ventral setation, only 3 short ventrolateral setae each side (character 91, state 3); and **6**, male aedeagal median lobe evenly narrowed apically (character 101, state 0: Fig. 2).

Homethina + Pentagonicina + Odacanthina. The presence of the spermathecal apical bulb and broader gonocoxae (characters 108, 117) are synapomorphies of this clade that excludes *Actenonyx*. The antennae are nearly uniformly elongate (character 5, states 1 and 2), and the apices of the elytra are generally separately rounded each side of the suture (character 61, state 1), though this condition is reversed in some *Cyphocoleus*, *Aeolodermus emarginatus*, and several species within Pentagonicina and Odacanthina.

Homethina subtrib. n. This subtribe is dramatically supported by the one segmented maxillary galea (character 2, state 1) that is appressed to the outer margin of the lacinia (character 3, state 1: Figs 26, 27). Although the state distributions for these two characters are identical in this analysis, a single-segmented maxillary galea is observed also in *Amerizus*, though in this taxon the galea is apically free of the lacinia, justifying the separation of these two attributes into distinct characters here. The mentum lacks a median tooth (character 21, state 0), a state shared with *Pentagonica* and some *Scopodes* spp. The humeri are tightly rounded to angulate (character 41, state 1: Figs 47–50) throughout the early-diverging lineages of this subtribe, although this condition is reversed



Figures 44–45. Parsimony cladograms comprising exemplar taxa of Odacanthini used in phylogenetic analysis, rooted at the out-group *Celaenephes linearis* (tribe Lebiini): **44**, 852-step length strict consensus of 29 equally parsimonious trees of 835-step length (CI = 22, RI = 74) [A = subtribe Actenonycina; H = subtribe Homethina subtrib. n.; P = subtribe Pentagonicina; O = subtribe Odacanthina]; **45**, majority-rule consensus of 29 equally parsimonious trees with all resolved nodes present in 100% of the multiple equally parsimonious trees; i.e. the majority-rule consensus is the result of collapsing 8 nodes. Abbreviations for geographical distributions include: Af, Africa; As, Asia; Eu, Europe; NC, New Caledonia; Nea, Nearctic; Neo, Neotropical; NZ, New Zealand; Oz, Australia.

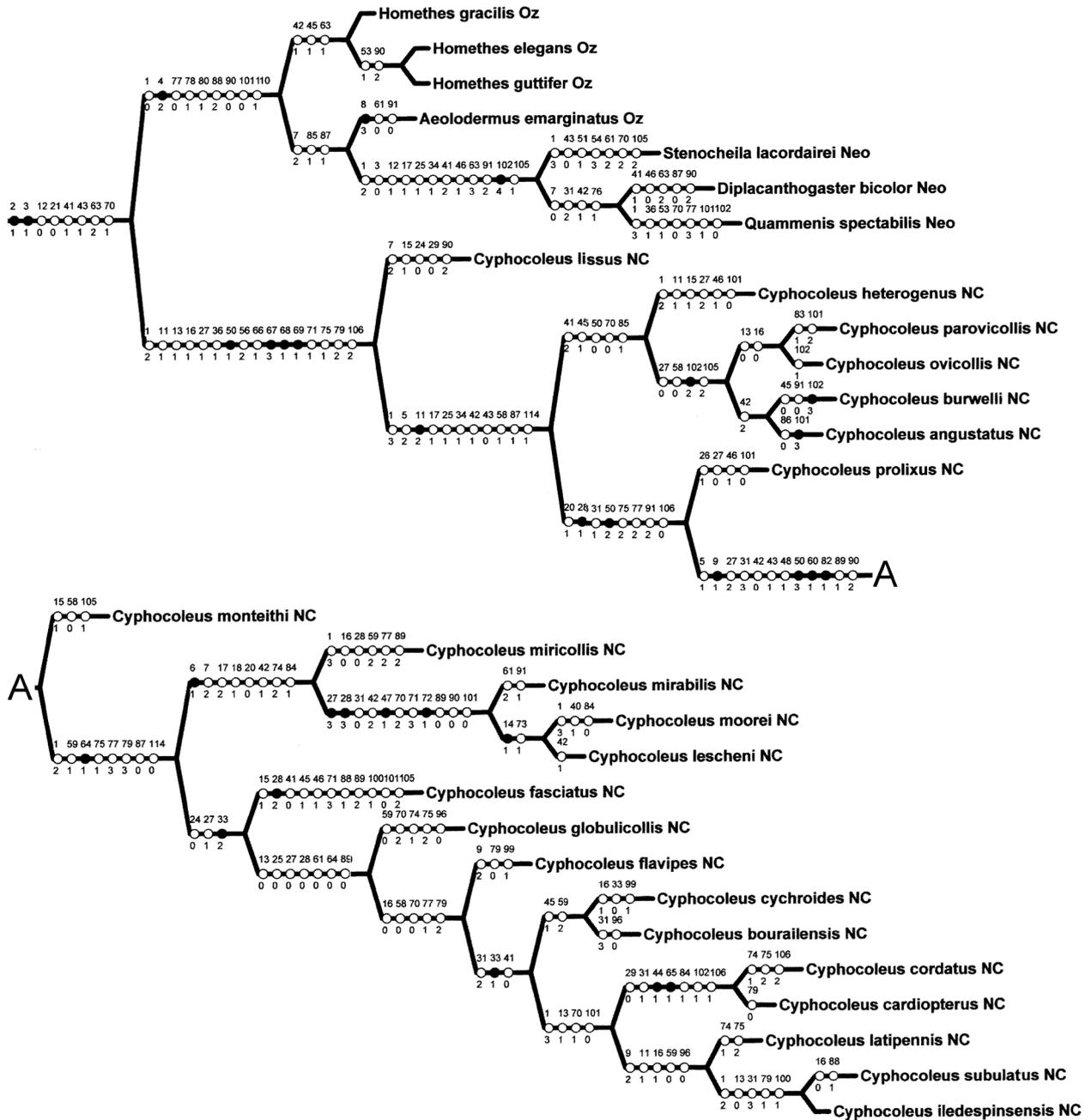


Figure 46. Parsimony cladogram of subtribe Homethina with characters indicated; character numbers above cladogram stems, state numbers below stems [cladogram divided into two parts joined at “A”]; geographic abbreviations as in Figs 44–45.

in homethine taxa with broad elytra (Figs 161–164). Also, the elytra basal margin is inflexed near the scutellum (character 41, state 1) in most taxa (Fig. 27), though also reversed in taxa characterized by narrow bodies (Figs 48–50). Most homethines bear a dense pelage of short to elongate microsetae over various parts of the body (e.g., the frons: character 70). These pelage setae culminate in the dramatically club-shaped setae of *Cyphocoleus mirabilis* and associates (Figs 101–103). This pelage may be reduced to inapparency in some *Cyphocoleus* spp., but careful examination in side view demonstrates that homethine cuticle is coated with microsetae (noted for *Aeolodermus* by Erwin and Zamorano 2014).

The Homethina divide into two sister clades: *Cyphocoleus* versus five other genera (Fig. 46). These five include: *Homethes* and *Aeolodermus*, both from Australia with the former also represented in Java and the Philippine Islands (Louwerens 1952), the South American *Stenocheila* and *Diplacanthogaster*, and *Quammenis* of Costa Rica. These genera are united by several characters related to microsculpture, coloration, and setation. All exhibit a pronotal surface with swirling microreticular ridges (character 78, state 1), and elytra with raised, granulate sculpticells (character 80, state 1). The femora are paler basally with a dark apex (character 88, state 2), and the apical maxillary palpomeres are densely covered with fine setae (character

4, state 2). Also, based on the female reproductive tracts available for study – i.e. *Homethes guttifer*, *H. gracilis*, *Aeolodermus emarginatus*, and *Stenocheila lacordairei* (Figs 35, 36) – the spermathecal gland ramifies into two arms, with the spermathecal gland duct exiting from the middle of those arms. Monophyly of *Cyphocoleus*, conversely, is based on characters representing mandibular elongation, eye modification, setal loss, wing loss, and modification of microsculpture. All *Cyphocoleus* exhibit elongate mandibles (Character 1) to varying degrees (Figs 47–50), whereas the Australian homethine taxa are characterized by shorter mandibles. Longer mandibles have evolved independently in the South and Central American homethines. The eyes (character 13) are reduced in most *Cyphocoleus*, though reversed to moderate size in eight taxa subordinate within the clade. The anterior supraorbital seta (character 11, state 1) is lost in all *Cyphocoleus* spp., and the posterior supraorbital seta (character 11, state 2) is lost during *Cyphocoleus* evolution, being absent in 17 of the 22 species. The prothoracic lateral seta is also lost in all *Cyphocoleus* (character 36), and except for one subordinate clade, the dorsal elytral setae (character 50, states 1, 2, and 3) are reduced in number or completely absent. A number of characters associated with flight wing loss (Darlington 1936) also define *Cyphocoleus*. These include, in addition to the obvious absence of flight wings (character 66): **1**, a very short metepisternum (character 67, state 3); **2**, a very tightly articulated abdomen (character 68); **3**, thick, brittle cuticle; and perhaps in association with thick cuticle, **4**, convex elytral intervals (character 56). Finally, the cuticle of *Cyphocoleus* often bears transverse microsculpture compared to the raised, isodiametric, or swirling microreticulate patterns of the Australian and New World homethines. Such transverse microsculpture is seen to differing degrees on the head (character 75), pronotum (character 77: reflected in Fig. 46 by loss at the base of the *Homethes*-subtended clade), and elytra (character 79).

Pentagonicina + *Odacanthina*. Cladistic support for monophyly of these two subtribes comes from six characters: **1**, neck very constricted (character 17, state 2: reversed in *Porocara* Baehr of Odacanthini); **2**, gena short before constricted neck (character 18, state 1: observed in *Pentagonicina* and *Lasiocera* Dejean of Odacanthina); **3**, elytral subapical sinuation nearly obsolete (character 63, state 0: a condition observed in most pentagonicines and stem odacanthines from *Lasiocera* to *Stenidia* Brullé); **4**, frons without visible microsculpture (character 74, state 1: extensively reversed to present in *Pentagonica*, some *Scopodes* spp., and several Odacanthini); **5**, tarsomeres dorsally glabrous (character 90, state 2: reversed to setose in *Pentagonica*, some *Scopodes*, and several Odacanthini); **6**, and finally, male aedeagal median lobe dorsal and ventral surfaces parallel near ostium, the ostial opening apical not dorsal (Figs 6–18).

Pentagonicina. The three genera placed in this subtribe exhibit numerous synapomorphies, with the rank of the taxon being the sole change in this historically well-recognized group. The labrum is broadly convex (character 0, state 1), covering the dorsal surfaces of the short

mandibles (character 1, state 0). The apical palpomeres are sparsely setose (character 4, state 1), and the mentum/gular suture is reduced laterally or absent altogether (characters 22 and 23, both state 1). These last characters are reversed in *Scopodes tasmanicus* and *Parascopodes cyaneus*. The pronotum bears a basal lobe that extends posterad between the hind angles (character 30, state 1) – again reversed in *Parascopodes* – but the pronotum is consistently angulate laterally (character 39, state 1), hence providing the basis for the taxon name. Deuve (1993) noted that the abdominal tergite VIII is broadly membranous in *Pentagonica* (character 92, state 2), and though this characters supports monophyly on the cladogram (Figs 44, 45), the broadly membranous condition is seen among many odacanthines.

Odacanthini. This very diverse, geographically cosmopolitan subtribe exhibits a broad array of characters and body forms, presumably associated with myrmeco-mimetic behavior while individuals are actively foraging. Focusing on the early-diverging lineages *Lasiocera*, *Eucollurius* Liebke, *Andrewesia* Csiki and *Porocara* allows focus on the odacanthine groundplan. Based on this cladistic analysis, the common ancestor of Odacanthini is characterized by: **1**, frons punctate (character 10, state 1); **2**, submentum with two setae each side (character 19, state 0); **3**, mentum with a median tooth (character 21, state 2); **4**, surface of pronotal disc distinctly punctate (character 32, state 1); **5**, elytral striae punctate (character 59, state 1); **6**, frons without microsculpture between punctures, glossy (character 74, state 2); **7**, pronotal disc (between punctures) without microsculpture, glossy (character 77, state 3); **8**, femora with apex dark (character 88, state 2); **9**, male aedeagal median lobe gracile (character 96, state 0: Figs 8, 9); **10**, male aedeagal median lobe with dorsal and ventral surfaces parallel from basal bulb to base of ostial opening (character 97, state 1: Figs 8–18); and **11**, female bursa copulatrix basally broad with common oviduct elongate basad the spermatheca (character 107, state 1: Figs 39–43).

Taxonomic treatment

Odacanthini Laporte, 1834: 40 [sensu n.]

Homethina subtrib. n.

<http://zoobank.org/AEDC73A8-C144-4635-999D-098AEEA7AEE5>

Cyphocoleus Chaudoir 1877: 188

Atongolium Park & Will 2008: 100 (syn. n.)

Type species. *Cyphocoleus heterogenus* Chaudoir 1877 (designated by Bousquet 2002).

Nomenclatural note. When Bousquet (2002) designated the type species for *Cyphocoleus*, he chose the variant spelling *C. heterogenus* (Chaudoir, 1877: 191), not mentioning the alternate spelling of *C. heterogenus* that was published in the same article (Chaudoir 1877:

196). Fauvel (1882) cited the species as *C. heterogenus*, choosing the correct Latin formation of the name, though he did not mention the alternate spelling. Subsequent authors (Fauvel 1903, Csiki 1931, Lorenz 2005) followed Fauvel's (1882) usage of *C. heterogenus* without mention of the "heterogenus" variant later cited by Bousquet (2002). Having cited both name variants together here – and therefore acting as first reviser under Article 24.2.3 (I.C.Z.N. 1999) – I designate *C. heterogenus* as the correct original spelling for the type species of *Cyphocoleus*.

Diagnosis. Though quite variable in body proportions and appearance (Figs 47–50, 82–85, 99–103, 161–164), the genus *Cyphocoleus* is amply diagnosed from other Odacanthini based on the following combination of characters: **1**, mandibles elongate, their length measured from anterior condyle to tip $>1.8\times$ distance from anterior margin of antennal articulatory socket to anterolateral labral margin; **2**, maxillary galea 1-segmented and appressed to outer margin of lacinia (Figs 26, 27) [synapomorphy of Homethina]; **3**, only posterior supraorbital seta present, or both supraorbital setae absent; **4**, pronotal lateral and basal setae absent [a configuration shared with *Quammenis spectabilis*: Homethina, and *Actenonyx bembidioides*: Actenonycina]; **5**, discal elytral intervals convex, not flat; **6**, elytral sub-

apical situation very distinctly, angularly concave; **7**, metathoracic flight wings vestigial, that configuration associated with a flightlessness syndrome that includes metepisternum broader than long, tightly articulated metathorax and abdomen [those somites functionally fused], elytra fused at the suture, and very thick and brittle cuticle of elytra and abdominal ventrites; **8**, head, prothorax, and elytra with pelage of secondary setae, those setae ranging from very short spike-like microtrichia, to elongate, paddle- or club-shaped setae (Figs 101, 102); and **9**, transverse microsculpture, or the absence of any microsculpture on frons and pronotal disc. In addition, several characters exhibited by *Cyphocoleus* spp. are shared with various other subtribes of Odacanthini. An elongate scape, length $2.4\text{--}4.9\times$ breadth is observed in all Homethina (Fig. 46). The submentum with only the inner seta each side is shared across Actenonycina, Homethina and Pentagonicina (Fig. 44). The mentum also lacks a median tooth: a character shared with other Homethina, *Pentagonica*, and some *Scopodes* spp. And the proepisternum is smooth, not punctate as observed in many Odacanthina (Fig. 46). Metatarsomeres 1–3 have narrow dorsolateral sulci both sides, and are broadly convex medially. Metatarsomere 4 bears both subapical and apical setae (Habu 1978).

Identification key to adults of *Cyphocoleus* spp. known from New Caledonia

- 1 Elytral striae impunctate; elytral intervals of subequal convexity, although the 5th and 7th intervals may be indistinctly more convex in beetles of some species; body surface always smooth, without varnish-like exudate that may trap environmental debris (Figs 47–50, 82–84)..... 2
- Elytral striae punctate, either shallowly punctate with punctures elongate and most evident on discal striae 1–5, or distinctly punctate with deep round punctures in all striae; elytral intervals often carinate, especially the 3rd, 5th or 7th intervals; body surface of all mature individuals covered with varnish-like exudate that may trap environmental debris (Figs 85, 99–103, 121–125, 161–164) (teneral individuals may lack this environmental patina) (e.g. Fig. 104)..... 8
- 2 Head capsule basally constricted posterad gena, neck constricted (Fig. 48–50, 82–84); pronotal lateral marginal bead subangulately joining straight basal margin; body size larger, standardized body length 9.1–13.1 mm..... 3
- Head capsule broad basally, not constricted behind eyes (Fig. 47); pronotal lateral and basal marginal beads continuous and evenly convex across median base; body size smaller, standardized body length 6.7–8.2 mm 1. *C. lissus* sp. n.
- 3 Pronotum broadest before midlength, pronotal front angles subangulate and slightly protruded (Figs 50, 82–84) to angulate and protruded (Fig. 49); elytral lateral margin not or only slightly expanded outside anterior series of lateral elytral setae, the elytral basal margin evenly rounded laterad humeral angle..... 4
- Pronotum broadest in basal half, narrowed apically toward very narrow head, pronotal front angles narrowly rounded, not protruded (Fig. 48); elytral lateral margin with distinct lateral expansion outside anterior series of lateral elytral setae, the elytral basal margin nearly straight between bases of striae 6 and 9 2. *C. prolixus* sp. n.
- 4 Pronotal front angles either minutely protruded, subangulate, or not protruded and obtusely rounded (Figs 50, 82–84) 5
- Pronotal front angles extremely protruded, acute (Fig. 49)..... 3. *C. heterogenus* Chaudoir
- 5 Pronotum broader (Figs 50, 82), MPW/PL = 0.78–0.90; lateral marginal depression broader, area mesad lateral marginal bead depressed 6
- Pronotum narrower (Figs 83, 84), MPW/PL = 0.68–0.77, lateral marginal depression very narrow, discal convexity extended nearly to lateral marginal bead 7
- 6 Eyes more convex, ocular ratio 1.47–1.55 (Fig. 50); apical abdominal ventrite of males with two setae each side; male aedeagus with internal sac bearing an apical "cockscorn" of stout macrotrichia (Fig. 56) 4. *C. parovicollis* sp. n.
- Eyes less convex, ocular ratio 1.41–1.44 (Fig. 82); apical abdominal ventrite of males with one seta each side; male aedeagus with internal sac bearing a large sclerotized tooth at midlength..... 5. *C. ovicollis* Fauvel
- 7 Elytral basal groove nearly straight, meeting lateral margin at obtusely angled humerus (Fig. 83); elytra piceous with silvery reflection; male aedeagal median lobe with narrowly rounded apex (Fig. 86) 6. *C. burwelli* sp. n.

- Elytral basal groove more distinctly curved laterally to meet lateral marginal bead at anteriorly projected, right-angled humerus (Fig. 84); elytra with violaceous reflection; male aedeagal median lobe with apical knob-like expansion (Fig. 87) 7. *C. angustatus* sp. n.
- 8 Pronotum tubular, distinctly longer than broad, MPW/PL = 0.59–0.83, front angles acute, protruded, or represented by setose, horn-like, digitiform processes that are longer than their diameter (Figs 85, 99–103) 9
- Pronotum more orbicular, MPW/PL = 0.86–1.10, bordered laterally by convex lateral marginal bead that is much more elevated than anterior margin inside front angles; front angles obtuse, not or only slightly protruded (Figs 104, 121–125, 161–164) 13
- 9 Elytra subellipsoid, basal carina recurved anterad to meet lateral margin at angulate humerus (Fig. 99), or humeri very narrowly projected laterally (Figs 101–103); elytral striae 1–9 with large, deep punctures even near apex, though punctures are more widely spaced apically; head capsule orbicular with deep cervical constriction and genae distinctly curved anterad neck 10
- Elytra broadly ellipsoid, disc convex, appearing inflated, humeri broadly rounded (Fig. 85); elytral striae shallowly punctate; head elongate, cervical constriction shallow, genae gradually constricted to neck 8. *C. montiethi* sp. n.
- 10 Pronotal disc smooth each side of median impression; pronotal front and hind angles presented by horn-like, digitiform processes (Figs 101–103); body including digitiform pronotal processes bearing a sparse pelage of very thick, club-shaped setae, these setae longitudinally arrayed on the elytral intervals 11
- Pronotal disc transversely wrinkled each side of median impression; pronotal front angles acute, projection continuously margined by basal and lateral marginal bead (Fig. 99); body surface covered with sparse pelage of very short, fine setae 9. *C. miricollis* Fauvel
- 11 Eyes very small, little convex, 8 ommatidia along maximal horizontal diameter of eye; body size smaller, standardized body length 4.8–5.4 mm 12
- Eyes small but moderately convex, 12 ommatidia along maximal horizontal diameter of eye; body size larger, standardized body length 6.5–7.0 mm 10. *C. mirabilis* (Park & Will)
- 12 Pronotum without lateral marginal expansion between very elongate anterior and posterior digitiform processes (Fig. 102) 11. *C. moorei* (Park & Will)
- Pronotum with elevated lateral marginal expansion between short, nub-like anterior pronotal process and elongate posterior digitiform process (Fig. 103) 12. *C. lescheni* sp. n.
- 13 Body size smaller, standardized body length 4.8–7.5 mm; pronotum much broader apically than basally, APW/BPW = 1.76–4.0 (Figs 121–125, 161–164) 14
- Body size larger, standardized body length 8.1–8.9 mm; pronotal apical width only slightly broader than basal width, APW/BPW = 1.28–1.40 (Fig. 104) 13. *C. fasciatus* sp. n.
- 14 Pronotum continuously bordered laterally and basally by uniformly elevated marginal bead that convexly crosses median base (Figs 121–124); pronotal disc smooth to shallowly wrinkled, the median disc either extended convexly to lateral carina, or delimited laterally by broad, shallow longitudinal impressions that define a broadly planar lateral marginal depression 15
- Pronotal lateral marginal bead sinuously adjoining median basal margin which bears a much less elevated basal bead or no bead at all (Figs 125, 161–164); pronotal disc deeply and distinctly transversely wrinkled, the median disc delimited by distinct longitudinal impressions that may be deep and narrowly incised (Figs 125, 161), or more broadly, more shallowly, and more irregularly incised (Figs 162–164) 18
- 15 Pronotal disc distinctly wrinkled transversely, wrinkles extended nearly to lateral carina, lateral longitudinal impressions indistinct, broad and shallow (Figs 121, 122); elytra ellipsoid, maximum breadth only slightly anterad midlength 16
- Pronotal disc smoother, transverse wrinkles very shallow to obsolete, median disc delimited by distinct longitudinal impressions that define broadly planar lateral depressions (Figs 123, 124); elytra cordiform, maximum breadth distinctly anterad midlength, the posterior half distinctly tapered to the narrow apex 17
- 16 Elytral margin broadly extended laterally outside anterior series of lateral elytral setae, the basal margin distinctly, sinuously recurved anterad parascutellar seta, humeri broadly protruded anteriorly (Fig. 121); supraorbital setae absent, vertex glabrous mesad compound eyes; pronotal disc lacking distinct longitudinal parasagittal impressions, the transverse wrinkles extended evenly or nearly evenly to lateral marginal bead 14. *C. cychroides* Chaudoir
- Elytral margin only narrowly extended laterally outside anterior series of lateral elytral setae, the setae close to lateral marginal bead; elytral basal margin only slightly recurved, the broadly rounded humeri little protruded anteriorly (Fig. 122); posterior supraorbital seta present each side near hind margin of vertex; pronotal disc with broad, shallow longitudinal parasagittal impressions that interrupt transverse wrinkles and define a broad depression mesad lateral marginal bead 15. *C. latipennis* Fauvel
- 17 Eyes small in diameter but very convex, appearing “popeyed” (Fig. 123); internal sac of male aedeagal median lobe with large, ventral tooth-like projection incorporating densely packed macroscopicules (Fig. 135) 16. *C. cordatus* sp. n.
- Eyes small in diameter but little protruded, outer surface little convex (Fig. 124); internal sac of male aedeagal median lobe with diffuse, little sclerotized ventral projection incorporating numerous macroscopicules (Fig. 136) 17. *C. cardiopterus* Chaudoir

- 18 Pronotal and elytral surface with evident microsculpture, the sculpticells isodiametric to transverse resulting in a matte to subiridescent surface; elytra and ventral body surface glabrous except for macrosetae, vertex glabrous to sparsely covered by a few short setae (environmental patina may need to be removed from elytra to assess this character) (Figs 161–164)..... 19
- Cuticle of pronotum and elytra extremely glossy, surface microsculpture not traceable; body surface with well-developed pelage of microsetae, extremely dense and extremely evident on frons, elytra, and proepisterna (Fig. 125) 18. *C. globulicollis* Fauvel
- 19 Elytral striae deeply and distinctly punctate, their punctures expanding strial breadth (Figs 161, 162);..... 20
- Elytral striae punctate but punctures shallow and not expanding strial breadth (Figs 163, 164) 21
- 20 Pronotal median discal convexity delimited by deeply incised parasagittal impressions, the pronotal surface smooth, convex between parasagittal impressions and lateral marginal bead (Fig. 161); male aedeagal median lobe short, robust, with broad recurved tip (Fig. 153)..... 19. *C. flavipes* Fauvel
- Pronotal median discal convexity bordered laterally by broad, shallow parasagittal impressions, transverse wrinkles of disc extended across impressions to reach lateral margin (Fig. 162); male aedeagal median lobe gracile, elongate, shaft expanded slightly at midlength, apex evenly downturned to narrowly rounded tip (Fig. 154)..... 20. *C. bourailensis* sp. n.
- 21 Legs and antennal scape flavous, distinctly contrasted to piceous body (Fig. 163); apex of male aedeagal median lobe curved dorsally relative to broad shaft, ostium opening on ventral surface of shaft apex (Fig. 155–158)..... 21. *C. subulatus* sp. n.
- Legs and antennal scape fuscous, only slightly paler than piceous body (Fig. 164), tibiae and tarsi only slightly paler, brunneous; apex of male aedeagal median lobe correct relative to evenly narrowed shaft, ostium opening on left-ventral surface of shaft apex (Figs 159–160)..... 22. *C. iledespkinsensis* sp. n.

1. *Cyphocoleus lissus* sp. n.

<http://zoobank.org/83EFACA6-BFD1-4FF2-83B5-2A11764976AB>

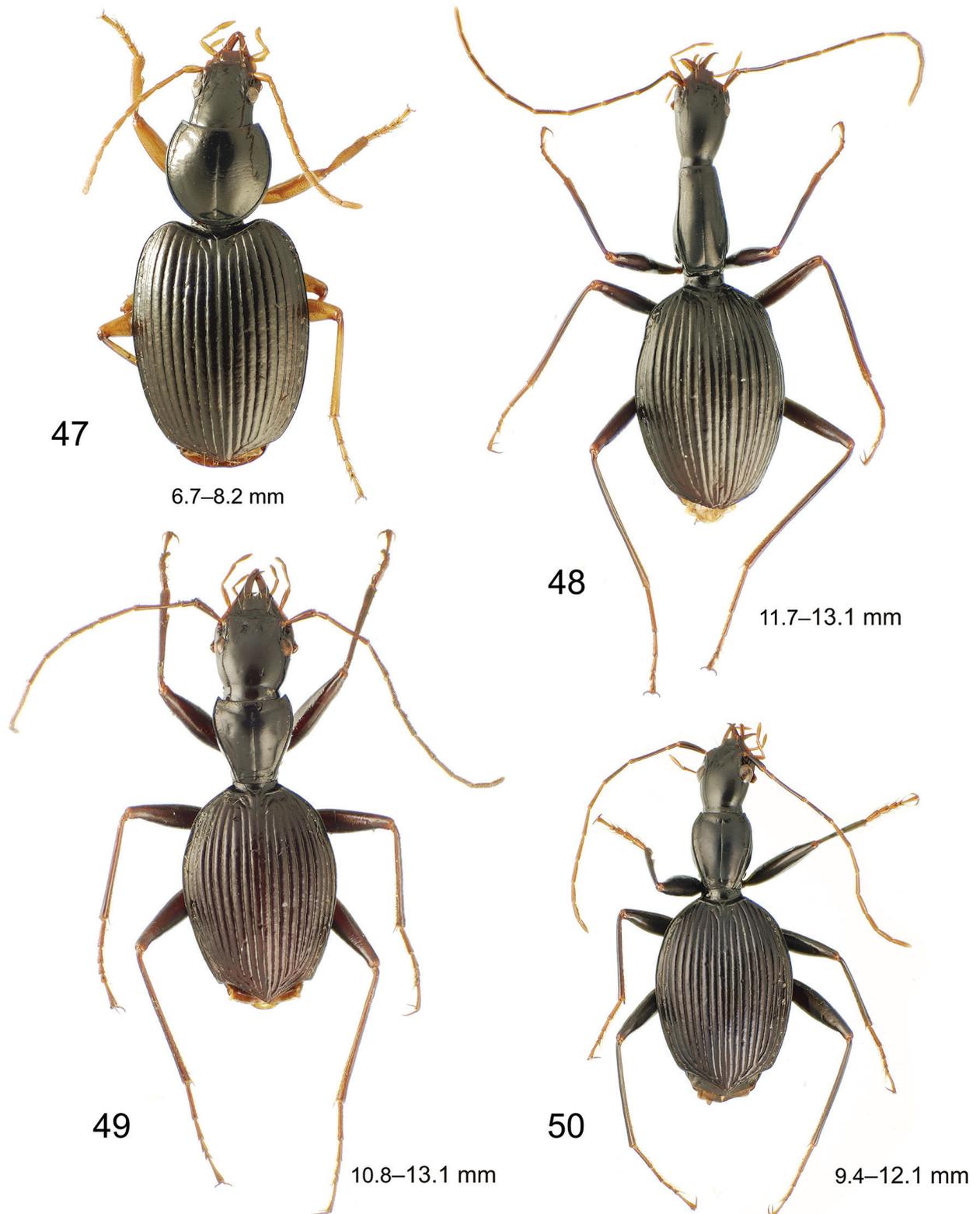
Figures 47, 51, 60, 66, 76

Diagnosis. Dorsal body surface smooth, glossy, with cyanotic iridescent reflection on elytral disc due to dense transverse microsculpture, antennae and legs contrastedly pale than dark body; head stout, broadest at juncture with prothorax, eyes small in diameter with outer surface extremely convex (Fig. 47), 16 ommatidia across horizontal diameter of eye; only posterior supraorbital seta present each side, anterior seta absent; pronotal disc extremely smooth, the lateral marginal bead convexly continuous across the median base in an even arc; elytral humeri broadly rounded, the humerus anterad the depressed scutellum; elytra with anterior and medial dorsal elytral setae, the posterior seta absent; standardized body length 6.7–8.2 mm.

