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Taxonomic review of Australian *Mecyclothorax* Sharp (Coleoptera, Carabidae, Moriomorphini) with special emphasis on the *M. lophoides* (Chaudoir) species complex

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Abstract

The Australian fauna of *Mecyclothorax* Sharp (Coleoptera: Carabidae: Moriomorphini) is reviewed, with special focus on species assigned to the monophyletic subgenus *Eucyclothorax* Liebherr: *M. isolatus*, **sp. n.** from Western Australia, *M. moorei* Baehr, *M. punctatus* (Sloane), *M. curtus* (Sloane), *M. blackburni* (Sloane); *M. eyrensis* (Blackburn); *M. peryphoides* (Blackburn); *M. darlingtoni*, **sp. n.** from Queensland; *M. jameswalkeri*, **sp. n.** from Western Australia; *M. lophoides* (Chaudoir); and *M. cordicollis* (Sloane). The last six species listed above–the *M. lophoides* species complex–have been the source of long-term confusion for taxonomists, with male genitalic characters providing trouble-free species circumscription. One new subspecies, *M. lewisensis estriatus*, **subsp. n.** from Queensland is added to the seven previously described taxa of the monophyletic subgenus *Qecyclothorax* Liebherr. The balance of the fauna consists of four species in the subgenus *Mecyclothorax*: **1** and **2**, the sister-species pair *M. lateralis* (Castelnau) and *M. minutus* (Castelnau); **3**, *M. ambiguus* (Erichson); and **4**, *M. punctipennis* (MacLeay). *Mecyclothorax fortis* (Blackburn), **syn. n.**, is newly synonymized with *M. minutus*. *Mecyclothorax ovalis* Sloane is recombined as *Neonomius ovalis* (Sloane), **comb. n.**, and a neotype is designated to replace the destroyed holotype. Phylogenetic relationships for the Australian *Mecyclothorax* are proposed based on information from 68 terminal taxa and 139 morphological characters. The biogeographic history of Australian *Mecyclothorax* is deduced based the sister-group relationship between *Mecyclothorax* and the *Amblytelus*-related genera, with both groups hypothesized to have originated during the late Eocene. Diversification within *Mecyclothorax* has occurred since then in montane rainforests of tropical Queensland, temperate forest biomes of the southwest and southeast, and in grasslands and riparian habitats adjacent and inland from those forests. Several species presently occupy interior desert regions, though no sister species mutually occupy such climatically harsh habitats. The *M. lophoides* species complex exhibits profound male genitalic diversification within the context of conserved external anatomy. This disparity is investigated with regard to the functional interaction of the male internal sac flagellum and female spermathecal duct. Though limited association of flagellar and spermathecal duct configurations can be documented, several factors complicate proposing a general evolutionary mechanism for the observed data. These include: **1**, the occurrence of derived, elongate spermathecal ducts in three species, two of which exhibit very long male flagella, whereas males of the third exhibit a very short flagellum; and **2**, a highly derived and exaggerated male flagellar configuration shared across a sister-species pair even though the two species can be robustly diagnosed using external anatomical characters, other significant genitalic differences involving male parameral setation, and biogeographic allopatry associated with differential occupation of desert versus forest biomes.

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Introduction

Although relatively few in number of species, the Australian *Mecyclothorax* have proved confusing throughout much of their taxonomic history. This is partly due to the description of species and associated deposition of type specimens by taxonomists working half a world away from Australia. Yet, the confusion has been also caused in part by the broad geographic distribution of the taxon across Australasia, Java, Borneo and Polynesia, with constituent radiations in islands and island continents distantly separated from each other. *Mecyclothorax* taxonomy started in mid-19th century Berlin with Erichson's (1842) study of the insect fauna of Vandiemensland, a treatise predominantly focusing on Coleoptera, but also treating some Orthoptera *s.l.*, Hymenoptera, Diptera, and Hemiptera. Among Carabidae, Erichson perceived and described as new the distinctive genera *Lestignathus*, *Amblytelus* and *Scopodes*, but he consigned one apparently unremarkable new species from Melbourne–*Anchomenus ambiguus* Erichson–to a Bonelli (1810) genus now recognized as a monophyletic, holarctically restricted taxon of tribe Platynini (Liebherr 1991, 1994a, Schmidt 2014). Throughout much of the mid-19th century, species were described in Bonelli's *Anchomenus* that are now known to be members of a broad array of phylogenetically distant, morphologically disparate, and geographically disjunct platynine taxa including, non-exhaustively: **1**, Neotropical *Glyptolenus* Bates (e.g. *Anchomenus chalybaeus* Dejean, 1831; Whitehead 1974); **2**, Hawaiian *Blackburnia* Sharp (e.g. *Anchomenus corruscus* Erichson, 1834; Liebherr and Zimmerman 2000); **3**, Asia-Pacific *Metacolpodes* Jeannel (e.g. *Anchomenus laetus* Erichson, 1834; Liebherr 2005); **4**, South American *Incagonum* Liebherr (e.g. *Anchomenus aeneum* Reiche, 1843; Liebherr 1994b, Moret 2005); **5** New Zealand *Ctenognathus* Fairmaire (e.g. *Anchomenus colensonis* White, 1846; Larochelle and Larivière 2007); **6**, Australasian *Notagonum* Darlington (e.g. *Anchomenus lafertei* Montrouzier, 1860; Darlington 1952); **7**, Mediterranean and Macaronesian *Paranchus* Lindroth (e.g. *Anchomenus nicholsii* Wollaston, 1864; Machado 1992); **8**, Mexican *Elliptoleus* Bates (e.g. *Anchomenus vixstriatus* Bates, 1878; Bates 1882); and **9**, Holarctic *Agonum* Bonelli (e.g. *Anchomenus* (*Agonum*) *charillus* Bates, 1883; Habu 1978). Consistent with the use of *Anchomenus* as a catch-all genus, Chaudoir (1854) described the second *Mecyclothorax* from Australia as *Anchomenus lophoides*. As with Erichson, this description was done remotely, in the Ukraine (Ball and Erwin 1983), based on specimens from Melbourne sent to Chaudoir by the English entomologist André Melly. Then in 1867 Australia received its first home-grown descriptions for species of *Mecyclothorax*: *Phorticosomus lateralis* Castelnau and *P. minutus* Castelnau. Castelnau's confusion concerning placement of these species was evident in that he described the two species destined for future membership in *Mecyclothorax* within an assemblage of five new species he assigned to Schaum's (1863) genus *Phorticosomus*; these also including one future *Simodontus*, as well as two currently recognized *Phorticosomus*. Castelnau's specimens of the two future *Mecyclothorax* species were deposited in the Museo Civico in Genoa after his death in 1880, not with the balance of his Australian collections deposited in Museums Victoria, Melbourne (Evenhuis 2012). It was not until Barry Moore visited Genoa in 1968 that these specimens were compared to those of other Australian taxa.

When William MacLeay (1871) described *Cyclothorax punctipennis* from Gayndah, N.S.W., Australia witnessed the beginning of a local network of taxonomists that would describe the bulk of Australian *Mecyclothorax*. However, at that early date MacLeay admitted his confusion regarding placement of his species, writing: "I am not at all sure of the position of this genus, the dilitation of the tibiae in the male is so slight as to be in most instances unnoticeable (MacLeay 1871: 105)." His placing the species after *Acupalpus* and before *Abacetus* suggests an ambiguous placement within generalized Harpalinae. The *Cyclothorax* name then traveled to the middle of the Pacific, at the eastern end of the generic distributional range, where Thomas Blackburn recognized the similarity between Hawaiian species he was collecting and MacLeay's species. Blackburn (1878a, 1878b, 1879, 1881, 1882) described 21 species that he placed in *Cyclothorax*, forever moving the center of diversity of the genus to Hawaii. Blackburn was able to continue his study of the genus when he was assigned in 1882 as rector to a church in Port Lincoln, South Australia (Lea 1912). During the remainder of his life he described several thousands of Australian beetle species, including four future *Mecyclothorax*: understandably including two junior synonyms of Castelnau names, the types for those specimens unavailable to him as they had sailed for Europe.

The closing of the 19th century saw Thomas G. Sloane take up description of *Mecyclothorax* from specimens he collected or received from colleagues (Sloane 1895, 1898, 1900). With Sloane the confusion concerning *Cyclothorax* began to dissipate: "I believe Dr. Sharp has placed *Cyclothorax* in the tribe Feronini, but it is evident this is not its true position, which cannot be far from *Amblytelus* ... (Sloane 1895: 447)." Nonetheless on that same page he also wrote: "A species of *Cyclothorax* is found everywhere in south-eastern Australia ... I believe it to be identical with *C. ambiguus*, Erichs., and that *C. lophoides*, Chaud., is also founded on it. I do not feel that *C. punctipennis*, Macl., is a distinct species from *C. ambiguus*, though it is quite likely that it is (Sloane 1895: 447)." Sloane was also the first taxonomist to look carefully at more than the dorsal surface of card-mounted specimens. Of *M.* (*Eucyclothorax*) *punctatus*, treated below, he wrote: "The episterna of the metasternum are punctate, and probably more of the undersurface as well, but not having detached the specimen before me from the card to which it is gummed, the episterna only have been seen (Sloane 1898: 473)." Of the last *Mecyclothorax* he described–*M. cordicollis* (Sloane) (Sloane 1900)–he wrote

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of his confusion, but in fact he had deduced the specific differences between *M. cordicollis* and *M. peryphoides*, confirmed by results of this study completed 118 years later: "This is the species I formerly regarded as *C. peryphoides*, Blkb.* but Mr. Blackburn has informed me that it differs from that species. The only difference the description of *C. peryphoides* suggests to me is the darker colour of the legs in that species, a character that seems of little value, but probably *C. peryphoides* has the prothorax more strongly sinuate near the base, the basal angles more marked, and perhaps a coarser puncturation on the basal area" (Fig. 2H versus 2I). Sloane (1903) was also the first to point out homonymy of *Cyclothorax* MacLeay, 1871 with *Cyclothorax* Frauenfeld, 1868, solving that issue by nomenclaturally uniting *Cyclothorax* MacLeay with *Mecyclothorax* Sharp, 1903.

The beginning of the modern era of Australian *Mecyclothorax* taxonomic research is synonymous with Moore's (1984) type examinations and associated male dissections, which clearly defined the species boundaries between the two most commonly encountered Australian species, *M. ambiguus* and *M. punctipennis*. Moore was able to examine the types of the long-mysterious *Anchomenus lophoides*, available at the Paris Museum after more than a century of seclusion in the Chaudoir and Oberthür private collections, and he established its independence from *M. ambiguus* while proposing its close relationships to *M. cordicollis*, *M. peryphoides*, and *M. eyrensis*. Moore also described the first two Queensland species of subgenus *Qecyclothorax* Liebherr, which laid the foundation for Baehr's (2003) comprehensive revision.

Material and methods

This taxonomic review is based on 3273 specimens of Australian *Mecyclothorax* held in 21 institutional or personal collections (codens used in species treatments): American Museum of Natural History, New York (AMNH); Australian Museum, Sydney (AMS); Australian National Insect Collection, Canberra (ANIC); The Natural History Museum, London (BMNH); Bernice P. Bishop Museum, Honolulu (BPBM); California Academy of Sciences, San Francisco (CAS); Carnegie Museum of Natural History, Pittsburgh (CMNH); Cornell University Insect Collection, Ithaca (CUIC); Essig Museum of Entomology, University of California, Berkeley (EMEC); Field Museum of Natural History, Chicago (FMNH); Martin Baehr Collection, Munich (MBC); Museo Civico Storia Naturale, Genova (MCG); Museo Civico Storia Naturale, Milano (MCM); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museum national d'Histoire naturelle, Paris (MNHN); Museums Victoria, Melbourne (MVM); Queensland Museum, Brisbane (QMB); South Australian Museum, Adelaide (SAMA); University of Alberta Strickland Museum, Edmonton, CA (UASM); Western Australian Museum, Welshpool (WAM); Zoological Museum, University of Copenhagen (ZMUC).

Laboratory methods follow Liebherr (2015, 2018). The qualitative configuration of various features of the beetles was quantified using a variety of ratios. Three ratios were used to assist in description of the eyes: **1**, the ocular ratio, or the maximum head width across the eyes divided by the minimum breadth of the frons between the eyes (MHW/mFW); **2**, ocular lobe ratio, or the length of the compound eye measured from above divided by length of the protruded ocular lobe measured from the anterior margin of the eye to the groove at the ocular lobe-genal juncture (EyL/OLL); and **3**, eye convexity, or eye length divided by the maximal depth of the eye measured with the internal margin vertical in the field of view (EyL/EyD). Pronotal configuration was assessed using three ratios: **1**, maximal pronotal width divided by median pronotal length (MPW/PL); **2**, relative basal constriction of the pronotum, or the maximal pronotal width divided by pronotal breadth across the hind angles (MPW/BPW); and **3**, relative apical and basal pronotal widths (APW/BPW). The elytral configuration was described using the ratio MEW/EL, or maximum elytral width (usually situated near midlength) divided by elytral length, measured from the basal margin of the flattened posterior surface of the scutellum to the apex of the longer elytron (if elytral lengths differ slightly side to side). Presence or absence of macrosetae at specific positions on the bodies of *Mecyclothorax* beetles prove diagnostic for several taxa within the Australian fauna. Information regarding setal configuration is summarized using a setal formula comprising presence (+) or absence (–) of: **1**, the anterior and posterior supraorbital setae; **2**, the lateral and basal pronotal setae; **3**, the parascutellar seta; **4**, the dorsal elytral setal number (in these taxa 1-2); **5**, the subapical and apical elytral setae, the former situated in stria 7 apicad the lateral elytral setae of interval 8, the latter between the apex of stria 2 and the elytral apex. For ease of visualization, the various somites or structures–head, pronotum, elytra–are demarked by a slash: "/." Thus, ++/++/+2++ is the setal formula for presence of both supraorbital setae, both pronotal setae, the parascutellar seta, two dorsal elytral setae, and both the subapical and apical elytral setae. Standardized body length is used to assess body size, and consists of the sum of three measurements: **1**, head length measured as the distance from the middle of the labrum to the cervical carina at the posterior margin of the vertex; **2**, median pronotal length; and **3**, elytral length measured from the basal margin of the flattened posterior surface of the scutellum to the apex of the longer elytron (if elytral lengths differ slightly side to side).

Sclerites associated with the male aedeagal sac flagellum proved essential for species diagnosis and circumscription within the *M. lophoides* assemblage of cryptic species. Dissected aedeagi were temporarily slide-mounted in glycerin, and viewed under phase contrast microscopy using an Olympus BH2 scope. At least one male specimen from each collecting series was dissected, with the cleared aedeagal median lobe assessed for the configuration of the flagellum and the flagellar sheath. These

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two structures occur at the apex of the internal sac, with the flagellum near the gonopore, and the flagellar sheath situated to the right of the gonopore (Figs 7H, 14B, 14F, 14H). A broad sclerotized plate is situated to the left of the gonopore and flagellum; herein called the dorsal plate. The parameral configuration varies among the species treated, both in shape and setation (Figs 8, 13, 16). For diagnosis of the adelphotaxa *M. eyrensis* and *M. peryphoides*, the numbers of setae along the ventral margin of the right, or ventral paramere were assessed in 10 individuals of the former and 15 of the latter. The distributions of setal numbers were compared using the Wilcoxon rank-sum test for individual samples with unequal sample sizes (Snedecor and Cochran 1980).

Other structures of the male genitalia and female reproductive tract and gonocoxae are presented as in Liebherr (2018), with figured abbreviations presented in Table 1. Terminology of the female characters follows Liebherr and Will (1998). For presentation of male genitalic characters, and female reproductive tract characters, the numbers of individuals dissected, examined, and photographed are provided parenthetically (n = X) at the start of those sections. The numbers of individuals measured to calculate ratios of various external structures are presented at the beginning of each diagnosis. Specimens that were chosen for measurement included both the largest and smallest individuals, males and females, and representatives from multiple localities. Type label data are presented verbatim, including typeface.

Nomenclatural actions conform to The Code (I.C.Z.N. 1999). In order to clarify the ambiguous status of allotypes under the current version 4 of The Code (Santiago-Blay et al. 2008), the allotype for *M. darlingtoni*, sp. n. is designated as an allotypic paratype.

Cladistic methods are identical to those utilized in the earlier associated analysis of New Caledonian *Mecyclothorax* (Liebherr 2018), augmented with the following additional data. Two additional characters are reported, with these characters added to the end of the prior character matrix so as not to disturb the character numbering scheme presented in Liebherr (2018, pp. 6–11, Supplementary Material 1). These characters include:

137. Clypeus with: two setae, one each side (0); with four setae, two each side, the medial pair smaller (1).

138. Spermathecal duct: of equal width/sclerotization from base to spermatheca (0); sclerotized and broader basally, a narrow membrane at midlength (1, Fig. 9A–B).

Additional taxon-related information is also presented below, including the addition of the newly described species *M. isolatus* and *M. jameswalkeri*, the addition of male genitalic characters for *M. curtus* (characters 92–113) and both male genitalic and female reproductive tract characters for *M. punctatus* (characters 92–136). The previously mentioned *M.* sp. n. D (Liebherr 2018) is newly described as *M. darlingtoni*. Thus the present taxon-character matrix includes 68 terminals representing 67 species and 139 characters. The analysis is rooted at *Neonomius laevicollis* Sloane, a member of the subtribe Moriomorphina, and thus outside the ingroup representatives of this analysis which are all members of the subtribe Amblytelina (Liebherr 2018). Within Amblytelina, the genera related to *Amblytelus* Erichson comprise the primary outgroup to the various representatives of *Mecyclothorax* (Liebherr 2018, table 1).

Table 1. Key to abbreviations for morphological structures labelled in illustrations of male genitalia, female reproductive tracts, and female gonocoxae.

Abbreviation	Structure
af	apical face, male aedeagal median lobe
afs	apical fringe setae, basal gonocoxite
ams	apicomedial seta, basal gonocoxite
ans	apical nematiform setae, apical gonocoxite
bc	female bursa copulatrix
co	female common oviduct
des	dorsal ensiform seta, apical gonocoxite
dp	dorsal or left plate, male internal sac
fl	flagellum, male aedeagal internal sac
fp	flagellar plate, male aedeagal internal sac
fs	flagellar sheath, male aedeagal internal sac
gc1	basal gonocoxite, female
gc2	apical gonocoxite, female
gp	gonopore, male aedeagal internal sac
hg	hindgut
hs	helminthoid sclerite, female bursa
les	lateral ensiform setae, apical gonocoxite
ovo	ostial ventroapical operculum, male
r	ramus, female basal gonocoxite
sc	sagittal crest, male aedeagus
sd	spermathecal duct, female
sg	spermathecal gland, female
sp	spermatheca, female
ssd	sclerotized spermathecal duct, female
vss	ventrobasal spicular sclerite, male sac

Cladistic data were compiled using WinClada (Nixon 2002) with the search for most-parsimonious cladograms using the parsimony ratchet (Nixon 1999) with tree searches run using NONA (Goloboff 1999). Tree searches were conducted using standard WinClada defaults for 1000 iterations of the ratchet. Once the shortest trees were found using NONA and the ratchet, the results were checked using TNT (Goloboff and Catalano 2016). The TNT analysis used sectorial search, the ratchet, tree fusing, with the minimum tree cache set at 50 trees.

Results

Cladistic analysis

The NONA/WinClada analysis found 2 shortest trees of 1232 steps in 1000 iterations of the ratchet (C.I. = 0.21, R.I. = 0.67), with the strict consensus collapsing 1 node and resulting in a consensus tree length of 1235 steps (Fig. 1A). The TNT search for 1000 minimum-length trees, using sectorial search and the ratchet, also resulted in 2 trees of 1232-step length (3,572,933,738 rearrange-

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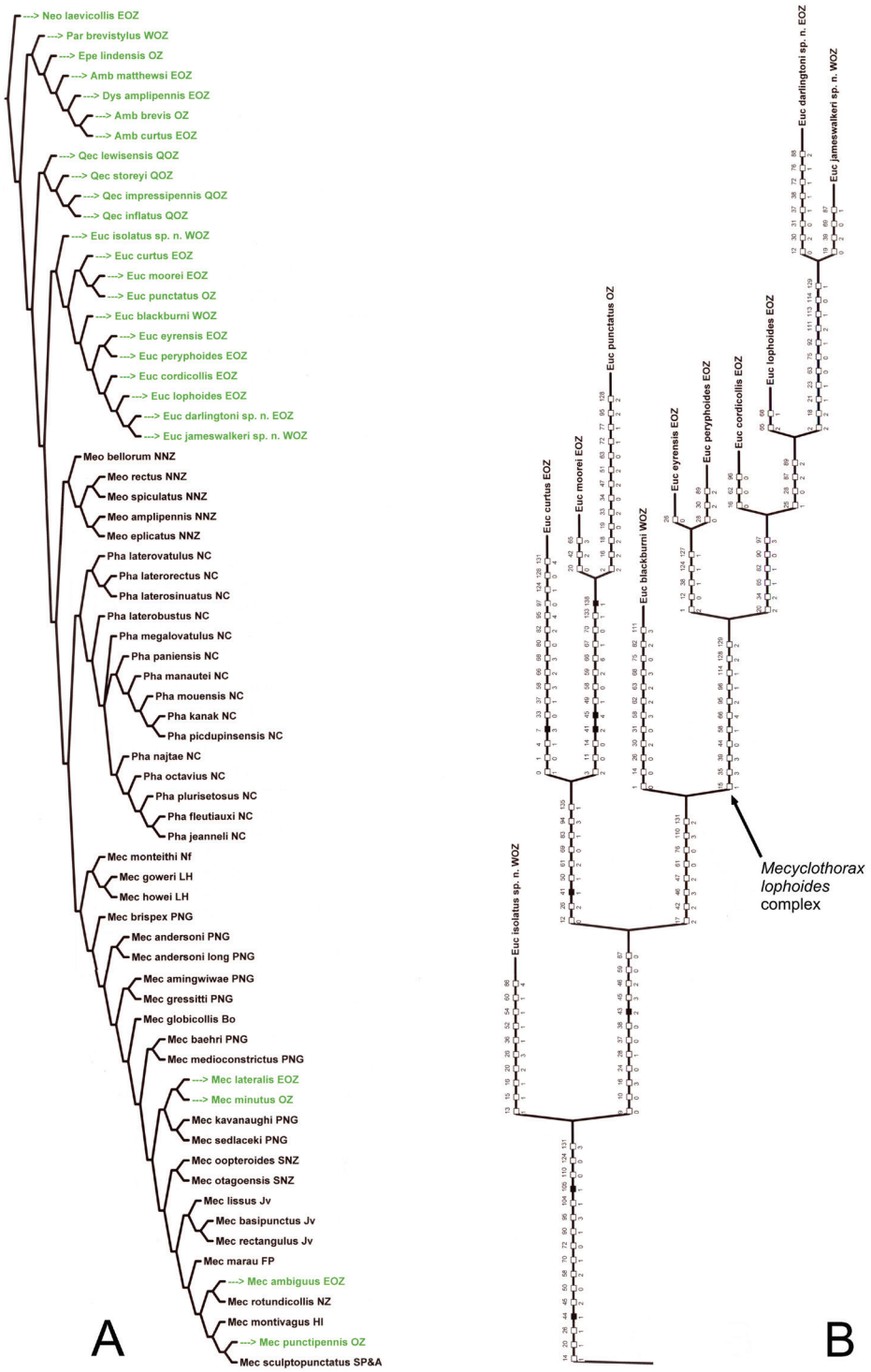

Figure 1. Cladograms resulting from cladistic analysis. Species terminals are labeled with species epithet and three-letter abbreviation of relevant generic or subgeneric name: Neo, *Neonomius* Moore; Par, *Paratrichothorax* Baehr; Epe, *Epelyx* Blackburn; Amb, *Amblytelus* Blackburn; Dys, *Dystrichothorax* Baehr; Euc, *Eucyclothorax* Liebherr; Qec, *Qecyclothorax* Liebherr; Meo, *Meonochilus* Liebherr and Marris; Pha, *Phacothorax* Jeannel; Mec, *Mecyclothorax* Sharp. Areas occupied by the included taxa are indicated by abbreviations following species epithets: **Bo**, Borneo; **EOZ**, eastern Australia, i.e. restricted to east of the Nullarbor Plain; **FP**, French Polynesia, Tahiti; **HI**, Hawaiian Islands, Maui; **Jv**, Java; **LH**, Lord Howe Island; **NC**, New Caledonia; **Nf**, Norfolk Island; **NNZ**, North Island of New Zealand; **NZ**, generally distributed across New Zealand; **OZ**, generally distributed across Australia; **PNG**, Papua New Guinea; **QOZ**, restricted to Queensland, Australia; **SNZ**, South Island of New Zealand plus Chatham Islands; **SP&A**, St. Paul and Amsterdam Islands; **WOZ**, western Australia, i.e. restricted to west of the Nullarbor Plain. **A.** Strict consensus cladogram of 2 equally most-parsimonious trees. Green-colored terminals represent mainland Australian taxa. **B.** Resolved cladistic relationships of 11 *Mecyclothorax* (*Eucyclothorax*) spp. represented in all cladograms. Character numbers are shown to left of cladogram edges, character states to right. Filled boxes represent characters that change to the indicated state only once on cladogram.

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ments tried). The consensus cladogram maintains monophyly of the five previously recognized *Mecyclothorax* subgenera (Liebherr 2018), although the subgenus *Qecyclothorax* is hypothesized to be the adelphotaxon of the other four subgenera. The four subgenera *Eucyclothorax*, *Meonochilus*, *Phacothorax*, and *Mecyclothorax s. s.* are hypothesized as successive sister groups (Fig. 1A). In all trees, relationships proposed for the Australian *Mecyclothorax* species are identical; e.g. Fig. 1B for the species of subgenus *Eucyclothorax*.

Cladistic analysis demonstrates the Australian *Mecyclothorax* fauna to be composed of several species or species assemblages interpolated among non-Australian taxa. The Queensland *Qecyclothorax* represent a the earliest divergent clade in Australia (Fig. 1A). Subgenus *Eucyclothorax*, a principal focus of this study, comprises the next divergent lineage (Fig. 1A–B). Subgenus *Mecyclothorax*, by far the most diverse component of the genus with over 350 species included (Liebherr 2013, 2015, 2017, 2018), is represented in mainland Australia by only four species; the adelphotaxa *M. lateralis* and *M. minutus*, and the more widespread species *M. ambiguus* and *M. punctipennis*. This subgenus diversified first in New Guinea, with species from Lord Howe and Norfolk Islands, and Borneo cladistically derived from that grade (Fig. 1A, Liebherr 2018). The Australian species pair *M. lateralis* plus *M. minutus* (Fig. 1A) are related to New Guinean taxa, whereas a third Australian species–*M. ambiguus*–is the adelphotaxon to *M. rotundicollis* of New Zealand. Most spectacularly, *M. punctipennis* is the most closely related species to not only *M. sculptopunctatus* of the St. Paul and Amsterdam Islands, but also to *M. montivagus*, the most generalized Hawaiian species that serves in this analysis as the surrogate representative for the 239 *Mecyclothorax* species that have radiated from a single ancestor in the Hawaiian Islands (Liebherr 2015).

Taxonomic treatment

At present, the best means to determine Australian *Mecyclothorax* beetles to genus is the key of Moore (1963), though the phylogenetic relationships of the Moore's recognized generic-level taxa are better represented in the analysis of Liebherr (2011a). It should be noted, however, that the relationships of the *Amblytelus*-related genera and *Mecyclothorax* should be assessed using the present analysis (Fig. 1A) as the enhanced taxonomic representation of Liebherr (2018) and this paper allow a more robust delineation of *Mecyclothorax* monophyly and its constituent subgenera.

Species treatments below follow one of three formats: **1**, a diagnosis and full description of external characters for all newly described taxa; **2**, an extended diagnosis presenting all salient external characters for previously described species of the *M. lophoides* species complex (see key below); and **3**, brief diagnostic combinations sufficient to allow determination of the balance of species in the subgenera *Eucyclothorax* and *Mecyclothorax*.

Genus *Mecyclothorax* Sharp

Mecyclothorax Sharp, 1903: 243 (type species *Cyclothorax montivagus* Blackburn by Andrewes 1939).

Cyclothorax MacLeay, 1871: 104 (not *Cyclothorax* Frauenfeld, 1868; type species *Cyclothorax punctipennis* MacLeay by monotypy; synonymy Sloane 1903).

Thriscothorax Sharp, 1903: 257 (type species *Cyclothorax unctus* Blackburn by original designation; synonymy Britton 1948).

Atelothorax Sharp, 1903: 269 (type species *Atelothorax optatus* Sharp by monotypy; synonymy Britton 1948).

Metrothorax Sharp, 1903: 269 (type species *Metrothorax molops* Sharp by Lorenz 1998; synonymy Britton 1948).

Antagonaspis Enderlein, 1909: 488 (type species *Antagonaspis sculptopunctata* Enderlein by original designation; synonymy Jeannel 1938).

Loeffleria Mandl, 1969: 54 (type species *Loeffleria globicollis* Mandl by monotypy; synonymy Baehr and Lorenz 1999).

subgenus *Phacothorax* Jeannel, 1944: 84 (type species *Phacothorax fleutiauxi* Jeannel by original designation; synonymy Liebherr and Marris 2009).

subgenus *Meonochilus* Liebherr & Marris, 2009: 10 (type species *Tarastethus amplipennis* Broun by original designation; synonymy Liebherr 2018).

subgenus *Eucyclothorax* Liebherr, 2018: 12 (type species *Cyclothorax blackburni* Sloane by original designation).

subgenus *Qecyclothorax* Liebherr, 2018: 14 (type species *Mecyclothorax storeyi* Moore by original designation).

