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A multigene phylogenetic analysis results in a redefinition of the genus *Notonomus* Chaudoir (Coleoptera, Carabidae) and descriptions of new species of the subgenus *Leiradira* Castelnau

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Bayesian analysis of four partial gene sequences (28S rDNA, wg, CAD and COI mtDNA) from exemplars of Abstract. all genera and 12 of 17 informal groups of the Notonomus-series of pterostichine carabids strongly supports a clade requiring redefinition of Notonomus Chaudoir, 1862. Notonomus is redefined to include all species currently placed in Notonomus by Lorenz (2005a) plus two Sarticus Motschulsky, 1865 species (S. blackburni (Sloane, 1895) and S. impar (Sloane, 1893)), all species of Leiradira Castelnau, 1867, Conchitella Moore, 1962 Loxodactylus Chaudoir, 1865 and Acanthoferonia Moore, 1965. Analysis of combined data places Sarticus sister to Notonomus with low support. Individual gene analyses indicated wg is in conflict with other loci and analyses exclusive of wg place Parhypates Motschulsky, 1866 sister to Notonomus with very high support. Leiradira species form a clade within Notonomus including Notonomus dimorphicus Darlington, 1961 and N. flos Darlington, 1961. Six new species of the subgenus Leiradira from Queensland are described; Notonomus (Leiradira) thynnefiliarum, N. (L.) vadosus, N. (L.) viridis, N. (L.) spectabilis, N. (L.) iridescens and N. (L.) barrae. Two additional species of Notonomus s.l. are described; Notonomus hephaestus from the Lamb Range, Queensland, which is part of a mimicry complex with Notonomus (Leiradira) aurifer (Darlington, 1961); and Notonomus nocturnocappellus, from New South Wales, which represents a unique combination of characteristics for the genus. Descriptions of all species of Notonomus (Leiradira) with a wide gula, a grouping equivalent to Darlington's concept of Leiradira, are given. An identification key to species of Notonomus (Leiradira), the two newly described Notonomus s.l. species and all recognised subgenera of Notonomus is provided.

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# Introduction

The bulk of work on the genus Notonomus Chaudoir, 1865 was done by Thomas Sloane in a series of ten papers published between 1890 and 1923. Of the 105 species-group taxa that were valid in the genus at the start of my study, Sloane had described 56. Earlier authors (e.g. Castelnau, Macleay, Dejean and Chaudoir), whose works are summarised by Sloane (1902), also published scattered descriptions. No additional species were described in the genus after Sloane's 1923 paper until Darlington (1953, 1961a) described new species from the Queensland tropics and Moore (1960, 1961, 1963) described new species from Victoria. Amazingly is has now been 50 years without any additional description of species, though in the intervening years some important nomenclatural issues and synonymies have been covered in catalogues by Moore (Moore et al. 1987) and Lorenz (2005a, 2005b) and two New Caledonian species attributed to Notonomus were moved to Prosopogmus Chaudoir, 1865 by Will (2011b).

Sloane's (1895) general treatment of carabids, his treatment of Sarticus Motschulsky, 1865 (Sloane 1903) and his two most substantial papers on Notonomus (Sloane 1902, 1913), express his significant reservations about the limits of Notonomus. At first he attempted to reconcile Australian taxa with the dominant European generic concepts of the time, e.g. Pterostichus Bonelli, 1810 and Platysma Bonelli, 1810. He then abandoned those taxa in favour of exclusively Australian genera, but still was plagued by doubts regarding generic limits. Though his overarching approach was practical, he waxed somewhat poetic when discussing the arrangement of Notonomus (Sloane 1902: 205): 'I offer a tabulation of the species known to me in which an attempt is made to arrange the species in a fairly natural order, or at least what seems to me a natural order. But, seeing that the species of a large genus in their relationships towards one another resemble the branches of a tree springing from one trunk, rather than a continuous chain, it is impossible to place them in a linear series by aid of a dichotomous table without species being separated sometimes from nearly allied congeners'. Though he explicitly was attempting to find a natural arrangement of Notonomus in his subsequent 1913 treatment he maintained that 'the extremely intricate manner in which the characters, on which the groups are founded, are diffused generally throughout the genus, owing, no doubt, to their being derived from numerous ancient stems, probably along many lines of descent, so that the relationships of the present-day species presents a bewildering labyrinth for the taxonomist to puzzle over'. Initially I intended to treat only a