Description (n = 5). Head capsule stout, frons broadly convex, the frontal grooves irregularly doubled anteriorly near clypeus; mandible length 2.0–2.1× distance from anterior margin of antennal articulatory socket to anterolateral margin of labrum; antennae filiform, moderately elongate, scape length 2.55× maximal breadth; eyes convex, but ocular ratio low due to very broad frons, MHW/mFW = 1.42–1.48; subgenera without fixed macroseta. Pronotum orbicular, hind angles completely untraceable due to evenly convex lateral and basal margin; front angles briefly protruded; notum only slightly wider than long, MPW/PL = 1.03–1.07; median longitudinal impression shallow, finely incised on disc, terminated basally in a well-defined dimple; anterior transverse impression traceable as obsolete impressed line, anterior convexity flat; proepisternum not visible from above; prosternal process convex anteriorly, with deep median groove on ventral surface that continues onto posterior face. Elytral disc moderately convex,

moderately broad, MEW/EL = 0.71–0.78; elytral intervals moderately and subequally convex across disc; striae indistinctly punctate to smooth, deep and well defined throughout length and in association with lateral elytral intervals; parascutellar seta present, articulatory socket not upraised; lateral elytral setae arranged as (5)6 + 1 + 7(8), the setal articulatory sockets not upraised above surface; both apical and subapical setae present; subapical sinuation moderately incised, convexly meeting lateral margin; apical margins of fused elytra rounded, the elytral apices slightly separated by curvature at suture. Mesepisternum smooth; metepisternum shorter than broad, dorsal length/diagonal width 0.80. Legs of moderate length, mt1 length/tibial length = 0.26; metacoxae bisetose; dorsal surfaces of tarsomeres with two dorsolateral rows of elongate setae; mt4 length to apex of outer lobe 1.6× median length, 3–4 ventrolateral setae each side. Abdomen with apical margin of apical ventrite broadly and very shallowly excavated to evenly convex; apical ventrite of male with one seta each side, of female with two setae each side. Microsculpture well developed on frons, consisting of isodiametric to slightly transversely stretched sculpticells; pronotum with dense transverse mesh over disc, but with isodiametric mesh medioapically on anterior margin; elytral intervals with dense transverse-line microsculpture; entire body surface with sparse pelage of fine microsetae, microsetae longer on frons and ventral body surface and shorter on pronotal disc and elytra. Coloration of head capsule rufopiceous; antennae pale throughout, brunneotestaceous; pronotum, proepipleuron and prosternum piceous; elytra rufopiceous basally, dark rufous apically; elytral epipleuron rufous; metepisternum piceous; abdomen rufobrunneous, ventrite 6 narrowly rufoflavous apically; femur, tibiae and tarsi flavous.

Male genitalia (n = 1). Male aedeagal median lobe robust, broadly parallel sided from base to apex of ostial



Figures 47–50. Dorsal habitus photographs of *Cyphocolleus* spp.: 47, *C. lissus* female, Mt. Humboldt; 48, *C. prolixus* male, Mt. Humboldt; 49, *C. heterogenus* male, Yahoué; 50, *C. parovicollis* male, Pic d'Amoa.

opening, dorsoventral breadth at midlength $0.25\times$ distance from tip to base of closed basal bulb (Fig. 51); lobe shaft slightly melanized, the internal sac visible through lobe wall in uneverted position; lobe apex parallel-sided,

length distad ostial opening $2.5\times$ dorsoventral breadth; tip of lobe narrowly rounded, slightly upcurved.

Female reproductive tract (n = 1). Bursa copulatrix vase-shaped, basally stalked, distance from base of gono-

coxites to spermathecal basal sclerite 2.75× maximum breadth (dissection compressed under cover slip) (Fig. 60); bursal walls thin, translucent, with broad band of short spicules lining lumen near midlength; basal gonocoxite with apical fringe of five setae (Fig. 66); apical gonocoxite acuminate with two lateral ensiform setae.

Types. Holotype female (QMB deposited in MNHN): NEW CALEDONIA / Mt. Rembai, 700–900 m / 9 May, 1984 / G. Monteith & D. Cook // **QUEENSLAND / MUSEUM LOAN / DATE:** April 2004 / No. LE 04.16 (green label) // female habitus photo / J.K. Liebherr 2015 // *Cyphocoleus* revision / measured specimen 1 / J.K. Liebherr 2015 // **HOLOTYPE** / *Cyphocoleus* / lissus / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (5 specimens). NEW CALEDONIA: Aoupinié, top camp, rainforest, 850 m el., Berlese sieved litter, 21°11'S, 165°18'E, 23-xi-2001, Monteith (QMB, 1; lot no. 1045); Ningua Res. camp, 1100 m el., pyrethrum trees & logs, 21°45'S, 166°09'E, 12–13-xi-2001, Burwell & Monteith (QMB, 1; lot no. 8639); Mt. Do, summit, 1000 m el., 21°45'S, 166°00'E, 21–22-xi-2003, Monteith (QMB, 1; lot no. 11421), forest litter 21°45'S, 166°00'E 03-xii-2009, Schuh (NMHW, 1); Mt. Humboldt, moss forest, 1400 m el., night collecting, 21°53'S, 166°24'E, 06-xi-2002, Burwell, Monteith & Wright (QMB, 1; lot no. 11139).

Etymology. The Latinized adjectival species epithet lissus is based on the Greek lissos, smooth (Brown 1956), signifying the smooth body surface of beetles comprising this species (Fig. 47).

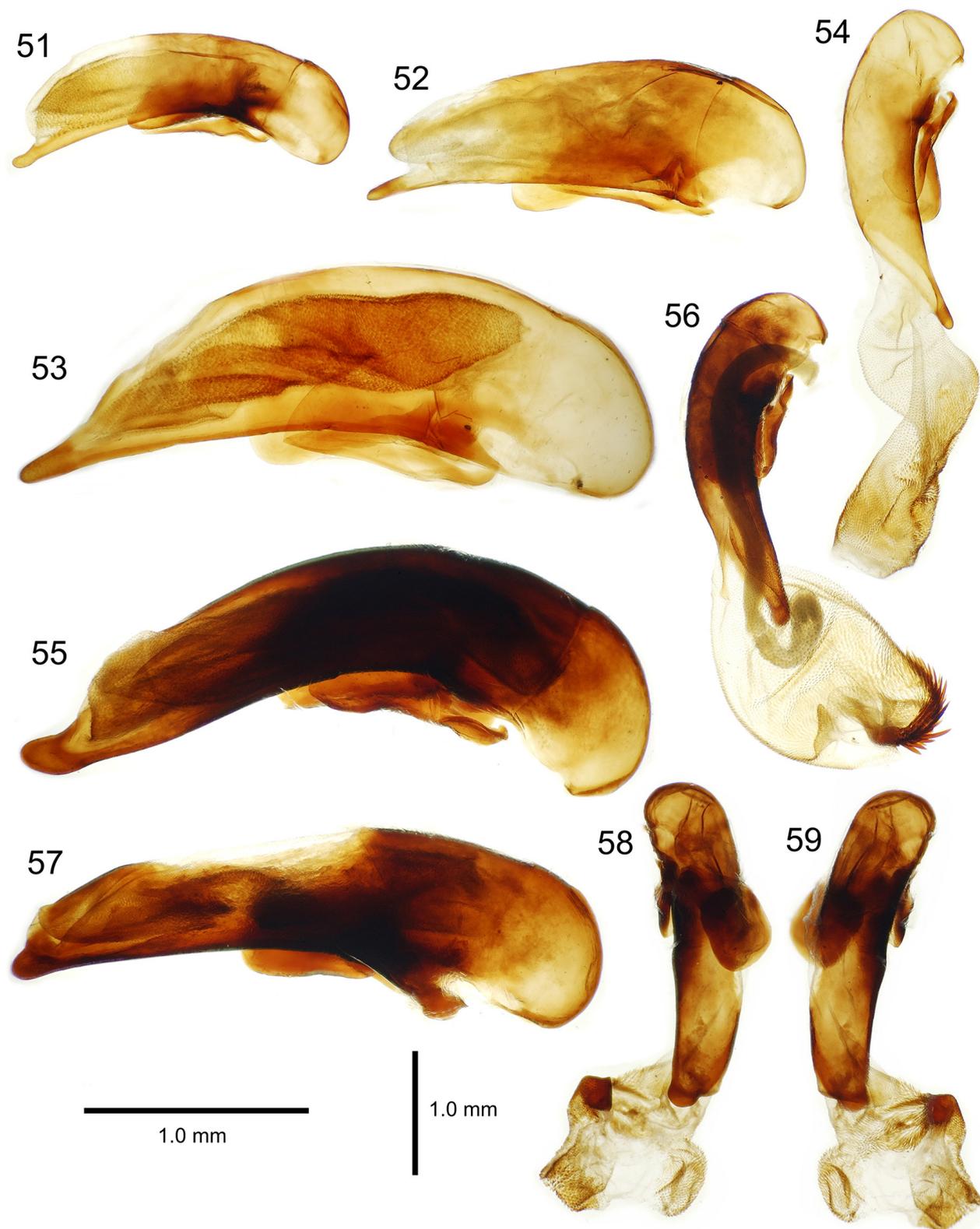
Distribution and habitat. Beetles of this species have been found at elevations from 700–1400 m, at localities ranging from Aoupinié to the north and Mt. Humboldt on the south (Fig. 76). Habitats include moss forest and rainforest, with specimens collected via pyrethrin fog of trees and logs, as well as in ground litter.

2. *Cyphocoleus prolixus* sp. n.

<http://zoobank.org/CE8A36DD-AD17-4CCD-8AF8-76358CCCBBE6>
Figures 48, 52, 61, 67, 77

Diagnosis. These remarkable beetles are uniquely diagnosed by the extremely elongate head and prothorax combined with broad, ovoid elytra (Fig. 48). In keeping with the elongate forebody, the mandibles are exceedingly long, their length 3.2× distance from anterior margin of antennal articulatory socket to anterolateral margin of labrum, and the antennae are also very elongate: scape length 3.6× maximum breadth. In stark contrast to *C. lissus* (Fig. 47), the head is broadest just posterad the mandibular articulation, and evenly reduced in width posteriorly to meet the narrow pronotum. The eyes are very small and oriented upward laterad the smooth, broadly convex frons. The elytral setation is also unique within *Cyphocoleus*; only the middle of three dorsal elytral setae present, whereas setae are absent from the anterior and posterior positions. Standardized body length among the largest for *Cyphocoleus* spp.; 11.7–13.1 mm.

Description (n = 3). Head capsule broadest anteriorly, a broad flange extended laterally laterad the antennal articulation and before the eye, the posterior articulatory condyle of mandible defining broadest portion of head; neck impression broad and shallow just before juncture of head and prothorax; eyes small though little convex, 17 ommatidia across horizontal diameter of eye; frons broad relative to eyes, ocular ratio 1.23–1.36; supraorbital setae absent; gena setose, a large macroseta present just laterad gula at position slightly posterad hind margin of eye. Pronotum elongate, parallel sided, MPW/PL = 0.44–0.50, broadest near basal third of length; proepimeron bulging outward, visible in dorsal view just laterad and posterad broadest portion of notum; pronotal front angle rounded, not protruded at all; lateral margin of pronotum defined by marginal bead from front angle to just inside subangulate hind angle, median base margined by low, broadly concave ridge; median longitudinal impression very shallow, finely incised; anterior transverse impression shallow, perpendicular to median impression, defining broad, slightly elevated anterior callosity; prosternal process with medially depressed anterior and ventral surfaces, the posterior surface between procoxae convex. Elytra broadly ovoid, the disc relatively flat and sides steeply sloped; discal elytral intervals broadly convex, the associated striae deep, impunctate; parascutellar seta present, articulatory socket not upraised above surface; elytral humeri narrow, humerus distinctly angulate just mesad base of fifth stria; elytral lateral margin distinctly concave laterad anterior series of lateral setae; lateral elytral setae arranged as 6 + 1 + (7)8; subapical and apical elytral setae present; subapical sinuation broadly, shallowly concave, meeting lateral margin at rounded-obtuse angle; elytral apices acutely rounded, slightly separated from each other laterad fused suture. Mesepisternum impunctate; metepisternum subquadrate, dorsal length 1.08× diagonal width. Legs extremely elongate, femora very thin, mt1 length/tibial length = 0.27; metacoxa bisetose; dorsum of tarsomeres covered with extremely short, sparsely distributed microsetae; mt4 outer lobe 1.56× median length, 3–4 ventrolateral setae each side. Abdomen with apical margin of apical ventrite broadly and very shallowly excavated to evenly convex; apical ventrite of male with one seta each side, of female with two setae each side. Microsculpture of frons very transverse, densely packed lines only loosely connected into a mesh; pronotal and elytral discs covered with dense transverse lines causing silvery and cupreous iridescence; dorsal body surface bearing a sparse distribution of extremely short microsetae; pro- meso- and metasternum with pelage of longer, more densely distributed setae, abdominal ventrites apparently glabrous except for fixed macrosetae. Coloration of head capsule rufopiceous anterad eyes, piceous toward pronotum; antennae rufobrunneous, palps and maxillae slightly paler, brunneous; pronotum, proepipleuron and proepimeron piceous; elytral disc rufopiceous, elytral epipleura rufopiceous, metepisternum piceous; abdominal ventrites rufobrunneous, apical ventrite 6 narrow rufoflavous apically; femora and tibiae rufobrunneous, tarsi rufoflavous.



Figures 51–59. Male aedeagal median lobe and associated parameres of *Cyphocoleus* spp., dextral view: **51**, *C. lissus*, Mt. Humboldt; **52**, *C. prolixus*, Mt. Humboldt; **53**, *C. heterogenus*, Yahoué; **54**, *C. heterogenus*, internal sac everted, La Foa; **55**, *C. parovicollis*, Me Maoya; **56**, *C. parovicollis*, internal sac everted, Me Maoya; **57**, *C. ovicollis*, Ningua Res.; **58–59**, *C. ovicollis*, internal sac everted, Mt. Do; **58**, laevoventral view; **59**, dextrodorsal view. Scale bars, 1.0 mm: horizontal scale for figures with transverse orientation; vertical scale for figures with vertical orientation.

Male genitalia ($n = 1$). Male aedeagal median lobe robust, broadest near parameral articulations, slightly narrowed toward distal margin of ostial opening, dorsoventral breadth at midlength $0.3 \times$ distance from tip to base of closed basal bulb (Fig. 52); lobe shaft slightly melanized, the internal sac visible through lobe wall in unevverted position; lobe apex parallel-sided, evenly downcurved to narrowly rounded tip, length distad ostial opening $4 \times$ dorsoventral breadth.

Female reproductive tract ($n = 1$). Bursa copulatrix elongate, columnar, distance from base of gonocoxites to spermathecal basal sclerite $4.5 \times$ maximum breadth (dissection compressed under cover slip) (Fig. 61); bursal walls thin, translucent, densely wrinkled in distal half of bursa; basal gonocoxite with apical fringe of five to six setae (sixth seta smaller) (Fig. 67)

Types. Holotype male (QMB deposited in MNHN): NEW CALEDONIA 11138 / $21^{\circ}53'S \times 166^{\circ}24'E$. 1400m. / Mt Humboldt, moss forest. / 6–7Nov2002. Monteith & / Burwell.pyreth, trees&logs // QUEENSLAND / MUSEUM LOAN / DATE: Nov. 2003 / No. LEN 1688 (green label) // male habitus photo / J.K. Liebherr 2015 // *Cyphocoleus* revision / measured specimen 2 / J.K. Liebherr 2015 // HOLOTYPE / *Cyphocoleus* / prolixus / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (2 specimens). NEW CALEDONIA: Mt. Humboldt, moss forest, 1400 m el., pyrethrum trees & logs, $21^{\circ}53'S$, $166^{\circ}24'E$, 06–07-xi- 2002, Monteith & Burwell (QMB, 2; lot 11138).

Etymology. The elongate prothorax exhibited by beetles of this species (Fig. 48) supports use of the adjectival species epithet prolixus; i.e. stretched out, long (Brown 1956).

Distribution and habitat. This species is known only from Mt. Humboldt at 1400 m el. (Fig. 77). The three specimens were collected from pyrethrin fog samples of trees and logs within moss forest.

3. *Cyphocoleus heterogenus* Chaudoir, 1877

Figures 28, 49, 53–54, 62, 68, 77

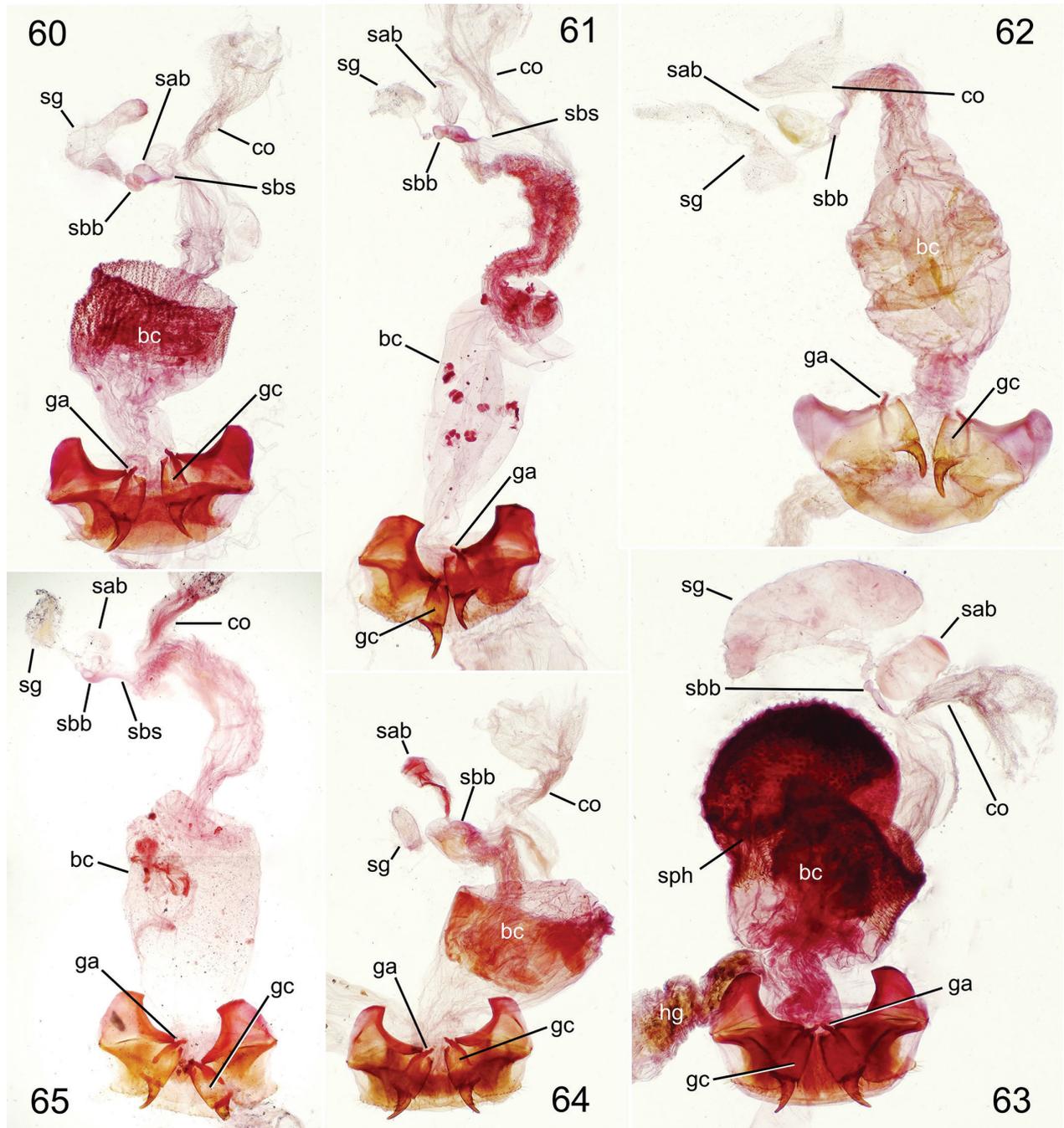
Diagnosis. Beetles as large as *C. prolixus*, standardized body length 10.8–13.1 mm, but head and prothorax much broader, the head much more developed at the expense of pronotal length (Figs 48, 49). Though the mandibles are shorter than in *C. prolixus*, with mandibular length $2.0 \times$ distance from antennal socket to anterolateral margin of labrum, the antennae are longer, with scape length $4.1 \times$ maximal breadth. The pronotum is unique among *Cyphocoleus* due to the extremely elongate, acutely protruded front angles. The presence of three dorsal elytral setae is shared only with *C. ovicollis* (Fig. 82), all other species exhibiting more reduced numbers of dorsal elytral setae or none at all.

Description ($n = 5$). Head capsule broad, robust, distance from clypeal-labral suture subequal to width across eyes; frons broadly convex, with small chevron-shaped indentation medially between front margins of eyes; eyes

moderately large, convex, 28 ommatidia across horizontal diameter; eyes moderately small, convex, ocular ratio 1.35–1.42; only posterior supraorbital seta present; neck distinctly impressed just before juncture with prothorax; gena glabrous, subgenal seta absent. Pronotum distinctly cordate, margin sinuately constricted basally; lateral marginal bead present from acute front angles to just mesad tightly rounded hind angles; median base margin by fine bead; proepisternum slightly bulging, visible in dorsal view along middle half of prothorax; median longitudinal impression shallow, finely incised; anterior transverse impression broad, shallow, obliquely meeting median impression; anterior callosity slightly convex; prosternal process with fine median ridge anteriorly between procoxae, medially depressed on ventral and posterior face. Elytra broadly ovoid, disc moderately convex with side only moderately depressed relative to disc; elytral striae impunctate; parascutellar seta present, articulatory socket not upraised above elytral surface; elytra narrow basally, humeri obtuse-angulate at base of fifth stria; lateral margin straight to slightly concave lateral anterior series of lateral elytral setae; lateral elytral setae arranged as $6 + 1 + 7-8$; subapical and apical elytral setae present; subapical sinuation distinctly invaginated, curvature greatest just mesad obtusely rounded juncture of sinuation and lateral margin. Mesepisternum impunctate; metepisternal dorsal length $0.86 \times$ diagonal width. Abdomen of males with apical margin of apical ventrite distinctly notched, the invagination smoothly rounded; apical ventrite of male with one seta each side, of female with two setae each side. Legs elongate, gracile, mt1 length/tibial length = 0.26; metacoxae bisetose; tarsomeres with short sparse setae dorsally; mt4 outer lobe $1.7 \times$ median length, 4–5 ventrolateral setae each side. Microsculpture of frons and vertex a stretched isodiametric mesh; pronotal disc and discal elytral intervals covered with fine transverse lines; dorsal surface of body apparently glabrous except for standard macrosetae; pro-, meso-, and metasternum and visible abdominal ventrites with sparsely distributed pelage of very short setae. Coloration of dorsum rufopiceous with cyanotic to cupreous iridescence due to microsculpture; antennae dark rufous, paler apically, palps brunneous; basal abdominal ventrites rufopiceous, ventrite 6 rufobrunneous, margin narrowly brunneous; femora rufopiceous, tibiae rufobrunneous, tarsi slightly paler, dark rufous.

Male genitalia ($n = 8$). Male aedeagal median lobe robust, broadly parallel sided in basal $3/4$ of length, then evenly narrowed to projected, narrow tip, dorsoventral breadth at midlength $0.25 \times$ distance from tip to base of closed basal bulb (Fig. 53); lobe shaft slightly melanized, the internal sac visible through lobe wall in unevverted position; lobe apex tapered to tightly rounded tip, length distad ostial opening $2.5 \times$ dorsoventral breadth; internal sac evenly covered with short melanized spicules in distal half, of sinuous shape but sides parallel in extension (Fig. 54).

Female reproductive tract ($n = 2$). Bursa copulatrix vase-shaped, basally stalked, distance from base of gono-



Figures 60–65. Female reproductive tract, ventral view, for *Cyphocoleus* spp.; **60**, *C. lissus*, Mt. Humboldt; **61**, *C. prolixus*, Mt. Humboldt; **62**, *C. heterogenus*, Yahoué; **63**, *C. parvicollis*, Mandjéla; **64**, *C. monteithi*, Mt. Mou; **65**, *C. miricollis*, Forêt Nord. For abbreviations see Table 1.

coxites to spermathecal basal sclerite 2.4× maximum breadth (dissection compressed under cover slip) (Fig. 62); bursal walls thin, translucent, with broad band of spicules lining lumen near midlength; basal gonocoxite with apical fringe of seven to eight setae (Fig. 68); apical gonocoxite broadly rounded at apex with three lateral ensiform setae.

Type. Holotype male (MNHN): Ex Musæo / Chaudoir (red-inked white label with red border) // HOLOTYPE / *Cyphocoleus* / heterogenus / Chaudoir 1877 (black-bor-

dered red label). Holotype status is based on Chaudoir's (1887: 193) statement "Cet insecte m'a été cédé par M. Sallé." Yahoué hereby designated type locality.

Distribution and habitat. Found throughout Grande Terre, from Mt. Ignambi and Mt. Panié on the north, to Forêt de Thi on the south (Fig. 77, Suppl. material 3). Beetles have been collected from pyrethrin spray samples from trees and logs, with and without epiphytes, from under a rock near a dead tree, from *Freycinetia* axils, and by hand during night.

4. *Cyphocoleus parovicollis* sp. n.

http://zoobank.org/8894D2DB-88B0-4205-B69F-9C4A8C34245D
 Figures 50, 55–56, 63, 69, 78

Diagnosis. This species and its following adelphotaxon are difficult to diagnose practically (Figs 50, 82), yet are clearly separate species. They can be diagnosed by the more convex eyes in beetles of this species, ocular ratio 1.47–1.55, and presence of four apical abdominal setae in males – two setae each side of apical visible abdominal ventrite – versus two apical abdominal setae – one each side – in males of *C. ovicollis*. The pronotum is generally narrower basally among individuals of this species – MPW/BPW = 1.87–2.10 – but the values overlap in the two species, with individuals of *C. ovicollis* ranging in values 2.04–2.29 for the same ratio. If a male is available, the identity based on abdominal setation can be confirmed based on the very different aedeagal internal sacs: that of *C. parovicollis* exhibiting an apical “cockscomb” of large, densely packed macrotrichia (Fig. 56). The allopatric geographic distributions can assist in the sorting of these two species, with *C. parovicollis* distributed to the north of *C. ovicollis* (Fig. 78). Standardized body length 9.4–12.1 mm.

Description (n = 5). Head capsule moderately broad, gena elongate anterad constricted neck (Fig. 50); frons broadly convex, but with variably developed chevron-shaped depression medially between eyes; supraorbital setae absent; mandibles elongate, length 2.5× distance from antennal articulatory socket to anterolateral margin of labrum; antennae very elongate, scape length 4.33× maximal breadth; supraorbital setae absent; gena glabrous, subgenal seta absent. Pronotum narrowly obovoid, MPW/PL = 0.78–0.88; front angles slightly protruded, right to slightly obtuse; lateral marginal bead continuous to obtuse-rounded basal angles and across straight median base; proepisternum bulging outward and so visible in dorsal view for middle half of pronotal length; median longitudinal impression deep, finely incised, terminated posteriorly in variably developed transverse depression; anterior transverse impression very shallow, obliquely paralleling anterior pronotal margin; prosternal process indistinctly depressed medially on ventral surface. Elytra narrowly subellipsoid, MEW/EL = 0.65–0.70; disc broadly and moderately convex; elytral striae deep, impunctate, associated intervals broadly convex; parascutellar seta present, socket not upraised above elytral surface; humeri very narrow, distinctly obtuse-angulate at base of fifth stria; elytral lateral margin convex laterad anterior series of lateral elytral setae; two to three dorsal elytral setae present (setae at anterior and middle positions always present, posterior seta present or absent); lateral elytral setae arranged as 6+1(0)+7; subapical and apical setae present; subapical situation broadly and slightly concave, joining lateral margin in a broad curve; elytral apices tightly rounded, slightly separated from suture. Mesepisternum impunctate; metepisternum dorsal length 0.93× diagonal width. Abdomen of males with distinct, narrow notch medially on apical margin of apical ventrite; females with two setae each side on apical margin of api-

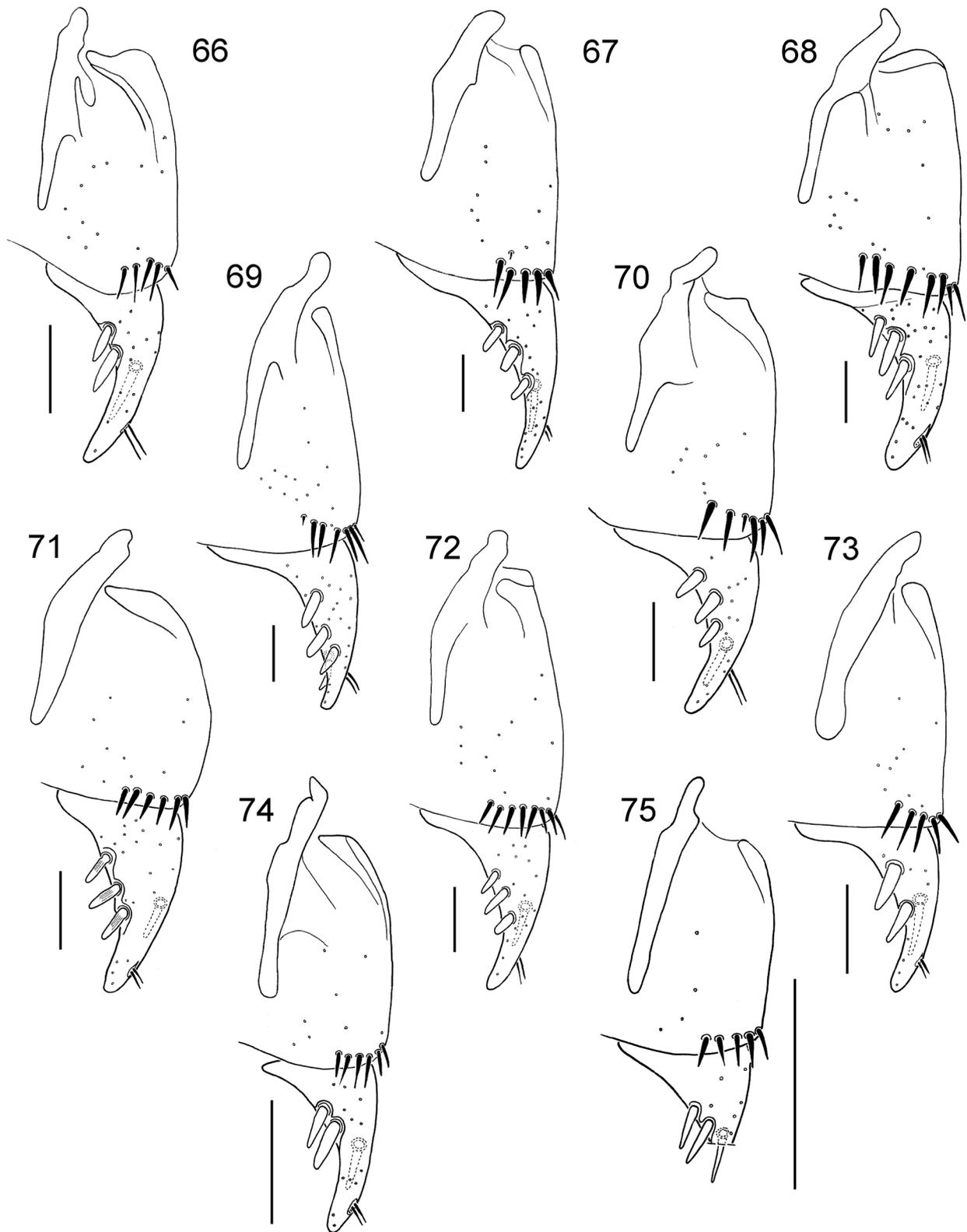
cal ventrite. Legs elongate, gracile, mt1 length/tibial length 0.26; metacoxae bisetose; tarsomeres with short, sparse seta on dorsum; mt4 outer lobe 1.5× median length, 4–5 lateroventral setae each side. Microsculpture of frons transversely stretched isodiametric mesh to distinctly transverse mesh on vertex; pronotal disc with dense transverse-line microsculpture loosely organized into a mesh; elytral disc with dense transverse lines resulting in cyanotic to cupreous iridescence; pro-, meso-, and metasternum with sparse pelage of short microsetae, abdominal ventrites and dorsal body surface apparently glabrous. Coloration of head capsule rufopiceous, antennae rufobrunneous with piceous cast on antennomeres 1–3; pronotum piceous, proepipleuron and proepisternum rufopiceous; elytra rufopiceous; elytral epipleuron rufous, metepisternum rufopiceous; femora and tibiae rufobrunneous, tarsi rufoflavous.