Diagnosis. Moore (1963) diagnosed *Mecyclothorax* based on: **1**, apical palpomeres glabrous; **2**, pronotum cordate; **3**, male parameres narrowed apically. These characters were chosen to differentiate *Mecyclothorax* from *Neonomius* Moore, a genus now placed far from *Mecyclothorax* in the subtribe Moriomorphina. The first character works well for *Mecyclothorax*, with the rare occurrence of very short setae on the apical palpomeres, those setae about 0.10× the palp's maximal diameter. Since Moore's pioneering exposition, pronotal shape has been shown worthless for diagnosing *Mecyclothorax* given the great diversity in shape among the Tahitian (Perrault 1984, Liebherr 2013), Hawaiian (Liebherr 2015), and New Caledonian species (Liebherr 2018). The male parameres differ in configuration among the various subgenera of *Mecyclothorax*, but as Moore proposed, both right and left parameres are elongate and setose apically (Liebherr 2018, fig. 5). Other characters that diagnose *Mecyclothorax* from various other taxa in tribe Moriomorphini, both symplesiomorphically and synapomorphically (Liebherr 2011a), include: **1**, labrum truncate to moderately and broadly emarginate apically; **2**, ligula truncate medially between the 2 marginal setae, paraglossae elongate; **3**, pronotal base at least moderately punctate; **4**, elytral humeral margin smooth, without tooth at humeral angle; **5**, female apical ventrite with median patch of 4–5 smaller setae.

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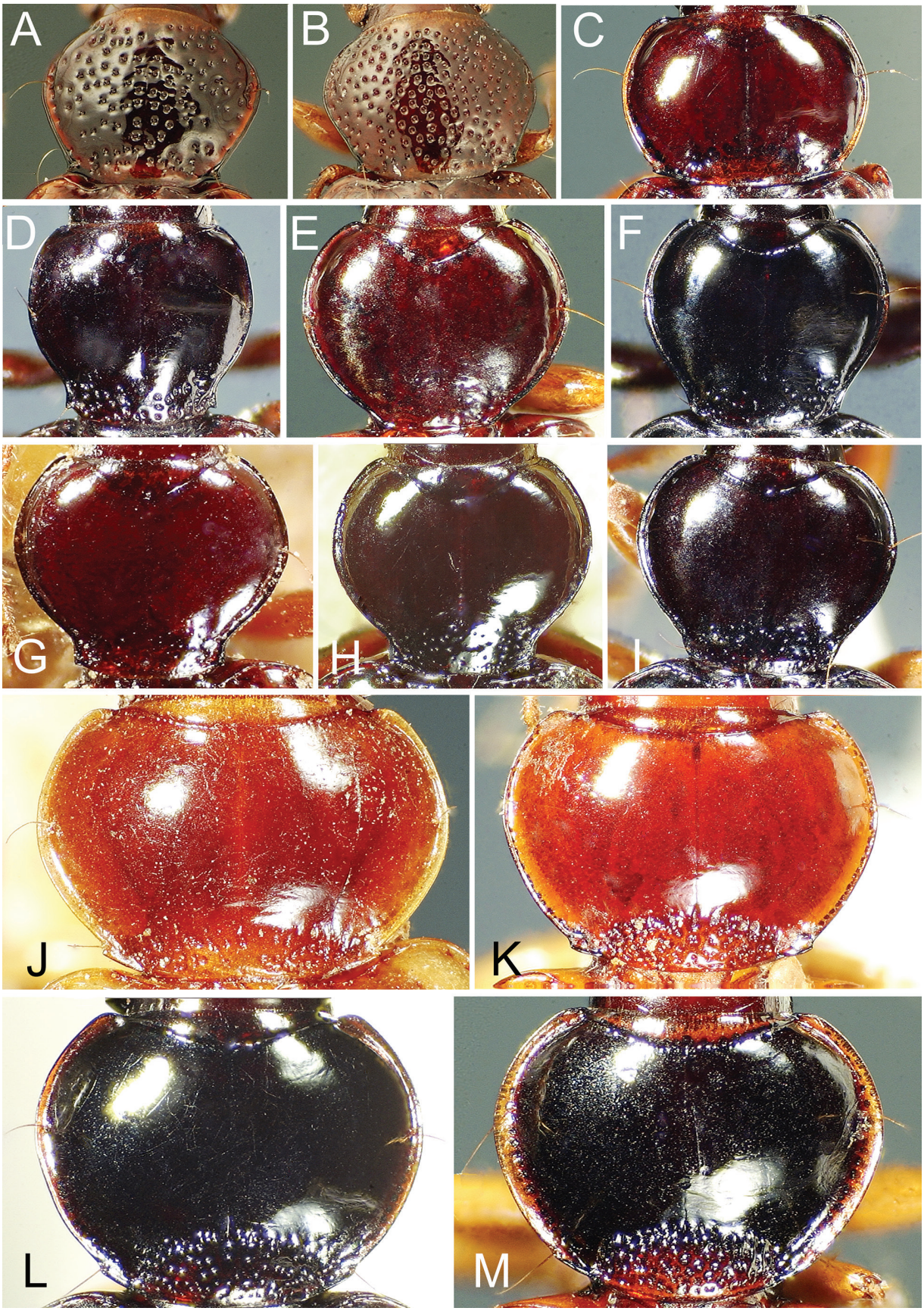

Figure 2. Pronota, dorsal view, of mainland Australian *Mecyclothorax* spp.: **A**, *M.* (*Eucyclothorax*) *moorei*; **B**, *M.* (*Eucyclothorax*) *punctatus*; **C**, *M.* (*Eucyclothorax*) *curtus*; **D**, *M.* (*Eucyclothorax*) *blackburni*; **E**, *M.* (*Eucyclothorax*) *darlingtoni*; **F**, *M.* (*Eucyclothorax*) *lophoides*; **G**, *M.* (*Eucyclothorax*) *eyrensis* lectotype; **H**, *M.* (*Eucyclothorax*) *peryphoides* holotype; **I**, *M.* (*Eucyclothorax*) *cordicollis*; **J**, *Mecyclothorax* (*s. s.*) *lateralis* paralectotype; **K**, *M.* (*s. s.*) *minutus* lectotype; **L**, *M.* (*s. s.*) *ambiguus*; **M**, *M.* (*s. s.*) *punctipennis*.

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Nomenclatural note. Sloane (1915) described *Mecyclothorax ovalis* from Manjimup, WA, with label data (ANIC): Manjimup, W.A. / 31.12.13 T. G. S. // Mecyclothorax / ovalis Sl. Type // Holotype [pink label]. The pink holotype label is consistent with those used by P. J. Darlington, Jr. during his curation of the Sloane collection in 1957 (Darlington 1962: 328). The specimen is mostly destroyed, with only partial remnants of the legs remaining glued to the card. As such, because the holotype specimen can no longer be used to diagnose the species nor the species' generic placement, a neotype is designated. As this neotype designation is required to stabilize both the concept of this species and the species' new generic combination, such an action is valid under Article 75 of The Code (I.C.Z.N. 1999). Therefore a Neotype male (MCZ specimen deposited in ANIC) is hereby designated: Mullewa, W.A. / Sept. 19 1931 // Australia / Harvard Exp., / Darlington // MCZ // Neotype / Mecyclothorax / ovalis Sloane / det. J.K. Liebherr 2004 [black-margined red label]. These specimens, both neotype and others in the series (MCZ) exhibit densely setose apical palpomeres as well as the small ovoid body diagnostic for *Neonomius* Moore (1963). The male genitalia conform to the configuration observed in the subtribe Moriomorphina (Liebherr 2011a), with both parameres broad, parallel-sided with rounded apices, and the right paramere ventrally setose, as observed in the generic type species *N. laevicollis* (Sloane) (Moore 1963, fig. 7). Based on these characters, Sloane's species is newly combined as *Neonomius ovalis* (Sloane), comb. n. Among species of *Neonomius*, *N. ovalis* is diagnosable from the sympatric *N. australis* (Sloane) by: **1**, the smaller body size, standardized body length 3.2–3.6 mm for the *N. ovalis* neotype series – agreeing with Sloane (1915; 451) – versus 5.0 mm for *N. australis* (Sloane 1915: 450); and **2**, the reddish-brown body color versus "black, nitid; legs piceous-red; antennae reddish (Sloane 1915, 450)" for *N. australis*. *Neonomius ovalis* can be diagnosed from the other two southeastern Australian species placed in the genus – *N. laevicollis* (Sloane) and *N. laticollis* (Sloane) – by the apically less convex elytral interval 8, versus the laterally compressed, subcarinate interval 8 characterizing those two species. The type locality for *M. ovalis* (Sloane) becomes Mullewa. That Moore et al. (1987) did not recognize Sloane's *Mecyclothorax ovalis* as a member taxon of *Neonomius* Moore is based on the lack of any other specimens in the ANIC beyond the destroyed holotype of *M. ovalis* Sloane, whereas Darlington made this nomenclatural connection, but only for specimens he deposited in the MCZ.

All other names placed under *Mecyclothorax* Sharp in Moore et al. (1987: 147–149) are treated below.

Key to the adults of the species of *Mecyclothorax* Sharp from mainland Australia

This key can be used to identify all mainland Australian species of *Mecyclothorax*. All previously recognized species of subgenus *Qecyclothorax* revised by Baehr (2003) are included, with his key couplets complemented by the addition of *M. lewisensis estriatus* subsp. n.

1 Prosternum punctate, either with punctures longitudinally oriented within a medial depression anterad procoxae, or more broadly distributed across the apical half of the prosternum (subgenus *Eucyclothorax* Liebherr) 2
– Prosternum smooth medially, though an impunctate depression may be present between procoxae 13
2 Proepisternum punctate either along the prosternal suture, or more broadly across apical half of entire sclerite..... 3
– Proepisternum impunctate near prosternal suture and on median surface, though punctures may be present in the proepimeral sutural groove 7
3 Pronotum densely punctate across entire surface, the punctures deep and round (Fig. 2A–B)..... 4
– Pronotal disc impunctate, punctures, if present, small and restricted to the pronotal base (Fig. 2D–I)..... 6
4 Elytral striae 1–5 present and evident on disc (Figs 3B–E, 4); elytra broad basally, lateral margins subparallel, humeri extended laterally so that the humeral angles lie laterad to the positions of pronotal hind angles 5
– Elytral striae 1–4 present on disc, though the punctures indicating the strial positions irregular and distant and stria 4 indicated by only a few very shallow punctures (Fig. 3A); elytra constricted basally, the lateral margins convexly divergent from humeral angles ..... *M. moorei* Baehr
5 Dorsal punctation denser and finer, pronotal discal punctures separated from each other by distances equal to the punctural diameters (Fig. 2B) ..... *M. punctatus* (Sloane)
– Dorsal punctures larger, less dense, pronotal discal punctures irregularly separated from each other by distances 1–2× setal diameters (see Baehr 2016a, fig. 1) ..... *M. punctatus peckorum* Baehr
6 Pronotum transverse, MPW/PL = 139–1.47, lateral margins broadly convex with hind angle indicated by denticle on convex lateral margin (Fig. 2C); elytra broad, lateral margins convex posterad rounded humeri, MEW/EL = 0.71–0.76 .... *M. curtus* (Sloane)
– Pronotum narrow, distinctly cordate with narrow base, MPW/PL = 1.09–1.12, lateral margins constricted and parallel anterad projected hind angles (Fig. 2D); elytra quadrate, narrow, lateral margins parallel, MEW/EL = 0.62–0.66 .... *M. blackburni* (Sloane)
7 Pronotum constricted basally, the lateral margins straight to sinuate anterad the well-defined hind angles (Figs 4, 5A–C) (*M. lophoides* species complex) 8
– Pronotum broadly ovoid, hind angles only suggested as change of curvature of lateral margin at basal pronotal seta (Fig. 3E) ..... *M. isolatus* Liebherr, sp. n.

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8 Pronotum quadrisetose, both lateral and basal setae present, pronotal basal margin not beaded medially, though margin may be beaded for short distance mesad hind angle (Fig. 2F–I)..... 9
– Pronotum bisetose, hind angles glabrous, pronotal basal margin beaded medially (Fig. 2E, 4A–B) 10
9 Pronotum very narrow basally relative to transverse breadth at midlength, MPW/BPW = 2.23–2.32 (Fig. 2E); posterior margin of eye in dorsal view broadly margined by gena, ocular lobe ratio = 0.84–0.88; parascutellar striole consisting of 4–5 isolated punctures..... *M. darlingtoni* Liebherr, sp. n.
– Pronotum narrow basally but less transverse at midlength, MPW/BPW = 1.68 (Fig. 4B); eyes covering most of ocular lobe, EyL/OLL = 0.95; parascutellar striole consisting of 7–8 isolated punctures .....*M. jameswalkeri* Liebherr, sp. n.
10 Dorsal body surface rufopiceous to rufous, legs paler with femora, tibiae and tarsi flavous (Fig. 5A–C); male aedeagal internal sac either with flagellum much longer than flagellar sheath (Fig. 14D–F), or with sheath bifurcated apically (Fig. 14G–H) .. 11
– Dorsal body surface piceous, legs dark, femora fuscous, tibiae and tarsi paler, brunneous with piceous cast (Fig. 4C–D); male aedeagal internal sac with flagellum and flagellar sheath of moderate, equal length, the flagellar sheath unbranched (Fig. 14A–C)..... *M. lophoides* (Chaudoir)
11 Elytral disc dark brunneous to rufopiceous, suture and lateral margins concolorous with disc, though apex may be broadly paler, rufoflavous (Fig. 5B–C); surface of discal elytral intervals subiridescent due to dense transverse-line microsculpture, sutural stria smooth or irregularly punctate in apical half (Fig. 12D–E); pronotal lateral margins shallowly concave anterad obtuse or obtuse-rounded hind angles (Fig. 2H–I), basal pronotal seta set in expanded marginal bead that is only slightly broader at hind angle versus anterad in lateral concavity..... 12
– Elytral disc rufous, suture and lateral margins with piceous cast (Fig. 5A); surface of discal elytral intervals glossy, microsculpture obsolete, vaguely defined transverse lines visible at margins of reflected microscope illumination, sutural stria distinctly punctate in apical half (Fig. 12C); pronotal lateral margins deeply, distinctly concave anterad slightly obtuse, well-projected hind angles (Fig. 2G), basal pronotal seta set in middle of upraised triangle defined laterally and basally by pronotal margins..... *M. eyrensis* (Blackburn)
12 Pronotal lateral marginal depression broader, margin upraised in a bead, hind angles obtuse, with marginal depression continued mesoposteriorly for short distance beyond basal pronotal seta (Fig. 2H); elytral apex concolorous with disc, only the lateral marginal depression near subapical sinuation narrowly paler (Fig. 5B); standardized body length 4.3–5.0 mm.....*M. peryphoides* (Blackburn)
– Pronotal lateral marginal depression very narrow, margin not upraised in a bead, hind angles obtuse-rounded, with marginal depression terminated posteriorly at basal pronotal seta (Fig. 2I); elytral apex broadly, diffusely paler, rufoflavous, in contrast to the dark brunneous disc (Fig. 5C); standardized body length 4.0–4.7 mm.....*M. cordicollis* (Sloane)
13 Elytra with a single dorsal elytral seta in third interval, situated near elytral midlength (Fig. 5D); standardized body length 2.6–3.7 mm (subgenus *Qecyclothorax* Liebherr)..... 14
– Elytra with two dorsal elytral setae in third interval (Fig. 6); standardized body length 4.9–6.4 mm (subgenus *Mecyclothorax* Sharp) 21
14 Clypeus bisetose; base of pronotum coarsely punctate, basal angles without seta, anterior transverse impression deep; male aedeagus inverted from ground-plan condition so that it everts toward right side..... 15
– Clypeus quadrisetose; base of pronotum not or sparsely punctate, basal angles with seta, anterior transverse impression barely indicated; male aedeagus oriented in groundplan condition so that apex everts toward left side..... 16
15 Pronotum not sinuate in front of base; aedeagus larger, apex shorter and wider, internal sac with two small spinose areas in front (Baehr 2003, fig. 1A) (Bellender Ker Range, Massey Range, QLD).....*M. storeyi storeyi* Moore
– Pronotum slightly sinuate in front of base (Baehr 2003, fig. 3A); aedeagus smaller, apex longer and narrower, internal sac without spinose areas in front (Baehr 2003, fig. 1B) (Bartle Frere Range, QLD) ..... *M. storeyi frerei* Baehr
16 Lateral margins of pronotum not perceptibly sinuate posteriorly (Baehr 2003, fig. 3G); genital ring with broad, moderately elongate apex (Baehr 2003, fig. 1E) 17
– Lateral margins of pronotum perceptibly sinuate posteriorly (Baehr 2003, fig. 3C, E); genital ring, when known, with narrow elongate apex (Baehr 2003, fig. 1C–D) 18
17 Spinose fields with apex of aedeagal ostium smaller, situated at left and right sides (Baehr 2003, fig. 1E) (southwestern part of Atherton Tbld.: Mt. Fisher, Mt. Hugh Nelson, Mt. Father Clancy, Malaan Rd. nr. Palmerston Hwy., QLD)..... ..... *M. inflatus inflatus* Baehr
– Spinose fields with apex of aedeagal ostium very large, situated only at the right side (Baehr 2003, fig. 1F) (Upper Boulder Creek at Water Hill Range, QLD) ..... *M. inflatus spinifer* Baehr
18 Inner striae of elytra at most lightly impressed and finely punctate..... 19
– Four inner striae of elytra impressed and finely punctate (Baehr 2003, fig. 3F; Isley Hills, ne. Atherton Tbld., QLD)..... ..... *M. impressipennis* Baehr
19 Inner four elytral striae evident on disc, consisting of distinct rounded punctures separated along the stria by 1–2 puncture diameters (Baehr 2003, fig. 3D)..... 20
– Only the sutural stria slightly impressed on elytral disc, striae 2–4 completely absent, the planar discal surface interrupted only by the puncture associated with the dorsal elytral seta (Fig. 5D; Brandy Creek nr. Conway N. P., QLD)..... ..... *M. lewisensis estriatus* Liebherr, subsp. n.

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20 Apex of aedeagus rounded off, genital ring with longer apex (Baehr 2003, fig. 1C); pronotum with comparatively wider base, ratio base/apex > 1.20 (Carbine Tbld., Thornton Peak, Mt. Pieter Botte, north of Thornton Peak, QLD) ..... *M. lewisensis lewisensis* Moore

– Apex of aedeagus sharply spined, genital ring with considerably shorter apex (Baehr 2003, fig. 1D); pronotum with comparatively narrow base, ratio base/apex < 1.17 (Mt. Hemmant, Mt. Halcyon, Roaring Meg Ck., mountain tops nr. Cape Tribulation, all north of Thornton Peak, QLD) ..... *M. lewisensis uncinatus* Baehr

21 Dorsal body coloration brunneous to rufous, legs concolorous or only slightly paler than lateral elytral intervals (Fig. 6A–B); parascutellar seta absent 22

– Dorsal body coloration rufopiceous to piceous, legs flavous, contrastingly paler than lateral elytral intervals (Fig. 6C–D); parascutellar seta present 23

22 Elytra bicolored, intervals 2–6 brunneous to rufopiceous, contrastedly darker than rufous sutural interval and flavous intervals 7–9 (Fig. 6A); elytra broad, MEW/EL = 0.78–0.81; body size larger, 5.2–6.4 mm ..... *M. lateralis* (Castelnau)

– Elytral disc, suture and margins concolorous, rufoflavous to rufobrunneous (Fig. 6B); elytra narrower, MEW/EL = 0.68–0.75; body size smaller, 4.9–5.7 mm ..... *M. minutus* (Castelnau)

23 Pronotal lateral marginal depression moderately broad, extended laterally as far as distance from lateral pronotal seta to marginal depression (Fig. 2L); elytral disc with well-developed transverse microsculpture, a mixture of transverse sculpticells 2–3× broad as long and loosely connected transverse lines, the surface with bluish iridescence; male aedeagal apex broadly subquadrate, the tip subangulate (Fig. 15C) ..... *M. ambiguus* (Erichson)

– Pronotal lateral marginal depression broad, extended laterally 3–4× as far as distance from lateral pronotal seta to marginal depression, the extended margin translucent (Fig. 2M); elytral disc glossy, ill-defined transverse lines and elongate sculpticells present over portions of surface; male aedeagal apex narrowly rounded, the tip slightly downturned (Fig. 15D) ..... *M. punctipennis* (MacLeay)

Subgenus *Eucyclothorax* Liebherr

Diagnosis. Beetles assigned to this subgenus have the prosternum punctate, with punctures either: **1**, distributed over the lateral reaches of the prosternum and medial reaches of the proepisternum; **2**, more generally distributed across both sclerites; **3**, lining a median depression anterad the prosternal process; **4**, lining the prosternal-proepisternal suture; or **5**, lining a transverse preapical depression (Liebherr 2018, fig. 2D–F). The pronotum may be distinctly punctate (Fig. 2A–B) or not (Fig. 2C–I), but in all species the median pronotal base is coplanar to only slightly depressed relative to the pronotal disc, not greatly depressed as in Australian species of subgenus *Mecyclothorax* (Fig. 2J–M). The vertex is transversely flat to convex, without a transverse dorsal impression, or neck. Generally the species conform to the full complement of standard setae; formula ++/++/+2++. However the basal pronotal seta is absent in *M. darlingtoni* and *M. jameswalkeri*, the parascutellar seta is polymorphically present or absent within *M. punctatus*, and *M. isolatus* exhibits only a single dorsal elytral seta. Body size ranges from small to moderately large, with standardized body length 2.7–6.0 mm.

All *Eucyclothorax* spp. are characterized by male genitalia that possess a flagellum, flagellar sheath, and dorsal plate at the apex of the internal sac, as well as robust aedeagal median lobes, i.e. dorsoventrally broad (Figs 7, 14). The female reproductive tract is configured with the spermathecal duct joined ventrally to the juncture of the common oviduct and the bursa copulatrix (Fig. 9). A helminthoid sclerite is present on the bursal wall ventrad the juncture of the spermathecal duct and common oviduct. Like all other *Mecyclothorax*, the gonocoxae have setae along the apicolateral margin of the basal gonocoxite (Fig. 10), and the apical gonocoxite has 1–3 (usually 2) lateral ensiform setae.

Mecyclothorax moorei Baehr

Figures 2A, 3A, 7A–B, 8A, 9A, 10A, 11A

Mecyclothorax moorei Baehr, 2009: 90.

Diagnosis (n = 2). This species is diagnosed by the broadly punctate pronotal disc (Fig. 2A), punctate head with a transverse line of about 5 large punctures between the posterior supraorbital setae, and convex, smooth elytra with only striae 1–4 in evidence, striae 2–4 only a series of small isolated punctures. The prosternum and proepisternum are also broadly punctate, the punctures large and separated from each other by a distances equal to the punctural diameters (Liebherr 2018, fig. 2F). The punctate pronotal disc, head, and prosternum + proepisternum are shared with *M. punctatus*, but the pronotal punctures are more numerous and less separated in *M. punctatus* (Fig. 2A–B), with about 30 punctures each side in *M. moorei*, and about 60 each side in *M. punctatus*. In addition, the elytral striae are more distinct in *M. punctatus*, with striae 1–5 present in the basal half of the elytra, though the punctures of stria 5 are smaller and shallower. The elytra of *M. moorei* are more ovoid, with the lateral margins more narrowly rounded behind the subangulate humeri (Fig. 3A–B). Whereas the parascutellar seta is present or absent in *M. punctatus*, and if present appearing short and narrow, this seta is well developed in *M. moorei*, with the setal articulatory socket set within a depression coincident with the base of the parascutellar striole, the seta as long as the breadth of 2–3 elytral intervals. The eyes of *M. moorei* are convex but they cover only the anterior 4/5

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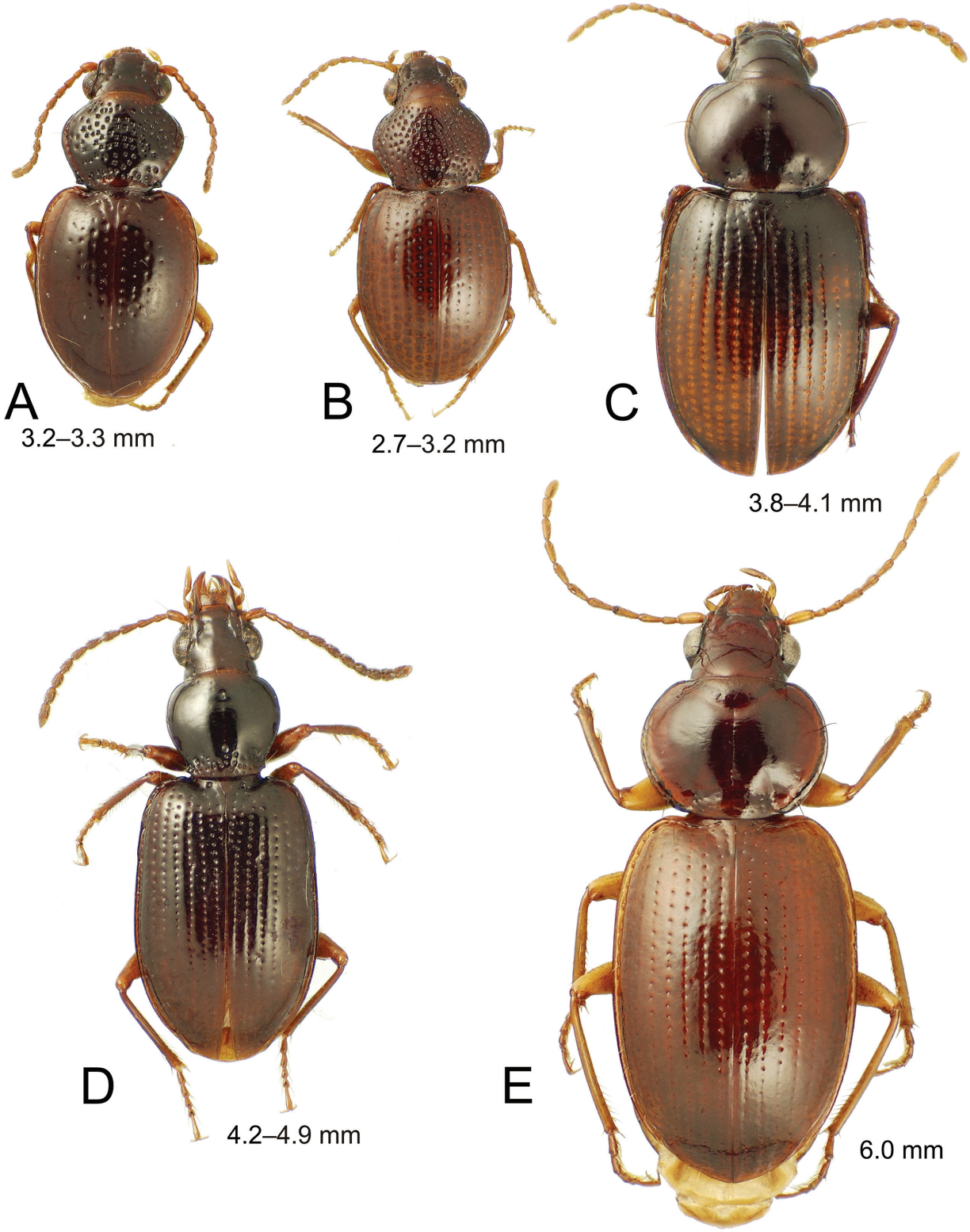

Figure 3. *Mecyclothorax* (*Eucyclothorax*) spp., dorsal view: **A**, *M. moorei*; **B**, *M. punctatus*, NSW; **C**, *M. curtus*; **D**, *M. blackburni*; **E**, *M. isolatus* holotype.

of the ocular lobe: EyL/OLL = 0.83–0.86. Finally, males of this species, *M. punctatus*, and *M. curtus* all exhibit 2 setae each side of the apical abdominal ventrite, an unusual character state within *Mecyclothorax*, and evidence of their monophyletic relationship within subgenus *Eucyclothorax* (Fig. 1B, character 83). Standardized body length 3.2–3.3 mm. Setal formula ++/++/+2++.