dramatic-looking undescribed species of Leiradira (N. (L.) barrae) that I had collected on Mt Lewis, QLD. I then received an abundance of undescribed species from G. Monteith (QM) and realised that Darlington (1961b) had left the status of Leiradira Castelnau 1867 and the Notonomus series taxa as 'something to be decided in the future, by the next reviser of the generic classification of Australian Pterostichini'. In the present paper I make my first foray into Sloane's labyrinth and take the first steps to revise the generic classification of Australian Pterostichini. I now have the excellent works by Sloane, Moore and Darlington to stand on, and DNA sequence data and analysis tools to address the taxonomic puzzle that is Notonomus.

#### Methods

#### Material examined and identification

Specimens for this study were provided by the following institutions: Australian National Insect Collection (ANIC), CSIRO, Canberra; Carnegie Museum of Natural History (CMNH); Cornell University Insect Collection (CUIC); Essig Museum of Entomology (EMEC), Berkeley; Museum of Comparative Zoology (MCZ) Harvard; Queensland Museum (QM), Brisbane; Zoological Institute (ZISP), St Petersburg.

Material from the QM was central to this study and those specimens are the product of many years of targeted surveys in the mountains of the wet tropics region by the QM staff; particularly Geoff Monteith. Data on specimens from those surveys has been analysed and published on using provisional code names. I list those code names and cite the papers where they published under the distributional information for the species below.

All holotype material is listed with verbatim locality data and unique identifier numbers below. All specimens of previously described species examined are listed in the material examined appendix and each includes a unique identifier number from a collection-specific tag found on each specimen. These numbers tie specimens to database entries that have the expanded, interpreted and often georeferenced data for the specimens. The full data is accessible via the Atlas of Living Australia (http://www.ala.org.au/), EssigDB (http://essigdb.berkeley.edu/), MCZBase (http://mczbase.mcz.harvard.edu/) or from in-house databases maintained by the individual institutions. Summary information is provided for each species below, which are listed alphabetically in Leiradira followed by the incertae sedis species.

In addition to specimens listed in the species descriptions below and in the material examined appendix, I curated and studied the pterostichine collection at ANIC, including their holdings of types and additional material in the Sloane and B.P. Moore collections. My work in that collection was instrumental in my assessment of the breadth and depth of sampling for this study. Identification of specimens is based on use of the literature cited herein and comparison with material in the ANIC collection.

## Taxon selection for analysis

Given the uncertainty of relationships within Pterostichini s.l., the taxa included in this analysis were selected from a parsimony analysis of a larger unpublished dataset including ~400 Pterostichini representing all North American genera, all but two North American subgenera, most South American genera, all New Zealand genera, all but three Australian genera and a wide sample across the diversity of genera and subgenera from Madagascar, New Caledonia, New Guinea, Africa and Europe. This larger exemplar dataset includes more or less complete sequence data (18S, 28S, CAD) and a partially coded matrix of ~100 morphological characters (K. Will,

unpubl. data). Though clearly preliminary, the genus-level taxa included herein as outgroups always group together with Notonomus-series taxa in the preliminary parsimony analyses. Based on that analysis and a general study of morphology, I exclude Delinius Westwood, 1864 and Lesticus Dejean, 1828 of the Delinius-series of Moore (1965), in which he includes Delinius, Lesticus and Leiradira. This informal group was based on similarity of mouthparts and antennae, but male and female genitalia and sequence data do not support a close relationship among these three. Delinius is part of a complex of genera related to Platycaelus Blanchard, 1843 (K. Will, unpubl. data), while Lesticus is part of the 'trigonotomi' taxa (Will and Kavanaugh 2012) and more closely related to northern hemisphere pterostichines. Moore included in the Notonomus-series Notonomus, Loxodactylus, Conchitella Moore, 1962, Rhabdotus Chaudoir, 1865 and Sarticus. Though Rhabdotus species do share an overall similar form with typical Notonomus, they are distinctly different in the features of the female genitalia. Rhabdotus females have an elongate gland duct diverticulum not known from any species of the genera included in this analysis (Fig. 5). A diverticulum is known in Euchroina (Ortuno 1996; Will 2002) and a variety of other pterostichines (Moore 1965; Liebherr and Will 1998). There are no obvious morphological synapomorphies linking Rhabdotus to any genus included in this analysis and sequence data used in the broader unpublished analysis places it very distantly.