Male genitalia (n = 4). Male aedeagal median lobe robust, broadly parallel sided to near distal margin of ostial opening, dorsoventral breadth at midlength 0.2× distance from tip to base of closed basal bulb (Fig. 55); lobe shaft brunneous, the internal sac obscured in uneverted position by the moderately melanized lobe wall; lobe apex with broadly rounded tip, tip skewed toward the left side of lobe, length distad ostial opening only slightly more than breadth; internal sac with apical “cockscomb” composed of densely packed, elongate, melanized, spike-like macrotrichia, the sac broadest at midlength (Fig. 56).

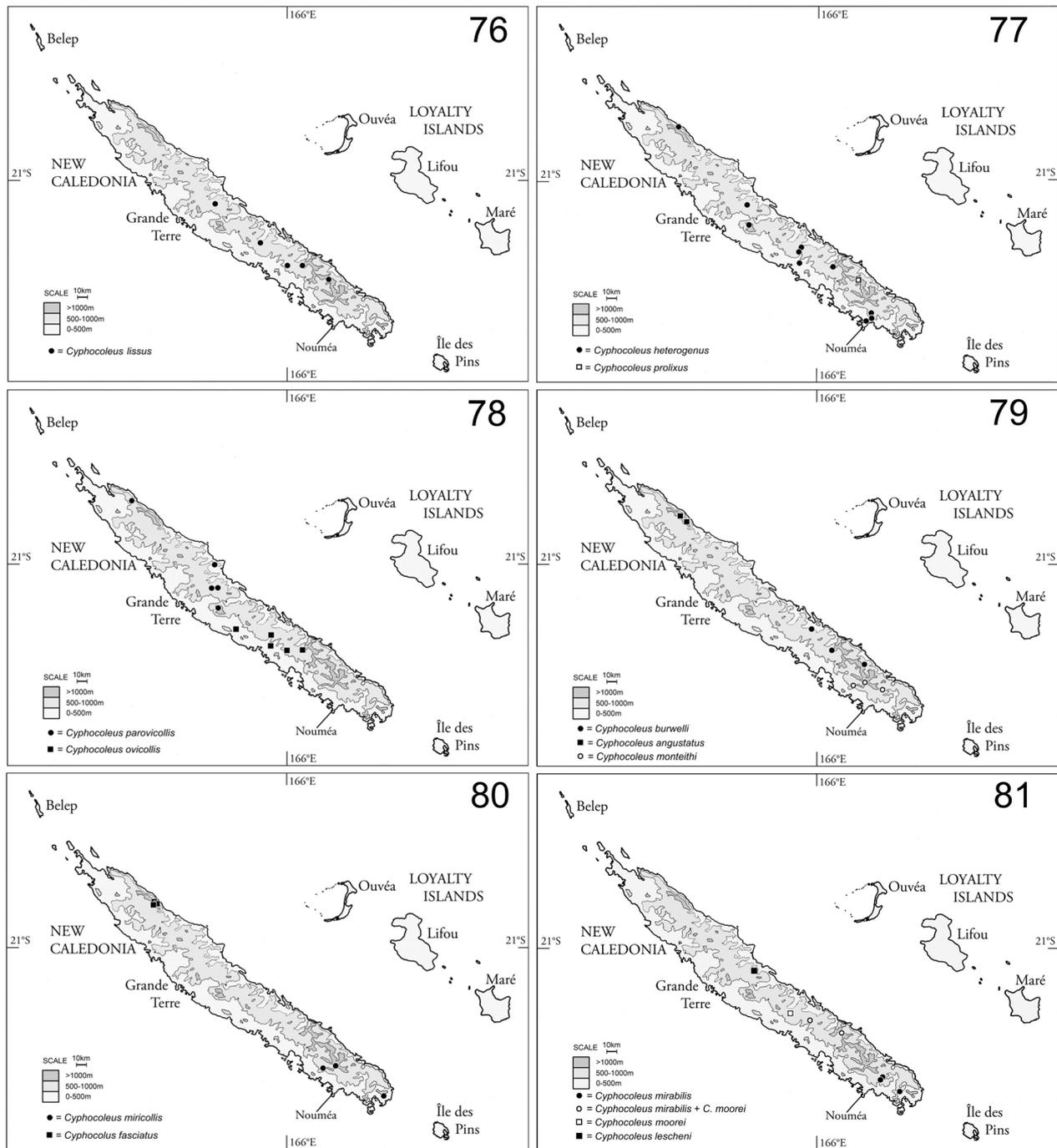
Female reproductive tract (n = 2). Bursa copulatrix vase-shaped, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite 1.8× maximum breadth (dissection compressed under cover slip) (Fig. 63); bursal walls thick, heavily pigmented by Chlorazol Black stain, with broad band of thick, densely packed spicules lining lumen over broadest part of bursa; basal gonocoxite with apical fringe of six setae, an additional small seventh seta observed in one individual (Fig. 69); apical gonocoxite acuminate with narrowly rounded apex and three lateral ensiform setae.

Type. Holotype male (QMB deposited in MNHN): NEW CALEDONIA 8682 / 20°58'Sx165°17'E.500m / Pic d'Amoa, N slopes / 24Nov2001. GBMonteith / Pyrethrum, trees & logs // QUEENSLAND / MUSEUM LOAN / Date: Nov. 2003 / no. LEN-1688 (green label) // *Cyphocoleus* / n. sp. / *ovicollis* male 9 / det. J.K. Liebherr 2015 // genitalia vial // HOLOTYPE / *Cyphocoleus* / *parovipennis* / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (30 specimens). NEW CALEDONIA: Mandjélie, above Pouébo 600–750 m el., 20°24'S, 164°32'E, 11–13-v-1984, Monteith & Cook (QMB, 1); Mt. Panié refuge, 1300 m el., 20°34'S, 164°46'E, 16–18-xi-2000, Bouchard, Burwell & Monteith (QMB, 1; lot no. 9938); Pic d'Amoa, N slopes, 500 m el., hand collecting, 20°58'S, 165°17'E, 10–11-xi-2001, Burwell & Monteith (QMB, 1; lot no. 8687); Aoupinié, 850 m el., 21°11'S, 165°19'E, 20–21-xi-2000, Bouchard, Burwell & Monteith (QMB, 2; lot no. 9930), summit, 1000 m el., pyrethrum trees & logs, 21°11'S, 165°16'E, 02-x-2004, Monteith (QMB, 1; lot no. 11665), 21°11'S, 165°19'E,



Figures 66–75. Female right gonocoxae, ventral view, for *Cyphocoleus* spp. illustrating apical fringe setae of basal gonocoxite 1, and two or three lateral ensiform setae, one dorsal ensiform seta, and two apical nematiform setae on apical gonocoxite 2; **66**, *C. lissus*, Mt. Humboldt; **67**, *C. prolixus*, Mt. Humboldt; **68**, *C. heterogenus*, Yahoué; **69**, *C. parovicollis*, Mandjéla; **70**, *C. ovicollis*, Ningua Res.; **71**, *C. burwelli*, Mt. Humboldt; **72**, *C. monteithi*, Mt. Mou; **73**, *C. miricollis*, Forêt Nord; **74**, *C. mirabilis*, Mt. Koghi; **75**, *C. lescheni*, apical gonocoxite damaged, Aoupinié. Scale bar, 0.10 mm.



Figures 76–81. Distribution maps of *Cyphocoleus* spp.: **76**, *C. lissus*; **77**, *C. heterogenus*, *C. prolixus*; **78**, *C. parovicollis*, *C. ovicollis*; **79**, *C. burwelli*, *C. angustatus*, *C. monteithi*; **80**, *C. miricollis*, *C. fasciatus*; **81**, *C. mirabilis*, *C. moorei*, *C. lescheni*.

12-xii-1993, Raven (QMB, 1); Me Maoya, near summit, 1400 m el., pyrethrum trees & logs, 21°22'S, 165°20'E, 12-xi-2002, Burwell & Monteith (QMB, 1; lot no. 11163); Me Maoya camp, 1150 m el., night collecting, 21°22'S, 165°20'E, 11–12-xi-2002, Burwell, Monteith & Wright (QMB, 15; lot no. 11159), pyrethrum trees & logs, 11–13-xi-2002, Monteith & Burwell (QMB, 5; lot no. 11158); Me Maoya, near summit, 1300 m el., pyrethrum trees & logs, 21°22'S, 165°20'E, 12-xi-2002, Monteith & Burwell (QMB, 2; lot no. 11169).

Etymology. The adelphotaxon status and great similarity of this species and *C. ovicollis* (Figs 46, 50, 82) is signified through use of *parovicollis* as this species' epithet: i.e. equal to *ovicollis*.

Distribution and habitat. This species is distributed in the northern half of Grande Terre, allopatric with its adelphotaxon, *C. ovicollis*, which is distributed to the south (Fig. 78). Beetles have been collected from tree trunks and downed logs via pyrethrin fog, and also by hand collecting at night.

5. *Cyphocoleus ovicollis* Fauvel, 1882

Figures 57–59, 70, 78, 82

Diagnosis. In juxtaposition to its cryptic adelphotaxon, this species can be diagnosed by the flatter eyes, ocular ratio 1.41–1.44, and presence of two apical abdominal setae in the males of this species – one seta each side of apical visible abdominal ventrite – versus four apical abdominal setae – two each side – in males of *C. parovicollis*. The pronotum is generally broader basally among individuals of this species – MPW/BPW = 2.04–2.29 – versus values of 1.87–2.10 in *C. ovicollis*. A male dissection will allow attribution of a series of specimens, with the male of *C. ovicollis* exhibiting an internal sac with a robust, mound-shaped tooth on the right side (Figs 58, 59). The allopatric geographic distributions also provide information as *C. ovicollis* (Fig. 78) is distributed to the south of *C. parovicollis*. Standardized body length 9.1–11.0 mm.

Description (n = 5). (The description of *C. parovicollis* can serve for this species, with the following exceptions). Head capsule with mandibles elongate, length 2.4× distance from antennal articulatory socket to anterolateral margin of labrum. Elytra more broadly subellipsoid, MEW/EL = 0.71–0.73; three dorsal elytral setae uniformly present; lateral elytral setae arranged as 6 + 1(0) + 7(8). Mesepisternum dorsal length 0.8× diagonal width.

Male genitalia (n = 5). Male aedeagal median lobe robust, broadly parallel sided in basal half, then tapered to narrowly rounded tip, dorsoventral breadth at midlength 0.2× distance from tip to base of closed basal bulb (Fig. 57); lobe shaft brunneous, the internal sac obscured in un-everted position by the moderately melanized lobe wall; lobe apex with evenly rounded tip, length distad ostial opening subequal to breadth; internal sac broadest at midlength, with large sclerotized plaque-like tooth on right side, and a ring of melanized microtrichia apically near gonopore (Figs 58, 59).

Female reproductive tract (n = 1). Bursa copulatrix vase-shaped, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite 1.7× maximum breadth (dissection compressed under cover slip) (as in Fig. 63); bursal walls thick, heavily pigmented by Chlorazol Black stain, with broad band of thick, densely packed spicules lining lumen over broadest part of bursa; basal gonocoxite with apical fringe of six to seven setae (Fig. 70); apical gonocoxite acuminate with narrowly rounded apex and three lateral ensiform setae.

Type. Holotype male (MNHN): *C. ovicollis* / FvI. // Ex-Musæo / Mniszech (white label with black border) // HOLOTYPE / *Cyphocoleus* / *ovicollis* / Fauvel 1882 (black-bordered red label). Type locality noted by Fauvel (1882: 248) as “probablement à Ourail,” with Bourail hereby designated type locality.

Distribution and habitat. The known distribution northern portions of Province Sud, from Bourail and Col d’Amieu on the north to Mt. Do and Ningua Reserve to the south (Fig. 78, Suppl. material 3). Specimens have been obtained in pyrethrin samples from trunks and logs

with and without epiphytes, via hand collecting, with one series of six specimens collected in a flight intercept trap, without doubt having climbed onto and into the trap.

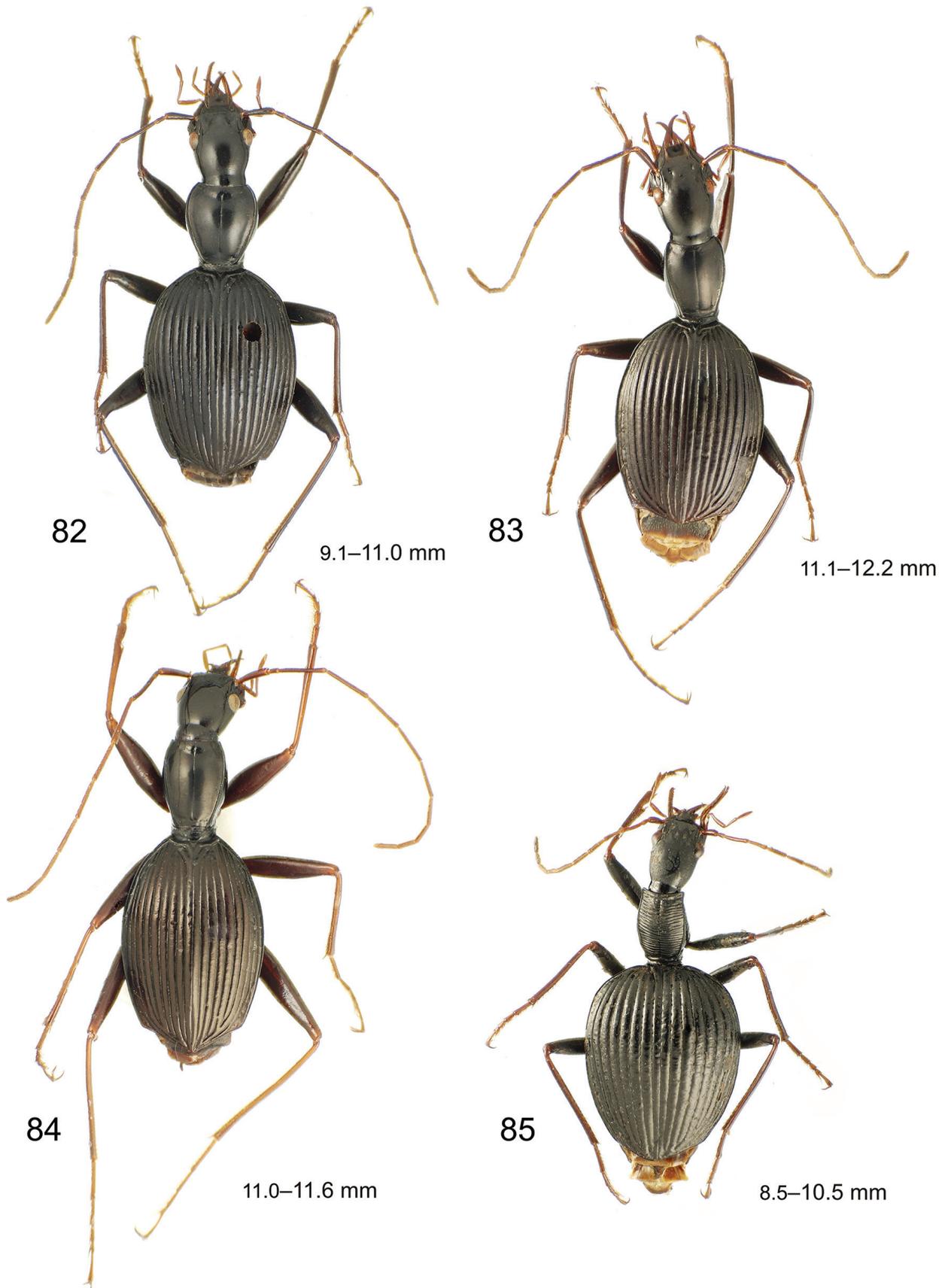
6. *Cyphocoleus burwelli* sp. n.

<http://zoobank.org/B5B3D4B3-E303-4330-B69C-7EB910795E93>

Figures 71, 79, 83, 86

Diagnosis. This species and the following, *C. angustatus*, comprise a second sibling species pair, these two characterized by the narrow body: i.e. pronotum and elytra. The pronotum of *C. burwelli* is more evenly ovate, with MPW/BPW = 1.72–1.83 versus values of 1.84–1.91 for *C. angustatus*. The pronotum is also relatively narrower overall, with MPW/PL = 0.68–0.72 compared to values of 0.72–0.77 recorded for *C. angustatus*. The elytra are narrower basally in *C. burwelli*, with MEW/HuW = 2.78–3.19 versus 2.60–2.79 for *C. angustatus*, and the humeral angle is obtuse versus very distinctly right angled to slightly acute in *C. angustatus* (Figs 83, 84). A male dissection can be used to confirm this diagnosis, with the aedeagal median lobe apex narrowly rounded in this species, and the internal sac bearing a stout apical tooth (Fig. 86). Standardized body length 11.1–12.2 mm.

Description (n = 4). Head capsule moderately elongate, trapezoidal, with broad flange basad posterior mandibular articulation, neck distinctly constricted (Fig. 83); frons broadly convex between hind margin of eyes, with shallow median dimple and progressively broadened frontal grooves anteriorly; eyes small and little convex, 23–28 ommatidia across horizontal diameter; supraorbital setae absent; mandibles elongate, length 2.4× distance from antennal articulatory socket to lateroapical margin of labrum; antennae elongate, scape length 4.2× maximal breadth; subgenal seta absent. Pronotum with front angles only slightly protruded, obtuse angulate; lateral marginal bead continuous to just mesad evenly rounded hind angles, basal margin not beaded medially; proepipleuron and propisternum bulging outward in basal half of pronotal length, visible in dorsal view; median longitudinal impression shallowly and finely incised, wavering along length; anterior transverse impression very shallow, barely traceable as oblique impression that reaches lateral marginal bead behind front angle; prosternal process flat anteriorly, flat to slightly depressed medially on ventral surface, convex posteriorly between procoxae. Elytra narrowly ellipsoid, moderately convex; elytral striae deep, impunctate, associated intervals moderately convex; parascutellar seta present, articulatory socket not upraised above surface of elytra; humeral angles obtuse-angulate, the juncture of basal and marginal grooves tightly rounded; lateral margin evenly convex outside anterior series of lateral elytral setae; two to three dorsal elytral setae present (setae at anterior and middle position present or absent, seta at posterior position always present); lateral elytral setae arranged as 6 + (7)8; subapical and apical elytral setae present; subapical situation slightly, evenly concave, situation meet-



Figures 82–85. Dorsal habitus photographs of *Cyphocoleus* spp.: **82**, *C. ovicollis* female, Ningua Res.; **83**, *C. burwelli* female, Mt. Canala; **84**, *C. angustatus* male, Mt. Panié; **85**, *C. monteithi* male, Dzumac Rd. jct.

ing lateral margin in broadly convex curve; elytral apices rounded, the apical margin invaginated to meet fused elytral suture. Mesepisternum impunctate; metepisternal dorsal length $0.9\times$ diagonal width. Abdomen of males with apical ventrite distinctly notched medially; two setae on apical margin of apical ventrite in males (one seta each side), four setae (two each side) present on apical margin of females. Legs elongate, gracile, mt1 length/tibial length = 0.27 ; metacoxae bisetose; tarsomeres with short, sparsely distributed setae on dorsal surface; mt4 length of outer lobe $1.3\times$ median length, 6–8 ventrolateral setae each side. Microsculpture of frons isodiametric, longitudinally stretched near median dimple, head microsculpture transversely stretched on clypeus and further posterad on vertex, becoming dense transverse lines before neck constriction; pronotal and elytral disc with dense transverse-line microsculpture; pro-, meso-, and metasternum, metacoxae and abdominal ventrites with sparsely distributed pelage of moderately elongate microsetae. Coloration of head and pronotum piceous with metallic cyanotic iridescence due to microsculpture; elytra rufopiceous with similar iridescence; ventral body surface uniformly dark, piceous to rufopiceous on medial portions of apical three abdominal ventrites, apical ventrite with pale, rufoflavous apical margin; legs slightly paler than ventrites, femora and tibiae rufobrunneous with piceous case, tarsi brunneous.

Male genitalia ($n = 1$). Male aedeagal median lobe robust, broadly parallel sided in basal half, then tapered to rounded tip, dorsoventral breadth at midlength $0.3\times$ distance from tip to base of closed basal bulb (Fig. 86); lobe shaft brunneous, the internal sac obscured in uneverted position by the moderately melanized lobe wall; lobe apex with tapered tip, length distad ostial opening subequal to breadth; internal sac broadest at midlength, with extremely large sclerotized apical tooth and a broad ring of melanized microtrichia over middle half of sac (Fig. 86).

Female reproductive tract ($n = 1$). Bursa copulatrix vase-shaped, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite $1.4\times$ maximum breadth (dissection compressed under cover slip) (as in Fig. 63); bursal walls thick, heavily pigmented by Chlorazol Black stain, with broad band of thick, densely packed spicules lining lumen over broadest part of bursa; basal gonocoxite with apical fringe of six to seven setae (Fig. 71); apical gonocoxite triangular with rounded apex (due to wear?) and three lateral ensiform setae.

Types. Holotype female (MNHB deposited in MNHN): Drs. F. Sarasin & J. Roux / Neukaledonien / Mt. Humboldt (on obverse of blue label) / Gipsel, 1600 m. / 18.9.1911 (on reverse of blue label) // *Cyphocoleus* / ovicollis Fauv. / Det. K.M. Heller 1914 // *Cyphocoleus* revision / measured specimen 1 / J.K. Liebherr 2015 // HOLOTYPE / *Cyphocoleus* / burwelli / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (3 specimens). NEW CALEDONIA: Ningu Reserve, near summit, 1300 m el., $21^{\circ}45'S$, $166^{\circ}09'E$, 13-xi-2001, Burwell & Monteith (QMB, 1); Mt. Humboldt, 1600 m el., $21^{\circ}53'S$, $166^{\circ}26'E$, 18-ix-1911, Sarasin

& Roux (SMTD, 1); Mt. Kanala, Wald, 800–1000 m el., $21^{\circ}34'S$, $165^{\circ}56'E$, 04-xi-1911, Sarasin/Roux (MNHB, 1).

Etymology. This species is named for Dr. Chris Burwell, Senior Curator of Insects, Queensland Museum, in recognition of the numerous specimens of *Cyphocoleus* he has collected: many representing previously undescribed species.

Distribution and habitat. The distribution of this species ranges from Mt. Humboldt on the south, to Mt. Canala on the north (Fig. 79). Collection sites range in elevation from 1000–1600 m.

7. *Cyphocoleus angustatus* sp. n.

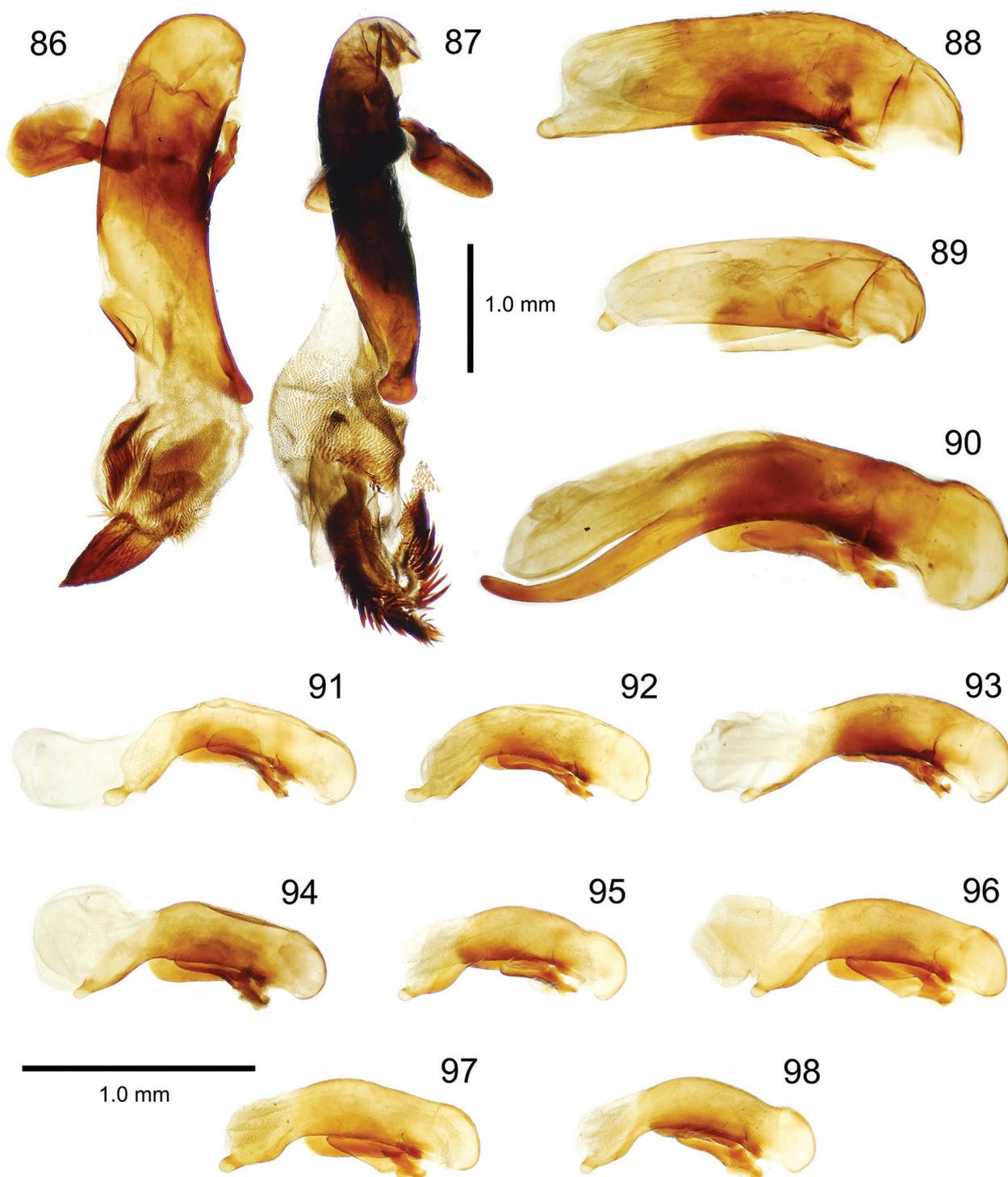
<http://zoobank.org/E414FE48-C4B8-4AF4-A7CA-3D377AE806EA>

Figures 29, 79, 84, 87

Diagnosis. As the second half of the sibling species pair also including *C. burwelli*, this species can be diagnosed by the more basally constricted pronotum, MPW/BPW = 1.84 – 1.91 versus values of 1.72 – 1.83 for *C. burwelli*. The pronotum is also relatively broader overall, with MPW/PL = 0.72 – 0.77 versus values of 0.68 – 0.72 for *C. burwelli*. The elytra are broader basally in *C. angustatus*, with MEW/HuW = 2.60 – 2.79 versus 2.78 – 3.19 *C. burwelli*. The humeral angle is positioned more anteriorly relative to the scutellum, and is very distinctly right angled to slightly acute in this species (Fig. 84). If a male can be dissected, the aedeagal median lobe apex is broadly expanded in this species, and the internal sac bears an apical “cockscorn” of densely packed macrotrichia (Fig. 87). Standardized body length 11.0 – 11.6 mm.

Description ($n = 3$). (The description of *C. burwelli* can serve for this species, with the following exceptions). Head capsule with mandibles exceedingly elongate; length $4.9\times$ distance from antennal articulatory socket to anterolateral margin of labrum; antennae exceedingly elongate, gracile, scape length $4.9\times$ maximal breadth. Pronotum margined basally with narrow, little upraised bead crossing median base between the distinctly margined, rounded hind angles. Elytra narrowly ovoid, extremely narrow basally; two dorsal elytral setae present at positions of middle and posterior seta; lateral elytral setae arranged as $6 + 1 + 7$, or $6 + 8$. Legs extremely elongate, gracile; metacoxae trisetose, two setae on lateral surface fore and aft, and a third large seta medial to posterior seta (short setae comprising part of ventral pelage also present); mt4 with length to apex of outer lobe $1.45\times$ median tarsomere length. Coloration of legs paler than piceous thoracic and rufopiceous abdominal ventrites, femora dark rufous with piceous cast, tibiae rufobrunneous, and tarsi paler, brunneous to rufoflavous.