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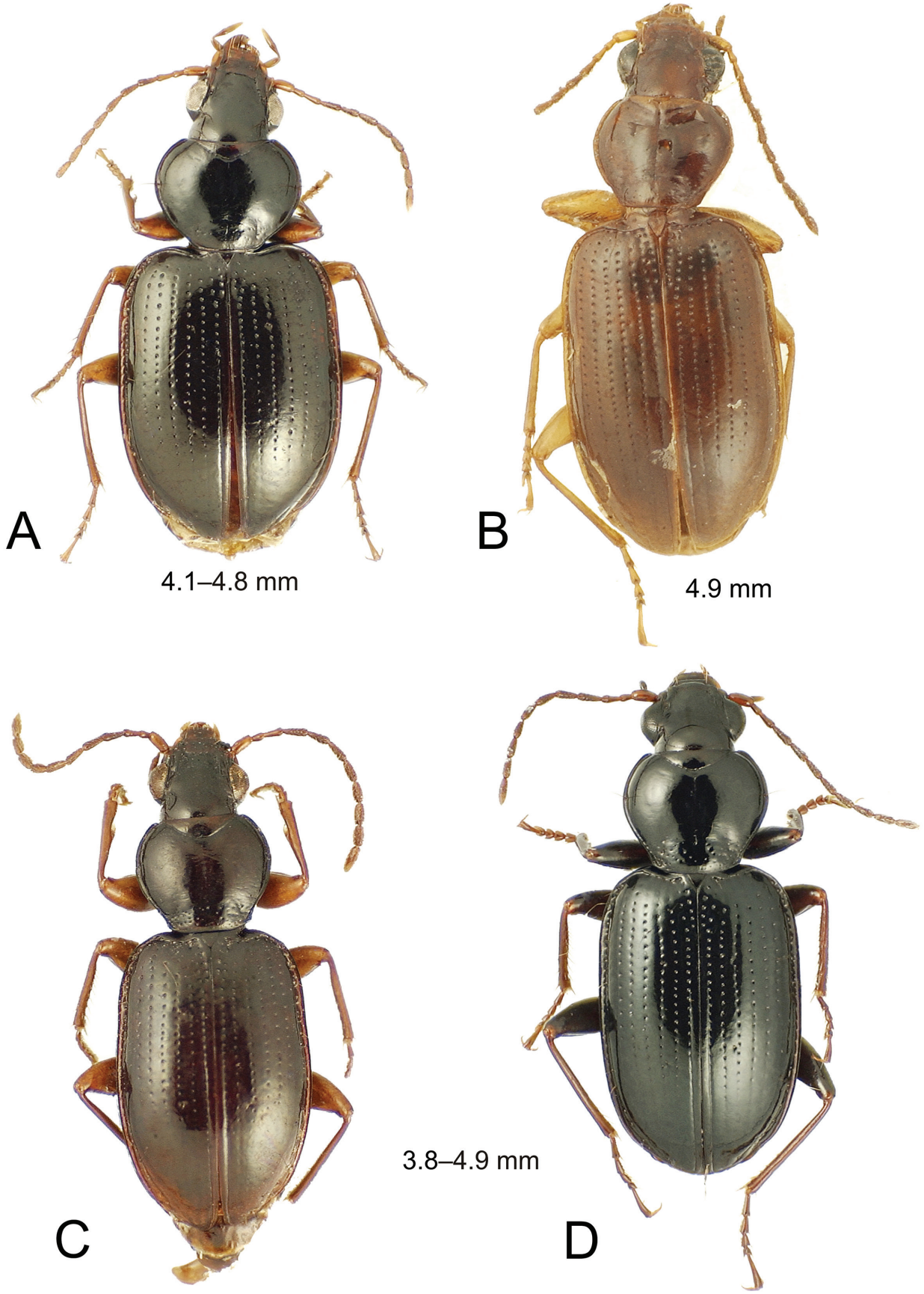

Figure 4. *Mecyclothorax* (*Eucyclothorax*) spp., dorsal view: **A**, *M. darlingtoni*; **B**, *M. jameswalkeri* holotype; **C**, *M. lophoides* lectotype, Melbourne; **D**, *M. lophoides*, ACT: Smoker's Gap.

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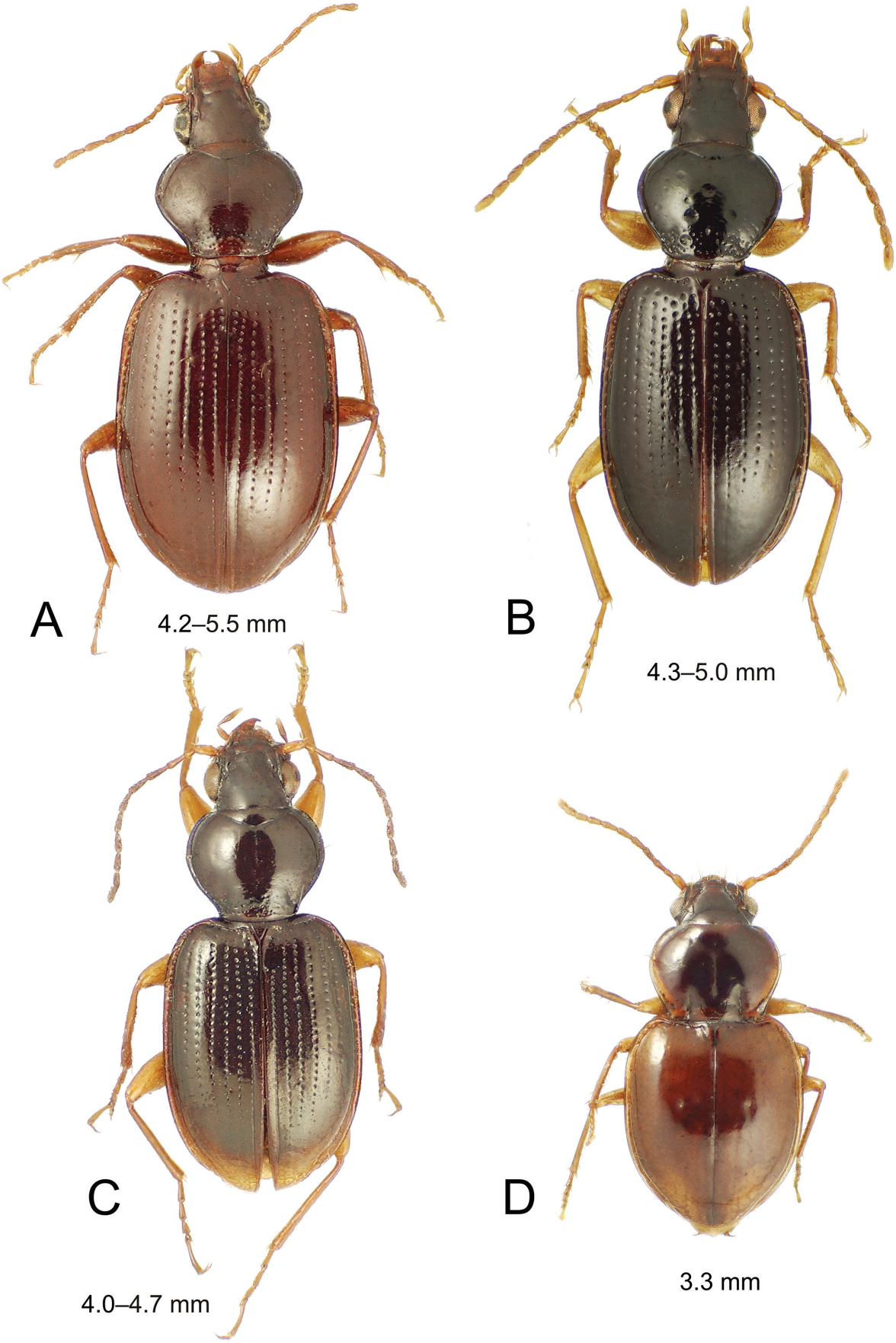

Figure 5. *Mecyclothorax* spp., dorsal view: **A**, *M.* (*Eucyclothorax*) *eyrensis*, paralectotype; **B**, *M.* (*Eucyclothorax*) *peryphoides*; **C**, *M.* (*Eucyclothorax*) *cordicollis*; **D**, *M.* (*Qecyclothorax*) *lewisensis estriatus* holotype.

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Male genitalia (n = 2). Aedeagal median lobe apex narrowly rounded and only slightly projected beyond apical ostial margin (Fig. 7A); aedeagal internal sac elongate, membranous, with apical dorsal plate, flagellum, and flagellar sheath (Fig. 7B); right paramere narrow, elongate, with 6 setae along the ventral margin, 1–2 apical setae, and the dorsal margin glabrous except for a small apical seta (Fig. 8A); left paramere broadly quadrate basally, the apical 1/3 of length very narrow in contrast to broad base.

Female reproductive tract (n = 1). Bursa copulatrix elongate, columnar (Fig. 9A); helminthoid sclerite elongate; spermathecal duct basally expanded and sclerotized, the more apical portion of duct membranous and of lesser diameter; basal gonocoxite with 2 larger setae laterally along apical margin (Fig. 10A), a very small seta medially near margin; apical gonocoxite broad basally, breadth more than half length; lateral ensiform setae elongate, ~ 0.60× length of apical gonocoxite; apical nematiform setae in subbasal sensory furrow.

Type information. Holotype male (AMS): site 32AR NSW Banda Rd about 4.5 km E Hastings Forest Hwy 31°09'S 152°25'E Mount Boss State Forest 17 1100m (NPWS Survey) 4 Feb–9 Apr 1993 M. Gray, G. Cassis (AMS K241125) (Baehr 2009).

Distribution and habitat. *M. moorei* is restricted to northeastern New South Wales (Fig. 11A), with populations allopatrically distributed relative to eastern populations of the more southerly distributed *M. punctatus*. Recorded elevations of collecting localities range from 110 m near Ramornie and 1100 m in Mt. Boss State Forest (Baehr 2009). Philip Darlington collected this species in Bellangry Forest NW of Wauchope (MCZ). All specimens are vestigially winged.

Mecyclothorax punctatus (Sloane)

Figures 2B, 3B, 7C, 8B, 9B, 10B, 11A

Cyclothorax punctatus Sloane, 1895: 449.
Mecyclothorax punctatus, Sloane, 1903: 585; Moore 1984: 163, fig. 12.
Mecyclothorax punctatus peckorum Baehr, 2016a: 94.

Diagnosis (n = 5). This species is most similar to *M. moorei*, with several diagnostic characters differentiating the two listed there. The eyes are large and convex, largely covering the ocular lobes; EyL/OLL = 0.92–0.96. The elytra are broad, with broadly rounded humeri (Fig. 3B). The single available female specimen assignable to *M. p. peckorum* has the elytral base broad, slightly different from the nominate form. However the pronotal and elytral strial punctures are deeper and less dense in *M. p. peckorum*–as reported in Baehr (2016a)–resulting in recognition of the two forms here. In addition, the parascutellar seta is much less in evidence among individuals of this species. When present it is short and fine, and it is certainly absent from the majority of examined specimens. Standardized body length 2.7–3.2 mm. Setal formula ++/++/±2++.

Male genitalia (n = 1). Aedeagal median lobe apex narrowly rounded and not projected beyond apical ostial margin (Fig. 7C); right paramere narrow, elongate, with ~10 setae along the ventral margin, 2 apical setae, and the dorsal margin with 3 small setae (Fig. 8B); left paramere broadly expanded basally, its dorsal margin convex, the apical 1/3 of length very narrow in contrast to broad base. Baehr (2016a, fig. 2) documents a short leftward expansion on the median lobe apex of *M. p. peckorum*. The parameral setation of the two subspecific forms is identical (Fig. 8B; Baehr 2016a, fig. 2).

Female reproductive tract (n = 1). Bursa copulatrix elongate, columnar (Fig. 9B); helminthoid sclerite elongate; spermathecal duct basally expanded and sclerotized, the more apical portion of duct membranous and of lesser diameter; basal gonocoxite with 3 larger setae laterally along apical margin (Fig. 10B); apical gonocoxite broad basally, breadth more than half length; lateral ensiform setae broad, elongate, length about 0.5× length of apical gonocoxite, setal surface longitudinal striate; apical nematiform setae in subbasal sensory furrow.

Type information. For *M. punctatus*, Lectotype female (SAMA) hereby designated: white card with "5104" and "N.S.W." in red ink // N.S. Wales // punctatus Sloane // J. 7252 / Mecyclothorax / punctatus / M.S. Wales / Cotype [red ink] // Lectotype ♀ / Cyclothorax / punctatus Sloane / det. J.K. Liebherr 2004 [red label with black border]. For *M. punctatus peckorum*, Holotype male (ANIC, not seen): Pemberton Warren N.P. WA 12 Jul. 1980 S. & J. Peck SBP106 // Berlesate karri litter and moss (Baehr 2016a).

Distribution and habitat. Following Baehr's (2016a) circumscription of this species, it is distributed across an easterly set of populations in southern New South Wales and northern Victoria (Fig. 11A), plus a disjunct set of western localities in the southwest region of Western Australia. Sloane wrote of the type series, "I have found it in considerable numbers under logs and the leaves of saplings at a place about twenty-five miles north-west from the town of Urana. It is sluggish in its movements (Sloane, 1895: 449–450)." Thus the type locality is very close to one of the localities where he collected types of *M. cordicollis* (Sloane 1900). More recently, specimens from the western localities have been collected via litter sifting of jarrah forest litter (*Eucalyptus marginata* Donn ex Sm.). All specimens are vestigially winged.

Mecyclothorax curtus (Sloane)

Figures 2C, 3C, 7D, 8C, 9C, 10C, 11B

Cyclothorax curtus Sloane, 1895: 448.
Mecyclothorax curtus Sloane, 1903: 585.

Diagnosis (n = 4). The transverse pronotum–MPW/PL = 1.39–1.47 with nearly impunctate median base and broadly convex margins (Fig. 2C), and broad, subpar-

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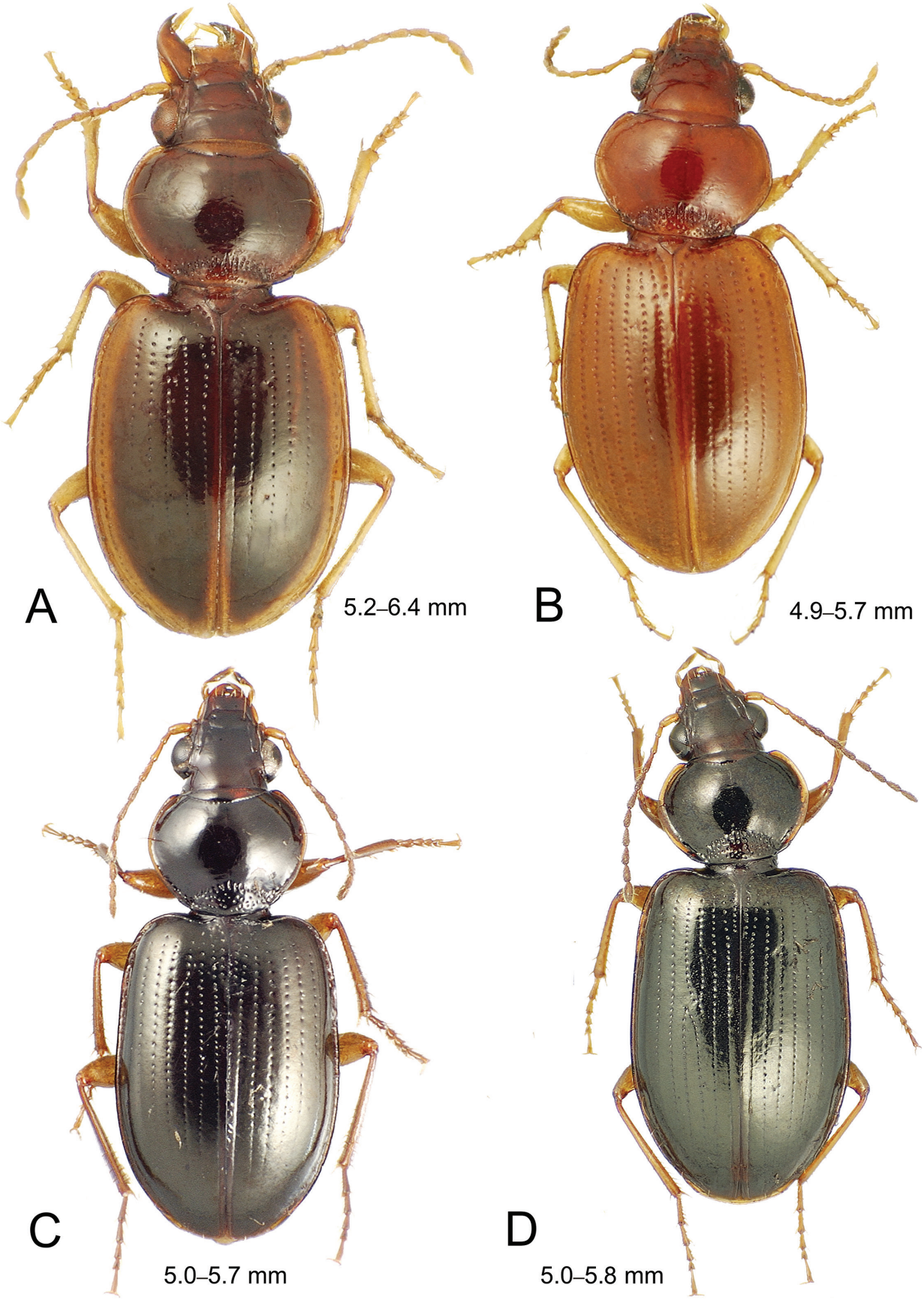

Figure 6. *Mecyclothorax* (*s. s.*) spp., dorsal view: **A**, *M. lateralis*; **B**, *M. minutus*; **C**, *M. ambiguus*; **D**, *M. punctipennis*.

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allel elytra (Fig. 3C), are unique within *Mecyclothorax*, unmistakably diagnosing this very rarely collected species. The pronotal hind angles are defined by denticles on a more broadly convex margin, the basal pronotal setae associated with a broadened marginal bead at their point of insertion. There are 5–6 minute punctures each side on the median base inside the laterobasal depressions, which are marked by 2–3 oblique lines of larger punctures associated with the depression (Fig. 2C, left side). Ventral prothoracic punctation is restricted to the lateral reaches of the prosternum (Liebherr 2018, fig. 2D). The lateral margins of the abdominal ventrites are also distinctly punctate, the punctures distributed densely and irregularly enough to give the surface a dented look. As in the above two species, both males and females have 4 setae along the apical margin of the apical abdominal ventrite. As in *M. punctatus*, the eyes are large and convex, EyL/OLL = 0.87–0.91. However unlike *M. punctatus* and *M. moorei*, the elytral striae are fully developed, with all striae evident nearly to the elytral apex. There is a well-developed carina immediately laterad stria 7 that extends from the position of the posterior series of lateral elytral setae to the elytral margin distad the well-developed elytral plica, parsimoniously interpreted as a parallelism also observed in *M. blackburni* (Fig. 1B, Liebherr 2018, fig. 2L). The apical palpomeres bear a sparse pelage of very short setae, a character otherwise only observed within the genus in Norfolk Island's *M. monteithi*. Standardized body length 3.8–4.1 mm. Setal formula ++/++/+2++.

Male genitalia (n = 1). Aedeagal median lobe apex narrowly rounded with broad dorsal expansion, the apical face of the lobe concave (Fig. 7D); flagellum short, associated with very elongate sclerotized saccal surface herein interpreted as flagellar sheath (single available male with sac uneverted); right paramere elongate but broad apically (Fig. 8C), the paramere more robust than in other *Eucyclothorax* (Figs 8, 13), and with ventral surface bearing only a single short seta complementing the 2 long apical setae, and the dorsal surface glabrous; left paramere broad basally (as in males of *M. moorei* and *M. punctatus*), but also broad apically, the apex more than half the breadth of base, a single longer seta present at apex.

Female reproductive tract (n = 1). Bursa copulatrix elongate, columnar (Fig. 9C); helminthoid sclerite with distal projection; spermathecal duct elongate, more than twice length of spermathecal reservoir, the duct moderately sclerotized, undulated along length; basal gonocoxite with a single large seta laterally along apical margin (Fig. 10C); apical gonocoxite very broad, the base extended and recurved basally so that lateral margin is distinctly concave; lateral ensiform setae broad, dorsal ensiform seta situated medially so that its apex extends beyond medial margin; apical nematiform setae in subbasal sensory furrow.

Type information. Holotype (ANIC): specimen on white triangle, lacking head and prothorax // C. curtus Sl. (type) / Bendigo. W.W.F. / 1176; "1176" is in Sloane's specimen list for 1893/94 (ANIC, unpubl. data).

Distribution and habitat. The lone holotype was collected by W.W. Froggatt at Bendigo, Victoria. Besides the holotype, I have had the opportunity to examine only a second specimen from Bendigo (MVM), two specimens from Sea Lake, Victoria (Fig. 11B; ANIC, MVM) and a single female from 27 km W Manangatan (ANIC). This last specimen is labeled "South Australia", but based on the locality data it must be from Victoria. Nothing is recorded concerning this species' habits, though occupation of a terrestrial microhabitat associated with forest vegetation near water would be consistent with the habits of its adelphotaxon, the sister-species pair *M. moorei* and *M. punctatus* (Fig. 1B). All specimens are vestigially winged.

Mecyclothorax blackburni (Sloane)

Figures 2D, 3D, 7E, 8D, 9D, 10D, 11B

Cyclothorax blackburni Sloane, 1898: 472.
Mecyclothorax blackburni Csiki, 1929: 487 (see Nomenclatural note).

Diagnosis (n = 5). Beetles of this species are very narrow-bodied, with a narrow, cordate pronotum (Fig, 2D), and narrow, subparallel elytra and an elongate head (Fig. 3D). The pronotal median base is coplanar with the disc, but distinguished by the presence of about 14 large deep punctures each side. The right pronotal hind angles protrude both laterally and posteriorly in association with a broadened marginal bead at the articulatory socket of the basal pronotal seta. Otherwise the pronotal lateral margin is extremely narrow, defined only by a marginal bead. Basally the elytral striae consist of series of closely spaced punctures, their separations equal to their diameters. Puncture size decreases, and puncture distances increase laterally and apically on the elytra, with stria 7 represented by only a few small punctures at mid-length. Interval 8 is broadly convex apically, and the elytral plica is well developed and evident in dorsal view. Ventrally, the body punctation includes a punctate median depression anterad the prosternal process, punctures along the lateral reaches of the prosternum, and a punctate anteapical groove (Liebherr 2018, fig. 2E). The lateral reaches of the mesosternum, metasternum, and all of the metepisternum are also intensely punctate. The basal 3 abdominal ventrites are covered with numerous small punctures laterally, and the suture between visible ventrites 2 and 3 is traceable only as a shallow groove. The apical margin of the male apical abdominal ventrite bears the usual 2 setae, 1 each side, but also 4 small medial setae in the position observed in *Mecyclothorax* females. Standardized body length 4.2–4.9 mm. Setal formula ++/++/+2++.

Male genitalia (n = 2). Aedeagal median lobe very broad and only slightly curved, the apex with subacuminate ventroapical projection and a broadly convex dor-

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soapical expansion resulting in a broadly concave apical face (Fig. 7E); flagellum short, flagellar sheath robust, and dorsal plate lightly sclerotized, difficult to discern in single available uneverted male; right paramere narrow, with 4 small setae ventrally and dorsal surface glabrous (Fig. 8D); left paramere broad basally, narrowly attenuate apically.

Female reproductive tract (n = 1). Bursa copulatrix elongate, extended dorsodistally beyond juncture of common oviduct and bursa (Fig. 9D); helminthoid sclerite robust, with distal projection; spermathecal duct straight and slightly longer than spermathecal reservoir, evenly, moderately sclerotized; basal gonocoxite with 1 larger seta apically, a smaller seta present or not (Fig. 10C); apical gonocoxite narrowly triangular, narrowed apically to acuminate apex; lateral ensiform setae narrow, moderately elongate; apical nematiform setae in apical sensory furrow.

Type information. Holotype male (SAMA): card mounted // TY Pinjarrah // Holotype M. blackburni / PJD Sl. [red label].

Nomenclatural note. Sloane (1903) proposed the replacement of *Cyclothorax* MacLeay (1871) (not Frauenfeld 1868) with Sharp's *Mecyclothorax* (1903), mentioning the new combinations of *M. lateralis* (Castelnau), *M. fortis* (Blackburn) = *M. minutus* (Castelnau) [NEW SYNONYMY herein], *M. punctatus* (Sloane), and *M. curtus* (Sloane). By not mentioning *M. blackburni*, nor also *M. eyrensis* (Blackburn), *M. peryphoides* (Blackburn), *M. cordicollis* (Sloane), *M. minutus* (Castelnau), and *M. punctipennis* (MacLeay), Csiki (1929) became the first to propose these combinations (see also below).

Distribution and habitat. *M. blackburni* is known only from coastal Western Australia (Fig. 11B) from Perth south to Harvey (ANIC, 2 specimens). The Perth locality is denoted as "Bridgel'a' (MVM, 1 specimen), which is here interpreted to be an abbreviation of Bridgeleigh, a remnant area of bush vegetation in Swan Valley, Wanneroo. Commander J.J. Walker, Royal Navy, collected a specimen at Fremantle in 1914 (BMNH). When Sloane (1898) described the species based on one specimen received from Arthur Lea he listed no biological information, and none accompanies the other four available specimens. Those four specimens are all macropterous.

Mecyclothorax isolatus, sp. n.

http://zoobank.org/B41F0209-F1AF-4C25-BAED-3315A834227C
Figures 3E, 11B

Diagnosis (n = 1). The larger body size, standardized body length 6.0 mm, ferruginous body color, and broadly transverse, ovoid pronotum (Fig. 3E) serve to diagnose this species from others of subgenus *Eucyclothorax*, except perhaps the smaller-bodied *M. curtus* (Fig. 3C). However the lateral margin of the pronotum is broadly rounded behind in this species, with the margin explanate in the region of the basal pronotal seta. The metathorax is remarkably abbreviated, more so than in any other Australian species of *Mecyclothorax*, with the metepisternum transversely broader than its lateral length. The elytra exhibit a subcarinate ridge along the eighth interval dorsad the subapical sinuation, reminiscent of such a carinate ridge observed in *M. blackburni*. The carinate ridge lies dorsad a well-developed internal elytral plica, with the plica and elytral margin fitting into a corresponding invagination along the margin of the apical abdominal ventrite, thereby forming, in concert with the conjoining of the elytra at the suture, a very robust, shell-like hindbody. Finally, there is a single dorsal elytral seta on each elytron (Fig. 3E), situated near midlength as observed in species of subgenus *Qecyclothorax* (Fig. 5D). Setal formula +/+/+/+/+/1/+/+.

Description. Head capsule elongate, frons with medial depression but otherwise convex mesad the deep, sinuous frontal grooves; frontal grooves deeply and obliquely continued onto clypeus toward lateral clypeal margins; labrum slightly emarginate apically; antennae filiform, antennomere 9 length 2.36× breadth; mandibles moderately elongate, overall length 1.57× distance from anterior condyle to lateroapical labral margin; eyes well developed and moderately convex, ocular lobe broadly projected, outer eye surface of same curvature behind as posterior portion of lobe meeting gena, ocular ratio = 1.47, ocular lobe ratio = 0.79; mentum tooth with sides obtuse, apex broadly rounded; ligular apex moderately narrowed, 2 ligular setae separated by 3 setal diameters; paraglossae thin, extended 1/2× as far past ligular margin as distance from base to ligular margin; mentum broad, breadth/length across the lateral lobes = 3.25. Pronotum broadly ovoid, MPW/PL = 1.31, without any indication of hind angles save a slight change of curvature of the lateral margin at the hind seta; articulatory socket of lateral seta 1 setal diameter mesad deepest part of marginal depression; median base convex, unmargined medially though broadly upraised mesad laterobasal depressions; base convex anterad basal margin, slightly depressed relative to convex disc, and separated from disc by broad, smooth oblique depressions that extend to laterobasal depressions; about 8 indistinct punctures each side from midline to mesal margins of laterobasal depressions, the depressions broadly extended to explanate lateral margin, with a low upraised tubercle in the middle of each depression; median longitudinal impression fine, well indicated, crossed by transverse wrinkles on disc; anterior transverse impression broad, shallow medially, not indicated laterally; anterior callosity slightly, broadly convex, a well-defined marginal bead along front of pronotum; front angle moderately protruded, tightly rounded; prosternal process broadly depressed between procoxae; prosternum smooth and convex medially, indistinctly punctate anterolaterally with an indistinct anteapical groove consisting of broad punctures that anastomose into a groove along lateral reaches; proepisternum impunctate, however prosternal-proepisternal suture lined with about 5 indistinct punctures; proepimeron with broadly raised posterior bead, the suture with proepisternum smooth. Mesepisternum punctate at its deepest portion, about

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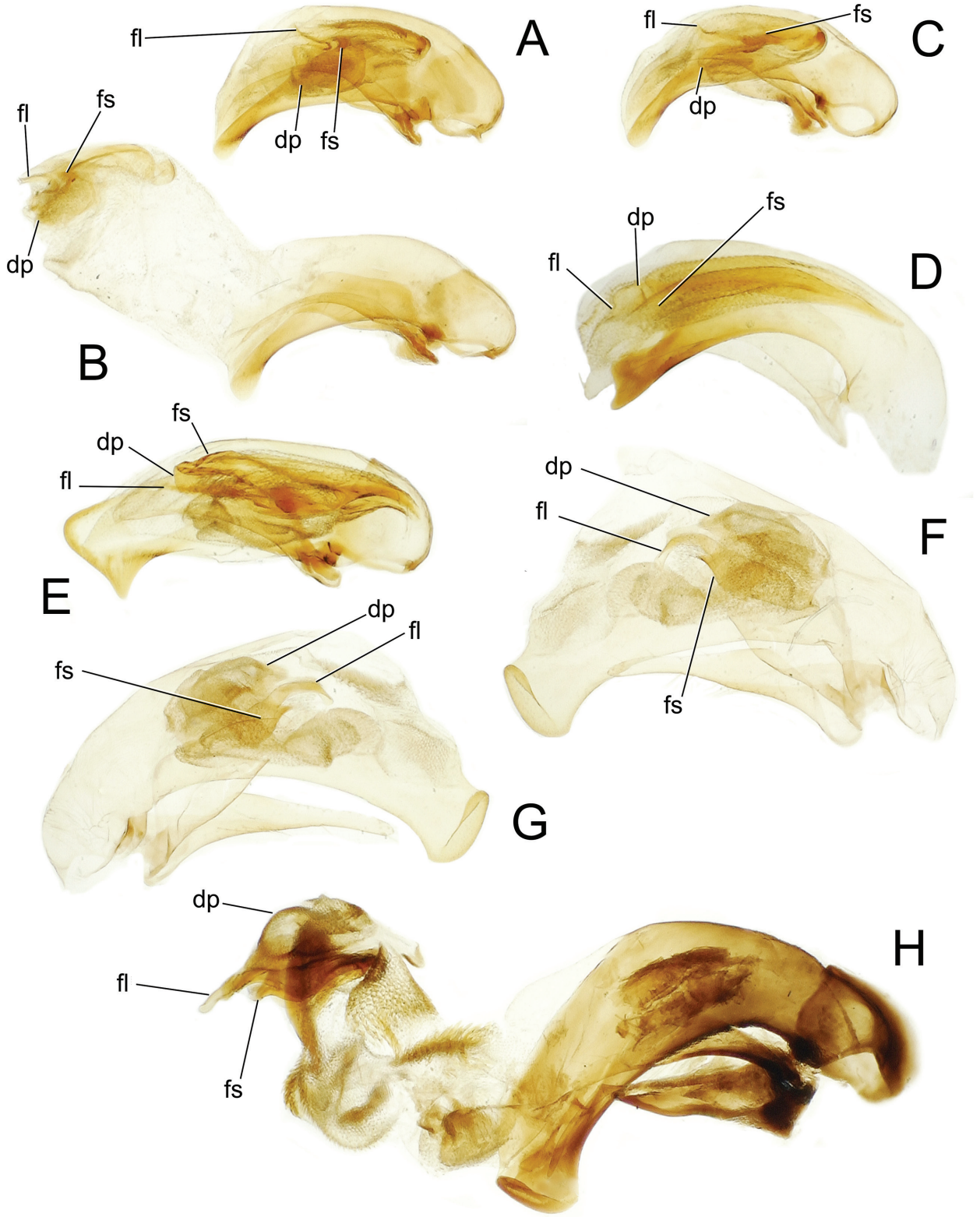

Figure 7. Male aedeagus, right view (unless stated otherwise), for *Mecyclothorax* (*Eucyclothorax*) spp.: **A**, *M. moorei*, NSW: Bellangry For.; **B**, *M. moorei*, NSW: Bellangry For.; **C**, *M. punctatus*, VIC: Sea Lake; **D**, *M. curtus*, VIC: Bendigo; **E**, *M. blackburni*, WA: Fremantle; **F**, *M. darlingtoni*, QLD: Woondom For. Res.; **G**. same specimen left view; **H**, *M. darlingtoni*, QLD: 30 mi. N Brisbane.