Among the Notonomus-series genera, Sarticus is the most species-rich genus next to Notonomus; however, Sarticus is very little studied so I have chosen to include a variety of body forms as exemplars from across the range of Sarticus (s. str.) (Fig. 1B). Unfortunately, no specimens of Sarticus (Coronacanthus W.J.Macleay, 1878) species were available. Parhypates Motschulsky, 1866 (Fig. 1A) includes a small number of species from Chile (Straneo 1986; Will 2011a) that are strikingly similar to Notonomus species (Fig. 1) and were consistently placed together with them in the preliminary analysis.

All species of Leiradira were studied and two species from each of the three subgenera in which Darlington (1961b) arrayed species are included in the molecular analysis. Groups within Notonomus established by Sloane (1913) and Darlington (1961a, 1961b) were used as guides for sampling within the genus. When possible, the nominal species for the group was included; (Table 1) as was the type species of the genus, Notonomus triplogenioides (Chaudoir, 1865) (Fig. 1C). Species from five small groups were not available for sequencing: cupricolor-group, atrodermis-group, excisipennis-group, lesueri-group and parallelamorphus-group. In addition, two species described herein, Notonomus nocturnocappellus and N. (Leiradira) barrae, were included in the molecular analysis as each of these has morphological character state combinations not found in any recognised species group. Though no DNA quality specimens are available for N. hephaestus and it is not included in the analysis, it is described here to draw attention to its unique combination of characters and apparent involvement in morphological and colour mimicry.

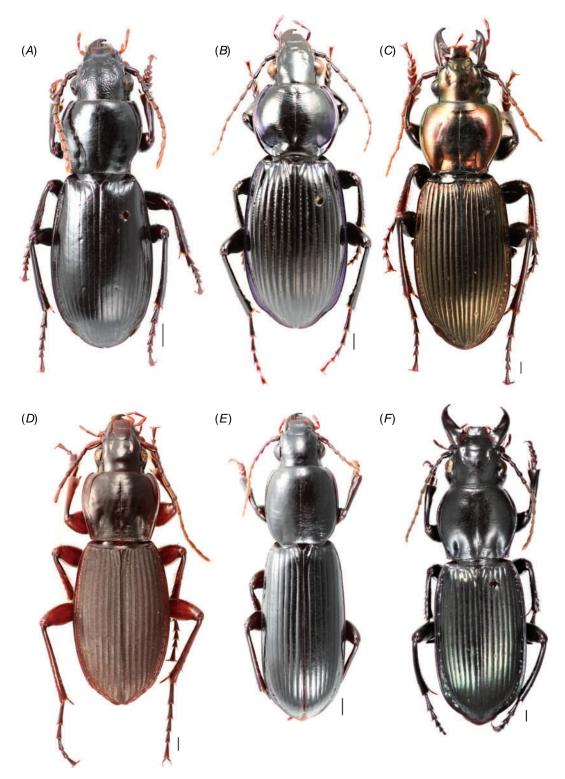


Fig. 1. Dorsal habitus of exemplars of genus-level taxa included in this study, scale bars = 1.0mm. (A) Parhypates nunni Straneo, 1987, (B) Sarticus (s.str.) cyaneocinctus (Chaudoir, 1865), (C) Notonomus (s.str.) triplogenioides, (D) Notonomus (Loxodactylus) carinulatus (Chaudoir, 1865), (E) Notonomus (Conchitella) clivinoides (Moore, 1962), (F) Notonomus (Acanthoferonia) ferox (Moore, 1965).