Male genitalia ($n = 2$). Male aedeagal median lobe robust, broadly parallel sided to near distal margin of ostial opening, dorsoventral breadth at midlength $0.2\times$ distance from tip to base of closed basal bulb (Fig. 87); lobe shaft melanized, the internal sac obscured in uneverted position by the moderately melanized lobe wall; lobe apex with



Figures 86–98. Male aedeagal median lobe and associated parameres of *Cyphocoleus* spp., dextral view: **86**, *C. burwelli*, internal sac everted, Ningua Res.; **87**, *C. angustatus*, dextroventral view, internal sac everted, Mt. Panié; **88**, *C. monteithi*, Parque Prov. Rivière Bleue, Haute Pourina; **89**, *C. miricollis*, Mt. Mou; **90**, *C. fasciatus*, dextral view, sac partially everted, Mt. Panié; **91–98**, *C. cychroides*; **91**, internal sac everted, Mandjélia; **92–93**, Mandjélia; **94**, internal sac everted, Hienghene; **95**, Touho; **96**, Tionaka Tal; **97**, Ateou; **98**, Pic d’Amoa. Scale bars, 1.0 mm: horizontal scale for figures with transverse orientation; vertical scale for figures with vertical orientation.

very broadly rounded tip, length distad ostial opening less than breadth; internal sac with well-developed apical “cockscomb” composed of densely packed, elongate,

melanized, spike-like macrotrichia, the basal half of sac densely covered with short, melanized microtrichia.

Types. Holotype male (QMB deposited in MNHN): NEW CALEDONIA / Mt Panié, 1300 m / 3-xi-1988 / R. Raven // QUEENSLAND / MUSEUM LOAN / DATE: Jan. 2004 / No. LE 04.01 (green label) // *Cyphocoleus* revision / measured specimen 1 / J.K. Liebherr 2015 male 2 // HOLOTYPE / *Cyphocoleus* / *angustus* / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (7 specimens). NEW CALEDONIA: Mt. Panié, 730 m el., under stones amongst ants, 20°32'S, 164°44'E, 24-viii-1914, Montague (BMNH, 2), 28-viii-1914, Montague (BMNH, 1), 1300 m el., 20°34'S, 164°46'E, 03-xi-1988, Raven (QMB, 1), refuge, 1350 m el., 20°34'S, 164°46'E, 08-09-xi-2001, Balke & Wewalka (ZSM, 2).

Etymology. The narrow, elongate pronotum and very narrow elytral humeri (Fig. 84) suggest the adjectival species epithet, *angustus*, based on the Latin *angustus*, or narrow (Brown 1956).

Distribution and habitat. This species is known only from Mt. Panié, with localities at 730 m elevation in 1914, and from 1300–1350 m elevation for more recently collected material (Fig. 79). P. D. Montague's specimens (see Turner 1919) are labeled as being collected "under stones amongst ants", although the level of interaction among beetles and ants, if any, is not known.

8. *Cyphocoleus monteithi* sp. n.

<http://zoobank.org/B88459B2-D6F8-486A-B85A-37EA2EA0135A>

Figures 64, 72, 79, 85, 88

Diagnosis. This species (Fig. 85) shares the very elongate prothorax and narrow head with *C. prolixus* (Fig. 48), however the pronotal disc is transversely wrinkled and the pronotal front angles are acutely extended as in *C. miricollis* below. These characters support this species' phylogenetic intercalation subordinate to the former, and as adelphotaxon to the latter plus all cladistically associated species (Fig. 45). The elytra are distinctly ovate and very convex, domed, the lateral intervals and margins very depressed relative to the disc. This is also the first of the species to be treated in this revision that bears an environmental patina: in this species a varnish-like coating that covers the body surface of the beetles, this coating deepest in depressed areas such as the transverse pronotal wrinkles and elytral striae. Body surfaces on the mouthparts, antennae, and at the base of the head between the constricted neck and anterior prothoracic margin are dramatically clear of this varnish. Standardized body length 8.5–10.5 mm.

Description (n = 5). Head capsule ellipsoid, genal surfaces behind eyes subparallel, then converging to distinctly constricted neck; frons with broad medial crest between eyes, fine arcuate wrinkles curving outward and posterad from crest, frontal grooves parallel, broadly depressed from position between hind margins of eyes to clypeus, broadest just posterad frontoclypeal suture; eyes small, convex, 20 ommatidia across horizontal diameter,

ocular ratio 1.39–1.50; supraorbital setae absent; mandibles moderately elongate, length 2.4× distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderately elongate, scape length 2.6× maximal breadth; gena setose, subgenal seta present just laterad gula about 2/3 distance from hind margin of eye to constricted neck. Pronotum elongate, tubular, MPW/PL = 0.59–0.69, base constricted relative to apex, APW/BPW = 1.28–1.40; median longitudinal impression finely and shallowly incised, causing interruptions in orientation of transverse wrinkles in some instances; anterior transverse impression broad, shallow, extended laterally to behind front angles; proepisternum bulging, extended beyond marginal bead of notum, with distinct, deeply engraved vertical wrinkles; prosternal process distinctly depressed medially anterad procoxae, flat to narrowly depressed medially on ventral surface, narrowly convex on posterior surface. Elytra inflated, based inflexed at scutellum and depressed along suture, intervals 3–5 convexly elevated; striae smooth with very widely spaced micropunctures along length (view cleaned specimen); parascutellar seta present, articulatory socket papillate, elevated above surrounding elytral surface; dorsal elytral setae absent; lateral elytral setae arranged as 6 + 7, their articulatory sockets slightly upraised above surrounding cuticle, often appearing clear of cuticular varnish; subapical and apical elytral setae present, articulatory sockets papillate and clear of varnish; subapical situation moderately concave, meeting lateral margin in broad curve; elytral apices rounded, moderately separated by invaginated margin at fused suture. Mesepisternum impunctate, metepisternal dorsal length 1.1× diagonal width. Abdomen with apical ventrite broadly, slightly concave medially; males with one seta each side apical margin of apical ventrite, females with two setae each side. Legs gracile, moderately elongate, mt1 length/tibial length = 0.27; metacoxae bisetose; tarsomeres with dorsal surface glabrous; mt4 with length to apex of outer lobe 1.8× median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture of head transverse, dense; pronotal and elytral disc with fine transverse lines; pro-, meso-, and metasternum plus abdominal ventrites with sparse pelage of extremely short microsetae, such extremely short setae also visible on head on frons, pronotum, and elytra (though cleaning the surface may remove setae). Coloration of head piceous, mandibles rufobrunneous, palps and antennae rufoflavous; pronotum, elytra and body ventrites and coxae piceous; femora piceous with rufobrunneous base and apex, tibiae rufopiceous dorsally, rufobrunneous on lateral and ventral surfaces, tibiae rufobrunneous.

Male genitalia (n = 6). Male aedeagal median lobe robust, broadly parallel sided from base to apex of ostial opening, dorsoventral breadth at midlength 0.25× distance from tip to base of closed basal bulb (Fig. 88); lobe shaft slightly melanized, the internal sac visible through lobe wall in unverted position; lobe apex parallel-sided, length distad ostial opening subequal to dorsoventral breadth; tip of lobe evenly, narrowly rounded.

Female reproductive tract ($n = 1$). Bursa copulatrix vase-shaped, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite $1.8\times$ maximum breadth (dissection compressed under cover slip) (Fig. 64); bursal walls thin, translucent basally, thicker and more heavily stained with Chlorazol Black stain near midlength, lumen without spicules, but bursal surface wrinkled in distal half; basal gonocoxite with apical fringe of seven to eight setae (Fig. 72); apical gonocoxite acuminate with narrowly rounded apex and three lateral ensiform setae.

Types. Holotype male (QMB deposited in MNHN): NEW CALEDONIA 11152 / 22°02'Sx166°28'E. 950m. / Dzumac Rd., junction / 26Jan2004. G.Monteith / pyrethrum, trees & logs // QUEENSLAND / MUSEUM LOAN / DATE: April 2004 / No. LE 04.16 (green label) // male habitus photo 1 / J.K. Liebherr 2015 // HOLOTYPE / Cyphocoleus / monteithi / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (22 specimens). NEW CALEDONIA: Mt. Ouin, 1100 m el., pyrethrum trees & logs, 22°01'S, 166°28'E, 09-xi-2002, Burwell & Monteith (QMB, 1; lot no. 11150); Dzumac Road junction, 950 m el., 22°02'S, 166°28'E, 09-xi-2002, Burwell, Monteith & Wright (QMB, 1; lot no. 11145), pyrethrum trees & logs, 09-xi-2002 Burwell & Monteith (QMB, 3; lot no. 11143), pyrethrum mossy trees, 04-xii-2003, Monteith (QMB, 3; lot no. 11458), pyrethrum trees & logs, 26-i-2004, Monteith (QMB, 8; lot no. 11522), flight intercept trap, 05-xii-2003–26-i-2004, Monteith (QMB, 1; lot no. 11465); Mt. Dzumac road, 700 m el., pyrethrum trunks & logs, 22°03'S, 166°28'E, 01-xii-2000, Monteith (QMB, 1; lot no. 9913); Mt. Mou summit, 1200 m el., 22°04'S, 166°21'E, 24-v-1984, Monteith & Cook (ANIC, 1; QMB, 1), moss forest, 1200 m el., hand collecting, 27–28-xii-2004, Monteith (QMB, 1; lot no. 12019); Rivière Bleue, Haute Pourina, 800 m el., pyrethrum trees & logs, 22°06'S, 166°38'E, 22-xi-2002, Monteith (QMB, 1; lot no. 11210).

Etymology. I take great pleasure in naming this extremely distinctive species (Fig. 85) for Dr. Geoff Monteith, Senior Curator of Insects Emeritus, Queensland Museum. His collecting activities involving numerous field expeditions to New Caledonia formed the taxonomic basis for this study.

Distribution and habitat. This species is known only from the southern portion of Grande Terre: localities range from Mt. Ouin on the north to Parc Provincial Rivière Bleue on the south (Fig. 79). Collection localities range from 700–1200 m el., with beetles collected via pyrethrin fog of trees and logs, hand collecting, and in a flight intercept trap into which one beetle was able to climb.

9. *Cyphocoleus miricollis* Fauvel, 1882

Figures 65, 73, 80, 89, 99

Diagnosis. This species shares the elongate prothorax with transversely wrinkled notum and acutely projected

front angles with *C. monteithi*, but the elytra are very flat, and the elytral striae distinctly punctate, the punctures expanding strial breadth (Fig. 99). The pronotum is narrowly trapezoidal, with broadly rounded hind angles and a deep transverse groove defining a broadly elevated pronotal basal margin, APW/BPW = 1.28–1.40. Based on the two examined specimens, it appears that this species carries a layer of environmental varnish similar to that observed for *C. monteithi* above (Fig. 85), not the abundant layer of environmental debris that coats individuals of *C. mirabilis*, *C. moorei*, and *C. lescheni* (Figs 100–103). Standardized body length 7.3–7.7 mm.

Description ($n = 2$). Head capsule ovoid with deeply constricted neck, genae distinctly incurved at back of head; frons with large, shallow chevron-shaped medial impression, frontal grooves broad and subparallel; eyes small, moderately convex, ocular ratio 1.30–1.50; supraorbital setae absent; mandibles moderately elongate, length $2.5\times$ distance from antennal articulatory socket to anterolateral margin of labrum; gena glabrous. Pronotum narrow, tubular, MPW/PL = 0.63–0.67; median longitudinal impression deep, interrupting orientation of deep transverse wrinkles, terminated anteriorly as a deep pit; anterior marginal bead very broad, the deep groove just posterad bead interpreted as anterior transverse impression; proepipleuron and proepisternum bulging outward, visible in dorsal view for much of pronotal length, proepisternum smooth. Elytra broadly ellipsoid, MEW/EL = 0.68–0.69; humeri broadly angulate laterad depressed scutellum and parascutellar interval; parascutellar setae present, articulatory socket papillate, elevated above elytral surface; elytral striae deeply incised, punctate, the punctures separated by about $5\times$ puncture diameter; elytral intervals distinctly convex, the sutural, third, fifth, and seventh interval subcarinate, most evidently so basally; dorsal elytral setae absent; lateral elytral margin straight to slightly concave laterad anterior series of lateral elytral setae; lateral elytral setae arranged as 6 + 6; subapical elytral seta present, apical seta absent; subapical sinuation distinctly concave, sinuation subangulately meeting lateral margin; elytral apices broadly rounded, margin deeply invaginated at fused suture. Mesepisternum impunctate; mesepisternum with dorsal length subequal to diagonal width. Abdomen of males and females with apical ventrite broadly, slightly concave medially; males with one seta each side of apical margin of apical ventrite, females with two setae each side. Legs gracile, moderately long; metacoxae bisetose; tarsomeres relatively broad and short, mt1 length $0.21\times$ tibial length; mt4 with long, broad apical lobes, length to apex of outer lobe $2.67\times$ median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture reduced, frons with surface shiny, transversely stretched isodiametric mesh traceable over portions of surface; pronotum glossy with fine transverse lines visible over portions of surface; elytral glossy on disc with transverse lines visible apically; body surface – head, pronotum, elytra, and ventral surfaces – with sparse pelage of very short setae (these setae may

be removed in part by cleaning). Coloration of head and pronotal disc rufopiceous; prothoracic ventrites piceous; elytra rufobrunneous; thoracic and abdominal ventrites rufopiceous, apical abdominal ventrite apically brunneous; femora and tibiae rufobrunneous, tarsi brunneous.

Male genitalia (n = 1). Male aedeagal median lobe robust, broadly parallel sided from base to apex of ostial opening, dorsoventral breadth at midlength 0.25× distance from tip to base of closed basal bulb (Fig. 89); lobe shaft slightly melanized, the internal sac visible through lobe wall in unevverted position; lobe apex parallel-sided, dorsoventral breadth slightly longer than length; tip of lobe evenly rounded.

Female reproductive tract (n = 1). Bursa copulatrix broadly columnar, distance from base of gonocoxites to spermathecal basal sclerite 2.7× maximum breadth (dissection compressed under cover slip) (Fig. 65); bursal walls thin, translucent, the lumen smooth; basal gonocoxite with apical fringe of five setae (Fig. 73); apical gonocoxite broad basally, but narrow for much of length, with narrowly rounded apex and two lateral ensiform setae.

Types. Lectotype male (IRSN) hereby designated: M^t Mou (white label glued to larger pink label) Coll. R. I. Sc. N. B. / Nouvelle Calédonie / rec. / Deplanche / ex. coll. Fauvel // type (pink label with black border) // Coll. et det. A. Fauvel / *Cyphocoleus* 1882 / miricollis n. sp. / R. I. Sc. N. B. 17.479 // LECTOTYPE / *Cyphocoleus* / miricollis / Fauvel 1882 (black-bordered red label // *Cyphocoleus* revision / measured specimen 1 / J.K. Liebherr 2015.

Distribution and habitat. Known from sites in the southern mountains of Province Sud, near Mt. Ouin, at Mt. Mou, and at Forêt Nord (Fig. 80, Suppl. material 3).

10. *Cyphocoleus mirabilis* (Park & Will), comb. n.

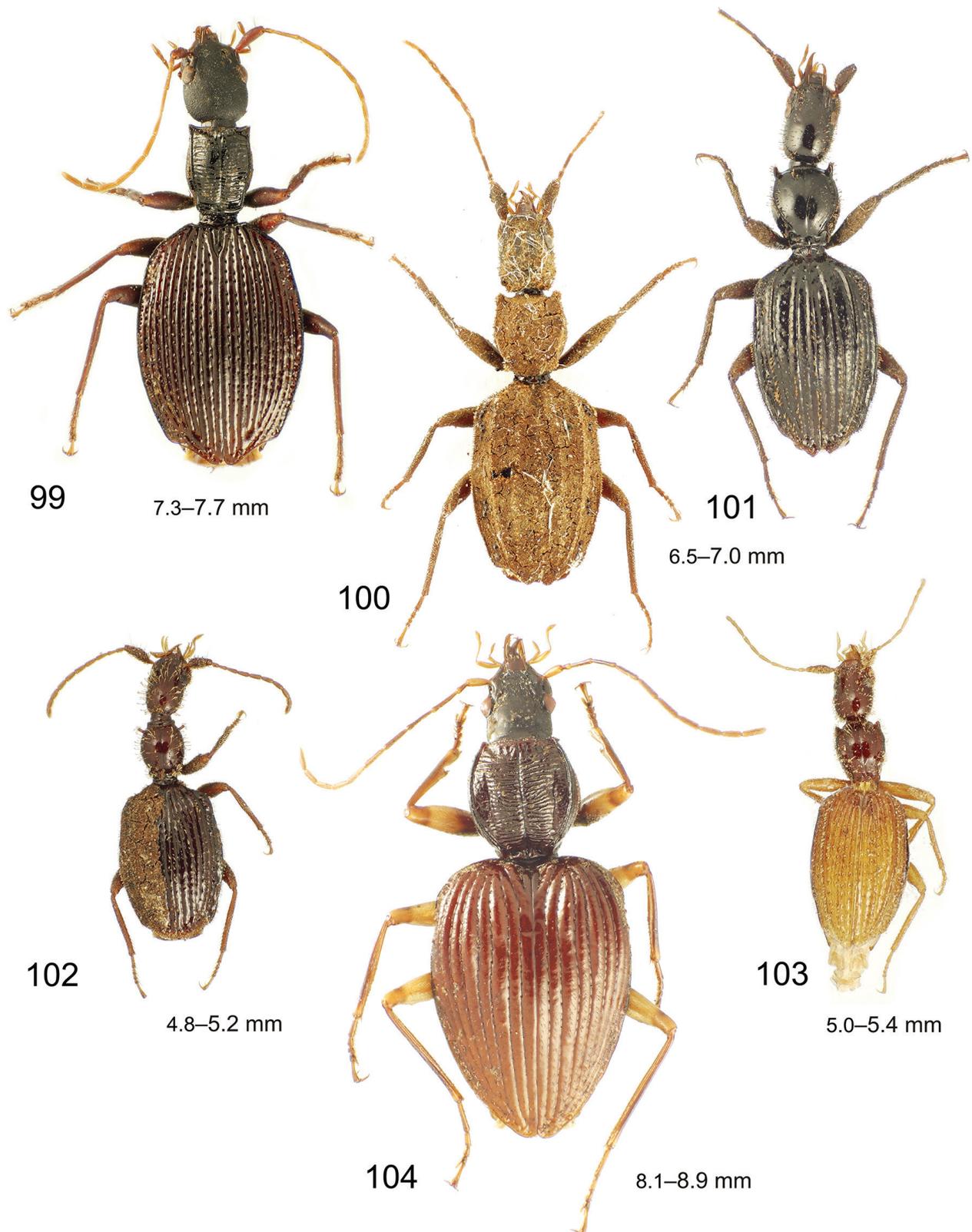
Atongolium mirabile Park & Will, 2008: 100.

Figures 30, 74, 81, 100–101, 105

Diagnosis. This species comprises one-third of a species triplet characterized by anterior and posterior projections on the front and hind angles of the pronotum (Figs 101–103), as well as presence of a pelage of setae that are club- or paddle-shaped: i.e. the setae are 2–3× broader apically than at their base. *C. mirabilis* is the largest-bodied of the three; standardized body length 6.5–7.0 mm, and also differs by the larger eye size: eyes slightly convex with 12 ommatidia present across a horizontal eye diameter. The apical abdominal ventrite bears a single seta on its apical margin in both males and females of this species, whereas females of the other two species in the triplet – *C. moorei* and *C. lescheni* – have two setae each side of the apical ventrite's apical margin. This species shares with *C. lescheni* the presence of a lateral marginal carina connecting the two pronotal processes, whereas *C. moorei* lacks such a carina. Conversely, dark rufous body coloration is shared among individuals of *C. mirabilis*

and *C. moorei* (Figs 101, 102) versus the pale brunneous and flavous coloration of *C. lescheni*.

Description (n = 3). Head capsule elongate, genae subparallel behind eyes and deeply converging at constricted neck; frons with small dimple-like depression medially between eyes, the dimple lined with isodiametric sculpticells; frontal grooves broad and deep, restricted to portion of frons anterad eyes; eyes small and slightly convex, a depressed groove continuous with groove at lateral edge of frons extended from eye dorsum to midpoint of eye hind margin; supraorbital setae absent; mandibles moderately elongate, length 2.0× distance from antennal articulatory socket to anterolateral margin of labrum; antennal scape broadly fusiform, length 3× maximal breadth; gena glabrous. Pronotum convex dorsally, with broadly spatulate processes at front and hind angles, the front processes flatter and broader in longitudinal orientation, the posterior processes more hornlike; lateral marginal carina extended and diminished behind posterior process, pronotal median base depressed but not margined; median longitudinal impression finely incised with surface sloping to meet at deepest portion; anterior transverse impression represented by oblique depressions that define an anterior pronotal collar about as wide as neck of head; proepipleuron and proepisternum bulging outward, visible in dorsal view in basal half of pronotal length; proepisternum smooth; prosternal process deeply depressed anterad procoxae, broadly depressed medially on ventral face, and depressed in an inverted “Y” pattern on posterior face resulting in a dorsomedial bump. Elytra only moderately convex overall, scutellum and sutural stria slightly depressed relative to stria 3; at midlength, sutural and fifth interval distinctly elevated, third interval slightly less so but it is also more elevated than intervals 2, 4, and 6; humeri very narrow, the basal groove present only from base of greatly elevated fifth interval to subangulate lateral margin just outside anterior series of lateral elytral setae; parascutellar and dorsal elytral setae absent; lateral elytral setae arranged 6 + 3 + 3, their articulatory sockets papillate, upraised above elytral surface: subapical elytral seta present, apical seta absent; subapical sinuation distinctly concave, the median portion of concavity upraised thereby elevating elytral margin; elytral apices tightly rounded, protruded, a deep invagination between them adjacent to the fused suture. Mesepisternum impunctate; metepisternal dorsal length subequal to diagonal width. Abdomen with very shallow, broad concavity medially on both male and female apical ventrite. Legs moderate, tarsomeres relatively short, mt1 length/tibial length = 0.21; mt4 length to apex of outer lobe 1.2× median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture absent on vertex except in median dimple; surface of pronotal and elytral disc glossy, indistinct transverse lines over portions of elytral surface; pelage of club-shaped setae well developed; setae on head capsule and pronotal moderately expanded, twice as broad apically as basally; setae broad and paddle-like on prothoracic lateral carina and anterior and posterior pronotal process-



Figures 99–104. Dorsal habitus photographs of *Cyphocoleus* spp.: **99**, *C. miricollis*, Forêt Nord; **100**, *C. mirabilis* female, environmental patina intact, Mt. Koghi; **101**, *C. mirabilis* male, environmental patina removed, Mt. Koghi; **102**, *C. moorei* female, environmental patina removed from forebody and right elytron, E. Table Unio; **103**, *C. lescheni* female, environmental patina removed, elytra reassociated with dissected specimen, Aoupinié; **104**, *C. fasciatus* male, teneral specimen lacking environmental patina, Mt. Panié.

es; elytra with broad paddle-like setae on sutural, third, and fifth intervals, setae narrower apically on intervals 2, 4, and 6; elytral lateral margin with short paddle-like setae, their length about half that of longer setae on odd intervals; ventral body surface and legs covered with dense pelage of short microsetae, the setae on legs more robust than those on ventrites. Coloration of head capsule dark rufous; antennal segments 1–4 rufobrunneous, outer antennomeres flavous with rufous cast; pronotum, elytra, and thoracic sclerites and abdominal ventrites dark rufous with a piceous cast; femora rufobrunneous, tibiae darker, rufopiceous, tarsi brunneous.

Male genitalia. Male aedeagal median lobe robust, broadly parallel sided in basal half, evenly tapered in distal half to subacuminate tip, dorsoventral breadth at midlength $0.22\times$ distance from tip to base of closed basal bulb (Fig. 29); lobe apex elongate, evenly tapered to subacuminate tip, dorsoventral breadth $0.2\times$ distance from distal margin of ostial opening to tip.

Female reproductive tract ($n = 1$). Bursa copulatrix vase-shaped, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite $2\times$ maximum breadth (dissection compressed under cover slip) (Fig. 105); bursal walls thin, translucent, lumen without spicules but bursal surface wrinkled in distal two-thirds; basal gonocoxite with apical fringe of six setae (Fig. 74); apical gonocoxite narrowly subtriangular with narrowly rounded apex and two lateral ensiform setae.

Type. Holotype male (MNHN): NEW CALEDONIA: $21^{\circ}45'S$, $166^{\circ}09'E$, Ningua Reserve Camp, 1100 m, 12–13.xi.2001, C. Burwell & G. Monteith, pyrethrum, trees & logs, 8639 (not examined; identification based on female paratype (QMB) and non-type male (MNHW))

Distribution and habitat. Known from across the southern third of New Caledonia, from Col d'Amieu on the north to Rivière des Pirogues on the south (Fig. 81, Suppl. material 3). All recorded microhabitats include tree trunks and downed logs, with beetles collected using pyrethrin fog. The elongate paddle-shaped setae distributed over the body surface are associated with a thick layer of environmental patina (Figs 100, 101).

11. *Cyphocoleus moorei* (Park & Will), comb. n.

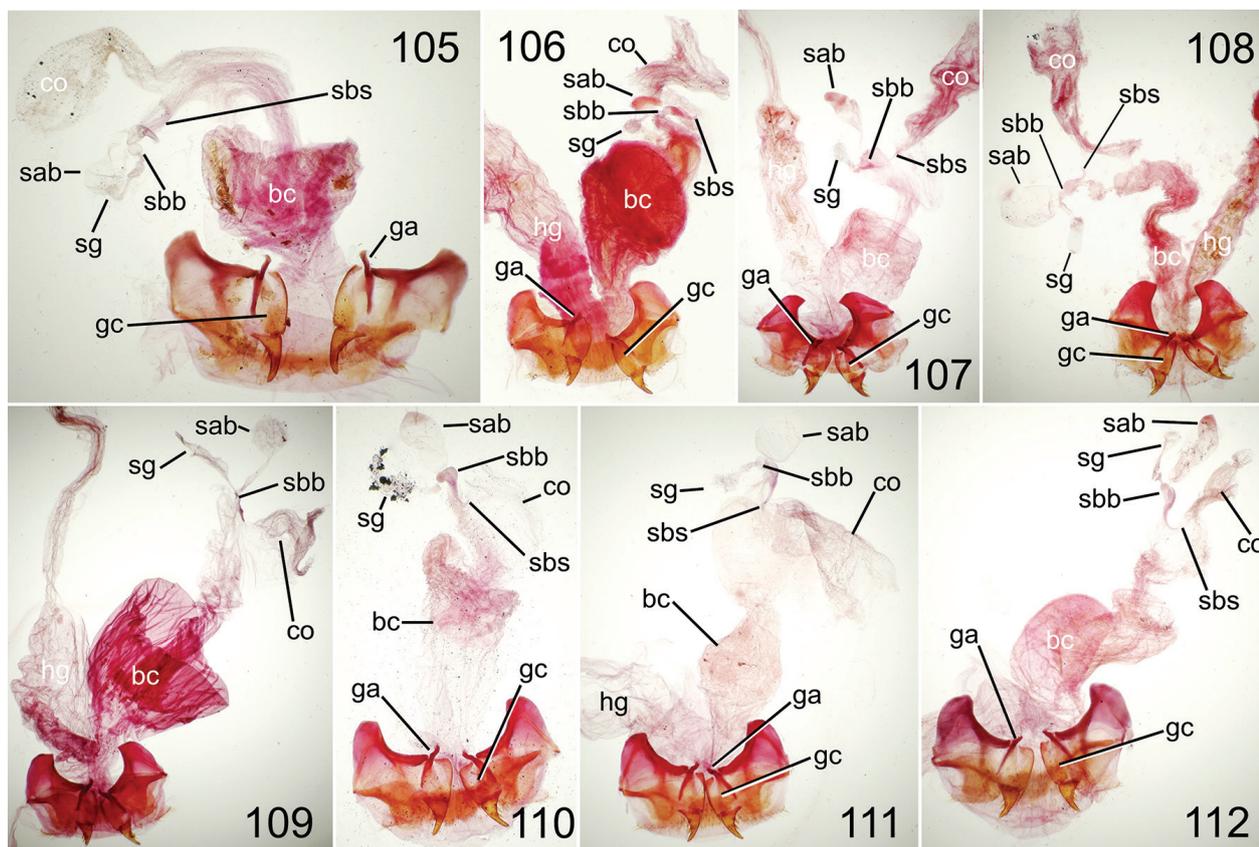
Atongolium moorei Park & Will, 2008: 101.

Figures 81, 102

Diagnosis. This second of the species triplet with anterior and posterior pronotal processes is unique in the absence of a lateral carina joining the processes, the pronotum fused to proepipleuron without any evidence of the shared suture (Fig. 102). The pronotal processes are both columnar, the anterior process half the height of the posterior, and both topped with a tuft of approximately nine club-shaped setae. The elytral intervals are distorted in this species, with the second interval absent basally due to convergence of the sutural and third intervals. Conversely, the fourth interval appears split basally, resulting

in the highly carinate fifth interval maintaining its fifth place position relative to the inner intervals throughout its length. The less convex sixth interval lies just laterad the carinate fifth interval, with the seventh interval very low and in part confused with the sequence of lateral elytral setae. The eyes of these beetles are very small in diameter, though slightly convex, with eight ommatidia horizontally across the diameter: the same ommatidial count as *C. lescheni* below. Standardized body length 4.8–5.2 mm.