6 deep punctures in 1–2 dorsoventral rows. Elytra with striae 1–5 composed of isolated punctures in basal half, less punctate though traceable in apical 1/3 of length, stria 6 represented by small, isolated punctures at mid-length, stria 7 absent except near apex mesad subcarinate eighth interval dorsad subapical sinuation; sutural stria broadly depressed in apical half in association with convex sutural interval, the elytra conjoined apically; stria 8

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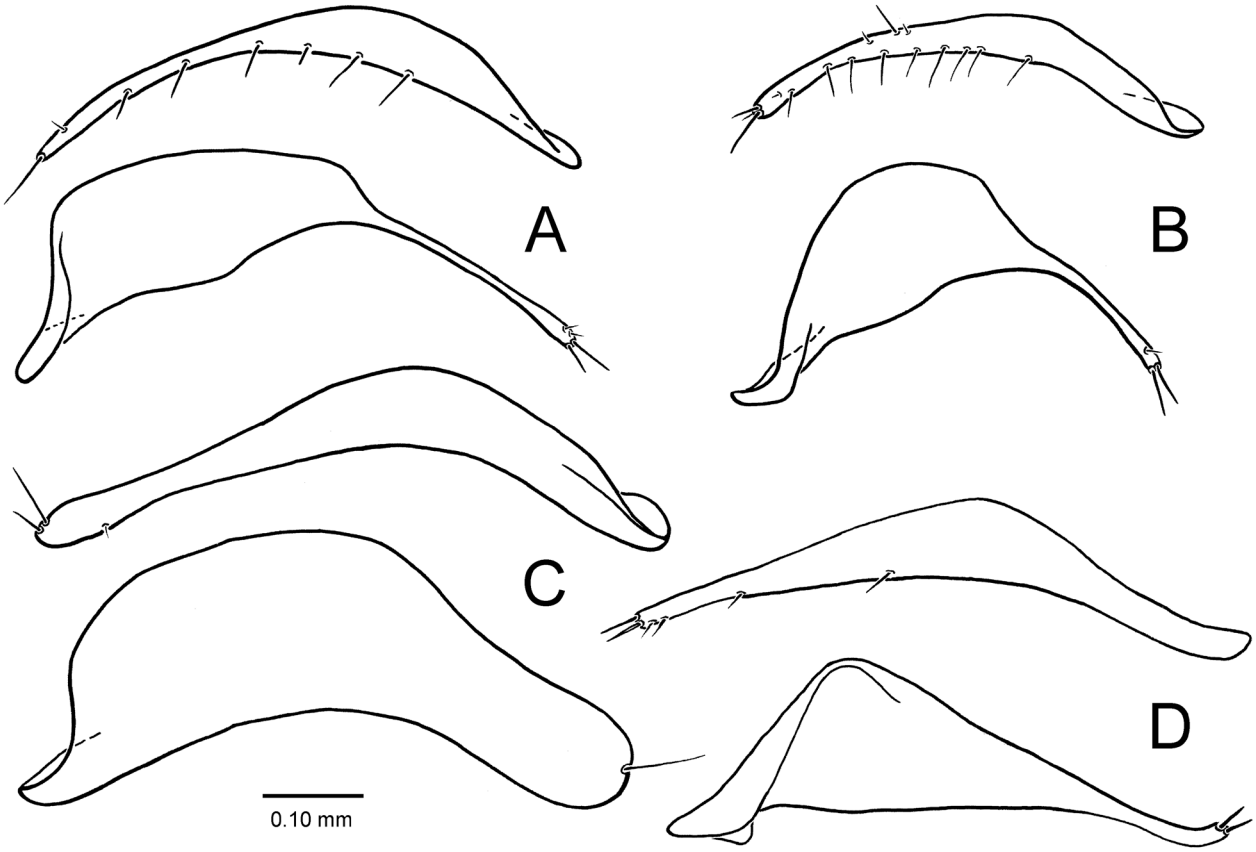

Figure 8. Male parameres of *Mecyclothorax* (*Eucyclothorax*) spp., ectal view, right paramere above in each pair, left paramere below: **A**, *M. moorei*, NSW: Bellangry For.; **B**, *M. punctatus*, VIC: Sea Lake; **C**, *M. curtus*, VIC: Bendigo; **D**, *M. blackburni*, WA: Fremantle.

a series of deep, interrupted punctures at midlength, deep and continuous mesad the posterior series of lateral elytral setae; lateral elytral setae arrayed in 7 + 6 (anterior series setae and posterior series setae), with the posterior seta of the anterior series slightly separated from the rest; subapical sinuation angulate, abruptly curved anteriorly, with well-developed internal elytral plica visible in quarter view, though obscured by the elytral margin in dorsal view. Metepisternum short, trapezoidal, maximum breadth 1.1× lateral length, metepimeron broadly convex posteriorly; metasternal process with sides acute, apex narrow, triangular with margin very broad medially in apex of process. Abdomen with broad linear depressions on lateral reaches of visible ventrites 3–6; suture between ventrites 1 and 2 deeply sinuous laterally, ventrite 2 depressed within sinuosity; female with 2 setae each side and a median patch of 4-5 smaller setae; apical margin of the female apical ventrite with deep emargination each side bordered laterally by a vertical, sclerotized border, these emarginations and lateral wall fitting into the elytral plica above. Microsculpture absent from frons, the surface glossy, micropunctures visible across the surface; pronotal disc and base with indistinct transverse microsculpture consisting of transverse lines and elongate meshes, these visible in surface irregularities such as wrinkles and depressions; elytral disc glossy with fine transverse lines faintly visible outside areas of reflection, elytral apex with transverse sculpticells visible in irregularly depressed areas associated with striae; metasternum glossy with indistinct transverse sculpticells, their breadth 2–3× length; abdominal ventrites glossy with swirling transverse mesh and transverse lines. Coloration of head rufous; antennomere 1 flavous, antennomeres 2–3 rufoflavous, 4–11 with brunneous cast; pronotal disc dark rufous, margins rufoflavous; elytral disc rufobrunneous, sutural interval concolorous, interval 9 and marginal depression, and apex narrowly rufoflavous; proepipleural margin rufous, rufoflavous ventrally, proepisternum rufous; elytral epipleuron broadly flavous, margin darker, brunneous, metepisternum rufoflavous; abdominal ventrites rufoflavous with dark rufous posterior margins, apical ventrite with apical half rufoflavous; femora flavous; tibiae brunneous.

Female reproductive tract (n = 1). The unique female holotype was not dissected, however the gonocoxae are exerted from the specimen allowing the following characters to be assessed: basal gonocoxite with 2 stout apicolateral setae, medioapical surface glabrous (as in Fig. 10A); apical gonocoxite extended laterally at base, basal width about 0.7× length, 2 stout lateral ensiform setae along lateral margin of coxite and an elongate dorsal ensiform seta present; apical nematiform setae within fossa at about 0.8× gonocoxite length. Thus the gonocoxal configuration is most like that of *M. moorei* (Fig. 10A), another early divergent species within subgenus *Eucyclothorax* (Fig. 1).

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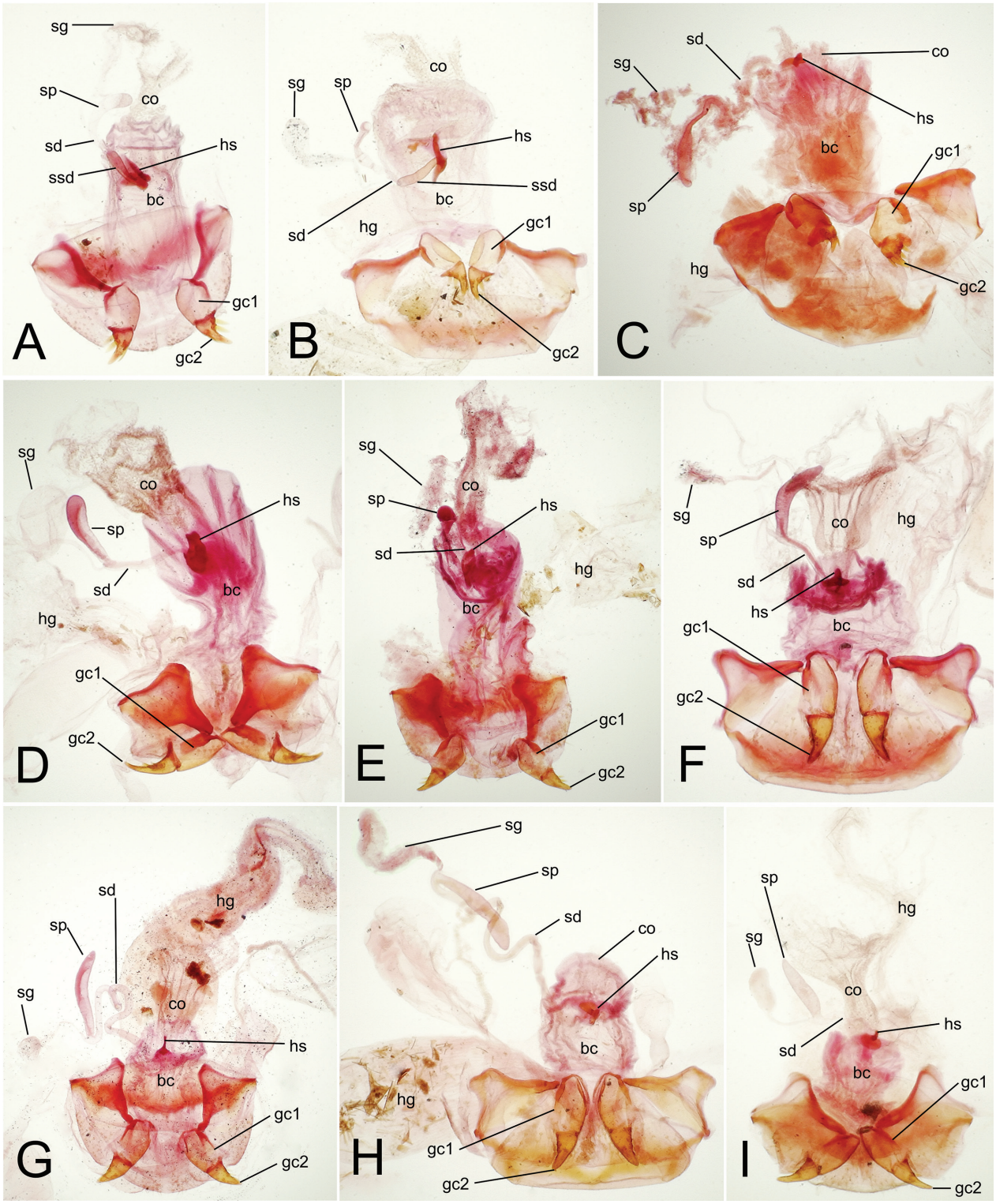

Figure 9. Female reproductive tract and gonocoxae of *Mecyclothorax* (*Eucyclothorax*) spp., ventral view: **A**, *M. moorei*, NSW: Werrikimbe N. P.; **B**, *M. punctatus*, VIC: Birchip; **C**, *M. curtus*, SA: Manangatan; **D**, *M. blackburni*, WA: Harvey; **E**, *M. darlingtoni*. QLD: Woondom For. Res; **F**, *M. lophoides*, ACT: Smoker's Gap; **G**, *M. eyrensis*, SA: Telowie Gorge; **H**, *M. peryphoides*, ACT: Black Mountain; **I**, *M. cordicollis*, NSW: Gosford.

Holotype female (ANIC): Walpole N.P. /Zig Zag Rd. WA / 20–27 June 1980 / S. & J. Peck SBP 70B // berlesate / rotted log / litter and / fungi // HOLOTYPE / Mecyclothorax / isolatus / J.K. Liebherr 2018 (black-margined red label).

Etymology. The adjectival species epithet isolatus signifies both the geographic isolation of this species that is distributed in the south coast region of Western Australia (Fig. 11B), as well as the phylogenetic isolation of this

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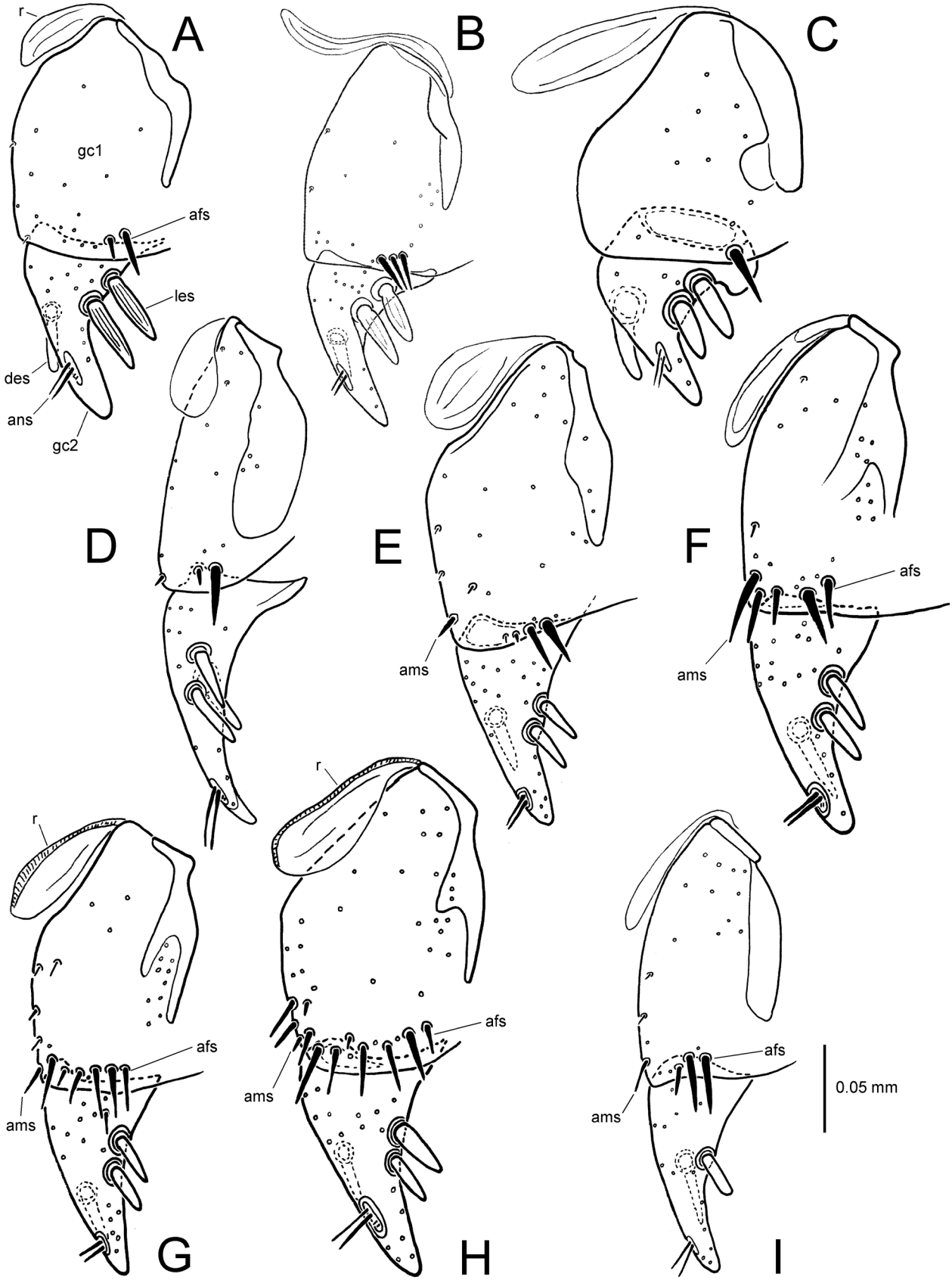

Figure 10. Left gonocoxa of *Mecyclothorax* (*Eucyclothorax*) spp., ventral view: **A**, *M. moorei*, NSW: Werrikimbe N. P.; **B**, *M. punctatus*, VIC: Birchip; **C**, *M. curtus*, SA: Manangatan; **D**, *M. blackburni*, WA: Harvey; **E**, *M. darlingtoni*. QLD: Woondom For. Res; **F**, *M. lophoides*, ACT: Smoker's Gap; **G**, *M. eyrensis*, SA: Telowie Gorge; **H**, *M. peryphoides*, SA: Blackwood; **I**, *M. cordicollis*, NSW: Gosford.

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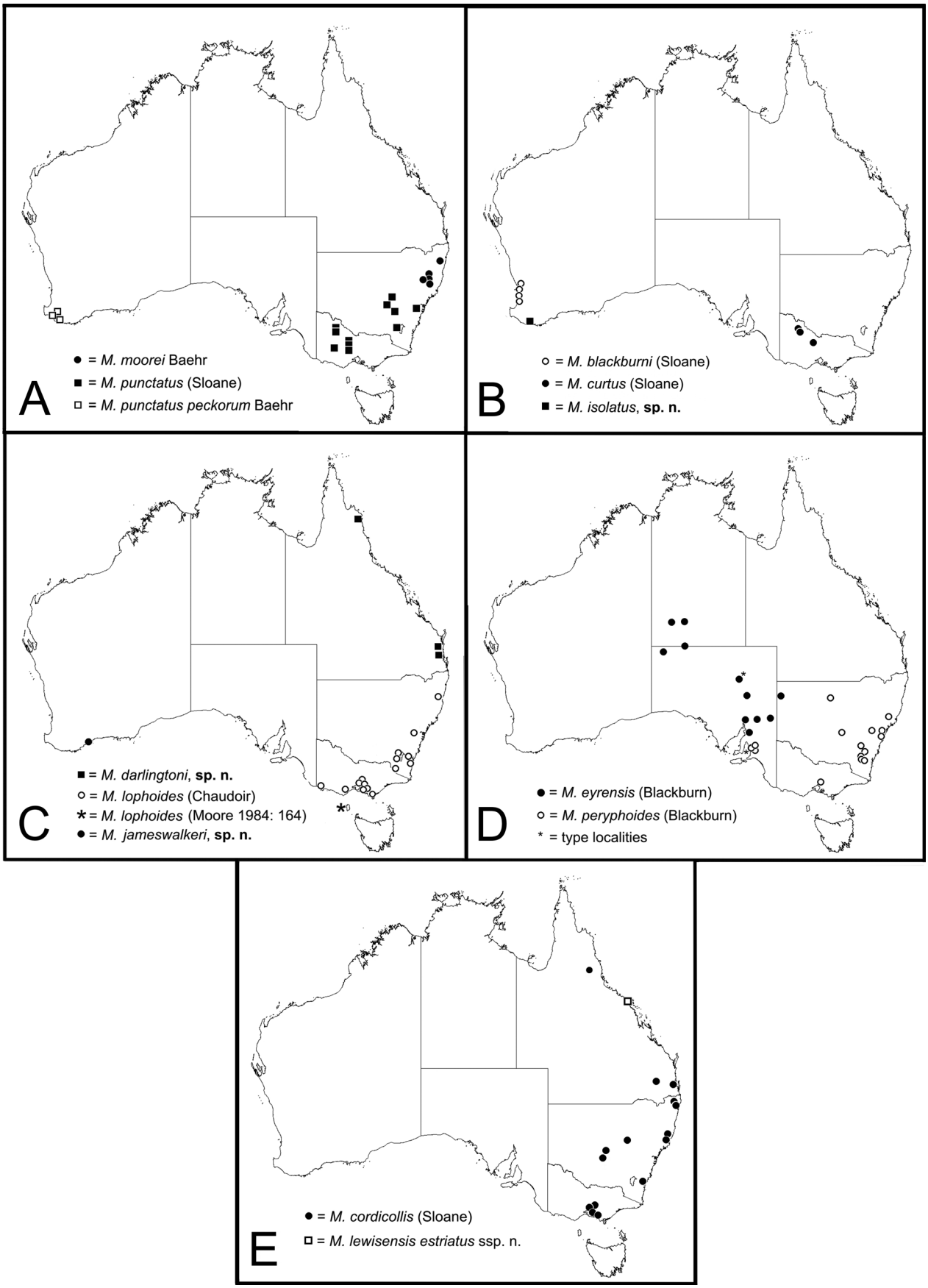

Figure 11. Distributional ranges of 11 *Mecyclothorax* spp. assigned to subgenus *Eucyclothorax*, plus newly described subspecies of *M. lewisensis*.

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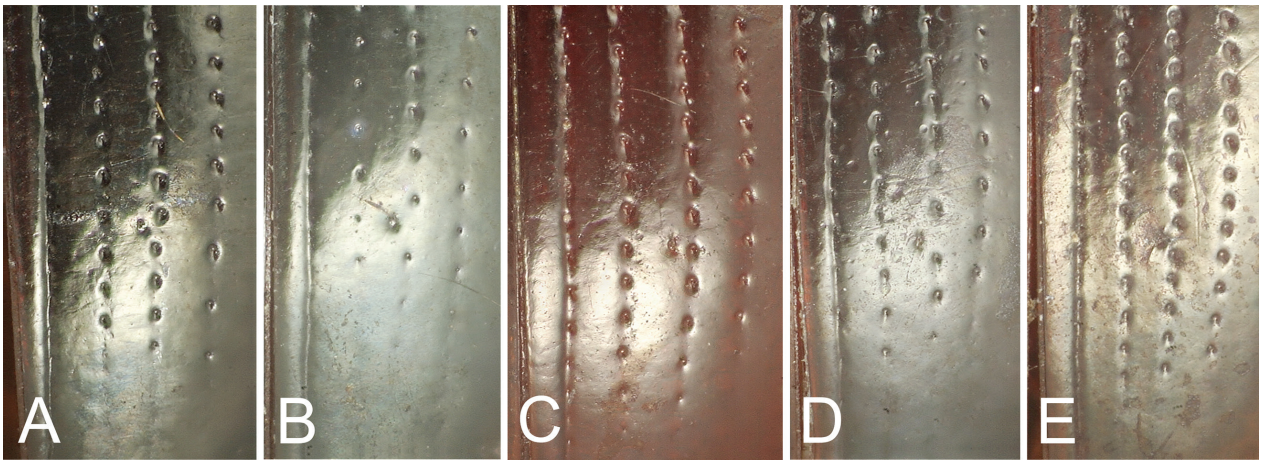

Figure 12. Distal portion of right elytron centered on apical dorsal elytral seta–sutural interval at left in view–showing differential punctation of sutural stria and striae 2 to 4: **A**, *M. darlingtoni* female; **B**, *M. lophoides* male; **C**, *M. eyrensis* paralectotype female; **D**, *M. peryphoides* male; **E**, *M. cordicollis*, paralectotype male.

species, as it comprises the adelphotaxon to all other species of subgenus *Eucyclothorax* (Fig. 1)

Distribution and habitat. This species is known only from the tingle tree (*Eucalyptus jacksoni* Maiden) forest in the south coast region of Western Australia (Fig. 11B). The single individual was collected in berlesate moist enough to support growth of fungal hyphae (S. B. Peck, pers. comm.). The vestigialized flight wings occur in concert with an extremely abbreviated metathorax and a well-developed plical lock between the elytra and apical abdominal ventrite. This species' adelphotaxic relationship to the remainder of subgenus *Eucyclothorax* (Fig. 1) supports its long-term term persistence in this region since the early diversification of all *Mecyclothorax*.

Mecyclothorax darlingtoni, sp. n.

http://zoobank.org/1D1DDE5B-6CB1-4A6F-A5AD-C9586A3087AC
Figures 2E, 4A, 7F–H, 9E, 10E, 11C, 12A, 13A

Mecyclothorax sp. n. D, Liebherr 2018: 3 (non-valid terminal in cladistic analysis).

Diagnosis (n = 5). This species and *M. jameswalkeri* are the only species of subgenus *Eucyclothorax* with glabrous hind pronotal angles (Fig. 2E). Of the two, *M. darlingtoni* is more broad-bodied (Fig. 4A–B), with: **1**, a more transverse and basally constricted pronotum, MPW/PL = 1.32–1.35, MPW/BPW = 2.21–2.32; and **2**, relatively broader elytra, MEW/EL = 0.70–0.75. Both species are characterized by large eyes, but the eyes of *M. darlingtoni* do not cover as much of the ocular lobe; EyL/OLL = 0.84–0.88. The parascutellar striole in this species is composed of 4–5 small, deep, isolated pits arcuately joining the basal groove. Standardized body length 4.1–4.8 mm. Setal formula ++/+–/+2++.