Table 1. Taxa included in phylogenetic analysis by group or subgenus

Species	Group or subgenus
N. aeques	aeques-grp
N. angustibasis	angustibasis-grp
N. australis	australis-grp
N. chalybeus	chalybeus-grp
N. dimorphicus	doddi-grp
N. flos	doddi-grp
N. minimus	kingi-grp
N. lateralis	lateralis-grp
N. auricollis	Leiradira
N. puella	Leiradira
N. mediosulcatus	mediosulcatus-grp
N. alternans	Metadira
N. aurifer	Metadira
N. opacicollis	opacicollis-grp
N. triplogenioides	s.str.
N. satrapa	satrapa-grp
N. sphodroides	sphodroides-grp
N. jacobi	Stomimorphus
N. tenuis	Stomimorphus
N. barrae	unplaced
N. nocturnocappellus	unplaced
N. violaceus	violaceus-grp

#### Measurements and methods

#### Morphological methods

Measurements were made using an eye piece graticule with a Leica MZ12s stereomicroscope. Standard body length (SBL) is representative of the overall length of specimens as viewed dorsally and is the sum of the distance from the base of the labrum to just anterior of the occipital suture + the length of the pronotum along its midline + the length of the left elytron from basal margin where it meets the scutellum to the apex of the elytron. The width of the elytra is the widest point viewed dorsally or as best estimated by summing the width of each elytron if pinning separated the elytra at the suture. The ocular ratio is the greatest apparent width over the eyes when viewed dorsally divided by the width between the eyes at the level of the anterior supra orbital seta.

Male and female genitalia were prepared using the same methods as Will (2002). Head capsules were prepared by first clearing of muscle tissue using warm KOH and then placing them in warm, dilute bleach. They remained in bleach until the membranous region, e.g. the gular sutures, were strongly contrasting white and so highly visible. All images were taken using a modified Microptics XLT digital imaging system and then edited to enhance clarity using standard image editing software. Maps were created using the Cartographer package ver. 1.31 in Mesquite ver. 2.75 (Maddison and Maddison 2011a, 2011b) using the Australia, shaded relief and coloured height base image from NASA (NASA/JPL/NGA 2004), which was modified for colour contrast and cropped to fit.

# DNA sequencing

Abbreviations used for loci are: 28S, 28S rDNA (aligned length 1157 bp); COI, cytochrome oxidase I (701 bp + 840 bp);

wg, wingless (462 bp); CAD, carbamoyl phosphate synthetase domain of the rudimentary gene (840 bp). Fragments for these genes were amplified using polymerase chain reaction, exo-sap cleaned and sequenced following the same procedures and primers given by (Will and Gill 2008). The only addition is the COI here includes the JER-PAT primer region and HCO-LCO region, both primer pairs from Simon et al. (1994). The use of these two primer pairs usually leaves a 50-100 bp gap unsequenced in the middle of the otherwise nearly complete COI gene. Assembly of multiple chromatograms for each gene fragment and initial base calls were made with Phred (Green and Ewing 2002) and Phrap (Green 1999) initiated within Mesquite's Chromaseq package ver. 1.0 (Maddison and Maddison 2011c) with subsequent editing by manual inspection within Mesquite. Multiple peaks at a single position were coded using IUPAC ambiguity codes. Sequences have been deposited in GenBank with accession numbers: 28S: KF551597-KF551638; CAD: KF551639-KF551680; COI (HCO-LCO region): KF551681-KF551722; COI (JER-PAT region): KF551765-KF551804; and wg: KF551723-KF551764. The GenBank sequence files include an EMEC##### that links to the complete specimen data in the publically available EMEC database http://essigdb.berkeley.edu/. The EMEC record and GenBank files include a KWW### that links the template DNA sample to the voucher specimen deposited in the EMEC.