Description ($n = 2$). Head capsule narrow elongate, genae parallel behind eyes, basally constricted to narrowly constricted neck (Fig. 102); frons depressed between the eyes relative to convex vertex; frontal grooves deep, broad, depressed mesad bases of antennae; supraorbital setae absent; mandibles moderately elongate, length $2.1\times$ distance from antennal articulatory socket to lateroapical margin of labrum; antennae only moderately elongate, apical antennomeres filiform; scape greatly swollen, flattened dorsoventrally so that it assumes the profile of a cricket bat at midlength, scape length $2.3\times$ maximal breadth; gena glabrous except for pelage, subgenal seta absent. Pronotum evenly ellipsoid in dorsal view, MPW/PL = 0.77; pronotal disc convex in both lateral and longitudinal dimensions, median base depressed relative to center of disc, with obsolete marginal bead defined by very shallow groove near margin; median longitudinal impression shallow, smooth, best defined by darker cuticle at deepest part; anterior transverse impression interpreted as deep transverse groove that defines upturned anterior collar; proepisternum bulging outward, visible in dorsal view, smooth; prosternal process broadly, medially depressed near front of procoxae, more narrowly depressed medially on ventral face, broadly medially depressed on posterior face. Elytra broad, moderately convex, little depressed laterally; scutellum depressed and basal margin medially inflexed at suture; humeri evenly sloped from scutellum to narrowly rounded margin just laterad front of anterior series of lateral elytral setae; parascutellar and dorsal elytral setae absent; fifth elytral interval subcarinate, more elevated than other moderately convex intervals; lateral elytral setae arranged as $6 + 3 + 3$, their articulatory sockets papillate, upraised above surrounding cuticle; subapical elytral seta present, apical seta absent; subapical sinuation distinctly concave, most concave portion of sinuation convexly upraised; elytral apices broadly rounded, separated by moderate invagination centered on fused suture. Mesepisternum impunctate; mesepisternum with dorsal length $1.1\times$ diagonal width. Abdomen of female with broad, shallow concavity medially, two setae each side. Legs moderately long, mt1 length/tibial length = 0.21; metacoxa bisetose; mt4 length to apex of outer lobe $1.2\times$ median length, 4–5 ventrolateral setae each side. Microsculpture of head absent, frons and vertex glossy; pronotal disc and lateral sclerites glossy; elytra without microsculpture on higher portions of intervals, fine transverse lines traceable in deeper portions of striae and punctures; head and pronotum with pilose pelage of elongate club-shaped setae; pronotal processes with tufts of pad-



Figures 105–112. Female reproductive tract, ventral view, for *Cyphocoleus* spp.: **105**, *C. mirabilis*, Mt. Koghi; **106**, *C. fasciatus*, Mt. Panié; **107**, *C. cychroides*, Pic d’Amoa; **108**, *C. latipennis*, Mt. Panié; **109**, *C. cardiopterus*, Mt. Mou; **110**, *C. globulicollis*, Col des Roussettes; **111**, *C. flavipes*, Nouméa; **112**, *C. subulatus*, Forêt de Thi. For abbreviations see Table 1.

dle-like setae at apices; elytral intervals lined with series of paddle-like setae of length similar to tufts on pronotal processes; elytral margin lined with very short paddle-like setae; ventral surfaces of head, thorax, and abdomen covered with sparsely distributed pelage of short microsetae, with similar-lengthed setae covering anterior surfaces of femora, dorsal surfaces of tibiae; tarsomeres setose dorsally, the setae arranged in two dorsolateral longitudinal series. Coloration of head, prothorax, elytra, and thoracic and abdominal ventrites rufous; antennal scape dark, rufopiceous, outer antennomeres 2–11 brunneous; femora rufoflavous, tibiae and tarsomeres brunneous.

Male genitalia. Male aedeagal median lobe robust, broadly parallel sided in basal half, ventral margin slightly convex near midlength, dorsoventral breadth at midlength $0.2\times$ distance from tip to base of closed basal bulb (Park and Will 2008; Fig. 3K); lobe apex tapered to subacuminate, slightly downturned tip, dorsoventral breadth $0.25\times$ distance from distal margin of ostial opening to tip.

Female reproductive tract. Not examined (see Park and Will 2008).

Type. Holotype male (MNHN): NEW CALEDONIA, $21^{\circ}45'S$, $166^{\circ}09'E$, Ningua Reserve Camp, 1100 m, 12–13.xi.2001, C. Burwell & G. Monteith, pyrethrum, trees & logs, 8639 (not examined; identification based on female paratype (QMB)).

Distribution and habitat. Known from slightly north of the distribution of *C. mirabilis* along the Sararaméa-Canala Road near Table Unio, though with a broad sympatric overlap with that species ranging from Col d’Amieu to Ningua Reserve (Fig. 81, Suppl. material 3). Specimens have been found in leaf litter, and by pyrethrin fogging of trees and logs. The elongate club-shaped setae over the body surface are associated with a 0.2 mm thick environmental patina incorporating plant-based detritus (Fig. 102).

12. *Cyphocoleus lescheni* sp. n.

<http://zoobank.org/D211D53A-BC34-491B-A11A-DDF3D4A36DB6>
Figures 75, 81, 103

Diagnosis. Among the triplet of species with setose pronotal processes, *C. lescheni* can be diagnosed by: **1**, presence of a carinate ridge between the anterior and posterior pronotal processes; **2**, small, flat eyes, eight ommatidia crossed on a horizontal diameter; **3**, elytra with seventh interval the most carinate, its convexity marking the border between a moderately flat disc bearing six intervals, and a much more vertical elytral margin with a pelage-seta bearing eighth interval. Standardized body length 5.0–5.4 mm.

Description (n = 2). Head capsule elongate, genae parallel behind eyes, basally constricted to well-defined neck; frons convex between eyes, frontal grooves linear and moderately convergent anterad, widest at fronto-clypeal suture; supraorbital setae absent; mandibles moderately elongate, length 1.9× distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderately elongate, apical antennomeres filiform; scape fusiform, broadened into a paddle-like shape, length 2.5× maximal breadth; gena glabrous except for pelage, subgenal seta absent. Pronotum orbicular; anterior pronotal process short, apically obtuse, the process flattened longitudinally; posterior pronotal process columnar, peg-like, slightly more than twice as long as broad; lateral ridge joining two process a low rounded carina; pronotal median base constricted, surface undulated with median and two lateral depressions separate by low rounded longitudinal ridges, lateral depressions bordering outside by similar low, rounded lateral longitudinal ridges; median longitudinal impression finely incised, moderately deep; anterior transverse impression interpreted as a punctulate transverse groove that defines a rounded anterior collar, the collar broadest medially, terminated laterally anterad pronotal processes; proepipleuron and proepisternum bulging outward, visible in dorsal view; proepisternum smooth; prosternal process medially concave anteriorly near front of procoxae, deeply medially depressed on ventral face, broadly depressed medially on posterior face. Elytra narrow, elongate, with scutellum and parascutellar interval depressed relative to very carinate seventh interval, the carination of that interval greatest at base; parascutellar and dorsal setae absent; humeri extended anterad at base of seventh interval, basal margins straight and narrowly diverging posterad humeral angle to position laterad anterior three lateral elytral setae where the margins become subparallel posteriorly; lateral elytral setae arranged as 6 + 3 + 4, the setal articulatory sockets papillate, raised as mounds above the surrounding cuticle; subapical elytral seta present, apical seta absent; subapical sinuation distinctly concave, margin upraised at middle of concavity, the sinuation subangulately meeting lateral margin. Mesepisternum impunctate; metepisternal dorsal length 1.3× diagonal width. Abdomen with apical margin of apical ventrite moderately concave medially in females, the middle pair of the four apical setae just laterad median concavity. Legs moderately elongate, gracile; mt1 length/tibial length = 0.21; mt4 length to apex of outer lobe 1.2× median length, with 4–5 ventrolateral setae each side. Microsculpture of head and pronotal disc glossy, without microsculpture; elytral disc with intervals glossy, indistinct isodiametric (?) sculpticells in deepest portions of striae; pelage well developed, comprising club-like to paddle-like setae; head capsule densely covered with club-like setae that are longest on posterior portion of head capsule, about half a long on frons, and very short, scale-like anterad and below eyes; pronotal disc pelage consisting of setae much like present on posterior portion of head, pronotal processes and lateral ridges with

apically broader, more paddle-like setae; elytral intervals lined with longitudinal series of club-like setae, the setae broader apically on odd intervals (sutural, 3, 5, 7), and shorter and narrower apically on even intervals; elytral lateral margin densely lined with short, thick setae; ventral body surface, femora and tibiae covered with very fine, apically narrowed microsetae; tarsomeres with and additional paired dorsolateral setae, four on mt1 and two on mt2–4. Coloration of head and pronotal disc rufous, pronotal lateral ridge somewhat darker due to deeper cuticle; elytra and abdominal ventrites rufoflavous, elytral lateral margin dark rufous (as in pronotal lateral carina); legs flavous.

Female reproductive tract (n = 1). Basal portion of one right gonocoxa available for study; basal gonocoxite with apical fringe of five setae; apical gonocoxite apparently subtriangular based on basal fragment, with two lateral ensiform setae.

Types. Holotype female (EMEC deposited in MNHN) (body pointed, fused elytra mounted on platen): NEW CALEDONIA, Prov. / Nord L'Aoupinié 24-iii-2007 / R. Leschen rotten wood / berlesate NC076 800m el. / 21°11'S/165°17'E // UC Berkeley / EMEC / 1137861 (pixelated bar code) // *Cyphocoleus* revision / measure specimen 1 / J.K. Liebherr 2015 // HOLOTYPE / *Cyphocoleus* / lescheni / J. K. Liebherr 2016 (black-border red label).

Paratype female (EMEC): Aoupinié, 800 m el., 21°11'S, 165°17'E, Berlesate rotten wood, 24-iii-2007, Leschen.

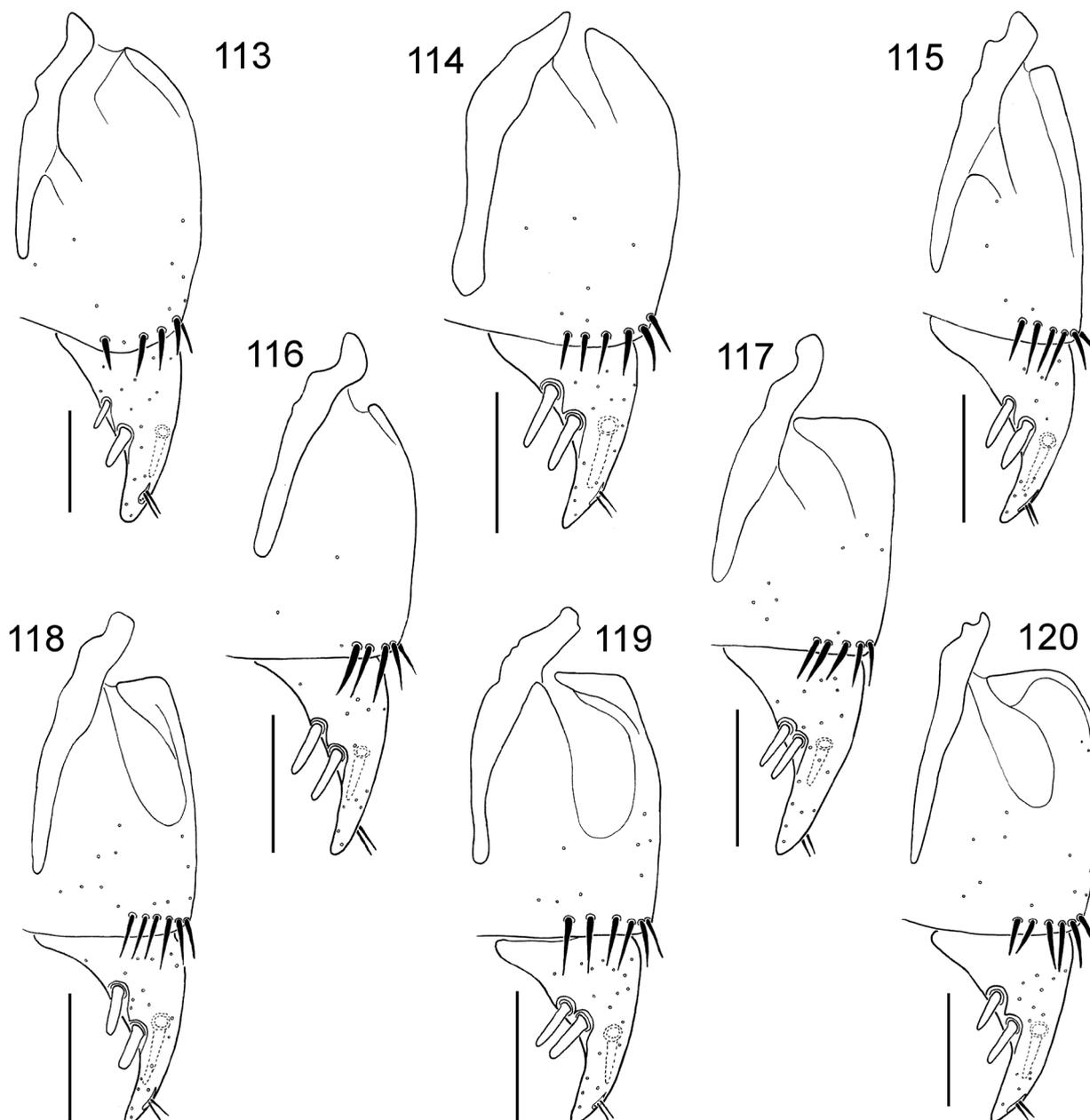
Etymology. We take great pleasure in naming this species for Dr. Richard A. B. Leschen, Curator, New Zealand Arthropod Collection and the collector of the two type specimens currently representing this species. Dr. Kipling W. Will is accorded author status based on his recognition of this species as undescribed from amongst the material collected during the 2007 New Zealand Arthropod Collection-University of California, Berkeley Essig Museum expedition.

Distribution and habitat. Both types of this species were collected from leaf litter by Berlese extraction. The long club-shaped setae afford the means for a thick layer of environmental patina to adhere to the body surface.

13. *Cyphocoleus fasciatus* sp. n.

<http://zoobank.org/C0597858-AACC-475B-BEA4-DE5CD75E2B35>
Figures 80, 90, 104, 106, 113

Diagnosis. This species (Fig. 104) comprises beetles of largest body size – standardized body length 8.1–8.9 mm – among those species characterized by orbicular pronota and broadly ovate, inflated elytra (Figs 121–125, 161–164). Indeed, *C. fasciatus* is the adelphotaxon to those taxa (Figs 44–46). Additionally, individuals of *C. fasciatus* exhibit legs with banded femora, their smoky piceous basal halves and subapical band contrasted to flavous bands in the apical half and at the apex (Fig. 104). The pronotal disc is distinctly transversely



Figures 113–120. Female right gonocoxae, ventral view, for *Cyphocoleus* spp. illustrating apical fringe setae of basal gonocoxite 1, and two lateral ensiform setae, one dorsal ensiform seta, and two apical nematiform setae on apical gonocoxite 2; **113**, *C. fasciatus*, Mt. Panié; **114**, *C. cychroides*, Pic d'Amoa; **115**, *C. latipennis* Mt. Panié; **116**, *C. cordatus*, Forêt Nord; **117**, *C. globulicollis*, Col des Roussettes; **118**, *C. flavipes*, Nouméa; **119**, *C. bourailensis*, Bourail; **120**, *C. subulatus*, Forêt de Thi. Scale bar, 0.10 mm.

wrinkled, with longitudinal parasagittal impressions defining a central disc and lateral flanges extended to the lateral marginal bead. As in the three preceding species – *C. mirabilis*, *C. moorei*, and *C. lescheni* (e.g. Fig. 100) – individuals of this species are capable of developing a very thick environmental patina that obscures their dorsal body surface under deep, anastomosing layers of debris derived from leaf litter and humus. In keeping with those species, and indicative of a proximal phylogenetic relationship, the lateral marginal ridge of the pronotum terminates posteriorly in a projection: in this species a stout, obtuse tooth.

Description ($n = 5$). Head capsule broad, stout, genae parallel behind convex, pop-eyed compound eyes; neck constriction broad, moderately deep dorsally but not evidenced laterally; ocular ratio 1.39–1.45, eyes with 20 ommatidia across horizontal diameter; frons medially rugose between eyes, frontal grooves distinctly doubled, the deep canaliculi separated by a distinct rounded ridge, groove convergent to frontoclypeal suture; supraorbital setae absent; mandibles moderately elongate, length $2.1\times$ distance from antennal articulatory socket to anterolateral margin of labrum; antennae elongate, scape length $2.9\times$ maximal breadth; gena setose, subge-

nal seta present. Pronotum orbicular, front angles briefly but acutely projected; lateral marginal bead subcarinate, elevated, terminated posteriorly in blunt, obtuse tooth that continues medially as a diminished basal marginal bead, though median base not margined; pronotal base constricted, set off from disc by median and two oblique lateral depressions; median longitudinal impression deep, moderately broad, undulated longitudinally with transverse wrinkles of disc not all aligned across impression; anterior transverse impression represented by an oblique series of longitudinal depressions that extend anterad at their ends as two to three longitudinal canaliculi crossing the anterior callosity; two linear parasagittal impressions present, these grooves extended from basal tooth $\frac{3}{4}$ pronotal length toward front angles; pronotal flanges laterad parasagittal impressions irregularly wrinkled, surface smoother than median pronotal disc; proepipleuron and proepisternum bulging outward, visible in dorsal view; proepisternum irregularly and obliquely wrinkled, the wrinkles oriented more or less longitudinally; prosternum rugose, the surface with deep, irregular wrinkles that are most distinct near anterior margin; prosternal process distinctly margined anteriorly by ridges surrounding procoxal cavities, broadly medially depressed on ventral face, narrowly carinate dorsally on posterior face. Elytra ovoid, disc elevated relative to depressed lateral margins, appearing somewhat cordate due to basal elevation of third to seventh intervals versus depressed scutellum and parascutellar interval; parascutellar seta present, situated at base of sutural interval, elevated on papillate articulatory socket; basal groove broadly rounded laterad depressed and inflexed scutellum; sutural, and elytral intervals 2, 4, and 6 moderately convex on disc, intervals 3, 5, and 7 elevated, subcarinate basally, the intervals broader where they are more convex; dorsal elytral setae absent; lateral elytral setae arranged as 6 + 7; subapical elytral seta present, apical seta absent; subapical situation well developed, concavity near lateral margin of situation extended ventrad to subangulately meet lateral margin, thus apical elytral margin not elevated inside situation; elytral apices broader rounded, separated by inflexed margin adjacent to fused suture. Mesepisternum impunctate, metepisternal dorsal length $0.9\times$ diagonal width; metasternum with deep, laterally ovoid median fossa at base of metasternal process. Abdomen with broad, shallow medial concavity at apex of apical ventrite in both males and females; males with one seta each side of apical ventrite, females with two setae. Legs elongate, gracile; metacoxae bisetose; mt1 length/tibial length = 0.27; mt4 length to apex of outer lobe $2.33\times$ median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture of head stretched isodiametric mesh, visible over portions of vertex, microsculpture obscured in rugose area of frons and in frontal grooves; pronotal disc glossy, indistinct sculpticells traceable only in deepest portions of wrinkles; elytral disc glossy, obsolete transverse lines visible over portions of apex; sparsely distributed pelage of short microsetae visible on head capsule, prothorax, meso- and

metasternum, and coxae; elytra with pelage of microsetae arranged in mediolongitudinal series along elytral intervals; legs sparsely covered with very short, fine microsetae in addition to the larger fixed setae, these short setae also arranged in irregular longitudinal series on the dorsal surfaces of tibiae and tarsomeres. Coloration (specimen clear of environmental patina is teneral; Fig. 104) generally piceous on head capsule, prothorax, elytra, and meso- and metathorax; elytral epipleura narrowly dark rufous dorsally; abdominal ventrites rufopiceous, apical ventrite rufoflavous marginally; femora with distinct flavous bands in apical half and at apex that contrast greatly with the piceous coxae, dark rufous trochanters, and smoky brunneous tibiae and tarsi.

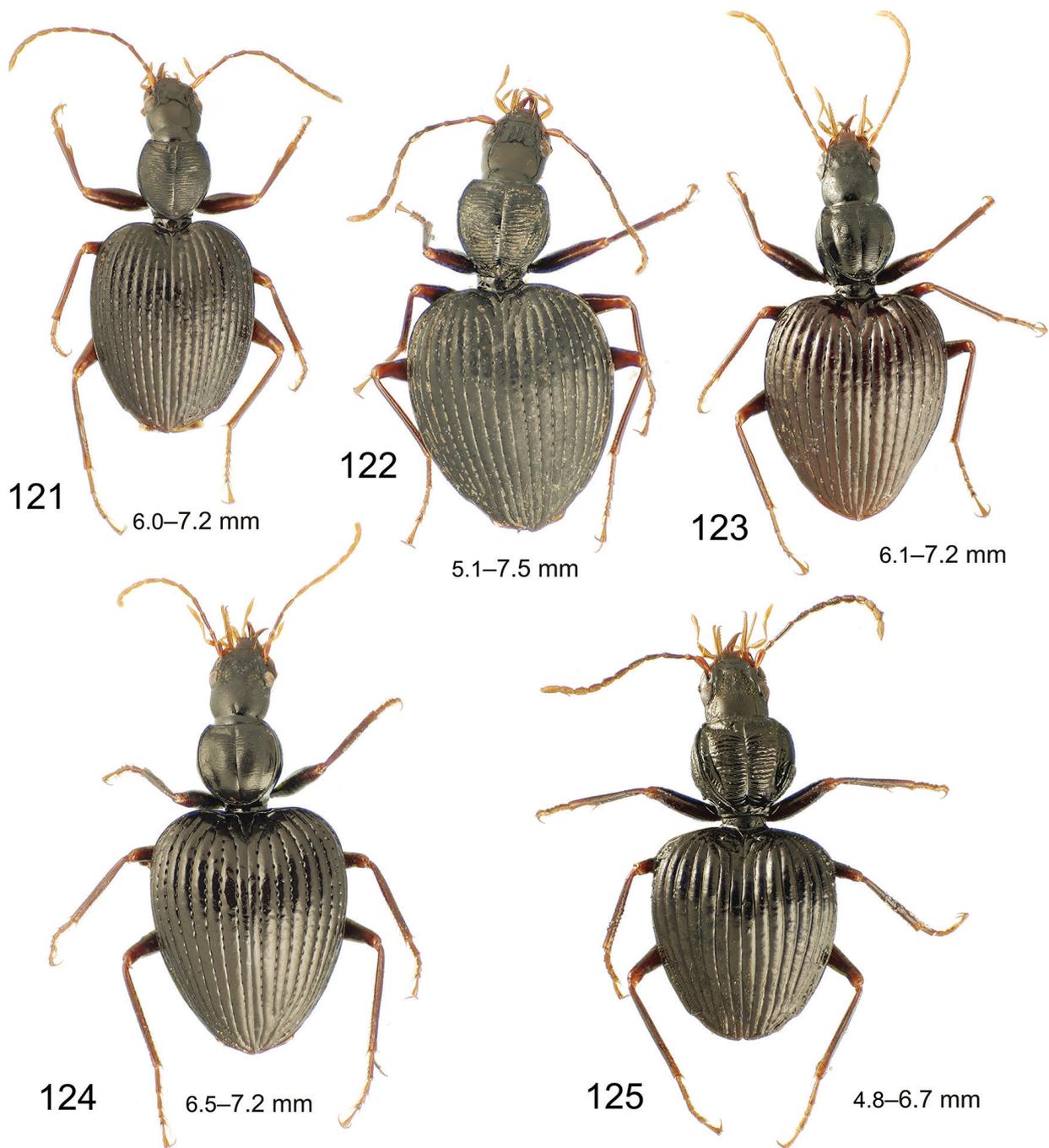
Male genitalia (n = 2). Male aedeagal median lobe robust basally, broadly parallel sided in basal half, evenly tapered in distal half to extremely elongate, curved, proboscis-like apex, dorsoventral breadth at midlength $0.16\times$ distance from tip to base of closed basal bulb (Fig. 90); lobe apex extended beyond ostial opening in a broad curve, tip tightly rounded, dorsoventral breadth at midlength of apical extension $0.13\times$ distance from distal margin of ostial opening to tip; sac with microtrichia, but without any heavily sclerotized structures.

Female reproductive tract (n = 1). Bursa copulatrix vase-shaped, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite $1.5\times$ maximum breadth (dissection compressed under cover slip) (Fig. 106); bursal walls thick, wrinkled, heavily stained with Chlorazol Black, luminal surface smooth; basal gonocoxite with apical fringe of five setae (Fig. 113), one very small on left gonocoxite; apical gonocoxite subtriangular with narrowly rounded apex and two lateral ensiform setae.

Types. Holotype male (QMB deposited in MNHN): NEW CALEDONIA / 20°34'Sx164°46'E / Mt Panie refuge, 1300 m / 16–18Nov2000.Bouchard / Burwell&Monteith.9938 // QUEENSLAND / MUSEUM LOAN / DATE: Nov.2003 / No. LEN 1688 (green label) // male habitus photo 1 / J.K. Liebherr 2015 // HOLOTYPE / *Cyphocoleus* / *fasciatus* / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (26 specimens). NEW CALEDONIA: Mt. Panié, 950–1300 m el., 20°34'S, 164°46'E, 14–16-v-1984, Monteith & Cook (QMB, 1), refuge, 1300 m el., 20°34'S, 164°46'E, 16–18-xi-2000, Bouchard, Burwell & Monteith (QMB, 10; lot no. 9938), 08–09-xi-2001, Burwell (QMB, 2; lot no. 8764), below Maruia refuge, 1300–1350 m el., 25-xi-2010, Wanat & Ruta (MNHW, 1), 1300–1600 m el., 20°35'S, 164°46'E, 15-v-1984, Monteith & Cook (ANIC, 2; QMB, 4), E trail, 1350–1600 m el., rainforest, 24-xi-2010, Wanat & Ruta (MNHW, 1), summit, 1600 m el., 20°35'S, 164°46'E, 09-xi-2001, Burwell (QMB, 3; lot no. 8769), 18-xi-2000, Bouchard, Burwell & Monteith (QMB, 2; lot no. 9939).

Etymology. The species epithet *fasciatus* is derived from the Latin to “envelop with bands (Brown 1956)”, referring to the banded pigmentation of the femora of beetles comprising this species (Fig. 104).



Figures 121–125. Dorsal habitus photographs of *Cyphocoleus* spp., environmental patina removed: **121**, *C. cychroides* male, Tionaki Tal; **122**, *C. latipennis* male, Mt. Panié; **123**, *C. cordatus* female, Forêt Nord; **124**, *C. cardiopterus* female, Mt. Mou; **125**, *C. globulicollis* female, Col des Roussettes.

Distribution and habitat. This species is known only from Mt. Panié at elevations ranging 950–1600 m (Fig. 80). Given the well-developed environmental patina borne by beetles of this species, they come in contact with ground litter during their activities. The well-developed pelage of microsetae on the dorsal body surface and prothoracic ventrites is associated with deep layers of environmental patina.

14. *Cyphocoleus cychroides* Chaudoir, 1877

Figures 107, 114, 121, 137

Diagnosis. Among all the smaller-bodied species with orbicular pronotum and cordate elytra (Figs 121–125, 161–164), this species stands out due to the narrowly orbicular pronotum, $MPW/PL = 0.88–0.94$, and pronotal disc that is evenly traversed by wrinkles but without longitudinal parasagittal impressions. The pronotal later-

al marginal beads arcuately extend to the narrow median base (Fig. 121). Some individuals of *C. latipennis* have the pronotum nearly as narrow, MPW/PL = 0.92–1.07, but beetles comprising *C. cychroides* differ by their lack of supraorbital setae, whereas *C. latipennis* is characterized by presence of the posterior seta, though it is located well behind the eye just anterad the constricted neck. The pronotal disc of *C. latipennis* also differs by the presence of parasagittal impressions, and median pronotal base not arcuately and continuously margined as in *C. cychroides*. Standardized body length 6.0–7.2 mm.

Description (n = 5). Head capsule narrowly ovoid, genae gradually narrowed to moderately constricted neck; eyes only slightly convex, oriented toward upper surface of head, ocular ratio quite variable, 1.20–1.56, about 18 ommatidia across horizontal diameter of eye; frons with paired, longitudinal depressions that surround a low median ridge; frontal grooves broad, deep, parallel, extended from just anterad hind margin of eye onto clypeus; mandibles elongate, length 2.1× distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderately elongate, scape length 2.75× maximal breadth; gena setose, subgenal seta present. Pronotum with front angles rounded, only slightly protruded; median base continuously margined, but bead straight along base; median longitudinal impression finely incised, slightly irregular as it traverses transverse wrinkles; anterior transverse impression a deep, oblique depression, defining a flat anterior callosity with indistinct longitudinal wrinkles; proepisternum slightly extended beyond marginal bead, narrowly visible in dorsal view; proepisternum mostly smooth, with indistinct vertical wrinkles; prosternal process broadly, medially depressed anteriorly, with paired, shallow longitudinal depressions ventrally, posterior face broadly convex. Elytra broadly cordate, basal groove sinuously incurved near depressed scutellum, continued in broad curve laterally around humerus, a slight hitch in the curve near base of third stria; discal intervals moderately convex, all intervals of subequal convexity; elytral striae deep, punctate, the punctures larger basally where they expand striae breadth; parascutellar seta present, articulatory socket papillate; dorsal elytral setae absent; lateral elytral setae arranged as 6 + 7, the articulatory sockets papillate; both subapical and apical elytral setae present, the articulatory socket for apical seta smaller; subapical sinuation well developed, lateral portion of concavity joined to depressed lateral margin in broad curve; elytral apices conjoined, no invagination of apical margin at fused suture. Mesepisternum impunctate; metepisternal dorsal length 1.1× diagonal width; metasternum with broad, shallow median fossa at base of metasternal process. Abdomen with apical margin of apical ventrite shallowly concave medially in both males and females; males with one seta each side of apical margin of apical ventrite, females with two setae each side. Legs moderately elongate; metacoxae bisetose; mt1 length/tibial length = 0.27; mt4 length to apex of outer lobe 1.6× median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture on vertex stretched isodiametric mesh, the

head capsule glossy; pronotal disc with evident transverse mesh visible within transverse wrinkles, the surface matte; elytral intervals covered with transverse-line microsculpture resulting in silvery iridescence; pelage little developed, glossy head capsule glabrous, pronotum and elytra with sparse distribution of exceedingly short microsetae, visible only in lateral view; ventrites and legs glabrous except for macrosetae. Coloration of body dorsum piceous, mouthparts, scutellum, and apical elytral margin rufopiceous; body venter including elytral epipleura rufopiceous; femora dark rufous; tibiae piceous medially, rufoflavous at base and apex; tarsi rufoflavous.