Description. Head capsule broad, vertex broadly convex between deep, sinuous frontal grooves, the grooves more shallowly continued onto clypeus; labrum broadly, moderately concave; mandibles moderately elongate, overall length 1.64× distance from anterior condyle to lateroapical labral margin; ocular lobes convexly projected, outer eye surface slightly more convex than posterior portion of lobe meeting gena; mentum tooth with sides acute, apex rounded; ligular apex moderately narrowed, 2 ligular setae separated by 2 setal diameters; paraglossae thin, extended 2× as far past ligular margin as distance from base to ligular margin; mentum breadth/length across lateral lobes = 2.58. Pronotum with articulatory socket of lateral seta touching marginal depression; hind angles obtusely rounded, margin anterad angle slightly concave (Fig. 2E); median base completely margined, the marginal bead uniform and continuous across width (Fig. 4A), base convex anterad basal margin, nearly coplanar with disc though disc is convex and upraised anterad toward middle of pronotum; about 6 minute punctures on base each side of midline, laterobasal depression a shallow longitudinal depression immediately anterad hind angle; median longitudinal impression fine, well indicated, crossed by oblique transverse wrinkles anterad base; anterior transverse impression deep, punctate medially, fine and deep to front angle; anterior callosity slightly convex, defined posteriorly by deep transverse impression; front angle slightly protruded, tightly rounded; prosternal process with broad deep median depression with 4 indistinct pits along its length; prosternum with anteapical groove that is deep and distinctly punctate laterally, smoother and more irregular medially, marginal bead of procoxal cavity bordered anteriorly by distinct, close-set punctures; proepisternum impunctate; proepimeron with broadly raised posterior bead, punctures along suture with proepisternum and anterad posterior bead. Mesepisternum punctate at its deepest portion, about 6 deep punctures in 1–2 dorsoventral rows. Elytra with striae 1–6 composed of isolated punctures in basal half, striae 2–6 reduced to absence in apical 1/3 of length (Fig. 12A), stria 7 absent except near apex from position of subapical sinuation to apical margin; sutural stria deeper in apical half in association with convex sutural interval, the

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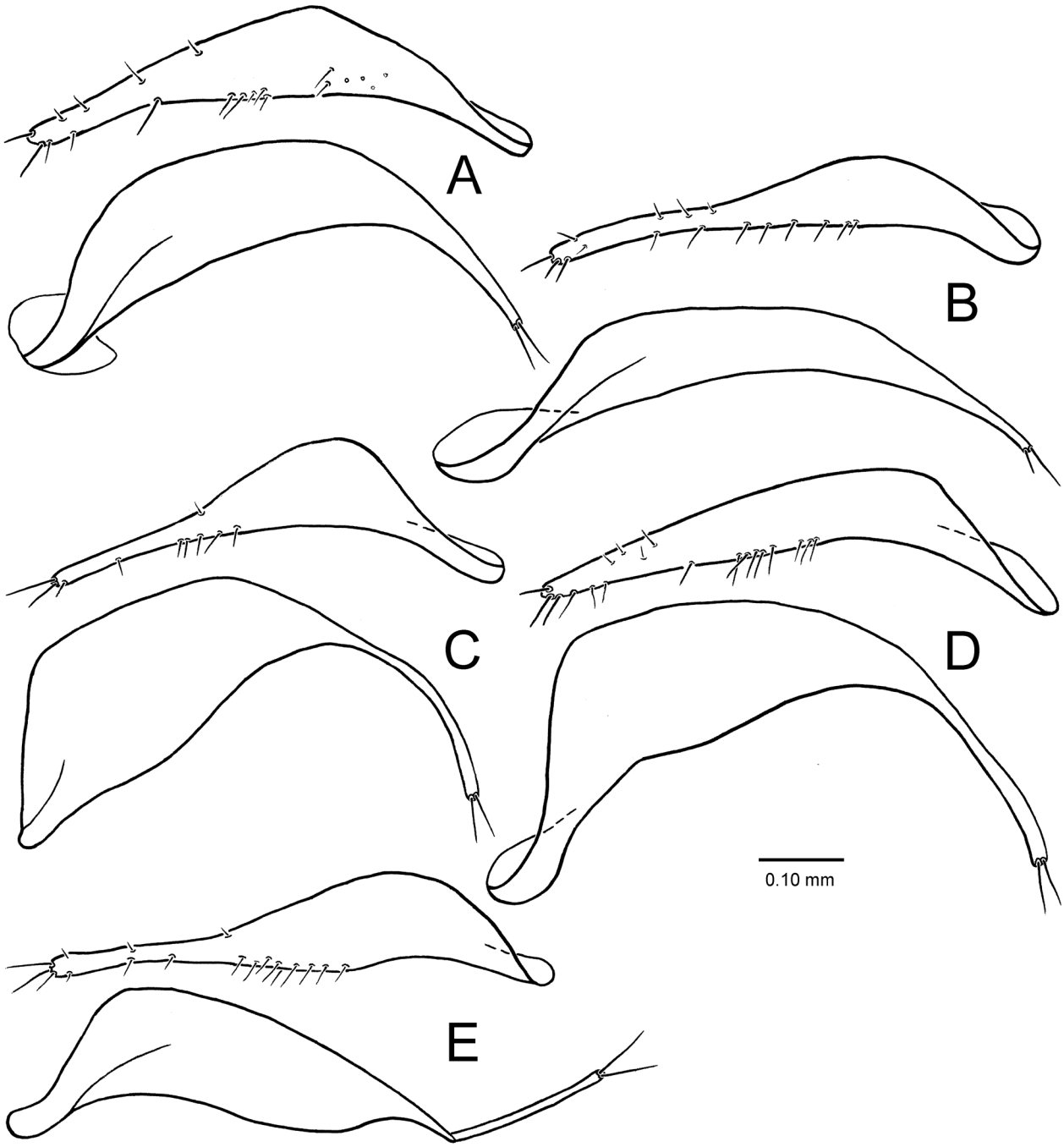

Figure 13. Male parameres of *Mecyclothorax* (*Eucyclothorax*) spp., ectal view, right paramere above in each pair, left paramere below: **A**, *M. darlingtoni*, QLD: Woondom For. Res.; **B**, *M. lophoides*, NSW: Blackheath; **C**, *M. eyrensis*, SA: Telowie Gorge; **D**, *M. peryphoides* holotype, SA: Woodville; **E**, *M. cordicollis*, NSW: Gosford.

suture smooth from near position of apical dorsal elytral seta to apex (Fig. 12A); stria 8 deep, punctate and bordering lateral marginal depression anteriorly, deeper, smooth and distinct mesad posterior series of lateral elytral setae; lateral elytral setae arrayed in 7 + 6 (anterior series setae and posterior series setae); subapical sinuation evident, abruptly curved anteriorly, but elytral plica covered by margin in dorsal view. Metepisternum moderately elongate, maximum width/lateral length = 0.63; metasternal process with sides acute, apex narrowly rounded, margin very broad medially in apex of process. Abdomen with linear wrinkles on lateral reaches of visible ventrites 1–2, more rounded depressions laterally on ventrites 3–6; suture between ventrites 1 and 2 deeply sinuous laterally; males with 1 seta each side along margin of apical ventrite, females with 2 setae each side and a median patch of 4–5 smaller setae; apical margin of the female apical ventrite with small convex projection medially. Microsculpture absent from frons, the surface glossy, micropunctures visible across the surface; pronotal disc with shallow transverse

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mesh, sculpticell breadth 3–4× length, pronotal base with evident, regular transverse mesh, sculpticell breadth 2–3× length; elytral disc glossy with fine transverse lines, loosely connected into a mesh and producing an iridescent reflection (Fig. 12A), elytral apex with elongate transverse mesh, surface iridescent; metasternum with distinct transverse mesh, sculpticell breadth 2–3× length; basal abdominal ventrites with swirling transverse mesh and transverse lines, surface iridescent. Coloration of vertex piceous, frons rufous near clypeus, clypeus rufoflavous; antennomeres 1–3 rufoflavous, 4–11 with piceous cast; pronotal disc piceous; margins concolorous; elytral disc dark rufous with iridescent reflection, sutural interval concolorous, interval 9 and marginal depression rufoflavous; elytral apex narrowly brunneous; proepipleuron margin piceous, dark rufous ventrally, proepisternum rufopiceous; elytral epipleura rufoflavous apically, dark rufous ventrally, metepisternum dark rufous; abdominal ventrites rufopiceous with amber posterior margins, apical ventrite with apical half rufobrunneous; femora flavous with brunneous cast; tibiae brunneous with piceous cast.

Male genitalia (n = 4). Male aedeagal median lobe robust, curved, with broad blunt apex, the apical margin curled toward right resulting in a dorsoventral crease (Fig. 7H); internal sac with a robust flagellar sheath, attenuate flagellum, and broad, well-sclerotized dorsal plate (Fig. 7G–H); right paramere elongate, broader basally, conchoid (Fig. 13A), ventral surface with ~9 setae along margin, dorsal margin with 4 setae; left paramere narrow basally, evenly narrowed to apex.

Female reproductive tract (n = 1). Bursa copulatrix elongate, columnar (Fig. 9E); helminthoid sclerite robust with distal projection; spermathecal duct straight, shorter than spermathecal reservoir, evenly sclerotized; basal gonocoxite with 3–4 setae along apical margin, 2 larger laterally and the balance small and positioned medially (Fig. 10E), an apicomedial seta present; apical gonocoxite subtriangular, apex narrowly rounded; lateral ensiform setae small relative to gonocoxite length; apical nematiform setae in apical sensory furrow.

Types. Holotype male (MCZ deposited in ANIC): c30 mi.N.of / Brisbane SQ / Mar. ‘58 / Darlingtons // HOLOTYPE / Mecyclothorax / darlingtoni / J.K. Liebherr 2018 (black-margined red label). Allotypic paratype female (MCZ deposited in ANIC): (same data as holotype, with black-margined red Allotype label).

Paratypes (61 specimens). AUSTRALIA: Queensland: Brisbane, 30 mi. N, iii-1958, Darlingtons (CUIC, 1; MCZ, 19); Mt. Webb, 3 km NE, 15. 03°S 145. 09°E, 03-v-1981, Calder (ANIC, 1); Woondom For. Res., Mothar Mtn. For. Dr., dry rainfor., palm gully, FMHD #2004-217, berl. wet litter along stream, Solidovnikov 1139, 26°15.77’S 152°49.48’E, 380-400 m, 09–xii–2004, Solidovnikov (CUIC, 2; FMNH, 24); FMHD #2004-218, berl. litter under palms, Thayer 1139, 26°15.77’S, 152°49.48’E, 09–xii–2004, Thayer (CUIC, 3; FMNH, 10); Thayer 1139, pyr. fog old logs, 26°15.77’S, 152°49.48’E, 380-400 m, 09–xii–2004, Thayer (FMNH, 1).

Etymology. The species commemorates Prof. Philip J. Darlington, who collected extensively across Australia during various expeditions undertaken throughout his career. He personally developed the most extensive collection of Australian Carabidae housed in North America, allowing American scientists the ability to work with the fauna. He also curated the Thomas G. Sloane collection after its receipt by C.S.I.R.O., stabilizing the specimens and thereby preserving their information for future researchers. Although he focused on the New Guinea carabid fauna (summarized in Darlington 1971), he rightfully viewed the New Guinean fauna as an extension of the Australian, making biogeographic connections underpinned by taxonomic relationships for much of the Australian Region (Wallace 1876).

Distribution and habitat. *M. darlingtoni* is broadly distributed along the Queensland coast, with recorded localities spanning the vicinity of Brisbane to Mt. Webb in northern Queensland (Fig. 11C). The extensive numbers of specimens collected in Woondom Forest Reserve (FMNH) were extracted from Berlese samples from mesic litter under palms, or from wet litter along a stream. The single specimen from the northerly and, based on present specimens, disjunct Mt. Webb locality is macropterous, as is one of the two specimens from Dalby, whereas all other specimens from southern Queensland are vestigially winged.

Mecyclothorax jameswalkeri, sp. n.

http://zoobank.org/27A7A15F-B09B-4B59-9F8E-CB0AA17A78A2
Figures 4B, 11C

Diagnosis (n = 1). This, the second of two Australian species of subgenus *Eucyclothorax*– with *M. darlingtoni*– characterized by the absence of basal pronotal setae, can be diagnosed by aspects of the narrow body, including: **1**, a narrow, basally constricted pronotum, MPW/PL = 1.28, MPW/BPW = 1.88; and **2**, narrow, subparallel elytra, MEW/EL = 0.64. Like *M. darlingtoni*, the prosternum of this species has a punctate medial depression anterad the prosternal process, in this instance lined with 7 punctures. The prosternal anteapical groove is continuous and distinctly punctate laterally, more irregular and smoother ventrally. The eyes are large and moderately convex, and they cover much of the ocular lobe; EyL/OLL = 0.95. The parascutellar striole is composed of 7–8 deep, isolated pits. Standardized body length 4.9 mm. Setal formula ++/+–/+2++.

Description. Head elongate with large eyes (Fig. 4B), vertex broadly convex between deep, sinuously convergent frontal grooves that continue anterolaterally onto clypeus, anterior supraorbital seta in deep depression behind frontolateral callous; labrum broadly, slightly emarginate; mandibles elongate, overall length 1.9× distance from anterior condyle to lateroapical labral margin; mentum tooth with obtuse side, apex shallowly bifid; mentum breadth/length across lateral lobes = 2.57. Pronotum with

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lateral setal articulatory socket within associated expansion of lateral marginal depression, the lateral marginal depression otherwise broad enough to observe microsculpture at its deepest part, its margin beaded; hind angle obtusely rounded, the lateral margin slightly sinuate before angle; medial base unmargined inside marginal bead that extends only slightly inside hind angle, convex, with ~10 small punctures each side from midline to laterobasal depression; laterobasal depression a narrow oblique groove extended from mesad sinuate lateral margin toward middle of disc; median longitudinal impression very fine and shallow, occluded by broad, shallow transverse wrinkles, deepest between arms of anterior transverse impression; anterior transverse impression smooth, continuous from near midline to rounded, slightly protruded front angles; marginal bead of procoxal cavity lined anteriorly with 3 small isolated punctures: proepisternum impunctate. Mesepisternum punctate at its deepest portion, about 9 deep punctures in 2–3 dorsoventral rows. Elytra with serially punctate striae 1–6, stria 7 absent except near subapical seta; elytral punctures round with distinct center point, separated by their diameter on disc, smaller in stria 6 where separated by 2 punctural diameters; sutural stria distinctly punctate basally, becoming smoother toward apical 1/4 of length, but sutural interval slightly convex (teneral condition?), the transition from punctate to smooth as in Fig. 12A; stria 8 deep, punctate and bordering lateral marginal depression anteriorly, deeper, smooth and distinct mesad posterior series of lateral elytral setae; lateral elytral setae arrayed as 7 + 6 (anterior series setae and posterior series setae); subapical sinuation evident, abruptly curved anteriorly, but elytral plica covered by margin in dorsal view. Metepisternum moderately elongate, maximum width/lateral length = 0.44; metasternal process acute, apex knob-like, margins upraised, twice at broad at apex; metathoracic flight wing macropterous, veins evident in folded condition under teneral elytra, apex reflexed. Abdomen with linear wrinkles laterally on visible ventrites 1–3, shallow rounded depressions laterally on ventrites 3–6; suture between ventrites 1 and 2 slightly sinuate, deep midway along suture; female with 2 marginal setae each side of apical ventrite plus a trapezoidal patch of 4 smaller medial setae. Microsculpture of frons indistinct, surface glossy, vertex with indistinct transverse mesh in parts; pronotal disc and median base with shallow transverse mesh, sculpticell breadth 3–4× length, sculpticells irregularly swirling in laterobasal depressions; elytral disc with transverse lines loosely connected into mesh, the surface subiridescent; elytral apex with transverse lines in a loose mesh, the convex, estriate surface iridescent. Coloration (assessed on single teneral specimen) of vertex rufous with brunneous cast; antennomeres 1–3 rufoflavous, 4–11 with piceous cast; pronotal disc dark rufous, margins paler, flavobrunneous; elytral disc rufobrunneous, sutural interval concolorous, lateral marginal depression rufoflavous, translucent; elytral apex broadly flavobrunneous; proepipleuron rufoflavous, proepisternum rufobrunneous; abdomen rufobrunneous, apical half of apical visible ventrite paler, rufoflavous; femora and tibiae flavous with brunneous cast.

Female reproductive tract (n = 1). The single teneral female specimen of this species was not dissected.

Holotype. Holotype female (BMNH): Albany / W. Australia / J.J. Walker // G. C. Champion Coll. / B. M. 1927–09 // HOLOTYPE / Mecyclothorax / jameswalkeri / J.K. Liebherr 2018 [black-bordered red label].

Etymology. This species commemorates James John Walker, Commander and Fleet Engineer, Royal Navy, active member and officer in many scientific societies–including President of the Linnean Society of New South Wales (Walker 1921)–and in retirement, an editor of the Entomologist's Monthly Magazine (Poulton 1939). Walker's collections from Australia and New Zealand were passed to George C. Champion, his brother-in-law, and then bequeathed by Champion to The Natural History Museum, London. Walker's collections were as far flung as the British Empire, with his naval duties taking him to places where he could collect. Among many other species, carabid beetles named after him include: *Protopaussus walkeri* Waterhouse (1897) from China; *Calosoma walkeri* Waterhouse (1898), junior synonym of *C. oceanicum* Perroud, from Australia; *Rhaebolestes walkeri* Sloane (1903) from New South Wales; *Duvaliomimus walkeri* (Broun 1903), *Megadromus walkeri* (Broun, 1903), and *Mecodema walkeri* Broun (1903), the last a junior synonym of *Mecodema howitti* (Castelnau 1867), all from South Island, New Zealand; and *Trirammatus walkeri* (Andrewes 1931) from Juan Fernandez Island. Walker's collecting acumen can be attested to by his discovery of this broad assortment of carabid diversity.

Distribution and habitat. The lone specimen of this species is from Albany, W.A. (Fig. 11C). We know nothing specific about the habitat in which this beetle was discovered. The specimen is macropterous with the wings bearing well-developed venation and a reflexed apex, the wing structures being visible through the very translucent elytra of the teneral specimen. Thus occupation of a riparian habitat requiring recolonization of habitat patches may be predicted (Darlington 1936, 1943).

Mecyclothorax lophoides (Chaudoir)

Figures 2F, 4C–D, 9F, 10F, 11C, 12B, 13B, 14A–C

Anchomenus lophoides Chaudoir, 1854: 135.
Platynus lophoides Gemminger & Harold, 1868: 373.
Cyclothorax lophoides Blackburn, 1892: 481.
Agonum lophoides Csiki, 1931: 848.
Mecyclothorax lophoides Moore, 1984: 164.
Cyclothorax punctipennis Blackburn, 1889: 1388 (misidentification?, Blackburn 1892: 481).

Diagnosis (n = 5). This species is characterized by a narrow, moderately cordate pronotum, the lateral margins slightly sinuate anterad obtuse, moderately projected hind angles (Fig. 2F); MEW/BPW = 1.57–1.68, MPW/

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PL = 1.18–1.22. The pronotal lateral marginal depression is very narrow, with only the narrowest indication of microsculpture between the convex disc and the marginal bead. The hind angle is obtuse, rounded at its apex, with the basal pronotal seta set slightly anterad the angle. The marginal depression continues for only a short distance mesad the hind angle. The median base is covered with ~10 erratically distributed small punctures each side of midline. The laterobasal depression is a longitudinal depression lined with 4–5 larger punctures, with the flat area between depression and the marginal bead also bearing several larger punctures. The prosternum is medially depressed from the prosternal process between the procoxae 1/2 the distance toward the anterior margin, the depression lined with 6–7 pits. The anteapical groove is shallowly punctate laterally, continuous and irregularly indented medially, and the marginal bead of the procoxal cavity is bordered anteriorly by about 3 very shallow punctures. The mesepisternum is punctate at its deepest portion, about 9 deep punctures in 2–3 dorsoventral rows. The elytra are narrowly subparallel (Fig. 4C–D), with the humeral angles distinctly obtuse; MEW/EL = 0.64–0.69. The parascutellar striole is composed of 4–6 small, deep, isolated punctures. Elytral striae 1–6 are present on the disc, though striae 2–6 are absent basally and from the apical quarter to half, the outer striae progressively shorter. The strial punctures are isolated, progressively so apically, and the sutural stria is smooth or only slightly punctate in the apical half (Fig. 12B). Body coloration varies from dark brunneous (Fig. 4C) to piceous (Fig. 4D), with the legs correspondingly brunneous to piceous; i.e. there is less contrast between leg and body color than in *M. peryphoides* (Fig. 5B) or *M. cordicollis* (Fig. 5C). The elytral apex may be slightly paler than the disc in the brunneous specimens, however any difference is gradual, not a distinct transition as in *M. cordicollis* (Fig. 5C). Elytral margins are concolorous with the disc in the darker specimens. Cuticular microsculpture is relatively less developed in this species than in *M. darlingtoni*, *M. jameswalkeri*, *M. peryphoides*, or *M. cordicollis*, with: **1**, frons glossy, indistinct transverse lines visible over portions of the surface; **2**, pronotal disc glossy with shallow elongate transverse microsculpture visible outside the area of reflection; **3**, flat elytral intervals covered with dense transverse lines producing an iridescent reflection. Standardized body length 3.8–4.9 mm. Setal formula ++/++/+2++.

Male genitalia (n = 12). Aedeagal median lobe dorsoventrally broad, the apex broadly rounded and slightly projected beyond the apical margin of ostium (Fig. 14A, C); flagellum elongate and hooklike, the flagellar sheath of similar length, its surface scabrous (Fig. 14A–B), dorsal plate ovoid, lightly sclerotized (Fig. 14B); right paramere expanded basally, narrowed beyond midlength, the ventral surface with ~9 setae along margin, dorsal margin with 4 setae in apical half (Fig. 13B); left paramere narrow basally, evenly narrowed to apex.

Female reproductive tract (n = 2). Bursa copulatrix squat, as broad as long (Fig. 9F); helminthoid sclerite broad basally, with distinct mediodistal projection; spermathecal duct straight, narrow, evenly sclerotized, as long as spermathecal reservoir; basal gonocoxite with 4–5 apical setae plus a large seta at the apicomedial angle (Fig. 10F); apical gonocoxite subtriangular, broadly rounded apically; lateral ensiform setae small, narrow; apical nematiform setae in apical sensory furrow.

Type information. Lectotype male (MNHN) hereby designated: pointed specimen // Musaeo Chaudoir [red typeface] // Lectotype [red label] // Museum Paris / ex. Coll. Oberthur // Mecyclothorax (Ch.) det. P. M. Johns. There are also a male paralectotype and a female paralectotype (MNHN).

Distribution and habitat. *M. lophoides* is allopatrically distributed to the south of its adelphotaxon *M. darlingtoni*, with localities ranging from northeastern New South Wales southward through eastern N.S.W. to Melbourne (Fig. 11C). Non-type material and repositories include: A.C.T.: Paddy's R. 1 mi. S Cotter Dam (ANIC, 1); Smoker's Gap 43 km SW Canberra (CAS, 10; CUIC, 2): NSW: Blackheath (MVM, 1); Braidwood (CUIC, 2; MCZ, 37); Mt. Kosciuszko (MCZ, 2); New England N. P., Thungutti Camp (ANIC, 3): VIC: Dandenong Ck. (MVM, 1); Gellibrand R., Otway Ranges (MCZ, 1); Oakleigh (MVM, 1); Portland to Pt. Fairy (CUIC, 1; MCZ, 21); Wilson's Promontory (ANIC, 1); Winchester (MCZ, 1).

Specimens of this species collected by John Nunn on King Island (Moore 1984: 164) were preceded temporally by beetles laid down from 143,000–75,000 years ago in subfossiliferous deposits at Yarra Creek, King Island, during the Pleistocene last interglacial (Porch et al. 2009). Long-term residence on King Island suggests the species can persist in communities ranging from the present more mesic, more seasonal forest types to the wetter, more aseasonal forests present on King Island during the Pleistocene. All specimens are vestigially winged.

Mecyclothorax eyrensis (Blackburn)

Figures 2G, 5A, 9G, 10G, 11D, 12C, 13C, 14D

Cyclothorax eyrensis Blackburn 1892: 480.
Mecyclothorax eyrensis Csiki, 1929: 488.

Diagnosis (n = 5). Among species of the *M. lophoides* complex this species stands out based on its rufous coloration (Fig. 5A), and distinctly cordate pronotum with projected, nearly right hind angles (Fig. 2G). In the most melanized specimens, the forebody–head and pronotum–may be rufopiceous, but the elytra retain rufous coloration, and the legs are pale, flavous, with a slightly smoky piceous cast. The eyes are moderately convex, MHW/mFW = 1.51–1.57, less convex than those of the other *M. lophoides* complex species (Figs 4, 5B–C). The pronotum is quite constricted basally, MEW/BPW = 1.76–1.82, and moderately transverse, MEW/PL = 1.22–1.28. The pronotal lateral marginal depression is moderately broad, with the marginal bead only slightly upraised. The me-

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dian base is minutely punctate, with 5–8 isolated punctures each side from midline to the ill-defined laterobasal depressions, those defined mostly by a longitudinal line of larger punctures, with several larger punctures also present between that line and the marginal bead. The hind angle is right to slightly obtuse, with the posterior margin transverse and anterad the convex median basal margin, which is smooth not beaded. The prosternum is flat to depressed medially, the medial area bearing a longitudinal series of 7 distinct punctures. The anteapical groove is deep and distinctly punctate laterally, continuous and more shallowly punctate medially, and the marginal bead of the procoxal cavity is bordered anteriorly by 5–6 strigose punctulae. The mesepisternum is covered with punctures, about 13 deep punctures arrayed in 3–4 irregular rows. The elytra are relatively broad, MEW/EL = 0.67–0.73, and flat medially on disc. Elytral striae 1–4 bear large punctures, those serial punctures close set enough on the disc to depress the intervening cuticle. Strial punctation is more strongly developed in this species than in other species of the *M. lophoides* complex (Fig. 12), with the sutural stria distinctly punctate mesad the posterior dorsal elytral seta. In this species cuticular microsculpture is less well developed than in the other *M. lophoides* complex species, with: **1**, frons smooth, glossy, with micropunctures sporadically visible across surface; **2**, pronotal disc glossy with sporadic micropunctures visible, very transverse lines sporadically visible laterally and near concavities of median longitudinal impression and laterobasal depression; **3**, elytral discal intervals largely glossy, with shallow transverse lines sporadically visible over surface (Fig. 12C), transverse microsculpture more developed on elytral apex where it forms an elongate transverse mesh, sculpticells 3–4× broad as long. Body coloration varies from a bright rufous, mostly in desert inhabiting beetles from the northern part of the range including the type locality of Leigh's Creek (Fig. 11D), to darker with rufopiceous head and pronotum and rufous elytra at localities on the southern edge of the range; Mt. Remarkable and Telowie Gorge. Even in the darker specimens, the base of the pronotum is an amber rufous, the cuticle appearing translucent. Standardized body length 4.2–5.5 mm. Setal formula ++/++/+2++.

Male genitalia (n = 10). Aedeagal median lobe broadest near basal 1/3 of length, ventral margin distinctly and evenly curved (Fig. 14D); internal sac bearing a long sinuous flagellum, a large bean-shaped dorsal plate, and a well-sclerotized, smooth flagellar sheath, the sheath length less than 1/4 flagellar length (Fig. 14D, as in Fig. 14F); right paramere expanded dorsally in basal half, the dorsal margin convex, 7–11 setae along ventral margin and ~1 on dorsal margin (Fig. 13C); left paramere broadly quadrate basally, extended as a narrowly attenuated whip to apex. Comparing the dissected aedeagi of 10 *M. eyrensis* males (e.g. Fig. 14D) and 16 *M. peryphoides* males (e.g. Fig. 14E) resulted in no discernible differences in overall shape of the median lobe, in curvature or expanse of the apex, in the basal bulb or development of the sagittal crest, nor in structures of the internal sac such as the flagellum, flagellar sheath, or dorsal plate (Fig. 14D–E). The only male genitalic differences noted between males of these two species involved the presence of fewer setae along the ventral margin of the right parameres of *M. eyrensis* versus *M. peryphoides* (e.g. Fig. 13C–D). To determine whether these differences could diagnose the species, the numbers of setae along the ventral margin of the right paramere in 10 individuals of *M. eyrensis* (setal numbers: 7, 7, 8, 8, 8, 8, 9, 11, 11, 11) were compared to those in 15 individuals of *M. peryphoides* (setal numbers: 9, 10, 10, 11, 11, 11, 12, 12, 13, 13, 13, 14, 15, 15, 17) using the Wilcoxon rank-sum test (Snedecor and Cochran 1980). The distribution of values resulted in a minimal $T_1 = 69$, below the threshold value of 84 for a $p = 0.01$ level of significance for difference between the two distributions (Supplementary material 2). Even though the values among individuals overlap slightly in the 9–11 setal counts, there is a statistically significant difference between the setal configurations of the two species. This significant difference augments the diagnostic differences found in the external characters.

Female reproductive tract (n = 3). Bursa copulatrix short, slightly longer than broad (Fig. 9G); helminthoid sclerite broad basally, with narrow, elongate mediodistal projection; spermathecal duct elongate, sclerotized enough to hold coiled configuration, length ~2× length of spermathecal reservoir; basal gonocoxite with 2–6 apical setae, 2–4 of those larger and the balance smaller, plus a similarly sized seta at the apicomedial angle (Fig. 10G); medial surface of basal gonocoxite with several smaller setae along length; apical gonocoxite subtriangular, narrowly rounded apically; lateral ensiform setae small, narrow; apical nematiform setae in apical sensory furrow.

Type information. Lectotype male (BMNH) hereby designated: platen mounted with "2710 T / L. C. (red ink) // Type (round, red-margined label) // Blackburn coll. 1910-236 // Cyclothorax eyrensis Blackb. // Lectotype Cyclothorax eyrensis Blackburn / J.K. Liebherr 2006 [black-margined red label]. The abbreviation "L. C." stands for Leigh Creek based on the labels below. Paralectotype female (SAMA): platen mounted with L. C. 2710 in red ink // Leigh Ck. C.A. / Blackb's Coll. // Cyclothorax eyrensis Bl. / Co-type // Mecyclothorax eyrensis Blkn / S. Australia / Cotype [red ink] // Paralectotype ♀ / Cyclothorax / eyrensis Blackburn / det. J.K. Liebherr 2004 [black-margined red label]. The type locality is Leigh Creek, South Australia.

Distribution and habitat. This species is distributed across the interior of southeastern Australia (Fig. 11D), in South Australia from Telowie Gorge to Mt. Remarkable (FMNH), eastward to western N.S.W., and northward into southern Northern Territory at Palm Valley and Stokes Creek in the Gill Range (FMNH). Localities and repositories for non-type material include: NSW: Silverton (ANIC, 1). NT: Gill Range, Stokes Ck. (CUIC, 1; FMNH, 2); Palm Valley (FMNH, 1). SA: Flinders Ranges, Bunyeroo Gorge (CUIC, 1; FMNH, 14), Telowie Gorge

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(CUIC, 2; FMNH, 5); Mann Range, 0.5 km N Angatja Homestead (CUIC, 1; FMNH, 1); Musgrave Range, 13 km N Ernabella (CUIC, 1; FMNH, 10), 15 km W Officer Ck. (FMNH, 10), 17 km W Jacky Pass (CUIC, 1); Mt. Remarkable (CUIC, 6; FMNH, 94); Wilmington (MVM, 3); Yunta (FMNH, 3). The extensive collections made by L. Watrous (FMNH) were obtained from sieved litter or reed drift from along dry or running streams. Nonetheless, and going against Darlington's generalization for riparian species, all observed individuals are vestigially winged.