All sequences are of approximately the lengths given above with a few exceptions. The 28S sequence for Notonomus (Conchitella) clivinoides failed to sequence clearly for the d1 primer and the included sequence starts at aligned position 879 and is derived from the d3i primer. Multiple peaks were seen in the COI from JER-PAT primers for N. (Conchitella) clivinoides, N. (Leiradira) jacobi and N. aeques. These are likely the result of nuclear pseudogenes and no sequences are included for this region of COI. Notonomus chalybaeus has an unreadable, multi-peak region at aligned positions 286–401. That region was omitted from the analysis.

# Alignment

Alignment of the protein-coding sequences was straightforward as the only insertions or deletions consist of six contiguous nucleotides, representing two amino acids, in species of Sarticus for wg. Multiple sequence alignment of 28S was performed by Opal ver. 2.1 (Wheeler and Kececioglu 2007), using default parameter values within Mesquite.

### Phylogenetic analysis

Models of nucleotide evolution where chosen with the aid of mrModelTest ver. 2.3 (Nylander 2004). Using the hierarchical likelihood ratio tests and AIC the chosen models were GTR+I+G for 28S (hLrt, AIC) and COI (hLrt, AIC); and wg (hLrt); GTR+G for CAD (hLrt); HKY+I+G for CAD (AIC) and SYM+I+G for wg (AIC). Analyses were conducted on each gene individually, as well as a matrix of the four genes concatenated together, partitioned by gene. For CAD and wg separate analyses were done for the models chosen by the two criteria. The resulting topologies for CAD and wg did not conflict within a locus, though support and resolution was slightly different. In each

case the model that resulted in the larger support values was used for the combined, partitioned analysis. Those models are GTR+G for CAD and GTR+I+G for wg. Bayesian analyses were conducted using MrBayes ver. 3.2 (Ronquist and Huelsenbeck 2003). Two runs of four chains each were run for 10 million generations, with trees sampled every 1000 generations. Runs all reached an average standard deviation of split frequencies below 0.01 (Huelsenbeck and Ronquist 2005), and likelihood scores and all parameter values reached a stable plateau, based on the tools in Tracer ver. 1.5 (Rambaut and Drummond 2007). For each analysis, the trees in a burn-in period of 50% of the generations were excluded, and the majority-rule consensus tree of remaining trees was calculated to determine Bayesian posterior probabilities (pp) of clades.

# Results

#### Phylogenetic results

#### Single gene analyses

The independent analyses of CAD and COI result in high and very high support, respectively, for Parhypates as the sister to Notonomus. Neither 28S nor wg provide resolution for the Parhypates, Sarticus and Notonomus node (Table 2; Fig. 2).

In all single gene analyses except for wg, monophyly of Parhypates, Sarticus (without N. blackburni) and Notonomus (including N. blackburni, Acanthoferonia, Conchitella, Loxodactylus and Leiradira) is found with very high support (Table 2). Though monophyly of Sarticus and Parhypates is also very highly supported in the analysis of wg alone, that analysis places those as sister taxa within Notonomus, rendering it paraphyletic. All analyses place N. blackburni, Acanthoferonia, Conchitella, Loxodactylus Chaudoir, 1865 and Leiradira species among the clade of species currently in Notonomus; however, only the relationship between Loxodactylus and N. blackburni is found in multiple analyses (Table 2).

Within the subgenus Leiradira, Notonomus dimorphicus Darlington, 1961 and N. flos Darlington, 1961 are sister taxa with very high support in all analyses and are found to be sister to N. alternans + N. aurifer Darlington, 1961 in CAD, wg and combined analyses. Species pairs corresponding to Leiradira s. str., Stomimorphus Straneo, 1953 and Metadira Darlington, 1961b are found to have very high support from multiple genes and no contrary support (Table 2; Fig. 2 nodes 5, 7 and 8).

# Combined analyses

Combined gene analyses result in very high support of the monophyly of Parhypates, Sarticus (without N. blackburni) and Notonomus (including N. blackburni, Acanthoferonia, Conchitella, Loxodactylus and Leiradira) (Table 2). In the combined analysis including all loci, Sarticus is placed as sister to Notonomus, but with low support (0.61 pp). The analysis excluding wg results in Parhypates + Notonomus with very high support. A monophyletic Leiradira (including N. flos and N. dimorphicus) is found in the combined analyses with high or very high support for all nodes (Table 2; Fig. 2).