Male genitalia (n = 10). Male aedeagal median lobe robust, broadly parallel sided over basal 2/3 of length, the lobe shaft angled ventrally ventral ostial opening, dorsoventral breadth at midlength 0.20–0.25× distance from tip to base of closed basal bulb (Figs 91–98); lobe apex sinuously curved, tip may be knob-like with a constriction distad ostial opening (Figs 91, 92) or abruptly narrowed distad ostial opening to a parallel-sided apex (Figs 93–98); internal sac membranous without melanized microtrichia, length slightly greater than breadth (Figs 91, 93, 94, 96). Although the male aedeagi of individuals assigned to *C. globulicollis* exhibit substantial variation in the configuration of the apex, all of this variation is exhibited among individuals from the same well-sampled site; Mandjélia. All individuals from this site share other external attributes, as well as the subangulate apex to the aedeagal median lobe, and so this variation is interpreted as infraspecific.

Female reproductive tract (n = 2). Bursa copulatrix vase-shaped, abruptly narrowed distally near spermatheca, distance from base of gonocoxites to spermathecal basal sclerite 3× maximum breadth (dissection compressed under cover slip) (Fig. 107); bursal walls thin, translucent, luminal surface smooth; basal gonocoxite with apical fringe of five to six setae (Fig. 114); apical gonocoxite broadly triangular with pointed apex and two lateral ensiform setae.

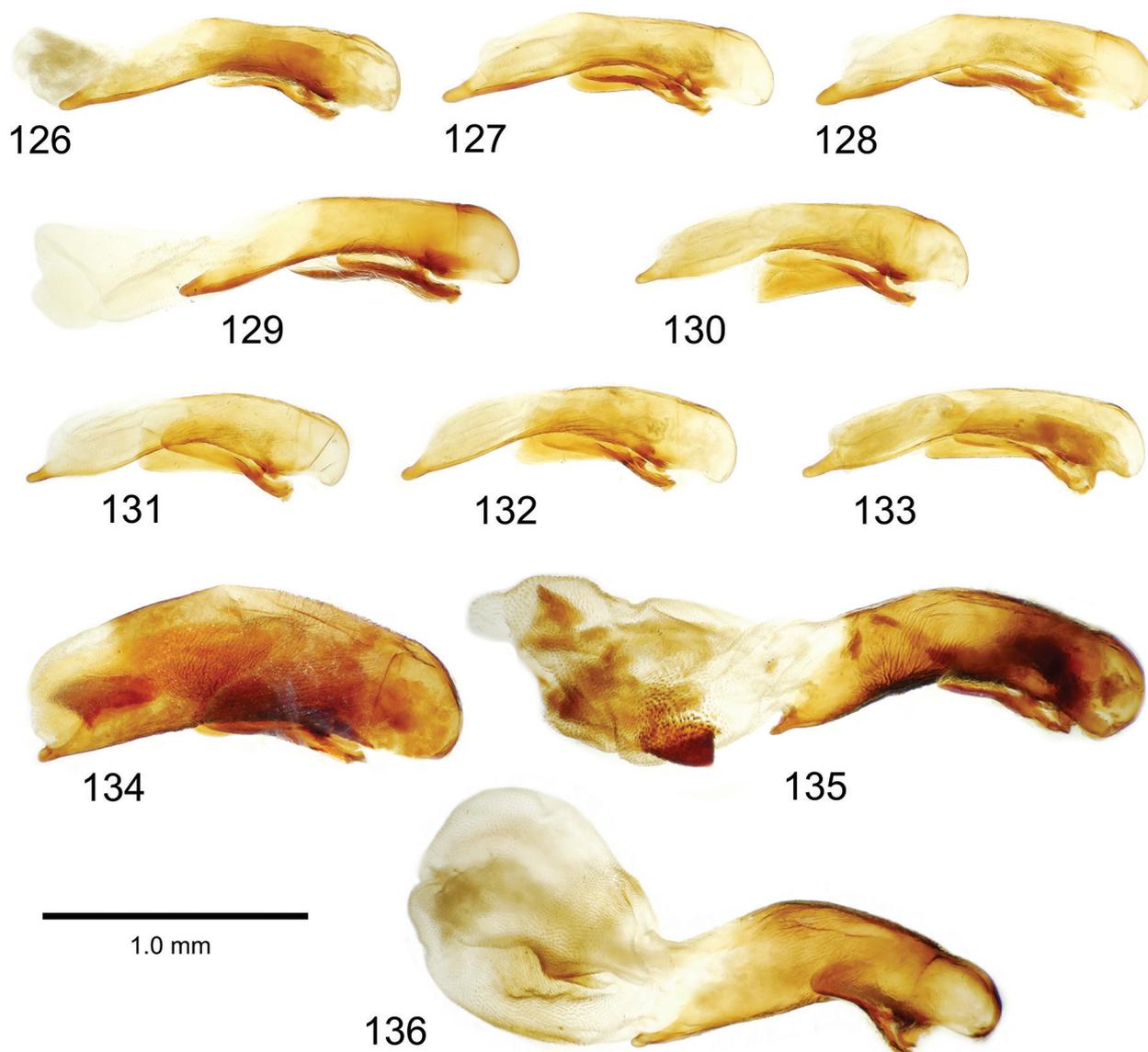
Types. Holotype male (MNHN): Ex Musæo / Chaudoir (red-inked white label with red border) // HOLOTYPE / *Cyphocoleus* / *cychroides* / Chaudoir 1877 (black-bordered red label). Holotype status is based on Chaudoir's (1877: 197) statement: "Il m'a été vendu par H.M. Deyrolle." Mandjélia summit, 750 m el. hereby designated type locality.

Distribution and habitat. Known from Province Nord. The recorded distribution is bounded by Canala on the south, and Col d'Amoss along the northeastern coast (Fig. 137, Suppl. material 3). Beetles have been collected from logs and trunks via the application of pyrethrin fog.

15. *Cyphocoleus latipennis* Fauvel, 1882

Figures 33, 108, 115, 122, 126–133, 138

Diagnosis. This species is characterized by presence of the posterior supraorbital seta, a configuration shared,



Figures 126–136. Male aedeagal median lobe and associated parameres of *Cyphocoleus* spp., dextral view: **126–133**, *C. latipennis*; **126**, internal sac everted, Mandjélia; **127–128**, Mandjélia; **129**, Mt. Panié; **130**, Pic d’Amoa; **131–132**, Aoupinié; **133**, Ouenarou; **134–135**, *C. cordatus*; **134**, Mt. Koghi; **135**, *C. cordatus*, internal sac everted, Forêt Nord; **136**, *C. cardiopterus*, Dzumac Rd. jct.

among the nine *Cyphocoleus* species with orbicular pronotum and cordate elytra (Figs 121–125, 161–164), only with *C. subulatus* and *C. iledespimensis*. This supraorbital seta is not close to the eye, but positioned far back on the head capsule close to the constricted neck. *C. latipennis* deviates from the other two species in exhibiting a very glossy vertex and glossy to transversely lined elytral intervals, versus a vertex covered with isodiametric sculpticells, and elytra with evident transverse-mesh microsculpture, best evidenced in the strial depressions. Standardized body length 5.1–7.5 mm.

Description ($n = 5$). Head capsule narrowly ellipsoid, genae gradually narrowed to moderately constricted neck; eyes only slightly convex, ocular ratio 1.46–1.53, 13–18 ommatidia across horizontal diameter of eye; frons with paired, elongate-ellipsoid depressions that surround a nar-

row elevated median carina; frontal grooves deepest and broadest just mesad eyes, sinuously convergent toward clypeus; mandibles elongate, length 2.3× distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderately elongate, scape length 2.75× maximal breadth; gena setose, subgenal seta present. Pronotum with front angles rounded, slightly protruded; median base depressed relative to disc, lateral margin sinuate anterad median basal margin that is straight across base; median longitudinal impression deep, broad, extended to anterior margin; anterior transverse impression defined by shallow groove where discal wrinkles terminate, anterior callosity crossed by numerous longitudinal wrinkles; proepisternum extended beyond marginal bead, visible in dorsal view, smooth; prosternal process broadly, medially depressed anteriorly and on ventral face, narrowly

carinate posteriorly. Elytra broadly ovoid, depressed mediobasally between parascutellar setae; basal groove subangulate basad sutural stria, lateral margin broadly and evenly extended outside humeral angle; discal intervals moderately convex, all intervals of subequal convexity; elytral striae deep, punctate, the punctures limited at the deepest portion of stria depression (and so easy to miss in uncleaned specimens); parascutellar seta articulatory socket papillate; dorsal elytral setae absent; lateral elytral setae arranged as 6 + 7, the articulatory sockets papillate; both subapical and apical elytral setae present, the articulatory socket for apical seta smaller; subapical sinuation moderately developed, lateral portion of concavity joined to depressed lateral margin in broad curve; elytral apices conjoined, no invagination of apical margin at fused suture. Mesepisternum impunctate; metepisternal dorsal length $1.0\times$ diagonal width; metasternum with broad, shallow median fossa at base of metasternal process. Abdomen with apical margin of apical ventrite shallowly concave medially in both males and females; males with one seta each side of apical margin of apical ventrite, females with two setae each side. Legs moderately elongate; metacoxae bisetose; mt1 length/tibial length = 0.27; mt4 length to apex of outer lobe $1.8\times$ median tarsomere length, 3–4 ventrolateral setae each side. Pelage little developed, glossy head capsule, pronotum, and elytra with only sparsely distributed, very short microsetae. Visible only in lateral view; pro-, meso-, and metasternum with evident pelage of microsetae, the setae longer than on dorsal surface; second and third abdominal ventrites with short, sparse microsetae medially, other ventrites and legs glabrous except for macrosetae. Coloration of body dorsum piceous, mouthparts rufopiceous; ventral surfaces of head and prothorax and thoracic sternites piceous, elytral epipleuron and abdominal ventrites to rufopiceous to dark rufous; femora dark rufous except for paler, rufolavous apex, tibiae and tarsi rufobrunneous.

Male genitalia ($n = 14$). Male aedeagal median lobe gracile, median lobe constricted near midlength, dorsoventral breadth at midlength $0.13\text{--}0.16\times$ distance from tip to base of closed basal bulb (Figs 126–133); lobe apex variously tapered to parallel sided basad broadly (Figs 128, 129) to narrowly rounded (Figs 126, 127, 130–133) tip; internal sac membranous without melanized microtrichia, length $2\times$ breadth (Fig. 129).

Female reproductive tract ($n = 3$). Bursa copulatrix narrowly elongate, distance from base of gonocoxites to spermathecal basal sclerite $7\times$ maximum breadth (dissection compressed under cover slip) (Fig. 108); bursal walls thin, translucent, luminal surface smooth except for thin band of very fine setae at midlength; basal gonocoxite with apical fringe of five to six setae (Fig. 115); apical gonocoxite subtriangular with pointed apex and two lateral ensiform setae.

Types. Holotype female (IRSN): Nelle. Calédonie (white label glued to larger pink label) Coll. R. I. Sc. N. B. / Nouvelle Calédonie / rec. / De- / planche / ex. coll. Fauvel // type (pink label with black border) // Coll. et det. A.

Fauvel / *Cyphocoleus* / *latipennis* Fauv. // HOLOTYPE / *Cyphocoleus* / *latipennis* / Fauvel 1882 (black-bordered red label. Fauvel (1882: 250) wrote: “je presume qu’il a été pris au Mont Mou”, with this locality considered the type locality.

Distribution and habitat. This is the most broadly distributed *Cyphocoleus* species, distributed along the length of Grande Terre (Fig. 138, Suppl. material 3). Specimens have been collected using pyrethrin fog applied to trunks and logs, from leaf litter, and also from flood debris.

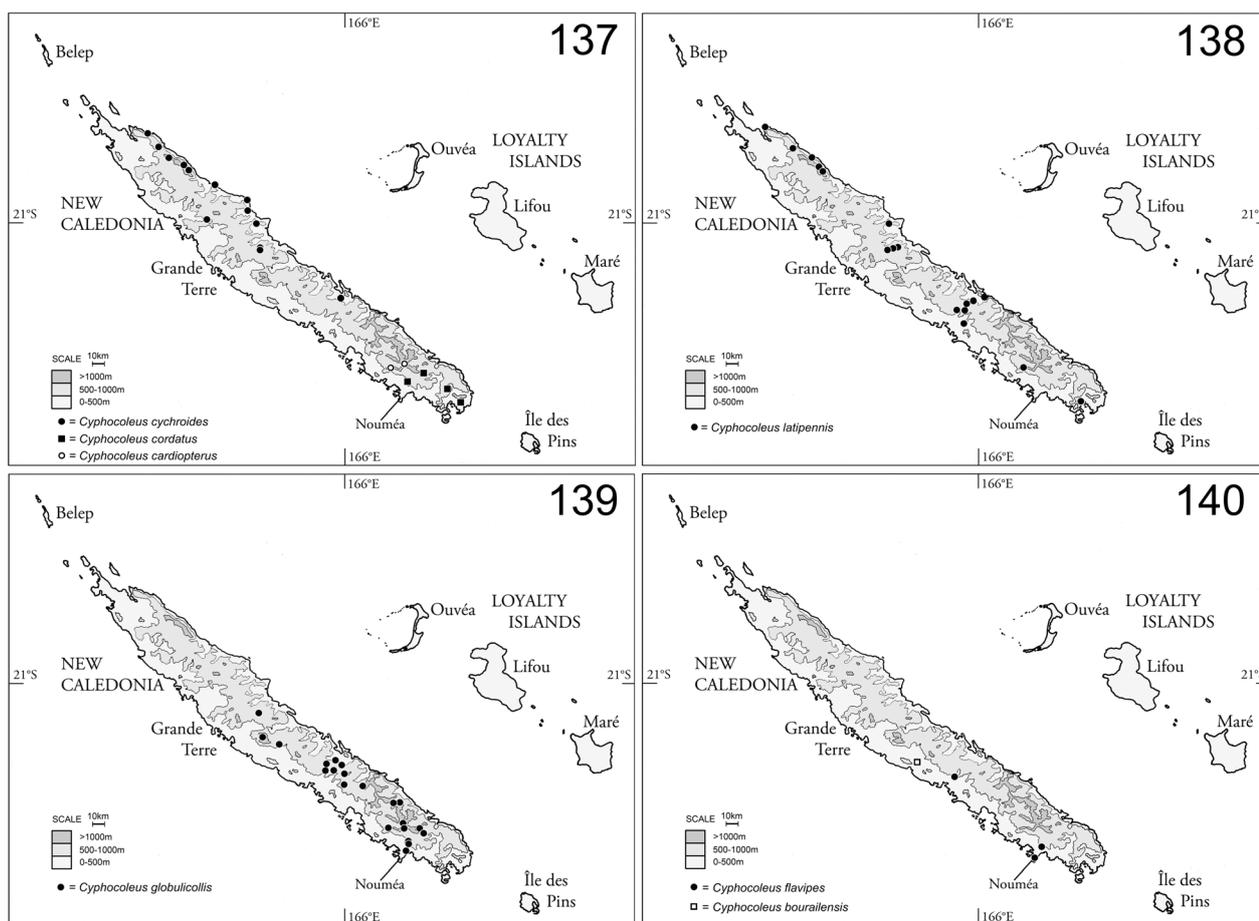
16. *Cyphocoleus cordatus* sp. n.

<http://zoobank.org/426B2B2A-6F48-4ABA-8601-EC74A69FB77E>

Figures 31, 116, 123, 134–135, 137

Diagnosis. This species and its adelphotaxon *C. cardiopterus* (Figs 123, 124) are characterized by an orbicular pronotum with lateral and basal marginal beads continuous arcuate around the pronotal base. The pronotal disc is at most shallowly wrinkled, and is covered with well-developed microsculpture, a transverse mesh on median disc, and isodiametric mesh laterad the shallow parasagittal impressions. Both species also differ from all other *Cyphocoleus* in the presence of a deep lateral fovea near the front of the mesepisternum, immediately posterad the hind margin of the proepimeron. The elytral striae of *C. cordatus* are punctate, the punctures limited to the depths of the very deep striae, whereas in *C. cardiopterus* the punctures are larger; expanding stria breadth to apex of elytra. The two species can also be diagnosed by elytral microsculpture; in *C. cordatus* the elytra bear transverse-line microsculpture, whereas in *C. cardiopterus* the beetles exhibit elytra covered with an isodiametric mesh. Standardized body length 6.1–7.2 mm.

Description ($n = 5$). Head capsule relatively broad, little narrower than prothorax, genae slightly convex anterad distinct, moderately constricted neck; eyes distinctly convex, oriented toward upper surface of head, ocular ratio quite variable, 1.43–1.50, 16 ommatidia across horizontal diameter of eye; frons with paired, rugose depressions that bracket median ridge, the ridge narrowed apically due to anterior broadening of depressions; frontal grooves broad, deep, expanded anterad to surround median frontal tubercle, their surfaces arcuately wrinkled; mandibles very elongate, length $2.6\times$ distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderate, scape length $2.5\times$ maximal breadth; gena setose, subgenal seta present. Pronotum with front angles angulate, anterior pronotal margin broadly concave; median base continuously margined, bead elevated across base well above scutellum; median longitudinal impression deep, finely incised at depth, straight, extended basally to deep transverse groove just inside basal marginal bead, extended anteriorly nearly to well-defined anterior marginal collar that extends to front angles; anterior transverse impression by deep



Figures 137–140. Distribution maps of *Cyphocoleus* spp.: **137**, *C. cychroides*, *C. cordatus*, *C. cardiopterus*; **138**, *C. latipennis*; **139**, *C. globulicollis*; **140** *C. flavipes*, *C. bourailensis*.

groove defining anterior limit of shallow transverse wrinkles, anterior callosity smooth, slightly convex behind anterior marginal collar; proepisternum extended beyond marginal bead, visible in dorsal view; proepisternum mostly smooth, with irregularities associated with shallow isodiametric microsculpture; prosternal process deeply, narrowly depressed medially before procoxae, narrowly medially depressed ventrally, posterior face with expanded triangular surface ventrally, median ridge invaginated dorsally. Elytra broadly cordate, basal margin sinuously recurved laterad depressed parascutellar striole, basal groove with deep pit at base of fourth stria; humerus broadly extended laterally at bases of striae 5–8, then evenly curved posterad outside anterior series of lateral elytral setae; discal intervals broadly convex, striae deep, all intervals of subequal convexity; parascutellar seta present, situated twice as far from basal margin than from suture, articular socket papillate; dorsal elytral setae absent; lateral elytral setae arranged as (5)6 + (1) + (7)8, the articular sockets papillate; both subapical and apical elytral setae present, their articular sockets subequal; subapical situation shallowly concave, lateral portion of concavity joined to depressed lateral margin in broad curve, medial portion near suture nearly straight; elytral apices conjoined or nearly so, no or little invag-

ination of apical margin at fused suture. Metepisternal dorsal length $0.9\times$ diagonal width; metasternum with deep, circular median fossa at base of metasternal process. Abdomen with apical margin of apical ventrite shallowly concave medially in both males and females; males with one seta each side of apical margin of apical ventrite, females with two setae each side. Legs moderately elongate; metacoxae bisetose; $mt1$ length/tibial length = 0.24 ; $mt4$ length to apex of outer lobe $1.6\times$ median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture on vertex dense transverse mesh; pelage little developed, head capsule, pronotum, and elytra with sparse distribution of exceedingly short microsetae, visible only in lateral view; pro-, meso-, and metasternites, and mediobasal portions of visible abdominal ventrites 2 and 3 with exceedingly short setae, other ventrites and legs glabrous except for macrosetae. Coloration of head capsule and prothorax piceous; elytra dark rufous with silvery iridescent reflection due to microsculpture; pterothoracic ventrites and elytral epipleura rufopiceous, abdominal ventrites rufous; femora dark rufous with piceous cast; tibiae rufobrunneous; tarsi rufoflavous.

Male genitalia ($n = 4$). Male aedeagal median lobe robust, broadly parallel sided over basal $3/4$ of length, dorsoventral breadth at midlength $0.33\times$ distance from tip to

base of closed basal bulb (Figs 134, 135); lobe apex only briefly extended beyond ostial opening, tip rounded (Fig. 134) to subacuminate (Fig. 135); internal sac with large, heavily sclerotized, obtuse ventral tooth, the tooth surrounded by short, heavily sclerotized microtrichia (Fig. 135); sac length 2× breadth.

Female reproductive tract (n = 1). Bursa copulatrix vase-like, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite 2.75 maximum breadth (dissection compressed under cover slip) (as in Fig. 109); bursal walls thin, translucent, luminal surface with thick band of long thick setae surrounding midlength; basal gonocoxite with apical fringe of four to five setae (Fig. 116); apical gonocoxite narrowly subtriangular with narrowly rounded apex and two lateral ensiform setae.

Types. Holotype male (QMB deposited in MNHN): NEW CALEDONIA 11822 / 22°19'Sx166°55'E 480 m / Forêt Nord site 1.rainfor. / 2–3 Dec 2004 pyrethrum / CJ Burwell & GB Monteith // QUEENSLAND / MUSEUM LOAN / Date: July 2005. No. LE 05.24 [green label // HOLOTYPE / *Cyphocoleus* / *cordatus* / J.K. Liebherr 2016 (black-bordered red label).

Paratypes (18 specimens). NEW CALEDONIA: Rivière Bleue, Haute Pourina, 800 m el., pyrethrum trees & logs, 22°06'S, 166°38'E, 22-xi-2000, Monteith (QMB, 4; lot no. 11210), Pourina track, 900 m el., pyrethrum trees & logs, 18-xi-2001, Monteith (QMB, 1; lot no. 8735), L'Houp Geant Trail, 330 m el., litter, rooting, 22°09.5'S, 166°30.8'E 13-iii-2007, Will (EMEC, 1), pyrethrum spray mossy log, 22°09'S, 166°41.2'E, 13-iii-2007, Will (EMEC, 2); Mt. Koghi, 600 m el., leaf litter, 22°10.7'S, 166°30.4'E, 12-iii-2007, Will (EMEC, 1), montane forest, 22°10'S, 166°31'E, 22–24-v-1987, Platnick & Raven (AMNH, 2), 500 m el., pyrethrum trunks & logs, 22°11'S, 166°31'E, 22-xi-2000, Monteith (QMB, 1; lot no. 9931); Forêt Nord, site 1, rainforest, 480 m el., pyrethrum, 22°19'S, 166°55'E, 02–03-xii-2004, Burwell & Monteith (QMB, 5; lot no. 11822).

Etymology. The species epithet *cordatus* – the Latin adjective heart-shaped (Brown 1956) – signifies the cordate elytral shape characterizing both this species and its adelphotaxon, *C. cardiopterus* (Figs 123, 124).

Distribution and habitat. This species is restricted to the southern portion of Grande Terre, allopatrically south of the distribution of its adelphotaxon, *C. cardiopterus* (Fig. 137). Beetles have been collected via pyrethrin spray of mossy logs and tree trunks, as well as within leaf litter.

17. *Cyphocoleus cardiopterus* Chaudoir, 1877

Figures 109, 124, 136, 137

Diagnosis. The diagnosis of *C. cordatus* should be consulted to determine the characters that uniquely circumscribe this species and its adelphotaxon (Fig. 46). *C. cardiopterus* (Fig. 124) can be diagnosed from its sister species (Fig. 123) by the presence of distinctly punctate

elytral striae, the punctures expanding striae breadth to apex of elytra. The two species can also be diagnosed by elytral microsculpture; isodiametric in this species versus transverse-line microsculpture in *C. cordatus*. Standardized body length 6.5–7.2 mm.

Description (n = 5). (The description of *C. cordatus* can serve for this species, with the following exceptions to accompany the diagnostic characters presented above). Lateral elytral setae arranged as 6 + (1) + 7(8), articulatory sockets slightly upraised above cuticular surface, not papillate; elytral disc rufopiceous, without iridescent reflection.

Male genitalia (n = 1). Male aedeagal median lobe robust, broadly parallel sided over basal 2/3 of length, dorsoventral breadth at midlength 0.3× distance from tip to base of closed basal bulb (Fig. 136); lobe apex only briefly extended beyond ostial opening, tip rounded; internal sac with broadly angled though lightly sclerotized area on ventral surface, the remaining sac surface with lightly sclerotized, very short microtrichia; sac length 2× breadth. The broad, lightly sclerotized region on the ventral sac surface corresponds in position to the heavy sclerotized sac tooth observed in males of *C. cordatus*, supporting the homology of these structures. That the structures are not identical is supported by the similar sclerotization of the median lobe, and by the different eye configurations (Figs 123, 124) that also diagnose these species.

Female reproductive tract (n = 1). Bursa copulatrix vase-like, basally stalked, distance from base of gonocoxites to spermathecal basal sclerite 2.75 maximum breadth (dissection compressed under cover slip) (Fig. 109); bursal walls thin, translucent, luminal surface with thick band of long thick setae surrounding midlength; basal gonocoxite with apical fringe of four to five setae (as in Fig. 116); apical gonocoxite narrowly subtriangular with narrowly rounded apex and two lateral ensiform setae.

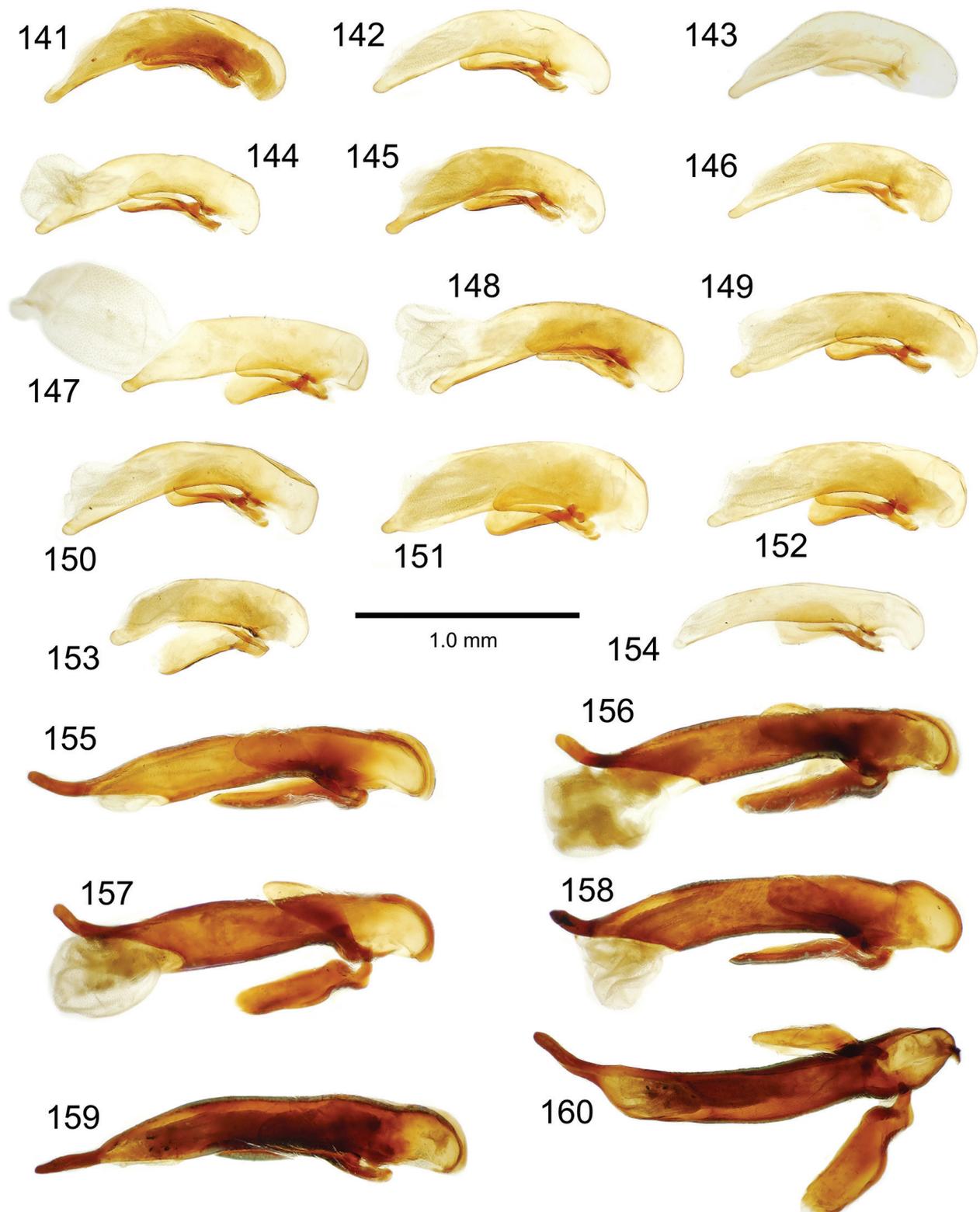
Type. Holotype female (MNHN): Ex Musæo / Chaudoir (red-inked white label with red border) // HOLOTYPE / *Cyphocoleus* / *cardiopterus* / Chaudoir 1877 (black-bordered red label). Holotype status is based on Chaudoir's (1877: 196) statement: "C'est également de M. Sallé que j'ai eu cet insecte." Mt. Mou hereby designated type locality.

Distribution and habitat. This species is known from Mt. Mou and near Mt. Dzumac, occupying a distribution allopatric and to the north of its adelphotaxon, *C. cordatus* (Fig. 137, Suppl. material 3).

18. *Cyphocoleus globulicollis* Fauvel, 1882

Figures 91–98, 110, 117, 125, 139, 141–152

Diagnosis (n = 5). Beetles comprising this species (Fig. 125) exhibit a pronotal disc with distinct transverse wrinkles bordered laterally by deep parasagittal impressions, and a body surface covered with a well-developed pelage of evident, elongate microsetae. These setae are especially visible on the vertex and frons, even occurring between



Figures 141–160. Male aedeagal median lobe and associated parameres of *Cyphocoleus* spp., dextral view: 141–152, *C. globulicollis*; 141, Aoupinié; 142, Me Maoya; 143, Col de Roussettes; 144, internal sac partially everted, Gelima; 145, Col d’Amieu; 146, Mt. Do; 147, internal sac everted, Ningua; 148–150, Mt. Dzumac Rd; 151–152, Mt. Koghi; 153, *C. flavipes*, Yahoué; 154, *C. bourailensis*, Bourail; 155–158, *C. subulatus*; 155, La Crouen; 156, Mt. Rembai; 157, Col d’Amieu; 158, Mt. Koghi; 159–160, *C. iledespinsensis*, Île des Pins; 159, dextral view; 160, ventral view.

the ommatidia on the surface of the slightly convex eyes: each eye with 12–13 ommatidia across the horizontal diameter. The elytra are broadly ovoid, with intervals 3–7 very convex, subcarinate basally. The elytral surface is glossy, with only very shallow transverse sculpticells visible over portions of the surface. Standardized body length 4.8–6.7 mm.