Mecyclothorax peryphoides (Blackburn)

Figures 2H, 5B, 9H, 10H, 11D, 12D, 13D, 14E–F

Cyclothorax peryphoides Blackburn 1889: 1392.
Cyclothorax peryphoides Sloane, 1895: 446.
Mecyclothorax peryphoides Csiki, 1929: 489.
Mecyclothorax cordicollis Jeannel, 1940: 100 (misidentification).
Mecyclothorax lophoides Liebherr, 2011a: 292, table 2 (misidentification).

Diagnosis (n = 5). Among the species of the *M. lophoides* complex characterized by darker bodies and contrastingly pale legs (Figs 4B, 5B–C), this species has an ellipsoid elytra with large strial punctures, a pronotum with distinct obtuse hind angles, and concolorous elytral disc and apex, i.e. without an apical flavous marginal band (Fig. 5B). The eyes are broadly convex, MHW/mFW = 1.60–166. The pronotal margins are sinuate anterad the well-defined hind angles, but the posterior margin behind the angle is at most slightly sinuate, and usually convex, smoothly meeting the curved median basal margin (Fig. 2H). Body coloration is dark, with the head, pronotum and elytra piceous. The pronotum is transverse and constricted basally–MEW/EL = 1.20–1.28, MPW/BPW = 1.63–1.71–though the basal constriction less than that observed in beetles of *M. eyrensis*; MEW/BPW = 1.76–1.82. The pronotal median base is covered with distinct punctures, about 20 punctulae each side from midline to the very shallow, poorly defined laterobasal depression (Fig. 2H). The pronotal lateral marginal depression is narrow, but broad enough for sculpticells to line the deepest part, and the margin is beaded. Like *M. eyrensis*: **1**, the prosternum is flat to depressed medially, the medial area bearing a longitudinal series of 4–7 distinct punctures; **2**, the anteapical groove is deep and distinctly punctate laterally, continuous and more shallowly punctate medially; **3**, the marginal bead of the procoxal cavity is bordered anteriorly by 5–6 strigose punctulae; and **4**, the concave mesepisternal surface is lined with 13 deep punctures arrayed in 3–4 irregular rows. The elytral striae are punctate on the disc, though the punctures are far enough apart that the cuticle is coplanar with the intervals between the punctures. Like *M. eyrensis*, the punctures of striae 1–6 are progressively more isolated laterally on the elytra, but the sutural stria is more shallowly and irregularly punctured mesad the posterior dorsal elytral seta in this species (Fig. 12C–D). Cuticular microsculpture is well developed in this species, with: **1**, frons covered with indistinct transverse lines, vertex with more well-developed sculpticells, transforming from transverse just behind posterior supraorbital setae to nearly isodiametric near pronotum; **2**, pronotal disc with indistinct transverse lines visible outside areas of direct reflection, irregular surface of pronotal base covered with irregular transverse mesh; **3**, elytral disc with transverse lines visible outside areas of direct reflection, apex covered with well-developed elongate transverse mesh. Standardized body length 4.3–5.0 mm. Setal formula ++/++/+2++.

Male genitalia (n = 16). As stated under *M. eyrensis*, the aedeagal median lobe and flagellar complex of that species and *M. peryphoides* show no differences (Fig. 14D–E). However the right paramere of this species bears significantly more setae (9–17) along its ventral margin.

Female reproductive tract (n = 3). Bursa copulatrix short, slightly longer than broad (Fig. 9H); helminthoid sclerite broad basally, with narrow mediodistal projection; spermathecal duct elongate, sclerotized enough to hold coiled configuration, length ~2× length of spermathecal reservoir; basal gonocoxite with 3–6 apical setae, 2–3 large and the balance smaller, plus a similarly sized seta at the apicomedial angle (Fig. 10H); medial surface of basal gonocoxite with larger setae apically; apical gonocoxite subtriangular, narrowly rounded apically; lateral ensiform setae small, narrow; apical nematiform setae in apical sensory furrow.

Type information. Holotype male (BMNH): platen mounted with "1614" in red ink and "T" in black ink on the obverse, with basal marginal black and red lines, the red crossed by an arrowhead // Type (round red-margined label) // Blackburn coll. 1910-236. // Cyclothorax periphoides [sic.], Blackb. Blackburn states the type locality as "Woodville, near Adelaide; a single specimen (Blackburn 1889: 1393)."

Distribution and habitat. This species is distributed (Fig. 11D) to the south of its sister species, *M. eyrensis*, in South Australia. The type locality of Woodville is near recent collections made at Belair Recreation Park, 10 miles S of Adelaide (FMNH), Blackwood, Sturt Gorge Reserve (ZMUC), and Hale Conservation Park SE Williamstown (FMNH). To the east the species is recorded from the following localities: A.C.T.: Black Mountain (CUIC, 8; EMEC, 1); NSW: Belmore (AMS, 1); Bogan R. (AMS, 1); "Calosoma" via Gundaroo (ANIC, 4); Federal Hwy. (ANIC, 1); Jerrawa (AMCS, 2); Mt. Wilson (CUIC, 1; FMNH, 4); Narrabeen (AMS, 1); Queanbeyan (ANIC, 1); Tuglo Wldlf. Ref. 48 km N Singleton (FMNH, 1); Weddin Mtns. N. P. (FMNH, 1); VIC: Lake Eildon N. P., Sebastopol Ck. (ZMUC, 1). Collections have been made via litter sifting along streams or in *Eucalyptus* (Myrtaceae) or mixed deciduous forest, or in rainforest on Mt. Wilson. As for *M. eyrensis*, even though this species occupies predominantly riparian situations, it appears to be vestigially winged.

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***Mecyclothorax cordicollis* (Sloane)**

Figures 2I, 5C, 9I, 10I, 11E, 12E, 13E, 14G–H

Cyclothorax cordicollis Sloane 1900: 563.
Mecyclothorax cordicollis Csiki, 1929: 488.

Diagnosis (n = 5). This species (Fig. 5C) and *M. lophoides* (Fig. 4C–D) include the smallest-bodied, most gracile beetles in the *M. lophoides* species complex, with standardized body length for this species = 4.0–4.7 mm. Individuals exhibit a flavous marginal band on the elytra, brunneous to rufobrunneous body, and pale, flavous legs. The pronotum is very similar to that of *M. lophoides* (Fig. 2F, I); moderately transverse, MPW/PL = 1.17–1.24, and basally constricted, MPW/BPW = 1.62–1.68, these values broadly overlapping those calculated from specimens of *M. lophoides*. The eyes are also similar in configuration in the two species: here MHW/mFW = 1.63–1.71, with the eyes covering most of the ocular lobe, EyL/OLL = 0.86–0.91. The pronotal lateral marginal depression is slightly broader in this species than in *M. lophoides*, with microsculpture evident in its deepest part. The pronotal hind angles are obtusely rounded, with the margin behind the angle smoothly curved onto median base. The marginal bead terminates at the laterobasal depression just mesad the hind angle, and the bead is only slightly broader at the setal insertion. The pronotal median base is covered with 10–13 large isolated punctures present each side of midline. The laterobasal depression is defined by a medially arcuate line of punctures commencing at the termination of the marginal bead mesad the basal seta. The prosternum is medially depressed from the prosternal process anterad slightly less than 1/2 the distance to the anterior margin, the depression broader anteriorly, and lined with ~8 pits. The anteapical groove is punctate laterally, continuous and indistinctly punctate medially, and the procoxal cavity marginal bead is bordered by 4–5 small punctures along its anterior margin. The mesepisternum is variously punctate, the deepest portion covered with about 9 shallow to deep punctures arranged in 2–3 dorsoventral rows. The elytra are broad basally, subparallel, and broad relative to their length (Fig. 5C), MEW/EL = 0.69–0.71, versus values of 0.64–0.69 for individuals of *M. lophoides* (Fig. 4C–D). The elytral disc is flat, with the sutural intervals apically raised into a callus. Elytral striae 1–6 are distinctly punctate on the disc, with the punctures nearly contiguous on the inner striae, however the intervening intervals are nearly flat. As in the other *M. lophoides* complex species, strial punctures are smaller and therefore further apart along the lateral striae, though in this species stria 6 is indicated until posterad midlength. As in *M. peryphoides*, the sutural stria is indistinctly punctate mesad the posterior dorsal elytral seta (Fig. 12D–E), but the punctures in striae 2–4 are more well developed, agreeing with *M. eyrensis*, but not *M. lophoides* (Fig. 12 B–C). Coincident with the presence of a flavous marginal band on the darker elytra, other body coloration tends toward the polychromatic: **1**, elytral epipleura dorsally flavous versus ventrally rufobrunneous adjacent to the metepisternum; **2**, coxae dark brunneous, trochanters rufous, femora flavous, and tibiae and tarsomeres brunneous with smoky cast. Cuticular microsculpture includes: **1**, vertex glossy with an indistinct transverse mesh in parts; **2**, pronotal disc glossy with an elongate transverse mesh restricted to transverse wrinkles, and a shallow elongate transverse mesh on the median base, sculpticells more irregular in the laterobasal depression; **3**, elytral disc with a shallow, elongate transverse mesh, sculpticell breadth 3–4× length, the convex apex covered with traceable transverse lines, the entire elytral surface subiridescent. Setal formula ++/++/+2++.

Male genitalia (n = 13). Aedeagal median lobe of moderate dorsoventral breadth (Fig. 14G), evenly curved as in *M. lophoides* (Fig. 14A); flagellar complex including a very short, spine-like flagellum, a bifurcated flagellar sheath, and a lightly sclerotized, ovoid dorsal plate (Fig. 14H); right paramere broader basally, conchoid, with ~12 setae along ventral margin and 2–3 small setae on dorsal margin (Fig. 13E); left paramere broadest basally, but evenly narrowed to whiplike apex, the apex flexible and often twisted relative to base when aedeagus mounted on slide.

Female reproductive tract (n = 1). Bursa copulatrix squat, as broad as long (Fig. 9I); helminthoid sclerite broad basally, with narrow elongate mediodistal projection; spermathecal duct straight and narrow, evenly sclerotized, of similar length to spermathecal reservoir; basal gonocoxite with 2–3 apical setae, 2 larger setae laterally, and a moderately sized seta at the apicomedial angle (Fig. 10F); apical gonocoxite subtriangular, narrowly rounded apically; 1–2 small lateral ensiform setae present; apical nematiform setae in apical sensory furrow.

Type information. Lectotype male (ANIC) hereby designated: 2nd specimen from left on 6-specimen platen, specimen annotated "♂ -w", male genitalia dissected and placed in polyethylene genitalia vial below labels // Cyclothorax Type / cordicollis Sl. MSS. / Colombo Plains 11/6/95 // C. cordicollis Sl. / Holotype / PJD not HT JKL 18 [pink label with Holotype crossed out] // ANIC Database / 25 014958 // ANIC Specimen [green label] / ANIC Image [orange label] // Lectotype / Cyclothorax / cordicollis / J.K. Liebherr 2017 [black-margined red label] / Mecyclothorax / cordicollis / (Sloane) ♂LT / det. J.K. Liebherr 2018. Although P.J. Darlington labelled these specimens as "Holotype", a lectotype must be designated given Sloane's description stating the multiple localities given as "Queensland–Brisbane (sent by Mr. Lea); N.S. Wales–Clarence River and Windsor (Lea), Grenfell, Junee, Urana, Mulwala (Sloane); Victoria–Ferntree Gully and Lilydale (Sloane) (Sloane 1900: 564)." Columbo Creek [Colombo Plains sic] is near and northwest of Lake Urana and the town of Urana, and so these specimens would correspond to the "Urana" locality of Sloane's list. Moreover, Sloane wrote regarding the habits of these beetles; "Found in damp situations near water, usually rare, but on July 11th, 1895, I found it very plentifully under sticks along the edge of a swamp about 20 miles north

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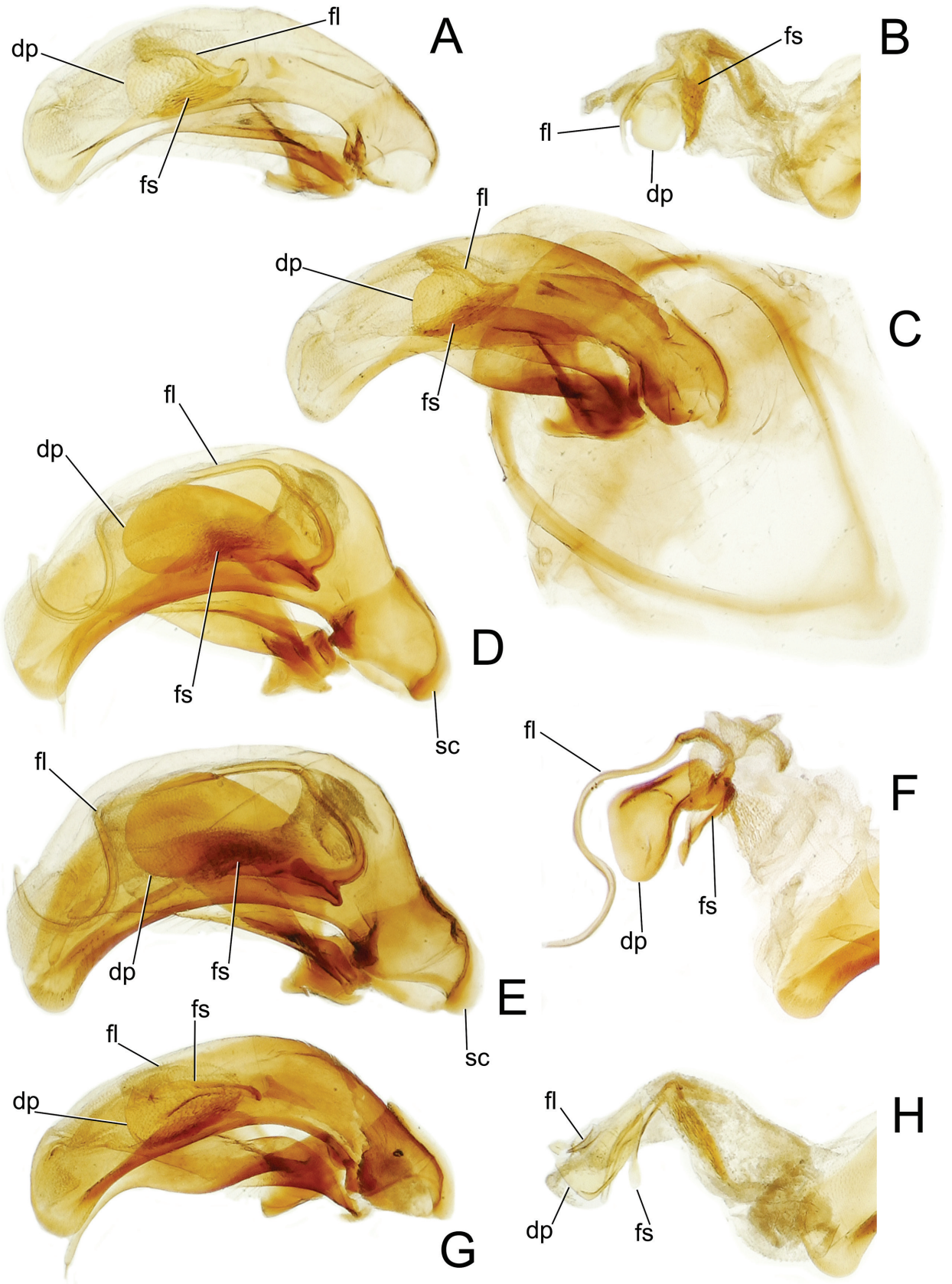

Figure 14. Male aedeagus, right view, for *Mecyclothorax* (*Eucyclothorax*) spp.: **A**, *M. lophoides*, ACT: Paddy's R.; **B**, *M. lophoides* everted internal sac, NSW: Braidwood.; **C**, *M. lophoides*, lectotype, aedeagus *in situ* with laterotergite IX, or ring sclerite, VIC: Melbourne; **D**, *M. eyrensis*, NSW: Silverton; **E**, *M. peryphoides* holotype, SA: Woodville; **F**, *M. peryphoides* everted internal sac, ACT: Black Mountain; **G**. *M. cordicollis*, VIC: Melbourne; **H**, *M. cordicollis* everted internal sac, NSW: Bodalla.

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from the town of Urana (Sloane 1900: 564)." As the label clearly reads "11/6/95" and Sloane wrote of "July 11th, 1895", some ambiguity concerning the date of this collection remains [though the label data would hold precedence]. However no such ambiguity can be countenanced regarding this collecting locality.

Distribution and habitat. Sloane (1900) described this species from specimens representing much of the distributional range as now known augmented by more than another century of collections (Fig. 11E), with the single notable exception of two specimens collected by the Darlingtons, ii–1958, at Ravenshoe, W of the Atherton Tableland (MCZ, 2). Localities and repositories of other non-type specimens include: NSW: Bodalla (CUIC, 1; MCZ, 10); Gosford (MVM, 2); Narrandera (MCZ, 1); Sydney vic. (CUIC, 1; MCZ, 15); QLD: Blunder (ANIC, 1); Brisbane vic. (CUIC, 2; MCZ, 9); Dalby (ANIC, 2); VIC: Dandenong Vy. (ANIC, 2); Lilydale (ANIC, 1); Melbourne (ANIC, 1); Powlett R. (ANIC, 1).

Sloane's perspicacity with regard to species boundaries is very evident in his sorting out this taxon from the very similar appearing beetles of *M. lophoides* and *M. peryphoides*. What we know about the habits of this species can be taken from Sloane's description, quoted above. The species is uniformly represented by vestigially winged individuals with the exceptions of macropterous beetles from two Queensland localities: **1**, one of two beetles from Ravenshoe; and **2**, two of two specimens from Dalby.

Subgenus *Qecyclothorax* Liebherr

Diagnosis. These robust-bodied species (e.g. Fig. 5D) are geographically restricted to Queensland, Australia, and have been recently revised by Baehr (2003). The pronotum of species in this subgenus is broad, with obtuse or obtusely rounded hind angles. Each elytron bears a single dorsal elytral seta just before midlength (Fig. 5D). The prosternum is medially depressed both between and anterad the procoxal cavities, a condition shared with most member species of *Eucyclothorax*, although punctures are not present in the depression. The elytral striae are reduced; striae 1–3 to 1–4 shallow to evanescent, striae 4– or 5–7 obsolete. Striae 1, 7, or both may be present apically on the elytra, but striae 4–6 are consistently absent there. The elytra are broadly convex, with interval 8 not, or only slightly upraised (*M. lewisensis*) relative to the general curvature of the elytral surface. The suture between abdominal ventrites 1 and 2 is nearly straight, with the second ventrite hardly depressed relative to the first. Body size is small for the genus; standardized body length 2.6–3.7 mm.

The male aedeagal median lobe internal sac bears a flagellum (Liebherr 2018, fig. 4E), and the ventral paramere is elongate-conchoid in shape, broadly to narrowly subtriangular with ventral setae present (Liebherr 2018, fig. 5B; Baehr 2003, fig. 1). The female bursa copulatrix is relatively short (Liebherr 2018, fig. 6D). The spermathecal duct joins the bursa copulatrix-common oviduct juncture.

Member species. Baehr (2003) recognized four species, three of them represented by two subspecies each, for a total of seven specific and subspecific forms. The subspecies described below is added to the inventory of *M. lewisensis*, resulting in three subspecies; *M. lewisensis*, *M. lewisensis uncinatus*, plus the newly described subspecies.

Mecyclothorax lewisensis estriatus, subsp. n.

http://zoobank.org/88C1027C-46AE-4BB2-975F-D327B10E55B7
Figures 5D, 11E

Mecyclothorax lewisensis Moore, 1984: 165.
Mecyclothorax lewisensis uncinatus Baehr, 2003: 74.

Diagnosis (n = 1). This taxon is distinguished from all others of subgenus *Qecyclothorax* by the reduced elytral striation, with only the sutural stria evident, and the positions of all outer striae only traceable by the longitudinal tracks of trachea (Shelford 1915). As for all *Qecyclothorax*, the elytra exhibit only a single dorsal elytral seta positioned near midlength (Fig. 5D). Consistent with membership in *M. lewisensis*, this beetle exhibits a quadrisetose clypeus and a pronotum with explanate lateral margins that are indistinctly sinuate basally. The parascutellar seta are very short and fine, and they are set in shallow depressions, however careful examination allows their discernment along with the fine articulatory sockets from which they extend. Baehr used the comparative breadth of the pronotal base relative to its apex as one criterion to differentiate the two subspecies *M. lewisensis* and *M. l. uncinatus*: the former with a ratio APW/BPW < 0.83 (note inverted ratio herein versus Baehr 2003), the latter with APW/BPW > 0.85. In the single specimen of *M. l. estriatus*, APW/BPW = 0.85. Standardized body length for the type specimen below, 3.3 mm. Setal formula ++/++/+1++.

Description. Head broad, frontal groove deep, arcuately convergent toward clypeus, continued onto clypeus, terminated posteriorly midway between 2 supraorbital setae; eyes moderately convex, MHW/mFW = 1.52, covering much of ocular lobe, EyL/OLL = 0.83; antennae elongate, long enough so that apex would extend to basal 1/4 of elytra, antennomere 9 length/maximal breadth = 1.89; mentum tooth with sides acute, apex broadly rounded; ligular apex narrowed, slightly concave between ligular setae, setae separated by 2 setal diameters; paraglossae extended as far beyond ligular apical margin as distance from base to ligular margin. Pronotum transverse, MPW/PL = 1.41, moderately constricted basally, MPW/BPW = 1.35; lateral pronotal seta placed 1 diameter mesad lateral margin depression, depression very narrow at front, gradually widened to explanate at hind angle; basal margin nearly straight, slightly convex between laterobasal depressions, margin flat and effaced behind laterobasal depressions, a convex roll medially; median base depressed relative to disc, smooth with ~3 small punctures each side mesad laterobasal depression; laterobasal depression a linear to slightly outwardly ar-

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cuate line of 3–4 broad punctures, the area laterad line of punctures broadly convex to explanate lateral margin; median longitudinal impression fine, deep, adjacent depression covered with transverse wrinkles on disc; anterior transverse impression broad, evenly depressed fore and aft, the anterior callosity broadly, slightly convex to front margin; front angles slightly protruded, subangulate with marginal bead mesad angle that is continuous with transverse impression; prosternum depressed medially anterad procoxal cavities, the depression's surface irregular with 3 shallow irregularities disturbing the surface; anteapical groove very shallow laterally discontinuous, not present medially; lateral reaches of prosternum irregular, procoxal cavity with very fine marginal bead. Mesepisternum covered with 7 large, isolated pits on a smooth surface, the pits arranged in 2 dorsoventral rows; metepisternum nearly quadrate, lateral margin length 1.2× maximal width. Elytral broadly hemiovoid (Fig. 5D), convex laterally with sides nearly vertical, disc flattened; basal groove slightly curved laterad position of parascutellar striole, punctate near basal positions of striae 3 and 4 (indicated by tracheae; Shelford 1915), and straight laterally to obtusely angulate humeri; elytral striae obsolete, striae 1 and 2 traceable only by very small serial punctures on disc, stria 3 less easily traced as punctures are irregular and easily confused with micropunctures scattered over cuticle; dorsal elytral setae short, in depressions that span only 1/4-1/2 of third interval; only stria 7 evident on elytral apex as a broad shallow depression connecting the subapical and apical elytral setae; stria 8 deep, present from posterad anterior series of lateral elytral setae, slightly irregular along length behind anterior series of lateral elytral setae; lateral elytral setae arranged as 7 + 6–7 setae; subapical sinuation very broad and shallow, the elytral plica visible in dorsal view. Head capsule with reduced microsculpture, frons glossy and vertex covered with fine transverse lines; pronotal disc glossy, a transverse mesh present over parts, sculpticell breadth 2–3× length; pronotal base glossy, indistinct transverse mesh in laterobasal depression; elytral disc glossy, indistinct transverse lines outside area of reflection, apex glossy with indistinct transverse mesh in irregularly depressed areas. Coloration of head rufous on frons, darker on vertex; antennomeres 1 rufoflavous, 2–11 brunneous; Pronotal disc dark rufous, lateral margins broadly paler, rufoflavous, base a translucent amber; elytral disc rufobrunneous overall, but with a darker transverse field posterad dorsal elytral seta that continues along suture to apex leaving 2 paler lateroapical fields; sutural interval concolorous with adjacent intervals; proepipleuron rufoflavous with darker explanate margin; proepisternum dark rufous with subiridescent reflection; elytral epipleuron broadly rufoflavous, metepisternum rufobrunneous; abdomen rufobrunneous, apical 2/3 of apical ventrite flavous; femora flavous, tibiae flavous with rufous cast.

Female reproductive tract (n = 1). The unique female holotype was not dissected. Nonetheless, the gonocoxae extend from the abdominal apex, allowing the following characters to be assessed: basal gonocoxite with medioapical margin glabrous; apical gonocoxite broad basally with 2 lateral ensiform setae; apical nematiform setae in subbasal sensory furrow. These characters conform to states previously scored for *M. lewisensis* (Liebherr 2018) though they are not definitive.

Holotype female (QMB): QLD: 20°21'S, 148°43'E / Brandy Creek, 150 m / 20 Nov 1992 / Monteith, Thompson / & Janetzki, Pyrethrum // HOLOTYPE / Mecyclothorax / lewisensis / estriatus / J.K. Liebherr 2018 (black margined red label).

Distribution and habitat. The lone specimen of this subspecific taxon is from near the Queensland coast south of Cannonvale (Fig. 11E), approximately 600 km south of the localities near Mossman from where the other subspecies of *M. lewisensis* have been described (Baehr 2003, fig. 6).

Subgenus *M*ecyclothorax Sharp

Diagnosis. This subgenus comprises over 350 species (Liebherr 2018), and so morphological variation among the species is the most extreme observed among the various *Mecyclothorax* subgenera. However, throughout taxa of this subgenus, the labrum is emarginate apically, either distinctly and angularly as in *M. goweri* Moore of Lord Howe Island (Liebherr 2018, fig. 1A), or less so as in *M. aeneipennis* Liebherr of Haleakalā, Maui, Hawai'i (Liebherr 2015, fig. 7). The ligular margin is generally truncate with the ligular setae well separated (Liebherr 2018, fig. 1G), though as exceptions, the ligula is apically rounded in the Papuan taxa *M. brispex* and *M. andersoni* (Liebherr 2017, 2018, fig. 7). The prosternum exhibits a smooth to distinctly punctate anteapical groove, though never any other punctures, such as in the median depression observed among species of subgenus *Eucyclothorax*. The parascutellar striole is present, and may be smooth or punctate, with up to 8 punctures along its length (Fig. 6). Among the mainland Australian species, the pronotal median base is depressed relative to the disc, and punctate; a distinction noted by Blackburn (1889).

The male aedeagus has an internal sac with an apical flagellar plate surrounding the gonopore (Fig. 15E). The female reproductive tract most often has the spermathecal duct entering the bursa copulatrix mediodorsally (Fig. 17C–D), however the sister-species pair *M. lateralis* + *M. minutus* (Fig. 1A) revert to the plesiomorphic configuration wherein the spermathecal duct basally joins the juncture of the common oviduct and the bursa copulatrix (Fig. 17A–B).

Member species. This subgenus is represented by four species in mainland Australia. Numbers of taxa in the substantial radiations from Hawaii, the Society Islands, New Guinea, New Zealand, the Sundas, and Lord Howe, Norfolk, and St. Paul and Amsterdam Islands are summarized in Liebherr (2018: 15).

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Mecyclothorax lateralis (Castelnau)

Figures 2J, 6A, 15A, 16A, 17A, 18A, 19A

Phorticosomus lateralis Castelnau, 1867: 92 (as *Forticosomus*); Castelnau, 1868: 178.
Simodontus lateralis Chaudoir, 1873: 114 (see Nomenclatural note).
Cyclothorax lateralis Sloane, 1895: 448.
Mecyclothorax lateralis Sloane, 1903: 586.
Cyclothorax cinctipennis Blackburn, 1889: 1391 (synonymy Sloane 1895: 448).

Diagnosis (n = 5). This large-bodied species–standardized body length 5.2–6.4 mm–is further distinguished by the rufous to brunneous body with contrasting, flavous elytral margins (Fig. 6A). The labrum is broadly and distinctly emarginate apically. The ligula is truncate apically, with the 2 apical setae separated by 4 setal diameters, the ligular surface longitudinally depressed between the setal articulations. The paraglossae are elongate, apically extended beyond the ligular apical margin twice the distance from ligular margin to their base. The pronotum is robust, transverse, with a convex disc, and depressed and circularly punctate median base (Fig. 2J); MPW/BPW = 1.45–1.56, MPW/PL = 1.35–1.40. The prosternal process is broad, only slightly depressed between the coxae, and convex anterad the coxae. The prosternal anteapical groove is deep and narrow, with only slight irregularities along its length at its deepest part. As in its sister species *M. minutus*, the parascutellar seta is absent. The metepisternum is abbreviated, with lateral length about 2× maximum width, and the metathoracic wings are vestigial in examined material. The suture between visible ventrites 1 and 2 is sinuous, with the area behind markedly depressed. Microsculpture of the head is reduced, with frons glossy, vertex with indistinct transverse sculpticells; pronotal disc and median base glossy, indistinct transverse lines visible in places; elytral surface glossy with well-defined isodiametric sculpticells visible over entire surface, the apex with sculpticells more upraised; thoracic ventrites glossy, abdominal ventrites glossy medially but with isodiametric sculpticells visible in lateral depressions. Setal formula ++/++/–2++.