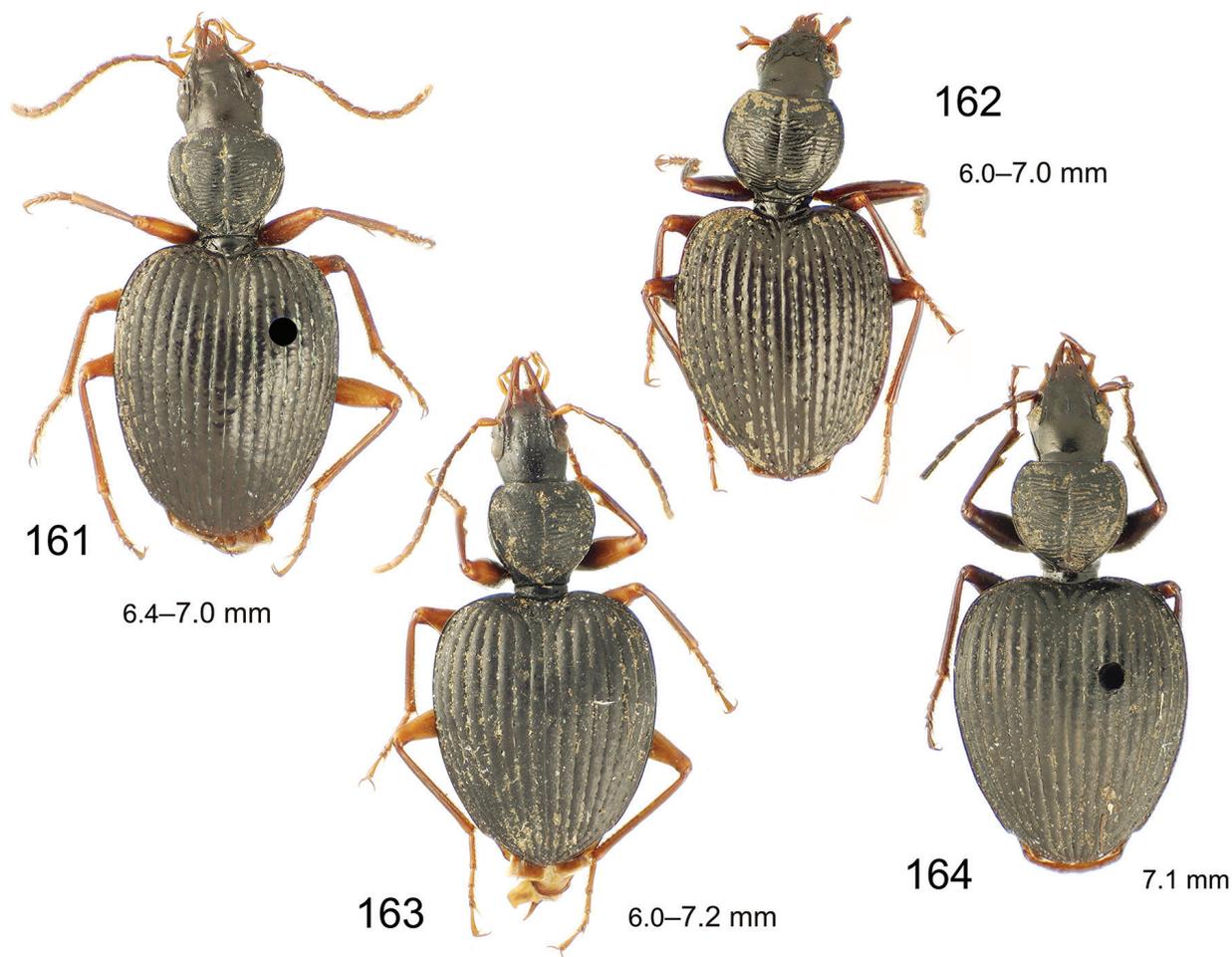
Description. Head capsule parallel-sided, appearing “reduviidoid”, the small, little-convex eyes only slightly extended beyond the genal profile in dorsal view; neck only slightly depressed medially, genae only indistinctly narrowed laterally before pronotal front angles; frons with narrow median longitudinal crest surrounded by flattened, rugose, lateral areas that lie mesad the deep, sinuous frontal grooves; frontoclypeal suture reduced, difficult to trace, frontal grooves apparently extended onto clypeus; mandibles elongate, length $2.1\times$ distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderately elongate, scape length $2.5\times$ maximal breadth; gena setose, subgenal seta present. Pronotum with front angles protruded, angulate, the angle right to slightly acute; lateral marginal carinae extended to base, slightly sinuate just before depressed median base, the marginal bead across base irregularly interrupted by convex basal wrinkles of disc; median longitudinal impression deep and broad, separating discal wrinkles, extended nearly to anterior margin but deepest at juncture with transverse anterior impression; anterior transverse impression a depressed oblique border defining an irregularly surfaced anterior callosity bearing distinct longitudinal wrinkles; proepisternum bulging, distinctly extended beyond marginal bead in dorsal view; proepisternal surface dimpled, the irregularities mostly short vertical wrinkles near dorsal margin with proepipleuron, short longitudinal wrinkles ventrally; prosternum deeply depressed medially from pronotal anterior marginal bead to prosternal process, process broadly, slightly depressed on ventral face, posterior face with depressed ventral triangle and rounded medial ridge above. Elytra broadly ovoid, parascutellar region depressed and inflexed, basal margin sinuously subangulate basad stria 4, then broadly extended and posteriorly curved; sutural intervals elevated and fused into median callosity on middle of disc, intervals 3, 5, and 7, and to a lesser degree intervals 4 and 6, subcarinate, very convex on elevated basal portion of disc immediately posterad apex of parascutellar striole; striae deep, not visibly punctate except in extremely clean specimens where very small elongate punctulae can be seen in the deepest portion of the striae, these elongate depressions separated from each other by twice their length or more; parascutellar seta present, articulatory socket distinctly papillate, very upraised; dorsal elytral setae absent; lateral elytral setae arranged as 6 + 6, the articulatory sockets distinctly papillate; both subapical and apical elytral seta present, the articulatory socket for apical seta much smaller, not papillate; subapical sinuation distinctly developed, lateral portion of concavi-

ty joined to depressed lateral margin in tightly rounded curve; elytral apices rounded, slightly separated by shallow invagination at fused suture. Mesepisternum impunctate; metepisternal dorsal length $1.1\times$ diagonal width; metasternum with deep, circular median fossa at base of metasternal process. Abdomen with apical margin of apical ventrite shallowly concave medially in both males and females; males with one seta each side of apical margin of apical ventrite, females with two setae each side. Legs moderately elongate; metacoxae bisetose; mt1 length/tibial length = 0.24; mt4 length to apex of outer lobe $2.0\times$ median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture on vertex densely transverse, shallow, difficult to trace on the glossy surface; higher areas between pronotal transverse wrinkles glossy, depressions of wrinkles and lateral flanges outside parasagittal groove covered with granulate isodiametric sculpticells, the surface matte; pelage well developed, head capsule, pronotum and elytra with densely distributed, evident microsetae, the setae on each elytral interval arranged in two irregular, longitudinal rows; prosternum with elongate pelage setae, meso- and metasternum largely glabrous, and meso- and metacoxae, and abdominal ventrites 2–3 medially with very short microsetae. Coloration of body dorsum piceous; thoracic sternites and elytral epipleura piceous, abdominal ventrites dark rufous; femora and tibiae rufopiceous, their articulation rufoflavous, tarsi rufobrunneous.

Male genitalia (n = 21). Male aedeagal median lobe variably robust, from gracile (Figs 144, 136) to more robust (Figs 147, 151, 152), dorsoventral breadth at midlength ranging from $0.16\text{--}0.22\times$ distance from tip to base of closed basal bulb (Figs 141–152); lobe apex little extended beyond ostial opening, rounded; internal sac membranous without melanized microtrichia, length $1.5\times$ breadth (Fig. 147). The substantial variation in robustness of the aedeagi for males assigned to *C. globulicollis* is not associated with geography, as a male from Mt. Dzumac Rd. in the southern portion of the range (Fig. 150) varies little from the male from Aoupinié at the northern margin (Fig. 141). Also two males from Mt. Koghi vary substantially in robustness (Figs 151, 152). All of these specimens exhibit the glossy cuticle with well-developed pelage of microsetae characteristic of *C. globulicollis*.

Female reproductive tract (n = 3). Bursa copulatrix columnar, distance from base of r gonocoxites to spermathecal basal sclerite $3\times$ maximum breadth (dissection compressed under cover slip) (Fig. 110); bursal walls thin, translucent, luminal surface smooth except for thin band of very fine setae over part of surface at midlength; basal gonocoxite with apical fringe of five to six setae (Fig. 117); apical gonocoxite broadly triangular with pointed apex and two lateral ensiform setae.

Type. Lectotype female (IRSN) hereby designated: Ile des Pins [and] M^e. Mou (two separate white labels glued to larger pink label) Coll. R. I. Sc. N. B. / Nou-



Figures 161–164. Dorsal habitus photographs of *Cyphocoleus* spp., environmental patina removed: **161**, *C. flavipes* Yahoué; **162**, *C. bourailensis*, Bourail; **163**, *C. subulatus*, Mt. Koghi; **124**, *C. iledespinoisensis*, Île des Pins.

velle Calédonie / ex. coll. Fauvel/ rec. Deplanche // type (pink label with black border) // Coll. et det. A. Fauvel / *Cyphocoleus* 1882 / *globulicollis* Fauv. // LECTOTYPE / *Cyphocoleus* / *globulicollis* / Fauvel 1882 (black-bordered red label).

Nomenclatural note. Fauvel (1882: 250) described this species listing specimens from Mt. Mou and Île des Pins. The lectotype specimen has two labels glued to the pink IRSN museum card (above), one specifying “Île des Pins,” the second “Mt. Mou.” As these two localities are impossible to reconcile geographically on a single specimen, and as numerous other specimens of this species are recorded from Mt. Mou and vicinity, Mt. Mou is designated type locality, with Île des Pins considered to represent an unverified locality for this species.

Distribution and habitat. This species is distributed in the southern two-thirds of Grande Terre, being known from Aoupinié on the north to Montagne des Sources on the south (Fig. 139, Suppl. material 3). Beetles have been found in leaf litter, and via the application of pyrethrin fog to trunks and logs. The well-developed pelage of microsetae is associated with a deep layer of environmental patina developing on these beetles.

19. *Cyphocoleus flavipes* Fauvel, 1882

Figures 111, 118, 140, 153, 161

Diagnosis. Like *C. globulicollis* (Fig. 125) in the transversely wrinkled pronotal disc with deep parasagittal impressions and head without supraorbital setae, but differing through: **1**, the much reduced dorsal pelage, the microsetae on head, pronotum, and elytra exceedingly short, visible only in lateral view; and **2**, elytral striae distinctly punctate, the punctures broadening striae and separated from each other by about their own diameter (Fig. 161). Microsculpture is also better developed in this species, with the vertex of head and the pronotal disc, including elevated portions between transverse wrinkles, covered with an evident transverse mesh. The elytral intervals bear evident isodiametric and slightly transversely stretched sculpticells arranged in an irregular, transverse pattern. Standardized body length 6.4–7.0 mm.

Description (n = 5). Head capsule broad, genae short, neck only slightly constricted; eyes moderately convex but profile not exceeding curvature of gena on posterior portion of eye, ocular ratio 1.47–1.56, 15–16 ommatidia across horizontal diameter of eye; frons with well-de-

veloped median carina that is surrounded by transversely wrinkled median spot; frontal grooves narrow between eyes, sinuously extended anterad to a deep, rounded depression just posterad frontoclypeal suture; mandibles elongate, length $2.2\times$ distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderately elongate, scape length $2.75\times$ maximal breadth; gena setose, subgenal seta present. Pronotum with front angles rounded, only slightly protruded, very obtuse; lateral marginal bead distinctly sinuate before depressed median base that is margined medially by an irregularly depressed bead continuous with the base of the median longitudinal impression; median longitudinal impression deep, broad, extended nearly to anterior marginal bead, with pit-like depression near juncture with anterior transverse impression; anterior transverse impression a shallow, irregular border on the anterior margin of the discal transverse wrinkles, defining a rugose, longitudinally wrinkled anterior callosity; proepisternum bulging, extended beyond marginal bead, visible in dorsal view, smooth; prosternal process convex anterad procoxae, slightly depressed medially on ventral face, broadly convex posteriorly. Elytra broadly cordate, basal margin slightly concave to base of fourth stria, then posteriorly curved across broad humeri; discal intervals moderately convex, all intervals of subequal convexity; elytral striae broad, deep, punctate, the punctures expanding strial breadth to elytral apex; parascutellar seta present, articulatory socket broadly papillate; dorsal elytral setae absent; lateral elytral setae arranged as $6 + 7$, the articulatory sockets papillate; both subapical and apical elytral setae present, the articulatory socket for apical seta smaller, not papillate; subapical situation distinctly concave, lateral portion of concavity joined to depressed lateral margin in tightly rounded curve; elytral apices conjoined, margin not invaginated at fused suture. Mesepisternum impunctate; metepisternal dorsal length subequal to diagonal width; metasternum with broad, shallow median fossa at base of metasternal process. Abdomen with apical margin of apical ventrite shallowly concave medially in both males and females; males with one seta each side of apical margin of apical ventrite, females with two seta each side. Legs moderately elongate; metacoxae bisetose; $mt1$ length/tibial length = 0.23; $mt4$ length to apex of outer lobe $1.9\times$ median tarsomere length, 3–4 ventrolateral setae each side. Pelage little developed, thoracic sternites with only a few very short microsetae, and abdominal ventrites and legs apparently glabrous except for macrosetae. Coloration of body dorsum piceous; prosternum piceous; meso- and metathoracic sternites and pleurites rufopiceous; abdominal ventrites rufous with piceous cast, apical margin of apical ventrite paler, brunnous to flavous; femora dark rufous basally and apically, but with flavous band just beyond midlength; tibiae rufous, matching femoral apex; tarsi brunneous.

Male genitalia ($n = 3$). Male aedeagal median lobe very short, broad, longer left paramere extended more than half distance from lobe tip to base of closed basal bulb (Fig. 153); lobe apex broadly extended beyond ostial opening,

tip broadly rounded, breadth of apical extension $0.6\times$ distance from tip to ostial opening; internal sac membranous without melanized microtrichia (uneverted view).

Female reproductive tract ($n = 2$). Bursa copulatrix columnar, distance from base of gonocoxites to spermathecal basal sclerite $3.5\times$ maximum breadth (dissection compressed under cover slip) (Fig. 111); bursal walls thin, translucent, luminal surface smooth except for thin band of very fine setae at midlength; basal gonocoxite with apical fringe of five to seven setae (Fig. 118); apical gonocoxite subtriangular with pointed apex and two lateral ensiform setae.

Type. Lectotype female (IRSN) hereby designated: Yahoué Août / feuille morts au pied / d'un arbre (white label glued to larger pink label) Coll. R. I. Sc. N. B. / Nouvelle Calédonie / rec. / Savés / ex. coll. Fauvel // type (pink label with black border) // Coll. et det. A. Fauvel / *Cyphocoleus* / *flavipes* n. sp. / R. I. Sc. N. B. 17.479 // LECTOTYPE / *Cyphocoleus* / *flavipes* / Fauvel 1882 (black-bordered red label).

Distribution and habitat. This species is known only from the disjunct localities of Fonwhary in the northern portion of Province Sud, and Yahoué and Nouméa in the south of New Caledonia (Fig. 140, Suppl. material 3). The lone historical collecting record with ecological information includes a beetle collected in dead leaves at the base of a tree.

20. *Cyphocoleus bourailensis* sp. n.

<http://zoobank.org/7C2143D4-CD0B-4045-A06A-B9419D8DB79A>

Figures 119, 140, 154, 162

Diagnosis. This species shares the well-developed dorsal microsculpture, transversely wrinkled pronotum, and punctate elytral striae with *C. flavipes* (Fig. 161). But in beetles of this species, the pronotal transverse wrinkles are continuous across the pronotum, continued from the parasagittal impressions to the marginal bead, and the elytral strial punctures are larger and more circular causing greater lateral expansion of the striae (Fig. 162). The legs are also darker overall, without the pale median band on the femora as observed in *C. flavipes*. Standardized body length 6.0–7.0 mm.

Description ($n = 5$). Head capsule broad, genae short, neck only slightly constricted; eyes moderately convex but profile not exceeding curvature of gena on posterior portion of eye, ocular ratio 1.44–1.61, 16 ommatidia across horizontal diameter of eye; frons with chevron-shaped median elevation surrounded by hemicircular depressions, the broad part of the chevron continued anteriorly as median flat area bordered by frontal grooves; frontal grooves narrow with lateral marginal carina to mesad eyes, sinuously extended anterad to a broad, rounded depression just posterad frontoclypeal suture; mandibles moderately elongate, length $1.9\times$ distance from antennal articulatory socket to anterolateral margin of labrum; antennae of moderate proportions, scape length $2.4\times$ maximal breadth;

gena setose, subgenal seta present. Pronotum with front angles rounded, only slightly protruded, very obtuse; lateral marginal bead slightly sinuate before depressed median base that is margined medially; median longitudinal impression finely incised, interrupted in part by transverse wrinkles, extended nearly to anterior marginal bead; anterior transverse impression a shallow, irregular border on the anterior margin of the discal transverse wrinkles, defining an irregularly, longitudinally wrinkled anterior callosity; proepisternum not extended beyond marginal bead in dorsal view, anteriorly with irregularly, arcuately wrinkled from front to dorsal margin; prosternal process slightly concave anterad procoxae, broadly and deeply depressed medially on ventral face, broadly convex posteriorly. Elytra broadly cordate, basal margin concave from scutellum to third stria, then extended anteriorly across broadly rounded humerus; small pits at the base of the parascutellar and third stria; discal intervals moderately convex, all intervals of subequal convexity; elytral striae finely incised at depth, deep, distinctly punctate, the punctures greatly expanding strial breadth throughout their length; parascutellar seta present, articulatory socket papillate; dorsal elytral setae absent; lateral elytral setae arranged as 6 + 7, the articulatory sockets papillate; both subapical and apical elytral setae present, the articulatory socket for apical seta smaller, not papillate; subapical sinuation distinctly concave laterally, subangularly meeting lateral margin, margin slightly convex medially in dorsal view; elytral apices conjoined, margin not or minutely invaginated at fused suture. Mesepisternum impunctate; metepisternal dorsal length subequal to diagonal width; metasternum with broad, shallow median depression at base of metasternal process. Abdomen with apical margin of apical ventrite shallowly concave medially in both males and females; males with one seta each side of apical margin of apical ventrite, females with two setae each side. Legs moderately elongate; metacoxae bisetose; mt1 length/tibial length = 0.25; mt4 length to apex of outer lobe 1.8× median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture well developed on head, isodiametric sculpticells on median elevation, vertex and neck with more transverse sculpticells defining a regular mesh; elevated portions of pronotal disc with shallow transverse-mesh microsculpture, wrinkled lined with granulate isodiametric sculpticells; elytral intervals with mix of transverse mesh, sculpticell breadth 3× length, and transverse lines loosely joined into a mesh; pelage little developed, head apparently glabrous, prothoracic and elytral disc with extremely short microsetae visible only in lateral view. Coloration of body dorsum piceous; prosternum piceous; meso- and metathoracic sternites, and abdominal ventrites dark rufous, apical margin of apical ventrite paler, brunneous to flavous; femora and tibiae dark rufous to match abdomen, tarsi slightly paler, brunneous.

Male genitalia (n = 3). Male aedeagal median lobe gracile, parallel sided, dorsoventral breadth at midlength 0.18× distance from tip to base of closed basal bulb (Figs 154); lobe apex extended little beyond distal margin of

ostial opening, broadly rounded; internal sac membranous without melanized microtrichia (uneverted view).

Female reproductive tract (n = 1). Bursa copulatrix columnar, distance from base of gonocoxites to spermathecal basal sclerite at least 2× maximum breadth (dissection broken); bursal walls thin, translucent, luminal surface smooth in portion examined; basal gonocoxite with apical fringe of five setae (Fig. 119); apical gonocoxite broadly subtriangular with pointed apex and two lateral ensiform setae.

Types. Holotype female (MNHN): (dissected female, pointed with abdominal ventrites glued onto second point below) Bourail // *Cyphocoleus* revision / measured specimen 1 / J.K. Liebherr 2015 // *Cyphocoleus* / n.sp. latipennis / female 1 Bourail / det. J.K. Liebherr 2015 // genitalia vial // HOLOTYPE / *Cyphocoleus* / bourailensis / J.K. Liebherr 2016 (black-margined red label).

Paratypes (7 specimens found in header-labeled series including holotype and labeled paratype; General Coleoptera Collection, MNHN): Bourail (dissected female remounted as holotype); 6 unlabeled (2 dissected males remounted on point and platen, 1 undissected male on original platen, 1 undissected male remounted on point (Fig. 162), 2 teneral specimens on original platens).

Etymology. The species epithet is based on the type locality Bourail, with the -ensis suffix denoting this locality.

Distribution and habitat. As this species is known only from a single series of specimens with the header specimens labeled Bourail, we know only the general collecting locality: Bourail (Fig. 140).

21. *Cyphocoleus subulatus* sp. n.

<http://zoobank.org/6839CC5D-ED40-4D10-BE41-1717E4A57D8E>

Figures 1, 26, 27, 32, 112, 120, 155–158, 163, 165

Diagnosis. Among species with orbicular pronotum and broadly cordate elytra, this species (Fig. 163) shares the possession of the posterior supraorbital seta with only *C. latipennis* (Fig. 122) and *C. iledespkinsensis* (Fig. 164). Beetles of *C. subulatus* can be diagnosed from the former by presence of evident, transversely stretched isodiametric microsculpture on the head, not the shallow, difficult to trace transverse-line microsculpture of *C. latipennis*. Conversely, this species can be diagnosed from the latter by the pale antennae, and femora with flavous ground color and dark basal and apical bands, versus the uniformly fuscous antennae and femora observed in *C. iledespkinsensis*. The eyes of this species are more convex, ocular ratio 1.54–1.57 compared to those of *C. iledespkinsensis*, where the broad, little convex eyes result in a ratio of 1.49. If a male can be dissected, the differences in the aedeagal median lobes are distinctive (see male genitalia sections for the two species descriptions). Standardized body length 6.0–7.2 mm.

Description (n = 5). Head capsule ovoid, neck moderately constricted with genae moderately convergent behind eyes in dorsal view; eyes moderately convex, outer profile extended beyond curvature of gena behind eye,

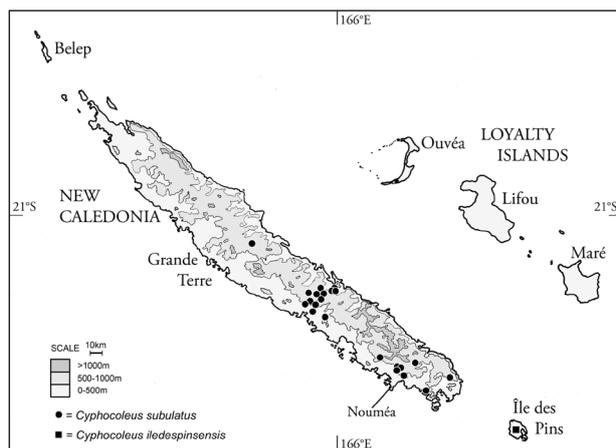


Figure 165. Distribution map of *Cyphocoleus subulatus* and *C. iledespinoisensis*.

16–18 ommatidia across horizontal diameter of eye; frons with well-developed median carina that is surrounded by transversely wrinkled median flat spot; frontal grooves narrow, sinuous anteriorly from between eyes onto clypeus, frontoclypeal suture obsolete; mandibles moderately elongate, length $1.9\times$ distance from antennal articulatory socket to anterolateral margin of labrum; antennae moderately elongate, scape length $2.5\times$ maximal breadth; gena setose, subgenal seta present. Pronotum with front angles tightly rounded, slightly protruded, nearly right; lateral marginal bead distinctly sinuate before depressed median base that is margined medially by narrow bead; median longitudinal impression narrowly and finely incised, extended from just inside basal marginal bead nearly to anterior marginal bead, transverse wrinkles on either side of impression not aligned; anterior transverse impression very shallow, irregularly impressed in association with shallow longitudinal wrinkles on anterior callosity; proepisternum not visible in dorsal view, smooth ventrally, with fine vertical wrinkles along dorsal margin; prosternal process slightly convex medially anterad procoxae, with shallow medial depression ventrally, broadly convex posteriorly. Elytra broadly cordate, basal margin slightly concave to base of fourth stria, then posteriorly curved across broad humeri; discal intervals convex, intervals 3–5 slightly more convex, broader basally; elytral striae deep, narrow, impunctate; parascutellar seta present, articulatory socket papillate; dorsal elytral setae absent; lateral elytral setae arranged as 6 + 7, the articulatory sockets papillate; both subapical and apical elytral setae present, the articulatory socket for apical seta smaller, not papillate; subapical sinuation distinctly concave, lateral portion of concavity joined to depressed lateral margin in broad curve, medial margin convex to suture; elytral apices conjoined, margin not or only slightly invaginated at fused suture. Mesepisternum impunctate; metepisternal dorsal length subequal to diagonal width; metasternum with broad, shallow median fossa at base of metasternal process. Abdomen with apical margin of apical ventrite shallowly concave medially in both males and females;

males with one seta each side of apical margin of apical ventrite, females with two seta each side. Legs moderately elongate; metacoxae bisetose; $mt1$ length/tibial length = 0.25; $mt4$ length to apex of outer lobe $1.6\times$ median tarsomere length, 3–4 ventrolateral setae each side. Microsculpture well developed on pronotal disc, a combination of upraised isodiametric and transverse sculpticells, the surface matte; elytral microsculpture an irregularly present transverse mesh, sculpticell borders shallow, difficult to trace in glossier portions of surface; pelage little developed, head apparently glabrous, pronotal and elytral disc with sparsely distributed, extremely short microsetae, visible only in lateral view; prosternum with only a few very short microsetae, pterothoracic and abdominal ventrites and legs apparently glabrous except for macrosetae. Coloration of body dorsum and venter, including elytral epipleuron, uniformly piceous; legs paler, rufobrunneous with piceous cast except for flavous median femoral band (a minority of specimens lack this pale band and so have concolorous, rufobrunneous leg segments).

Male genitalia ($n = 7$). Male aedeagal median lobe elongate, heavily sclerotized, parallel sided from base to ostial opening; dorsoventral breadth at midlength $0.13\times$ distance from tip to base of closed basal bulb (Figs 155–158); elongate lobe apex extended beyond ostial opening in a broad dorsally directed curve, tip tightly rounded, dorsoventral breadth at midlength of apical extension $0.18\times$ distance from distal margin of ostial opening to tip; ostial opening on ventral surface of median lobe shaft (Fig. 157); sac covered with microtrichia, but without any heavily sclerotized structures, length at least $1.6\times$ breadth.

Female reproductive tract ($n = 3$). Bursa copulatrix columnar, distance from base of gonocoxites to spermathecal basal sclerite $4\times$ maximum breadth (dissection compressed under cover slip) (Fig. 112); bursal walls thin, translucent, luminal surface smooth except for thin band of very fine setae at midlength; basal gonocoxite with apical fringe of five to six setae (Fig. 120); apical gonocoxite broadly subtriangular with pointed apex and two lateral ensiform setae.

Types. Holotype male (ANIC deposited in MNHN): NEW CALEDONIA / Col d'Amieu, 1800–2000 / 12–13 Dec., 1973 / G.B. & S. R. Monteith // HOLOTYPE / *Cyphocoleus* / *subulatus* / J.K. Liebherr 2016 (black-margined red label).

Paratypes (239 specimens). NEW CALEDONIA: Aoupinié, top camp, 850 m el., pyrethrum trees & logs, $21^{\circ}11'S$, $165^{\circ}18'E$, 02–03-xi-2001, Burwell & Monteith (QMB, 2; lot no. 8716); La Crouen, $21^{\circ}33'S$, $165^{\circ}55'E$, 16-iii-1961, Sedlacek (BPBM, 1); Col d'Amieu, 545–610 m el., $21^{\circ}33'S$, $165^{\circ}48'E$, 12–13-xii-1973, G. & S. Monteith (ANIC, 13), 18–19-xii-1973, G. & S. Monteith (ANIC, 2); Col d'Amieu, 6 km NNE, 300 m el., $21^{\circ}33.5'S$, $165^{\circ}51'E$, 13-xi-2000, Bouchard, Burwell & Monteith (QMB, 3; lot no. 9924; QMB, 2; lot no. 9923), pyrethrum trees & logs, 11-xi-2001, Burwell (QMB, 2; lot no. 8678), 390 m el., ex nr. *Mirasmius*, $21^{\circ}33.5'S$, $165^{\circ}45.6'E$, 16-iii-2007, Leschen (EMEC, 1; NZAC, 1); 440 m el., fogging logs,

21°33.5'S, 165°45.3'E, 16-iii-2007, Leschen (NZAC, 1); Mt. Kanala, 21°34'S, 165°56'E, 03-xi-1911, Sarasin & Roux (SMTD, 1); Ciu nr. Mt. Canala, rainforest, 21°34'S, 165°57'E, 01–03-i-1955 Wilson (MCZ, 2); Table Unio road, 500 m el., 21°34'S, 165°46'E, 14-xi-2000, Bouchard, Burwell & Monteith (QMB, 2; lot no. 9946), 800 m el., 21°34'S, 165°46'E, 14-xi-2000, Bouchard, Burwell & Monteith (QMB, 1; lot no. 9934); Canala, 4 km S Mia, 380 m el., 21°34.7'S, 165°58.3'E, river valley, rainforest, Wanat & Ruta (MNHW, 1); Mt. Rembai 650 m el., 21°35'S, 165°51'E, 09-v-1984 Monteith & Cook (QMB, 3), 700–900 m el., rainforest litter, 21°35'S, 165°51'E, 09-v-1984, Monteith & Cook (QMB, 9); Col d'Amieu Forest Station, 400 m el., 21°35'S, 165°50'E, 08–09-v-1984, Monteith & Cook (QMB, 4); Mt. Rembai top junction, 780 m el., hand collecting, rainforest, 21°35'S, 165°51'E, 30-xii-2004, Monteith (QMB, 1; lot no. 12007); Plateau de Dogny trail, 870 m el., litter, 21°37.2'S, 165°52.5'E, 15-iii-2007, Leschen & Will (EMEC, 1); Plateau de Dogny trail, 245 m el., flood debris, 21°37.8'S, 165°52'E, 15-iii-2007, Leschen (NZAC, 1), Will (EMEC, 12); Col d'Amieu litter, 21°37'S, 165°49'E, 06-ix-1990, Raven (QMB, 1); Farino, 5 km N, 400 m el., night collecting, 21°37'S, 165°46'E, 14-xi-2002, Burwell & Monteith (QMB, 2; lot no. 11186); Col d'Amieu, west slope, 470 m el., pyrethrum logs, 21°37'S, 165°49'E, 17-xi-2002, Monteith (QMB, 5; lot no. 11180), hand collecting, 21°37'S, 165°49'E, 25-xi-2003, Monteith (QMB, 1; lot no. 11426), pyrethrum trees & logs, 21°37'S, 165°49'E, 25-xi-2003, Monteith (QMB, 8; lot no. 11427), pyrethrum log w/ epiphytes, 21°37'S, 165°49'E, 27-i-2004, Monteith (QMB, 1; lot no. 11517), pyrethrum log w/o epiphytes, 21°37'S, 165°49'E, 27-xi-2004, Monteith (QMB, 14; lot no. 11516), pyrethrum trees & logs, 21°37'S, 165°49'E, 29-ix-2004 Monteith (QMB, 1; lot no. 11667); Sarraméa, 2 km NE, 280 m el., 21°38'S, 165°52'E, 30-xi-2009, Schuh (NMHW, 2); Table Unio, 700–1000 m el., 21°43'S, 165°47'E, 10-v-1984, Monteith & Cook (QMB, 1); Sarraméa, Plateau de Dogny, Bois mort, 21°46'S, 165°55'E, 23-vi-1971 (MNHN, 5); Mt. Mou, 380 m el., small stream, 22°04'S, 166°20'E, 23-xi-2009, Jäch (NMHW, 1); Col de la Pirogue, 22°05'S, 166°19'E, 23-i-1962, Krauss (BPBM, 2); Rivière Bleue, Kaori Geant, 22°06'S, 166°39'E, 11-xi-2000, Bouchard, Burwell & Monteith (QMB, 9; lot no. 9957), pyrethrum trunks & logs, 22°06'S, 166°39'E, 11-xi-2000, Monteith (QMB, 14; lot no. 9954), 160 m el., pyrethrum trees & logs, 22°06'S, 166°39'E, 19-xi-2002, Monteith (QMB, 2; lot no. 11202); 11–21-xi-2002, Monteith & Wright (QMB, 1; lot no. 11203), Pont Germain 160 m el., 22°06'S, 166°39'E, 11-xi-2000, Bouchard, Burwell & Monteith (QMB, 9; lot no. 9950), L'houp Geant Trail, 350 m el., 22°09'S, 166°41.2'E, 26-xi-2009, Jäch (NMHW, 1); Mt. Koghi, 22°10'S, 166°31'E, 26–30-i-1963, Kuschel (BPBM, 1), 480 m el., 24-x-2008, fogged log, Wanat (MNHW, 4), 500–800 m el., 23–27-x-1967, J. & M. Sedlacek (BPBM, 3), 500–750 m el., m, 25–26-x-1967, J. & M. Sedlacek (BPBM, 2), 610–670 m el., 20–23-xi-1973, G. & S. Monteith (ANIC, 8), 12–13-ii-1977, J. Balogh (RScC, 2), 500 m el., 26-viii-1978, S. & J. Peck (CNC, 2),

400 m el., 26-v-1984, Monteith & Cook (ANIC, 3), 400 m el., 26-v-1984, Monteith & Cook (ANIC, 2), rainforest 500 m el., sifted litter, 23-v-1987, Raven (QMB, 2), pyrethrum trunks & logs, 27-xi-2000, Monteith (QMB, 1; lot no. 9942), 750 m el., pyrethrum trunks & logs, 29-xi-2000, Monteith (QMB, 8; lot no. 9944); 500 m el., hand collecting, 27-i-2002, Monteith (QMB, 1; lot no. 8917), night collecting, 02–03-xi-2002, Burwell, Monteith & Wright (QMB, 2; lot no. 11088), 500 m el., 22-xi-2000, Bouchard, Burwell & Monteith (QMB, 2; lot no. 9932), dung pitfalls, 22-xi-2000, Monteith (QMB, 3; lot no. 9933), pyrethrum trunks & logs, 22-xi-2000, Monteith (QMB, 12; lot no. 9931), 700 m el., 22°10.5'S, 166°30.8'E, 12-iii-2007, Will (EMEC, 1), 550 m el., small streams, 22°10.5'S, 166°30.3'E, 25-xi-2009, Jäch (NMHW, 2), 485 m el., beating fungi & dead branches, 22°10.7'S, 166°30.4'E, 12-iii-2007, Leschen (EMEC, 2; NZAC, 1); Mt. Chapeau de Gendarme [= Mt. Malaoui], forest brook, under rocks, 22°11'S, 166°30'E, 22-x-1944, Herron (MSUC, 5), low pasture, 22-x-1944, Herron (MSUC, 1), under logs, 22-x-1944, Herron (MSUC, 1); Forêt de Thi to Hamma, 700–800 m el., 22°13'S, 166°32'E, 16-vii-1958, Malkin & Rageau (BPBM, 2); Forêt de Thi, 100–300 m el., 22°13'S, 166°32'E, 25-iii-1961, Sedlacek (BPBM, 2), 05-viii-1966, Oesterr. NC Exped. (RScC, 1), 30-x-1967, J. & M. Sedlacek (BPBM, 1), 100–300 m el., 07-ix-1979, Nishida (BPBM, 1), 150 m el., 21-v-1984, Monteith & Cook (ANIC, 2; QMB, 3); Pic du Grand Kaori, site 2, rainforest, 250 m el., hand collecting, 22°17'S, 166°53'E, 22–24-xi-2004, QMB Party (QMB, 2; lot no. 11772), pyrethrum, rainforest, 22–24-xi-2004, Monteith & Burwell (QMB, 1; lot no. 11773); Rivière des Pirogues Headwaters, 350–400 m el., 22°19'S, 166°44'E, 22-v-1984, Monteith & Cook (ANIC, 2; QMB, 4); Forêt Nord, site 2, rainforest, 200 m el., day hand collecting, 22°19'S, 166°55'E, 02–03-xii-2004, QMB Party (QMB, 3; lot no. 11829).

Etymology. The Latin adjectival *subulatus*, awl-shaped or pointed (Brown 1956), forms the basis this species' epithet based on the distinctively pointed male aedeagal median lobe (Figs 155–158).

Distribution and habitat. This species is known from the southern half of Grande Terre, with a northerly outlying locality, based on current specimens, at Aoupinié (Fig. 165). Beetles have been abundantly collected along the Sarraméa-Canala Road, and also in the mountains outside Nouméa. Localities range in elevation from 100–900 m. Collecting situations are quite diverse, including dead branches with fungi, pyrethrin fogged logs with and without epiphytes, the margins of small streams, and within flood debris.

22. *Cyphocoleus iledespkinsensis* sp. n.

<http://zoobank.org/FB56B4A9-0CB0-416E-8751-AC6DC4B08B11>
Figures 159–160, 164, 165

Diagnosis (n = 1). This species can be characterized as a dark, fuscous version of *C. subulatus*, its adelphotax-

on (Fig. 46). Only the less convex eyes (Fig. 164) – ocular ratio 1.49 – and the uniformly dark legs externally diagnose this species from its sister. The male genitalia can be referred to if a male is available for dissection. Standardized body length 7.1 mm. The two species are absolutely allopatric, with this species restricted to Île des Pins and *C. subulatus* distributed across the southern 2/3 of Grande Terre (Fig. 164).

Description. (The description of *C. subulatus* can serve for this species, with the following exceptions to accompany the diagnostic characters presented above). Head capsule narrowly ovoid, neck distinctly constricted with genae moderately convergent behind eyes in dorsal view; 17 ommatidia across horizontal diameter of eye; frons with narrow, elevated median carina that is surrounded by ovoid, transversely wrinkled median flat spot; frontal grooves narrow, sinuous anteriorly from between eyes onto clypeus, separated from supraocular groove by narrow ridge, frontoclypeal suture obsolete laterally, broadly and shallowly evident medially; mandibles moderately elongate, length $2.1\times$ distance from antennal articulatory socket to anterolateral margin of labrum. Pronotum with front angles tightly rounded to angulate, slightly protruded, obtuse; median longitudinal impression narrowly and deeply incised; anterior transverse impression indicated laterally as oblique depressions extended toward front angles, absent medially where anterior wrinkle is extended anteriorly onto anterior callosity, very fine longitudinal irregularities traversing callosity. Elytral subapical sinuation distinctly concave, lateral portion of concavity joined to depressed lateral margin in tightly rounded curve; elytral apices rounded, narrowly separated by shallow invagination at fused suture, Abdomen with apical margin of apical ventrite shallowly concave medially in female, two setae each side of concavity. Microsculpture on elytral intervals much reduced, surface glossy, a transverse mesh or transverse lines present in depressed undulations of surface. Coloration of body dorsum and venter, including elytral epipleuron, uniformly piceous; legs rufopiceous.

Male genitalia ($n = 1$). Male aedeagal median lobe elongate, heavily sclerotized, parallel sided from base to ostial opening; dorsoventral breadth at midlength $0.13\times$ distance from tip to base of closed basal bulb (Figs 159); elongate lobe apex porrect in dextral view (Fig. 159), curved to the right in ventral view (Fig. 160), dorsoventral breadth at midlength of apical extension $0.14\times$ distance from distal margin of ostial opening to tip; ostial opening on left-ventral surface of median lobe shaft (Fig. 160).

Type. Holotype male (MNHN): (dissected, remounted on platen) // I. / des / Pins // *Cyphocoleus* revision / measured specimen 1 / J.K. Liebherr 2015 // genitalia vial // HOLOTYPE / *Cyphocoleus* / iledespinsensis / J.K. Liebherr 2016 (black-bordered red label).

Etymology. The species epithet is based on the type locality Île des Pins; the -ensis suffix denoting this locality.

Distribution and habitat. The lone holotype is labeled only “I. des Pins” leaving the ecological situation and exact locality within which this species may occur

a mystery. To extrapolate from the known habitat of its sister species, *C. subulatus*, we can predict that beetles of this species occupy dead branches with fungi, rotten logs with and without epiphytes, and the margins of small streams.

Discussion

***Cyphocoleus* radiation.** The New Caledonian *Cyphocoleus* fauna exhibits substantial disparity in body forms. However when these forms are aligned using cladistic principles, the disparate body plans become explainable as the sequential evolution of salient characters, with these characters transforming the end products of the lineage in dramatic fashion. The groundplan for *Cyphocoleus* is built on a common ancestor who lacked flight wings, and thus evolved thickened cuticle and the robust body form as observed in *Cyphocoleus lissus* (Fig. 47). The eyes were small relative to the head, with the elongate head capsule not constricted into a neck. The elytra bore dorsal elytral setae in the third interval just as do most Carabidae. Also, the cuticular surface of the elytra bore very fine and short microsetae, these setae arranged in alternating rows down the lengths of the elytral intervals. In the groundplan these setae are so small as to be unapparent except with careful examination laterally across the cuticular surface.

The two successive branching lineages to come from the common ancestor – the clade of five species subtended by *C. heterogenus*, and *C. prolixus* (Fig. 46) – were transformed by the evolution of an elongate prothorax (Figs 48–50, 82–84). This prothoracic elongation is associated with narrowing of the pronotum, this narrowing resulting in distension of the proepisternum outside the dorsal profile of the notum. This tubularization of the prothorax is also a synapomorphy of all Odacanthina subordinate to *Lasiocera*. The head capsule is also constricted basally into a neck just before the juncture with the pronotum. These taxa also exhibited evolutionary increase in body size, with body lengths the largest in the radiation: 9.1–13.1 mm versus 6.7–8.2 mm for *C. lissus*. The bodies of these large beetles are also extremely narrow, with the legs greatly elongate. Thus these beetles are predicted to be exceedingly agile in their habitat, moving above the surface of mosses and other epiphytes on their long legs.

The sister group to the *C. prolixus* lineage (Fig. 46: A) adds several highly unique characters to the narrow, elongate body plan. It is at this point in the phylogeny of *Cyphocoleus* that the elongate pronotum evolves transverse wrinkles (Fig. 85). In *C. monteithi* we see the elytra transformed from narrow, little-convex sheaths to a globose, domed carapace that is substantially broader than the forebody (Fig. 85). It is also in *C. monteithi* and all subsequent descendant taxa that the varnish-like environmental patina is developed. In *C. monteithi* this patina consists of a surface varnish that can be flaked off using a minuten nadeln by the taxonomist interested in observing surface

microsculpture or punctation of the elytral striae. In association with the evolution of this patina, the dorsal elytral setae are absent, though the parascutellar seta, the lateral series of elytral setae in the eighth interval, and the subapical and apical elytral setae remain. But these setae are situated at the top of papillate cuticular projections ensuring that the setal articulatory sockets are raised high above the surrounding elytral surface. Although it is as yet only informed conjecture, the strict phylogenetic association of environmental patina, dorsal setal loss, *and* papillate raising of articulatory sockets for those setae that remain suggests a selective interaction of varnish and setal evolution.

Subsequent to evolution of the environmental patina, the *Cyphocoleus* splits into two disparate clades. The first *C. miricollis* clade includes beetles that are smaller—body lengths 4.8–7.7 mm—but with significantly punctate striae on the elytra (Figs 99, 101–103). These punctate elytral striae are associated with very convex intervals, with carinae developing when odd intervals are more convex than even intervals (Fig. 101). These beetles also exhibit a greatly constricted neck resulting in a pedunculate head. The antennal scapes are broadened to achieve the profile of a cricket bat in *C. mirabilis*, *C. moorei*, and *C. lescheni*. The prothorax of the initially divergent extant taxon, *C. miricollis*, is similar to that of *C. monteithi* in dimensions, possession of deep transverse wrinkles, and prominent front angles (Figs 85, 99). These pronotal front angles, and hind angles as well, transform to prominent processes that may be flat and paddle-like (Fig. 101), or circular and expanded apically (Figs 102, 103) in the subsequently divergent species. It is also in these beetle species that the environmental patina is developed to its utmost condition, here as a means for complete crypsis as the body becomes covered with a dense, anastomosing mat of environmental debris. This debris appears to be wood fibres or fine bits of humus, and it is layered on the cuticle of the beetle's body within and to the height of a pelage comprising club-shaped setae. These setae are not positioned in the standard positions of carabid beetle macrosetae, but are an extreme development of pelage setae present in the *Cyphocoleus* groundplan. In the extreme case of *C. mirabilis*, *C. moorei*, and *C. lescheni*, the anastomosed layer of debris extends from the glossy body surface to a depth equal to the apices of the club-like setae and the anterior and posterior pronotal processes. Setal reduction beyond absence of the dorsal elytral setae also evolved in this clade: **1**, all four species lack the apical elytral seta, though the subapical elytral seta remains; **2**, *C. mirabilis*, *C. moorei*, and *C. lescheni* lack the parascutellar seta. That progressive thickening of the environmental patina was evolutionarily associated with progressive setal loss suggests that the presence of a very thick patina infused with environmental debris reduced the functionality of underlying setae, undercutting any selective advantage to their retention.

The adelphotaxon to the *C. miricollis* clade represents the final iteration of body form in *Cyphocoleus*, i.e. beetles with orbicular pronotum and broadly cordate elytra (Figs

104, 121–125, 161–164). As opposed to *C. miricollis* and associates, the head is not pedunculate, and the pronotum lacks prominent front angles. In *C. fasciatus* however, the pronotum exhibits prominent denticles at the hind angles, homologous (but only under fast character optimization) with the hind pronotal processes observed in *C. mirabilis* and allies. The pronotum of *C. fasciatus* and many taxa in this clade exhibit the usual median longitudinal impression, but also parasagittal impressions that longitudinally divide the surface of each side of the notum: e.g. *C. globulicollis* (Fig. 125). Although the elytral intervals are very convex on these beetles' cordate elytra, all intervals are of subequal development with the presence of elytral carinae. Also, the domed elytra appear completely fused into a carapace, as the elytral apices are tightly conjoined at the suture, without any apical emargination (Fig. 1). This would suggest that the elytra serve to maintain body integrity as the beetle moves between parallel surfaces: e.g. in the subcortical zone of decaying woody plants, between layers of terrestrial humus or debris, or within loose soil.

At 8.1–8.9 mm body length, *Cyphocoleus fasciatus* is the largest-bodied taxon in this clade, evolutionarily retaining a larger body size similar to that of *C. monteithi* (8.5–10.5 mm). All subsequently evolved taxa in the orbicular pronotum + cordate elytra clade measure 4.8–7.5 mm body length, with body sizes among all of the species broadly overlapping. Beetles representing this body form have been collected from a broad variety of ecological situations. This is especially so for the abundantly collected *C. subulatus*, where individuals have been found associated with dead wood, fungi, epiphytes, and stream margins with associated flood debris. Thus this body form is associated not only with the greatest number of known species, but also with the largest variety of microhabitats.

Environmental Patina Function. The development of a varnish-like patina that obscures the deeper features of the cuticle, such as pronotal transverse wrinkles and elytral striae, evolved once within *Cyphocoleus* in the common ancestor of *C. monteithi* and its adelphotaxon (Fig. 46). In its simplest state, the patina covers the cuticular surface, however environmental debris is not trapped within it, at least for the specimens studied for this revision. Beetles exhibiting this type of patina possess pelage setae over the body surface that are short and fine, the setae acuminate apically. In *C. fasciatus*, with longer pelage setae that are acuminate apically, the patina may be much thicker, incorporating environmental material: presumably fine plant fibres or particles of humus. The ultimately developed patina incorporating a thick layer of environmental debris is observed on beetles with elongate club-shaped setae: i.e. *C. mirabilis* and adelphotaxon (Fig. 46). Conversely, in species that exhibit a thin varnish-like patina without debris—e.g., *C. flavipes* and adelphotaxon (Fig. 46)—the dorsal pelage setae are much shorter, often unapparent except under high magnification. Nonetheless, presence of the pelage does not inevitably lead to patina development. The

ventral surfaces of beetles that exhibit dorsal pelage setae long enough to be associated with a debris-infused dorsal patina, exhibit setose ventral surfaces clean of debris. These ventral surfaces with pelage setae are predominantly the thoracic sternites, the metacoxae, and in some species the medial portions of the abdominal ventrites. Why these setose ventral surfaces remain clean of debris is unknown. Must some cuticular wax or other hydrocarbon be present to allow debris to adhere between the pelage setae? Do the beetles groom the ventral surfaces differently to maintain clean surfaces where the legs articulate? Does the manner of beetle locomotion promote development of patina materials on the dorsal surfaces? Regardless of how the patina is emplaced on the dorsal surfaces, its restricted presence there strongly suggests a primary role in crypsis.

Cenozoic History of New Caledonia. There is little controversy whether New Caledonia is associated with the Lord Howe Rise, and that this region of eastern Gondwana progressively rifted from the eastern margin of Australia from Late Cretaceous to Paleocene, 90–61 Ma (McLoughlin 2001, Schellart et al. 2006, Ladiges and Cantrill 2007). However the initial subduction of the Pacific Plate under the margin of Australia at 90 Ma was followed by accelerated Pacific Plate subduction that caused 1200 km of eastward movement of the subduction zone and crustal extension of the Lord Howe Rise (Schellart et al. 2006, fig. 3). This crustal extension resulted in the opening of several backarc basins and subsidence of various crustal blocks including New Caledonia. This geological scenario has been alternately interpreted to allow the continuous existence of subaerial lands coincident or near New Caledonia since Late Cretaceous (Ladiges and Cantrill 2007), or to disallow such subaerial lands until the Eocene, when it is hypothesized that New Caledonia or volcanic islands near it once again became subaerial (Schellart et al. 2006, Grandcolas et al. 2008). Thus there are starkly alternative histories hypothesized for New Caledonia that are relevant for any biogeographic analysis based on endemic New Caledonian taxa: **1**, New Caledonia or an area close to it has persisted subaerially since the Late Cretaceous; or **2**, New Caledonia includes Cretaceous formations however they are irrelevant for biogeographic analysis because the main island, Grand Terre, was submerged prior to 37 Ma.

The biogeographic pattern exhibited by Homethina is consistent with amphiantarctic vicariance of Gondwana. Initial isolation of the Australian and South American mammal faunas is hypothesized to have started 64 Ma, with vicariance completed by 50 Ma (Woodburne and Case 1996); marsupials thus exhibiting a Gondwanan vicariant biogeographic pattern (Sanmartín and Ronquist 2004). Geological isolation of Australia and South America formerly adjoining Antarctica was fully achieved 35–30 Ma through nearly coincident opening of the Australo-Antarctic Gulf and Drake Passage (McLoughlin 2001, Lawver and Gahagan 2003, Livermore et al. 2005). Thus the age of the common ancestor of

Homethes + Aeolodermus and (*(Quammenis + Stenocheila) + Diplacanthogaster*) is constrained to be no younger than 30–35 Ma (Fig. 166). Given that *Cyphocoleus* is the sister group to these five genera, the common ancestor of Homethina must be dated to before 30–35 Ma as well. Ober and Heider (2010) estimated the age of the common ancestor of tribes Peleciini and Odacanthini to be 100–105 Ma using the r8s method and sequence data from 28s rDNA plus the wingless gene. Their taxon sampling of Odacanthini included species of *Actenonyx*, *Pentagonica*, *Scopodes*, plus species in six genera of Odacanthina: three of the four odacanthine subtribes recognized here. They estimated the time of divergence of Pentagonicina and Odacanthina at 65 Ma. Integrating the currently proposed subtribal relationships (Figs 45, 46) with a date of origin of 100 Ma for the tribe and 65 Ma for the ancestor of Pentagonicina + Odacanthina supports the origin of Homethina between the time of origin of the tribe, 100 Ma, and the divergence of Pentagonicina and Odacanthina, 65 Ma. Thus under this interpretation, the diversification of the Cretaceous-aged Odacanthini was temporally concordant with Gondwanan vicariance, and therefore occupation of New Caledonia by *Cyphocoleus* supports Grand Terre's consistent presence as a subaerial entity throughout the Cenozoic. This interpretation also supports the occupation of a consistently subaerial New Zealand by *Actenonyx* over that same Era, as *Actenonyx* would have been present on New Zealand long before the Oligocene drowning event proposed for 34–23 Ma (Campbell and Hutching 2007).

What if we were to accept the geological scenario whereby New Caledonia subsided completely during crustal extension of the Australian Plate, and only re-emerged 37 Ma? This could be rectified with the molecular dating estimates by hypothesizing the extinction of lineages related to *Cyphocoleus*, these extinct lineages “marking time” at “an undisclosed location” during the interval between the Cretaceous origin of Odacanthini and an Eocene reemergence of New Caledonia (Fig. 166, dashed line denoting post-submergence dispersal). By this reasoning *Cyphocoleus* could represent a retenant clade (Sharma and Wheeler 2013); i.e. a clade that experienced a substantial extinction bottleneck and radiated recently. Based on Sharma and Wheeler's (2013) criteria, however, *Cyphocoleus* does not present the attributes of a retenant clade, as it is a speciose and anatomically disparate radiation, and many of the taxa are known only from single localities (Figs 77, 79, 80, 81, 140, 165). Nonetheless, if one assumes post-emergence colonization over water from Australia less than 37 Ma as the basis for the New Caledonian *Cyphocoleus* radiation, it would require the window of opportunity for dispersal to last only 2–5 Ma, being constricted at an upper bound by amphiantarctic vicariance across the Australo-Antarctic Gulf, 35–32 Ma. Given the phylogeny of Odacanthini, a similar temporal eclipse and subsequent dispersal event must also be implicated as the basis for the New Zealand endemic *Actenonyx*. In this instance,

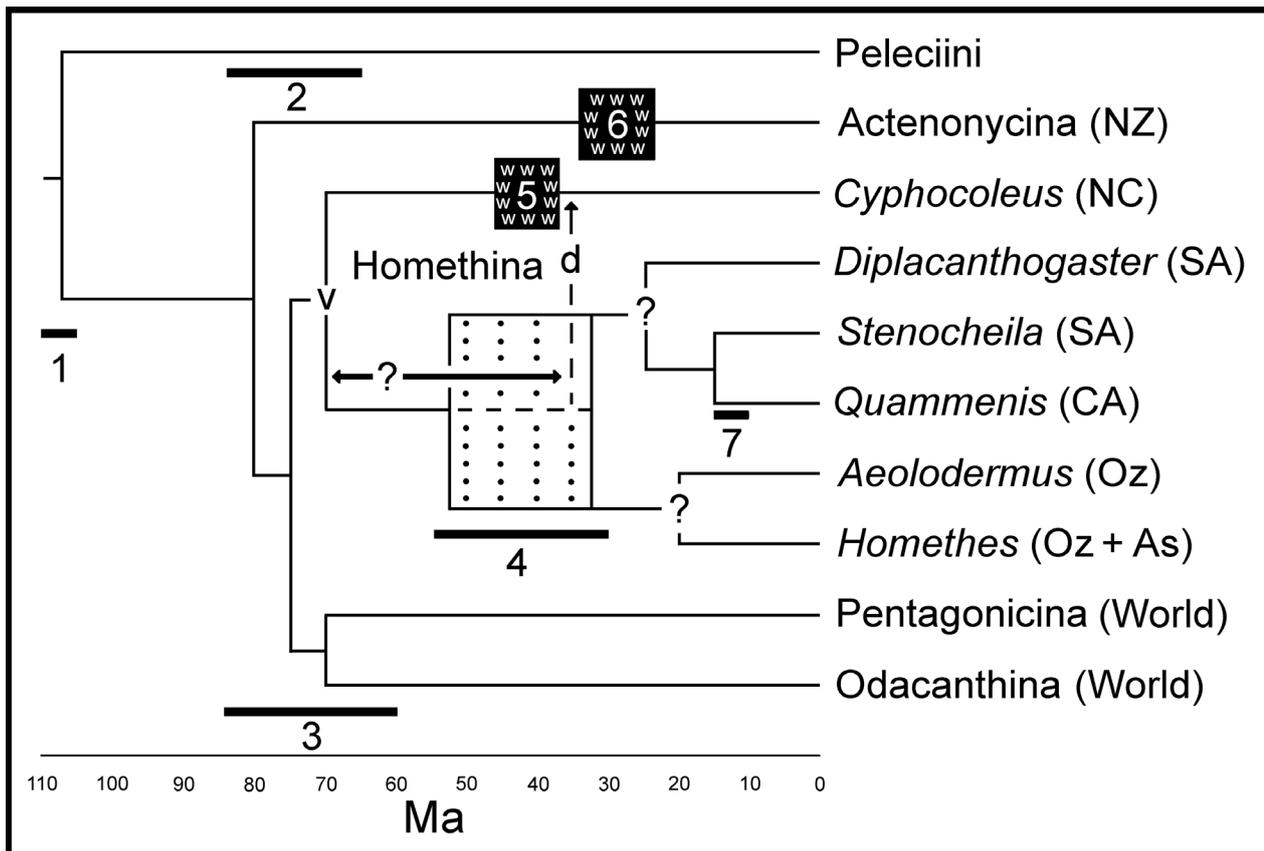


Figure 166. Diversification history of odacanthine subtribes and generic-level taxa within Homethina placed in temporal context defined by major geological events and molecular dating estimates (Ober and Heider 2010). Major events and dating estimates constraining historical relationships of the represented taxa include: **1**, 100–105 Ma, estimated age of origin of Odacanthini relative to its proposed adelphotaxon Peleciini (Ober and Maddison 2008, Ober and Heider 2010); **2**, 84–65 Ma, estimated divergence times of lineages within Odacanthini, represented in this study by Actenonycina, Pentagonicina, and Odacanthina (Ober and Heider 2010); **3**, 84–61 Ma, rifting of Zealandia, including New Caledonia and New Zealand, from Australia (McLoughlin 2001, Ladiges and Cantrell 2007); **4**, 50–30 Ma, extended rifting and increased isolation of Australia and South America from Antarctica due to opening of the Tasman Sea at 50 Ma (Woodburne and Case 1996, Sanmartín and Ronquist 2004), development of the Australo-Antarctic Gulf at 35–32 Ma (McLoughlin 2001, Lawver and Gahagan 2003), and opening of Drake Passage at 34–30 Ma (Livermore et al. 2005); **5**, 46–37 Ma, hypothesized submergence of New Caledonia (Grandcolas et al. 2008); **6**, 34–23 Ma, hypothesized Oligocene drowning of New Zealand (Campbell and Hutching 2007); **7**, 15–10 Ma, closing of Panamanian Isthmus establishing subaerial contact between South and Central America (Montes et al. 2015). Time of divergence of *Cyphocoleus* unconstrained due to lack of molecular-dating data. Under vicariance hypothesis (v), the ancestor of *Cyphocoleus* was emplaced on Zealandia in Late Cretaceous (event **3**). Under dispersal scenario (d with dashed line), *Cyphocoleus* dispersal to New Caledonia is constrained at the lower bound by reemergence of Grande Terre after putative Oligocene submergence (event **5**), and at upper bound by amphiantarctic vicariance at Austral-Antarctic Gulf that isolated Antarctica from Australia (event **4**).

one would have to find a land mass that the New Zealand precinctive *Actenonyx* could occupy until after the proposed 34–23 Ma Oligocene drowning of New Zealand (Campbell and Hutching 2007), as the common ancestor of the Australian and South American Homethina certainly evolved more than 30 Ma, and *Actenonyx* is hypothesized to have evolved long before that as the product of the first Cretaceous-aged divergence event within Odacanthini. Having ancestors of both *Actenonyx* and *Cyphocoleus* colonize their respective present-day microcontinental ranges during different spans long after the Cretaceous origin of the tribe Odacanthini beggars credulity. Nevertheless, arguing from the various attri-

butes of the extant New Caledonian *Cyphocoleus* radiation—flightlessness, morphological disparity, geographic endemism—may not satisfy all biogeographers regarding the contribution of *Cyphocoleus* to knowledge of New Caledonia’s Cenozoic biogeographic history. Yet based on this revision, and the attendant phylogenetic context proposed for *Cyphocoleus*, two very explicit, alternative biogeographic explanations become available. The more general and less assumption-laden vicariance-based hypothesis is preferable under a logical parsimony framework. Additional investigation of the date of the origin for the *Cyphocoleus* radiation will test this currently preferred general hypothesis.

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Supplementary material 1

Checklist of taxa represented in cladistic analysis of Odacanthini

Authors: James K. Liebherr

Data type: Taxonomic checklist

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Supplementary material 2

NONA format data file for cladistic analysis of Odacanthini

Authors: James K. Liebherr

Data type: Phylogenetic analysis data file

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Supplementary material 3

Specimen records for previously described *Cyphocoleus* spp.

Authors: James K. Liebherr

Data type: Species distributions and specimen repositories

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