Male genitalia (n = 1). Aedeagal median lobe moderately broad dorsoventrally, apex narrowly rounded and slightly projected beyond ostium (Fig. 15A); flagellar plate large and lightly sclerotized; right paramere narrow and elongate (Fig. 16A), ventral margin setose, with >20 setae along margin, setae more densely distributed in basal half; left paramere broadly subquadrate basally, apically attenuated into a whip-like apex.

Female reproductive tract (n = 1). Bursa copulatrix broadest at midlength, its surface membranous and covered with pleat-like wrinkles, apex narrowed (Fig. 17A); spermathecal duct narrow, elongate, about twice length of spermathecal reservoir; basal gonocoxite broad, 2–4 setae along apical margin (Fig. 18A), several setae along median margin; apical gonocoxite broadly rounded apically, mesal and lateral margins subparallel; a single broad lateral ensiform seta, its length about 1/3 length of apical gonocoxite; apical nematiform setae in large, apical positioned sensory furrow.

Type information. Lectotype female (MCG) designated by Straneo (1941): specimen glued to platen // Lateralis / Cast. / Paroo riv. // Australia / Paroo River / Coll. Castelnau // LECTOTYPUS / Forticosomus / lateralis / Castelnau, 1867 / des. S.L. Straneo, 1941 [orange label] // Forticosomus / lateralis // Mecyclothorax / lateralis Cast / holotypus / Det. B.P. Moore ‘68 // MUSEO GENOVA / Coll. Castelnau. A female paralectotype accompanies the lectotype. It bears only the newer “Australia / Paroo River / Coll. Castelnau” label and Straneo’s orange PARALECTOTYPUS label. As noted by Straneo (1941: 89), the paralectotype is teneral. For *C. cinctipennis* Blackburn, holotype (BMNH; label data not recorded): Torrens River, S.A. (Moore et al. 1987).

Nomenclatural note. In the paragraph within which Chaudoir (1873) combined *Phorticosomus minutus* Castelnau with *Simodontus* Chaudoir (pp. 113–114), Chaudoir writes “Je crois que son *Ph. lateralis* est encore une espèce de *Simodontus*, qui m’a semblé différente du *curtulus* (p. 114).” Such a statement falls short of a nomenclatural act proposing a valid new combination. Csiki (1929) interpreted Chaudoir (1873) to have officially combined *Ph. lateralis* with *Simodontus*, however his listing the page of that action as Chaudoir (1873: 113) suggests that he did not see the work personally, thus leading him to give Chaudoir credit for a nomenclatural act that Chaudoir did not commit. Sloane agreed that Chaudoir did not combine *Ph. lateralis* with *Simodontus*, writing: “*Ph. lateralis* is a species of *Mecyclothorax*. *Ph. minutus*, from the Paroo River, has been examined by Chaudoir, who referred it to *Simodontus* ... (Sloane, 1915, 462).” Moore’s labelling of the lectotype as holotype was corrected in Moore et al. (1987), where the presence of a paralectotype was also noted.

Distribution and habitat. This species is distributed in interior Victoria, western New South Wales and southeastern South Australia (Fig. 19A). Localities and repositories for non-type specimens I have examined include: SA: Lucindale (MCZ, 1); Pt. Lincoln (MVM, 1); VIC: Bendigo (MVM, 1); Birchip (MVM, 1); Evansford (BMNH, 15); Lake Hattah (MVM, 1); Maldon (MVM, 1); Wedderburn (MVM, 1). These records represent beetles collected between 1911 and 1950, none with any ecological data, and so nothing can be reported with confidence concerning the ecological preference of this species: but see *M. minutus* below. This species is polymorphic for flight-wing configuration, with 3 brachypterous individuals observed among the 27 beetles examined; 2 of the individuals from Evansford exhibit wings that are broad, slightly more than half as long as the elytra, and without a reflexed apex. Other examined individuals have vestigialized wings, with the wing stubs shorter than the metanotum.

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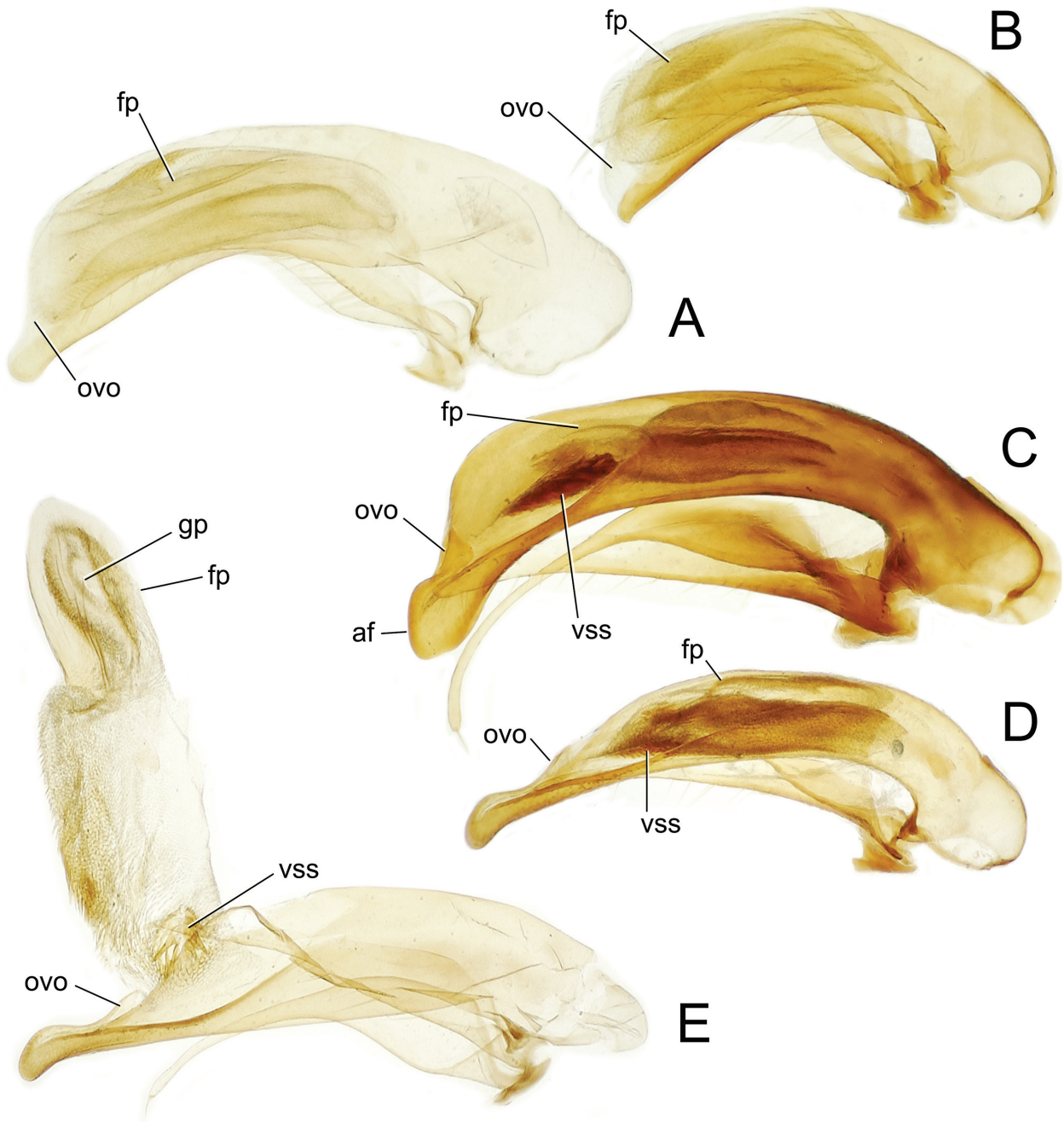

Figure 15. Male aedeagus, right view, for *Mecyclothorax* (*s. s.*) spp.: **A**, *M. lateralis*, VIC: Lake Hattah; **B**, *M. minutus*, WA: Merredin; **C**, *M. ambiguus*, VIC: Penshurst; **D**, *M. punctipennis*, ACT: Black Mountain; **E**, *M. punctipennis* internal sac everted, NSW: Kosciuszko N. P., Bullock Hill Tr.

Mecyclothorax minutus (Castelnau)

Figures 2K, 6B, 15B, 16B, 17B, 18B, 19B

Phorticosomus minutus Castelnau, 1867: 92 (as *Forticosomus*); Castelnau, 1868: 178.
Simodontus minutus Chaudoir, 1873: 113.
Mecyclothorax minutus Csiki, 1929: 488.
Cyclothorax fortis Blackburn, 1889: 1390 (NEW SYNONYMY).
Mecyclothorax fortis Sloane, 1903: 486.

Diagnosis (n = 5). This species shares the rufous to brunneous body color (Fig. 6A–B) and lack of the parascutellar seta with *M. lateralis*, however the beetles are smaller–standardized body length 4.9–5.7 mm–and the elytral lateral and apical margins do not markedly contrast with the elytral disc. In teneral individuals the margins may appear somewhat paler, partly due to reflection of the underlying abdominal tergites through the cuticle, and partly due to a smoky infuscation of the median elytral disc. However, the difference in coloration from disc to

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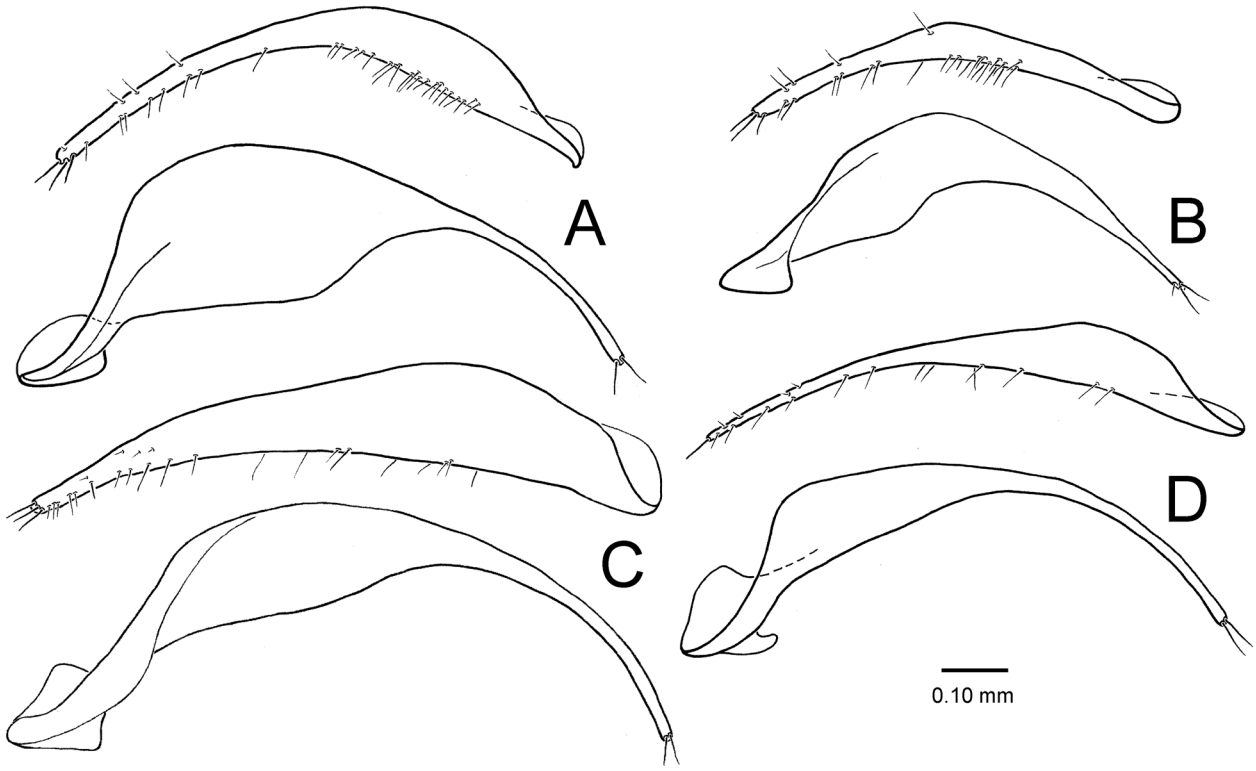

Figure 16. Male parameres of *Mecyclothorax* (s. s.) spp., ectal view, right paramere above in each pair, left paramere below: **A**, *M. lateralis*, VIC: Lake Hattah; **B**, *M. minutus*, WA: Merredin; **C**, *M. ambiguus*,VIC: Penshurst; **D**, *M. punctipennis*, ACT: Black Mountain.

margin is gradual, never marked. Males exhibit 2 setae each side of the apical ventrite margin, for a total of 4 apical setae, differing from *M. lateralis* which retains the plesiomorphic single seta per side: i.e. a total of 2 apical abdominal setae. The labrum is distinctly emarginate apically, the 2 sides subangulate medially. The ligula is truncate apically, with the 2 apical setae separated by 4 setal diameters, the ligular surface longitudinally depressed between the setal articulations. The paraglossae elongate, extending twice as far beyond the ligular apical margin as the distance from paraglossal base to ligular margin. The pronotum is transverse, with the depressed median base margined at the disc with strigose punctures (Fig. 2K); MPW/BPW = 1.47–1.56, MPW/PL = 1.42–1.51. The prosternal process is broad and only slightly depressed between the coxae, convex anterad the coxae. The prosternal anteapical groove is deep and narrow, smooth at depth. As in *M. lateralis*, the metepisternum is abbreviated, with lateral length about 2× maximum width, and the metathoracic wings are vestigial in examined material. The suture between visible ventrites 1 and 2 is sinuous, with a broad circular depressed area posterad the sinuosity. Microsculpture of the head is reduced, with frons and vertex glossy, the surface interrupted only by scattered micropunctures. Similarly the pronotal disc and median base are glossy, with indistinct transverse lines visible in places. The elytral surface is glossy with micropunctures covering the surface of the disc, the apex with margins of transverse sculpticells upraised. Ventrally, the thoracic ventrites are glossy; abdominal ventrites glossy medially but with swirling transverse sculpticells visible in lateral depressions. Setal formula ++/++/–2++.

Male genitalia (n = 1). Aedeagal median lobe moderately broad dorsoventrally, apex narrowly rounded and not projected beyond ostium (Fig. 15B); flagellar plate large and lightly sclerotized; Right paramere narrow, elongate, >20 setae along ventral margin, setae more densely packed in basal half, dorsal margin with ~4 small setae (Fig. 16B); left paramere slightly broadened basally, evenly narrowed to apex.

Female reproductive tract (n = 1). Bursa copulatrix broadest at midlength, its surface membranous, apex narrowed into an elongate projection covered with pleat-like wrinkles (Fig. 17B); spermathecal duct moderately narrow, elongate, about twice length of spermathecal reservoir; basal gonocoxite broad, 2–4 setae along apical margin (Fig. 18B), 1 seta at apicomedial angle, and several setae along median margin; apical gonocoxite broadly rounded apically, mesal and lateral margins subparallel; a single narrow, acuminate lateral ensiform seta, its length about 1/4 length of apical gonocoxite; apical nematiform setae in large, apical positioned sensory furrow.

Type information. For *P. minutus*, lectotype female (MCG) designated by Straneo (1941): specimen glued onto elongate trapezoidal point // riv. N.H. / Murray [blue label] // minutus / Cast. // N(ova) Hollandia / Riv. Murray / Coll. Castelnau //Forticosomus / minutus / Cast. // LECTOTYPUS / Forticosomus / minutus / Castelnau, 1867 /

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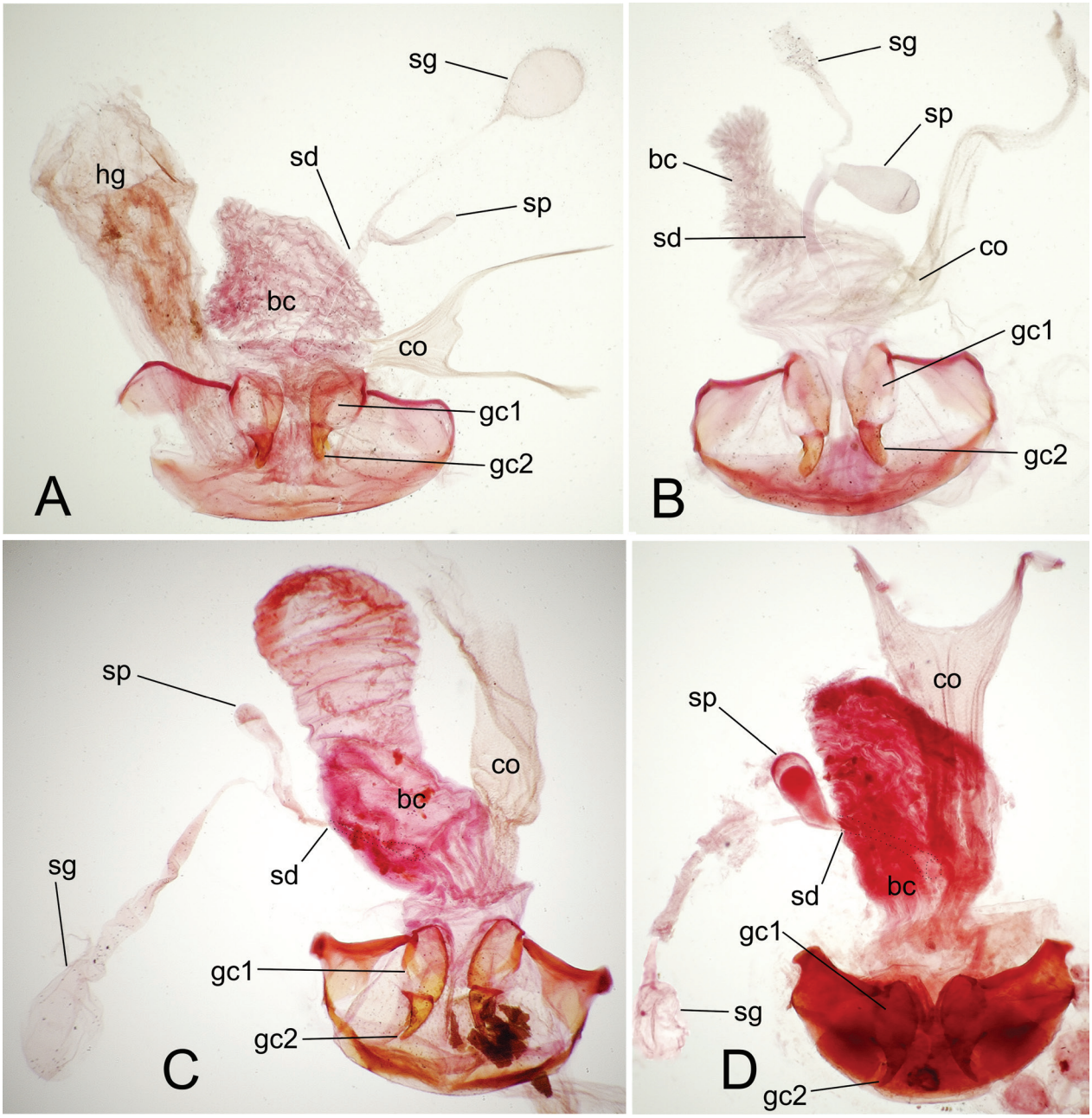

Figure 17. Female reproductive tract and gonocoxae of *Mecyclothorax* (*s. s.*) spp., ventral view: **A**, *M. lateralis*, VIC: Maldon; **B**, *M. minutus*, NSW: Lake Urana; **C**, *M. ambiguus*, NSW: Kosciuszko N. P., Thredbo R.; **D**, *M. punctipennis*, WA: Stirling Range N. P.

des. S.L. Straneo, 1941 // Mecyclothorax / minutus Cast / holotypus / Det. B.P. Moore ʻ68 // MUSEO GENOVA / Coll. Castelnau. Moore's labelling of this specimen as holotype, as done for *M. lateralis* above, is corrected in Moore et al. (1987) to reflect Castelnau's lack of mention of how many specimens from Paroo River were before him at description. For *C. fortis* Blackburn, lectotype male (BMNH) hereby designated: specimen mounted on white card with "913 T" on obverse, black and red lines at base, the red crossed by two triangles // round, red-margined Type label // Blackburn Coll. / 1910-236 // Cyclothorax fortis, Blackb. // Lectotype / Cyclothorax / fortis / Blackburn / J.K. Liebherr 2006 (black-margined red label). Female paralectotype (SAMA): specimen card-mounted with ventral surface upward, card with black and red line, "913" in red ink // S. Australia / Blackburn // Cyclothorax / fortis, Bl / Co-type // Paralectotype ♀ / Cyclothorax / fortis Blackburn / det. J.K. Liebherr 2004 [black margined, red label]. The lectotype (BMNH) was assigned based on its occupation of the first locality, Port Lincoln, mentioned in Blackburn's description (Blackburn 1889: 1391), with the paralectotype assigned to the second locality mentioned by Blackburn; "Yorke's Peninsula." Thus Port Lincoln becomes the type locality for the Blackburn name.

Distribution and habitat. This species exhibits a bicentric distribution, occupying the interiors of Western Australia, and New South Wales, South Australia and Victoria (Fig. 19B). Distributional records and institu-

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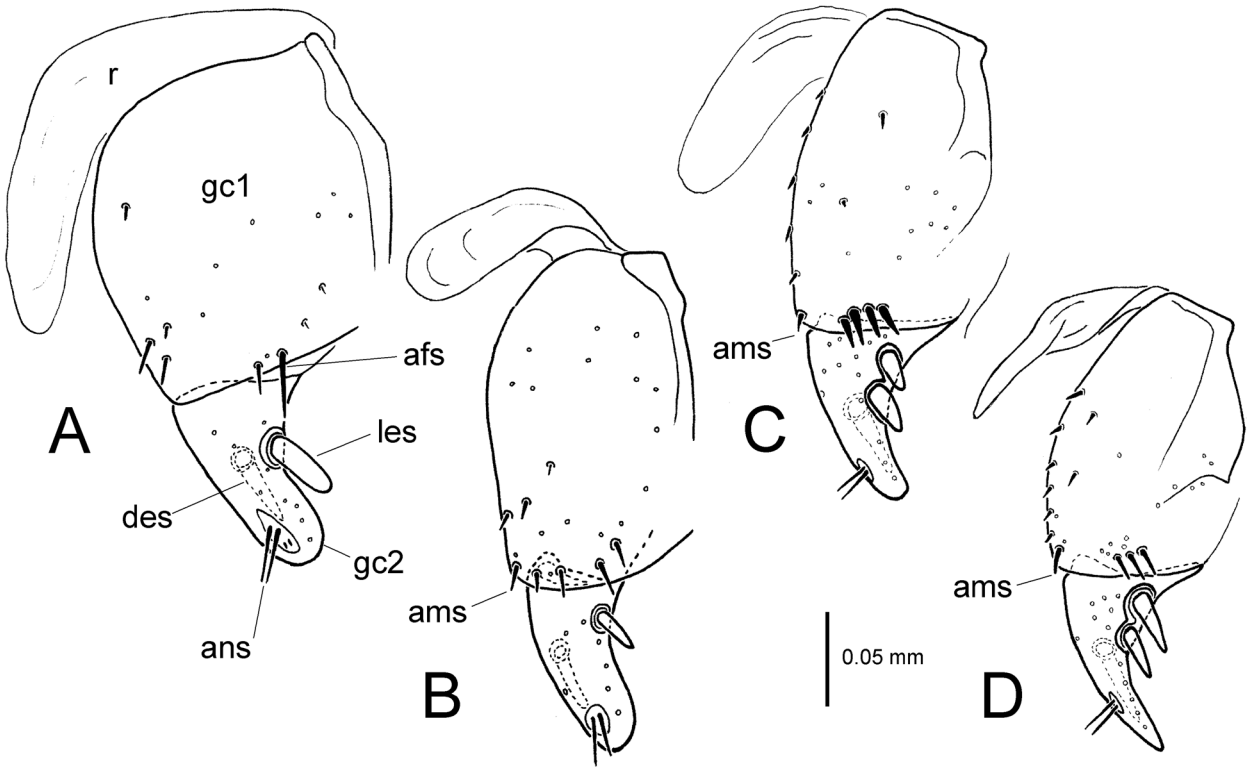

Figure 18. Left gonocoxa of *Mecyclothorax* (*s. s.*) spp., ventral view: **A**, *M. lateralis*, VIC: Maldon; **B**, *M. minutus*, NSW: Lake Urana; **C**, *M. ambiguus*, NSW: Kosciuszko N. P., Thredbo R; **D**, *M. punctipennis*, ACT: Black Mountain.

tional repositories for examined non-type specimens include: NSW: Bogan R. (MCZ, 1); Lake Urana Nat. Res. (EMEC, 17); SA: Koongawa, 4 mi. ESE (ANIC, 1); Pt. Augusta (BPBM, 7); Birchip (MVM, 1); Mallee Dist. (MVM, 3); Nyah (MVM, 1); WA: Burracoppin, 129 mi. S (WAM, 1); Coongardie, 85 km W (BPBM, 3); Hine's Hill, 10 mi. SW Merredin (CAS, 4); Hughden Rock (WAM, 2); Mullewa (MCM, 1; MCZ, 10); Newman Rock (ANIC, 1); Ravensthorpe, 50 mi. E (CAS, 1); Southern Cross, 14 mi. W (CAS, 1); Yellowdine, 18 km S (UASM, 2). Beetles constituting the sizable series collected by K.W. Will at Lake Urana Nature Reserve were found under rocks near pools of water in forest, by headlamp at night. As with most carabid beetles living in dry habitats, such nighttime entomological activity is a requisite for obtaining more than the odd specimen. Given the close, adelphotaxon relationship between *M. minutus* and *M. lateralis*, this type of habitat is suggested as the situation within which to find *M. lateralis* as well.

Mecyclothorax ambiguus (Erichson)

Figures 2L, 6C, 15C, 16C, 17C, 18C, 19C

Anchomenus ambiguus Erichson, 1842: 130.
Cyclothorax ambiguus Sloane, 1895: 447.
Mecyclothorax ambiguus Sloane, 1920: 153.
Cyclothorax lophoides Sloane, 1895: 447 (misidentification).

Diagnosis (n = 5). Moore (1984) deferred reliable diagnosis of this species from *M. punctipennis* based on the configuration of the male aedeagus (e.g. Fig. 15C–D), however the pronotal lateral margins are reliably narrower in individuals of this species (Fig. 2L). Although variable melanization of the pronotal disc and marginal depressions may confuse the appearance of the width of the lateral depressions, other aspects of the pronotum may be used, including: **1**, punctation of the median base, with about 20–22 punctures each side in this species versus nearly 30 deeper punctures each side in *M. punctipennis* (Fig. 2L–M); **2**, median base juncture with pronotal disc lined with deep, nearly round to moderately elongate punctures in this species, versus distinctly strigose depressions with 1–2 punctures in each depression for *M. punctipennis*. Microsculpture also varies unambiguously between the two species: **1**, in *M. ambiguus* a transverse mesh visible over portions of the pronotal disc and median base, best viewed adjacent to areas of reflected microscope light, versus glossy pronotal disc and median base, with only indistinct transverse lines within irregularities of the cuticular surface in *M. punctipennis*; and **2**, discal elytral intervals with well-developed transverse mesh, sculpticell breadth 2–3× length, and surface subiridescent in *M. ambiguus*, versus discal elytral intervals glossy, with at most indistinct transverse sculpticells visible at margins of fields of reflected light, the surface without any iridescence in *M. punctipennis*. The depth of elytral striae varies on the elytral apex, however in *M. ambiguus*, interval 8 is broadly convex adjacent to the well-developed stria 7 between the subapical and apical elytral setae, whereas in *M. punctipennis*, interval 8 is internally subcarinate and angularly depressed laterally (Liebherr

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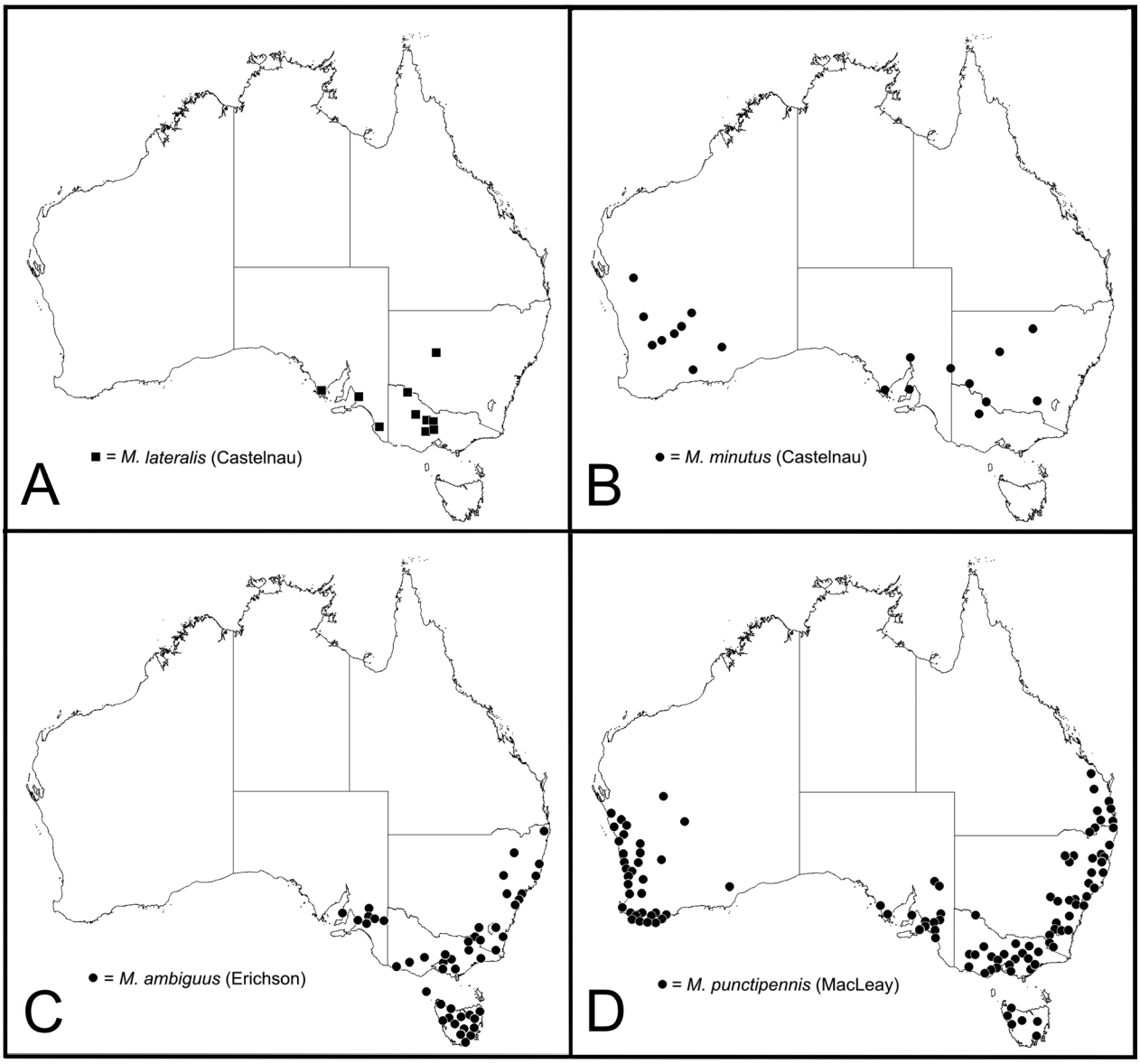

Figure 19. Distributional ranges of the four Mainland Australian *Mecyclothorax* (*s. s.*) spp.

2012a, fig. 7). For *M. ambiguus*, the mentum tooth has sides obtuse, the apex broadly rounded, whereas *M. punctipennis* is characterized by an acute mentum tooth with apex tightly rounded. The prosternal anteapical groove is deep and smooth here, but broader and distinctly punctate laterally, though smoother and slightly irregular medially, in *M. punctipennis*. In addition, the depressions surrounding the dorsal elytral setae span 1/4–1/2 of elytral interval 3 in this species, but up to 1/2–3/4 of the interval width in *M. punctipennis*. Standardized body length 5.0–5.7 mm. Setal formula ++/++/+2++.

Male genitalia (n = 3). Aedeagal median lobe gracile, narrow dorsoventrally relative to length, apex broad, expanded both ventrally and dorsally resulting in a nearly straight apical face (Fig. 15C); ostial ventroapical operculum well developed as a broadly triangular sclerite; flagellar plate very large, well-sclerotized with longitudinal ridges; aedeagal internal sac bearing a ventral spicular sclerite; right paramere slightly broadened basally, evenly narrowed to apex, ventral surface with ~20 setae along margin, additional very small setae may be present near apex (Fig. 16C); left paramere slightly expanded in basal half, apically narrowed to whip-like apex.

Female reproductive tract (n = 2). Bursa copulatrix elongate, columnar, length about 3× diameter when pressed under cover slip, surface membranous, translucent, wrinkled (Fig. 17C); spermathecal duct entering bursa copulatrix mediodorsally, duct length about 2× length of spermathecal reservoir; spermathecal gland duct long, >3× length of spermathecal reservoir; basal gonocoxite apical margin with 4 setae, 1 setae at apicomedial angle, and several smaller setae along medial margin (Fig. 18C); apical gonocoxite broad basally with 2 short, stout lateral ensiform setae, apex narrowly rounded; apical nematiform setae in sensory furrow near apex of apical gonocoxite.

Type information. Dissected and pinned male Lectotype (ZMHU): 3294 // ring sclerite and aedeagus on card

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// ambiguus / Er. / Van Diemens Land / Schayer [blue label] // LECTOYPE (red label) Mecyclothorax / "Anchomenus" / ambiguus / Erichson 1842 / designated by / B. P. Moore. An additional two male and one female paralectotypes (ZMUH) accompany the lectotype.

Distribution and habitat. This species is distributed throughout southeastern Australia including Tasmania and King Island (Fig. 19C). Localities and repositories for examined material include: NSW: Bodalla (MCZ, 4); Braidwood (MCZ, 41); Breakfast Ck. (MVM, 1); Cabramatta (BMNH, 1); Comboyne plateau (MCZ, 4); Cumberland (BMNH, 1); Greta (AMNH, 1); Kosciuszko N. P. (CUIC, 8; MCZ, 7); Mt. Wilson (FMNH, 1); Narrabeen Lagoon (FMNH, 5); Richmond R. vic. Wiangaree (MCZ, 8); Tallaganda St. For. (CAS, 1); Uralla (CAS, 3); SA: Adelaide (CAS, 1); Adelaide, 18 km E, Carey, 3 km SE (FMNH, 1); Adelaide, 8 km S, Waterfall Gully (FMNH, 1); Blackwood, Sturt Gorge Res. (ZMUC, 13); Goose Island (MVM, 3); Norton Summit, 10 km E Adelaide (FMNH, 2); Williamstown (FMNH, 1); Yorketown (CAS, 2; FMNH, 13); TAS: Burnie (MCZ, 8); Cockle Ck. (MCZ, 2); Florentine R. (MCZ, 3); Goulds Country (CMNH, 2); Hartz N. P. (MCZ, 2); Hastings (MCZ, 3); Hobart (MVM, 3); King Is. (MVM, 2); Launceton (FMNH, 1; MCZ, 1); Mersey R. Vy. (MCZ, 2); Mt. Ben Lomond (MCZ, 6); Mt. Field, base (MCZ, 7); Mt. Wellington (MCZ, 1); Parratah (MVM, 2); Queenstown (MCZ, 16); Smithton (CAS, 7); Tarraleah (MCZ, 3); Waldheim (MCZ, 1); Zeehan (CAS, 1); VIC: Ballarat (BMNH, 2); Bogong (MVM, 2); Dandenong (CAS, 2); Frankston (MVM, 1); Ferntree Gully (MVM, 1); Lakes Entrance (MVM, 1); Mt. Buller (MCZ, 1); Mt. Donna Buang (MCZ, 15); Mt. Hotham (MCZ, 3); Mt. Wogwog (EMEC, 1); Oakleigh (MVM, 2); Olinda (BMNH, 2); Penshurst (CUIC, 7); Port Melbourne (MVM, 2); Portland to Pt. Fairy (MCZ, 2); Pretty Vy. Dam (MVM, 1); Warburton (MVM, 6); Warrendyte (MVM, 1); Whiskey Ck. (MVM, 3); Yarra Glen (MVM, 1).

Mecyclothorax punctipennis (MacLeay)

Figures 2M, 6D, 15D–E, 16D, 17D, 18D, 19D

Cyclothorax punctipennis MacLeay, 1871: 105.
Mecyclothorax punctipennis Csiki, 1929: 487.
Cyclothorax obsoletus Blackburn, 1889: 1389 (synonymy Moore, 1984: 162).
Cyclothorax ambiguus Sloane 1898: 472 (misidentification).

Diagnosis (n = 5). For purposes of this review, all diagnostic external characters that distinguish this species from *M. ambiguus*–and therefore all other Australian species–are presented under *M. ambiguus*. Standardized body length 5.0–5.8 mm. Setal formula ++/++/+2++.

Male genitalia (n = 3). Aedeagal median lobe gracile, narrow dorsoventrally relative to length, the apex well extended beyond ostium, the tip downturned (Fig. 15D); ostial ventroapical operculum well developed, an elongate triangular sclerite; flagellar plate large, bearing longitudinal sclerotic ridges (Fig. 15E); base of aedeagal internal sac bearing a ventral spicular sclerite; right paramere narrow, elongate, bearing >12 setae along the ventral margin, 4 small setae long dorsal margin (Fig. 16D); left paramere narrow basally, narrowed to elongate, attenuated whip-like apex.

Female reproductive tract (n = 2). Bursa copulatrix elongate, columnar, length about 2× diameter when pressed under cover slip, surface thickened, wrinkled, (Fig. 17D); spermathecal duct entering bursa copulatrix mediodorsally, duct length about 2× length of spermathecal reservoir; spermathecal gland duct long, ~1.5× length of spermathecal reservoir; basal gonocoxite apical margin with 3 setae, 1 seta at apicomedial angle, and several smaller setae along medial margin (Fig. 18D); apical gonocoxite broad basally with 2 acuminate lateral ensiform setae, apex acuminate; apical nematiform setae in subbasal sensory furrow.

Type information. For *M. punctipennis*, lectotype male (ANIC): Gayndah, Queensland (Moore 1984). For *C. obsoletus* Blackburn, two syntypes (SAMA): Port Lincoln, S.A. (Moore 1984, Moore et al. 1987).

Distribution and habitat. This species is broadly distributed in numerous habitats across Australia (Fig. 19D). Recorded collection localities range in elevation from sea level to over 2000 m near the summit of Mt. Kosciuszko. These beetles are at home in leaf litter on the floor of *Eucalyptus* forests, under dense mats of dead leaves surrounding the bases of *Xantharrhoea* (Asphodelaceae) grass trees, in tussock grass clumps of high-elevation grasslands, under wrack on sea beaches, and in home gardens in urban settings. The species is monomorphically macropterous, with adults often collected at lights in great profusion.

Even given this species' catholic ecological preferences and propensity for winged flight, its geographic distribution is discontinuous across Australia (Fig. 19D). Moreover, the Western Australian populations of this bicentric species distribution interact little if at all with coastal populations east of the Great Australian Bight, based on geographic restriction of polymorphic male genitalic chiral antisymmetry to the populations inhabiting Western Australia (Liebherr and Will 2015). In contrast, all eastern populations monomorphically comprise males with plesiomorphic genitalic torsion, whereby the right side of the aedeagus is held ventrally when in repose. The Western Australian populations vary greatly in the proportions of left- and right-torsioned males, demonstrating that their mutual geographic isolation is great enough to preclude extensive homogenizing dispersal among populations.

Baehr (2000) reported a 1998 record for *M. punctipennis* from Rocky Cape N. P. as the first Tasmania record. However, Darlington material (MCZ) indicates *M. punctipennis* was present at Hobart in 1956–1957 (Liebherr and Will 2015). Tasmanian localities and repositories represented in material examined for this review (Fig. 19D) include: Corinna, West Tasmania (MCZ, 4); Hobart (MCZ, 8); Great Lake, north end (MCZ, 5); Waldheim nr. Cradle Mtn. (MCZ, 1); Zeehan, north (MCZ, 3).

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Discussion

Biogeographic History. The adelphotaxon relationship (Liebherr 2011a) between *Mecyclothorax* and genera allied with and including *Amblytelus* Erichson – i.e. *Epelyx* Blackburn, *Dystrichothorax* Baehr, *Paratrichothorax* Baehr, and *Trichoamblytelus* Baehr – requires both clades to be of equal age of origin. Baehr (2004) proposed an Eocene age of origin for the *Amblytelus* lineage, based on the restriction of *Paratrichothorax* and *Trichamblytelus* to coastal forests of southwest Australia. The late Eocene marine transgression would have isolated the ancestors of extant species in these genera from other lineages diversifying in eastern Australia, with subsequent aridification and periodic marine transgressions maintaining that isolation (Mast and Givnish 2002). Oligocene cooling allowed the evolution of rain forest communities, whereas Miocene drying (associated with the rise of Myrtaceae) resulted in the assembly of communities dominated by *Eucalyptus* (Crisp et al. 1999). The intense association of the tree-dwelling *Amblytelus* lineages with *Eucalyptus* forests allowed those taxa the opportunity to diversify over the past 20 Myr, with many of the more than 100 species evolving arboreal life styles (Baehr 2004, 2016b). *Mecyclothorax* spp., on the other hand, have been principally restricted to terrestrial microhabitats in southwest or southeast Australia, Queensland, New Caledonia, and especially New Guinea during the Miocene orogeny (Liebherr 2018). Species of the montane rainforest, Queensland *Qecyclothorax* have been principally collected in sieved litter from terrestrial situations, though some specimens have been collected via pyrethrin spray of mossy logs and trunk bases. The early divergence of *Qecyclothorax* in these rainforests is hypothesized to have occurred commencing in Oligocene when these communities were being assembled. Conversely, based on collecting records for Australian *Mecyclothorax* of the subgenus *Eucyclothorax*, we know that these species are distributed along waterways and in wetlands, often in association with open forest vegetation, fallen wood, and massed vegetation such as flood debris. Thus, like *Amblytelus*, this line could have diversified in the myrtaceous communities of southern Australia.

Though most of the diversification occurred in southeastern Australia, multiple east-west vicariance events of different ages are mandated by the cladistic taxon-area relationships of the taxa (Rix et al. 2015). The earliest east-west vicariance event would have isolated *M. isolatus* in the forests of the south west coastal region. That *M. isolatus* has a remarkably reduced metathorax and well-developed plical lock between the abdominal ventrites and elytra points to prolonged occupation of stable, persistent forest habitats (Southwood 1977) now conserved within Walpole-Nornalup National Park. Subsequently *M. blackburni* was isolated in Western Australia (Figs 1B, 11B) prior to diversification of the six species in the *M. lophoides* complex (Fig. 1B). Later in the history of that same clade, *M. jameswalkeri* was derived as a Western Australian isolate related to *M. darlingtoni* from Queensland and *M. lophoides* from southeast Australia (Figs 1B, 11C). The most recent east-west pattern involves widespread species with populations in both eastern and western Australia: **1**, *M. punctatus*, with the subspecific form *M. p. peckorum* described from the southwest Cape region; **2**, *M. minutus* (Fig. 19B); and **3**, *M. punctipennis* (Fig. 19D).

Within the subgenus *Mecyclothorax*, the vast majority of Australian Plate species evolved first in association with rainforest habitats in New Guinea (Fig. 1A; Baehr 2014, Liebherr 2017), and subsequently following overwater dispersal to locales such as Lord Howe and Norfolk Islands (Moore 1985, 1992), Borneo (Baehr and Lorenz 1999), Java (Andrewes 1933, Louwerens 1949, 1953), Timor Leste (Baehr and Reid 2017), New Zealand (Liebherr and Marris 2009), and most recently the Hawaiian and Society Islands. The colonizing taxon founding the very diverse Hawaiian radiation occupied terrestrial grassland, based on sharing of this habitat preference by the very close relatives *M. punctipennis* and *M. montivagus* (Fig. 1A, Liebherr 2015). The third species completing this triplet, *M. sculptopunctatus* of St. Paul and Amsterdam Islands, also occupies such an open habitat on these very small, windswept Indian Ocean islands (Jeannel 1940, plate IV, fig. 1), corroborating an open grassland habitat as the initial landing area for these island species. It is within the many Hawaiian species that have radiated from the common ancestor with *M. montivagus* that ecological diversification has reached its maximal range among known *Mecyclothorax*, with the evolution of alpine, riparian, and arboreal epiphyte-loving species (Liebherr 2015), as well as a cave-adapted troglophilic species (Liebherr 2008a). Even within the estimated 10% of *Mecyclothorax* species predicted to be discovered in New Guinea (Liebherr 2017), species have evolved to occupy alpine habitats–*M. sedlaceki* Darlington, *M. toxopei* Darlington, and *M. kavanaughi* Liebherr (Liebherr 2008b)–as well as dense lowland rainforest; *M. amingwiwae* Liebherr, *M. andersoni* Liebherr, and *M. gressitti* Liebherr (2017). Being highly complex geologically and largely unexplored, the New Guinea highlands on the active tectonic margin of the Australian plate are likely to provide further examples of ecological diversification within the genus.

Paleoecological research has resulted in the discovery of Australian subfossils assignable to *Mecyclothorax* (Sniderman et al. 2009). In deposits laid down ~1.84–1.56 Ma in the Stony Creek Basin, Victoria, subfossils determined as "*Mecyclothorax* '*punctatus*' grp n. sp." and "*Mecyclothorax* sp. 3 (*cordicollis* grp.)" were recovered. The site is within the present-day distributional range of *M. punctatus* (Fig. 11A), and so these subfossils presumably represent extant species or representatives of an ancestral population that evolved to become the extant species. Most parsimoniously then, the common ancestor of *M. punctatus* and its sister species *M. moorei* can be dated to the Pleistocene age of this assemblage (Fig. 1B). For the "*cordicollis* grp." taxon, the site lies within the distributional ranges of *M. lophoides*, *M. peryphoides*,

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and *M. cordicollis* (Fig. 11C–E). Given this contribution's sorting out of species in the *M. lophoides* species complex based on comprehensive use of external and male genitalic characters, more concise determination of these subfossils may allow more precise dating of cladogram nodes connecting these species (Fig. 1B). Regardless of the outcome of such a determination, the rate of speciation for these *Eucyclothorax* species is an order of magnitude lower than that observed in the Pacific Island radiations, where time between speciation is estimated to be 220,000 years for Hawaii (Liebherr 2015) and 300,000 years for the Society Islands (Liebherr 2013).

Genitalic Evolution. Confirmation of species assignment for specimens in the *M. lophoides* species complex is greatly assisted by examination of the male aedeagus, a finding in keeping with the utility of male genitalia for diagnosis of cryptic species in the Hawaiian *Mecyclothorax* fauna (Liebherr 2007, 2008a, 2011b, 2015), where numerous species may be sympatric across a limited portion of an island. In contrast, male genitialia vary infraspecifically within species of the New Caledonian *Mecyclothorax* subgenus *Phacothorax* on an island where often only two species occur sympatrically (Liebherr 2018). Even though the overall diversity of Australian *Mecyclothorax* is modest, the aggregate distributional patterns are more like those observed in Hawaii, as nine species are broadly sympatric across portions of New South Wales and Victoria (Figs 11, 19). Given the long duration of *Mecyclothorax* species in Australia (Sniderman et al. 2009), there has been abundant time for the evolution of discrete male genitalia, thereby assisting species recognition during the encounters of male and female beetles (Nagata et al. 2009, Okuzaki and Sota 2014). The only region of Australia where this pattern breaks down is Western Australia, where chiral antisymmetry occurs within populations of *Mecyclothorax punctipennis*. Here only that species and *M. minutus* share much of the region (Fig. 19), as the four *Eucyclothorax* species are allopatrically distributed within limited areas along the coast (Fig. 11A–C).

Species diagnosis within the *M. lophoides* complex (Fig. 1B) lies most specifically in differential characters of the internal sac flagellar complex (Figs 7F–H, 14). This is especially so for the sympatric species *M. lophoides*, *M. cordicollis*, and *M. peryphoides* (Figs 14B, F, H). A succession of taxonomists have routinely confused these closely related species (Fig. 1) because the external anatomical characters vary little among the species, and infraspecific variation blurs the subtle patterns of external character evolution. Yet the beetles' flagellar complexes differ very dramatically, with no possibility of misidentification given access to a male specimen. This disparity points to relative stasis in external anatomy during accelerated evolution of male genitalic characters. Two questions may be asked about this evolutionary disparity. Firstly, what are the functional ramifications for mating given the dramatic differences among species? Secondly, what are the evolutionary selection pressures that have resulted in accelerated genitalic evolution?

The internal sac flagellum of male tiger beetles functions during copulation as a semi-rigid structure that enters the female spermathecal duct (Schincariol and Freitag 1986). The *Cicindela* L. flagellum is elongate, sclerotized, and in cross-section U-shaped, with either the internal surface of the groove, or the convex outer surface of the flagellum bearing basally directed, microserrate teeth (tempers). These act to hold the flagellum in the duct when required, but can be detached from the duct's surface through flagellar flexion when removal of the flagellum is required (Freitag et al. 2001). The flagellum ranges from about half the length of the spermathecal duct to slightly longer than the duct in four species of *Cicindela* and *Pseudoxychila tarsalis* Bates (Freitag 1966, Freitag et al. 1980, Rodríguez 1999). In all instances, the flagellar diameter is similar to the diameter of the spermathecal duct, though the flagellar base is larger than the duct and presumably does not enter it. The flagellum cannot transfer sperm, as its base is closed, and it does not connect directly to the male gonopore. Its function includes opening of the spermathecal duct during the complicated multi-phase mating behavior of cicindelines (Schincariol and Freitag 1986), and possibly facilitating insertion of the spermatophore neck into the spermathecal duct (Rodríguez 1999), allowing sperm passage into the duct and to the spermatheca.

Aedeagal internal sac flagella occur throughout the Carabidae (Jeannel 1955, Maddison et al. 2013). In Hawaiian *Bembidion* Latreille beetles of the subgenus *Nesocidium* Sharp, the male flagellum length is subequal to the female spermathecal duct length, to 60–75% longer than the duct (Liebherr 2008c). Correspondence in length between male flagellum and female spermathecal duct was maximal in *Nesocidium* spp. with spermathecal ducts of uniformly narrow diameter, whereas species in which the male flagellum was longer than the duct included females with a basally broad duct, suggesting that the flagellum touches the walls of the duct, undergoing circular torsion and thus expanding the duct to its maximal diameter as it is pushed into the duct by the male. The presence of a short male flagellum is a groundplan character for the tribe Moriomorphini (Liebherr 2011a). Among species of *Mecyclothorax* subgenus *Eucyclothorax*, the flagellum ranges from a plesiomorphic shortened condition, as in *M. moorei*, *M. punctatus*, *M. curtus*, and *M. blackburni* (Fig. 7A–E), to the highly derived, elongate, and rigidly sinuous structure of *M. eyrensis* and *M. peryphoides* (Fig. 14D–F). The other species of the *M. lophoides* complex exhibit a flagellum of intermediate length; **1**, slightly longer than the associated flagellar sheath in *M. darlingtoni* (Fig. 7G–H): **2**, equal in length to the flagellar sheath in *M. lophoides* (Fig. 14B); and **3**, slightly shorter than the flagellar sheath in *M. cordicollis* (Fig. 14H). Among the females, most species have spermathecal ducts equal in length to the apical spermathecal reservoir, i.e. of moderate length (Fig. E–F, I). However, in females of *M. curtus*, *M. eyrensis*, and *M. peryphoides* the spermathecal duct is elongate, i.e. more than twice the length of the fusiform

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apical reservoir (Fig. 9C, G–H). In the species pair *M. eyrensis* + *M. peryphoides*, insertion of the long, semi-rigid and sinuous flagellum would make the spermathecal duct conform to the flagellar configuration.

The species pair *M. eyrensis* and *M. peryphoides* are also unique within subgenus *Eucyclothorax* in that the highly derived structures of the male aedeagal median lobe and internal sac are identical among males of both species, apparently violating one of the precepts of modern taxonomy that associate species diagnosis with male genitalic differences (Huber 2003). However parameral setation varies significantly among males of these species. This finding begs the question of how the male parameres interact with the external surface of the female abdomen during intromission, at the same time providing a genitalic difference between the species to accompany diagnostic external characters that include differences in: **1**, pronotal shape, especially at the pronotal hind angles; **2**, cuticular microsculpture; and **3**, coloration. The two species also occupy very different ecological zones in Australia; with *M. eyrensis* residing in the arid interior of South Australia, Northern Territory and New South Wales, whereas *M. peryphoides* occupies the more temperate grass- and woodland habitats to the south and east (Fig. 11D). Both species occupy riparian habitats within their respective distributions, perhaps the reason that *M. eyrensis* can persist in the dry interior, as the larvae would be seriously impacted were the occupied habitat too xeric during the period of larval development. Though only a single datum, the genitalic situation in *M. eyrensis* and *M. peryphoides* parallels that reported by Huber and Dimitrov (2014) for a sister-species pair of Taiwanese pholcid spiders: two species sharing highly distinctive yet identical male genitalia (i.e. chelicerae), while differing in body coloration and proportions, and occupying discrete ecological situations across allopatric distributions. Molecular divergence is minimal between the two pholcid species, supporting very recent speciation between them.

The second question posited above concerning the evolutionary basis for male and female genitalic correlations can be addressed preliminarily by the distribution of differences among the species in subgenus *Eucyclothorax*. It seems likely that genitalic characters provide specific cues for mate recognition (e.g. Nagata et al. 2009). Can such differences be interpreted as the results of sexual selection (Eberhard 1985, 2004)? Males of *M. moorei*, *M. punctatus*, and *M. curtus* exhibit short flagella (Fig. 7A–D), whereas the females exhibit several derived characters of the reproductive tract. Females of the sister species *M. moorei* and *M. punctatus* exhibit a basally sclerotized and bulbously expanded spermathecal duct (Fig. 9A–B). Females of *M. curtus* deviate from that by having a spermathecal duct that is elongate and moderately sclerotized (and therefore coiled when at rest), as observed in females of *M. eyrensis* and *M. peryphoides*. If we invoke runaway sexual selection to explain the association of elongate male flagella and spermathecal ducts of *M. eyrensis* and *M. peryphoides*, then how do we explain the similarly elongate duct in *M. curtus*, here in association with a short male flagellum? Moreover, given that we do not understand the function of the basally expanded and sclerotized spermathecal ducts in *M. moorei* and *M. punctatus* females, nor how the duct might interact with the male flagellum, currently we are best left to report the findings and introduce their use in phylogenetic inference. Finally, if we were to implicate the difference in parameral setation between *M. eyrensis* and *M. peryphoides* as the result of sexual selection, then we must posit the introduction of a novel focus of selection in the mating system at this point; a decidedly unparsimonious rescue attempt for a hypothesis compromised by the phylogenetic distribution of female spermathecal duct configurations.

Based on revisionary taxonomy for the *Mecyclothorax* faunas of the Hawaiian Islands (Liebherr 2006, 2007, 2008a, 2009a, 2009b, 2011b, 2015), the Society Islands (Liebherr 2012a, 2012b, 2013), New Zealand (Liebherr and Marris 2009), Papua New Guinea (Liebherr 2017), New Caledonia (Liebherr 2018) and now Australia, we have accrued information on genitalic correlates between the sexes for more than 350 species. Plucking from this cornucopia of genitalic riches, all manner of genitalic correlates among closely related species can be observed. The parapatric Moloka‘i sister species *M. lissopterus* Liebherr and *M. arcuatus* Liebherr of the *M. ovipennis* species group are not distinguishable based on external anatomy. However, genitalia of both sexes are both diagnostic and concordant with regard to size: **1**, the male aedeagal median lobe of *M. arcuatus* has a much longer and broader apex (Liebherr 2007, figs 75–78); and **2**, the female bursa copulatrix of *M. arcuatus* is much broader and more elongate (Liebherr 2007, figs 157, 159). In this instance, an elongate male median lobe is associated with an elongate female bursa, with the structures functionally related because the former enters the latter during intromission, followed by eversion of the male internal sac and transfer of the spermatophore. A second pair of allopatric *M. ovipennis* group sister species from Moloka‘i –*M. joni* Liebherr and *M. lisae* Liebherr –exhibit males with significantly different aedeagal median lobe lengths across species, but females with bursae of very similar lengths (Liebherr 2007 figs 71–74, 150, 152). A similar non-correlated pattern is observed among five sympatric species of Oahu’s monophyletic *M. brevis* species complex, with the male aedeagal median lobes and internal sacs varying dramatically among the species, but the known female bursae differing little (Liebherr 2009a, figs 6A–K, 9A, C). If we wish to implicate sexual selection across just these three examples, each involving most-closely related species, the first example of concordant transgender-based association of dramatically larger male and female genitalia in *M. arcuatus* would better fit the model of antagonistic sexual selection, whereas the latter two examples involving dramatic changes in male genitalia along with female genitalic stasis would fit conditions of Eberhard’s (2004) female choice model. Yet, the latter two examples consistent with observations of female choice also differ in that the former involves allo-

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patric sister species, and the latter involves five sympatric species. Females could choose among sympatric males, but not among allopatric males. Alternatively species-specific male genitalia could have evolved during allopatric speciation, with secondary sympatry enhancing either or both pre-mating sexual discrimination and post-mating reproductive isolation (Malone et al. 2015). Character displacement operating on characters of either system could reinforce divergence among secondarily sympatric species or populations (Brown and Wilson 1956). These myriad options point to the requirement for hypothesis testing specific to singular or closely associated evolutionary events when studying sexual selection (Simmons 2014). They also suggest that it is inappropriate to consider sexual selection as a singular factor responsible for the accelerated speciation of Polynesian *Mecyclothorax* beetles.

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Supplementary material 1
Data file for cladistic analysis of Australian *Mecyclothorax* Sharp
Author: James K. Liebherr
Data type: NONA format data file
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Link: https://doi.org/10.3897/dez.65.27424.suppl1

Supplementary material 2
Supporting data for Mann-Whitney rank-sum test of differences in parameral setation for *M. eyrensis* and *M. peryphoides* males
Author: James K. Liebherr
Data type: Word format table.
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