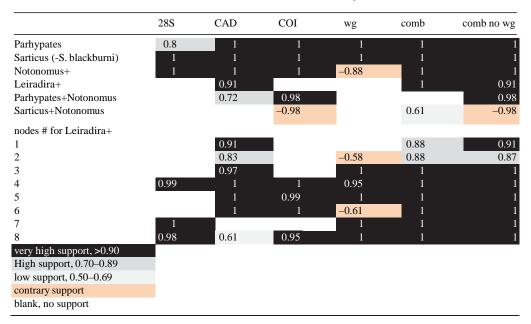
# Taxonomic results

#### Genera and subgenera

Based on the results of the phylogenetic analysis, a redefinition of Notonomus is required to better align the classification with genealogy. From my general examination of types, non-type specimens and descriptions, there is no obvious challenge to the monophyly of Notonomus as conceived here by any described species not included in this analysis. Therefore the genus encompasses all species of Notonomus as listed by Lorenz

 Table 2.
 Support for groups found in Bayesian analyses for each gene locus and combined analysis

 Node numbers refer to nodes indicated in Fig. 2



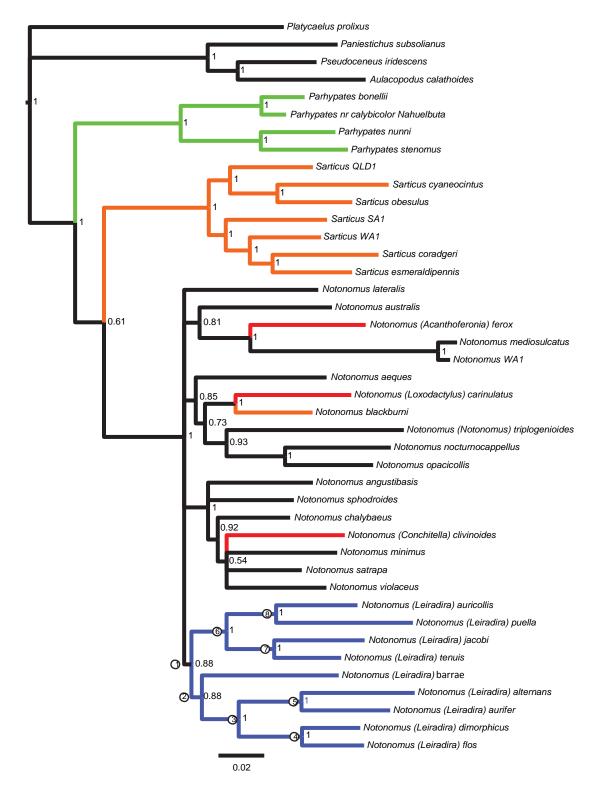


Fig. 2. Majority rule consensus tree from Bayesian analysis. Numbers at nodes are Bayesian PP values. Red numbers in circles are node numbers referred to in Table 2. Branch colours mark prior taxonomic groups: green – Parhypates, orange – Sarticus, blue – Leiradira, red – various small genera, black – distant outgroups and Notonomus.

(2005a) and the species listed below, which are described in or newly combined in Notonomus. Given that the relationships among species within Notonomus are not well supported or even known, the previously recognised genera that are reduced to subgenera are retained as working hypotheses. Of these only Leiradira includes more than two species and so those subgenera may call attention to the distinctiveness of the species, but provide little other information. Darlington used three subgenera of Leiradira (Leiradira s. str., Stomimorphus and Metadira) and these groups are likely to include close relatives. However, as some or all of the species in Darlington's doddi-group of Notonomus (including several undescribed species from Queensland (K. Will, unpubl. Data)) are very likely part of the Metadira clade and given species like N. barrae, which is morphologically distinct from all other Leiradira species, recognition of species groups corresponding to these previously recognised subgenera would be misleading and so they are not employed. Notonomus is a large genus and it will benefit from a subgeneric classification once an integrative taxonomic study is done for all the included species.

Notonomus Chaudoir, 1865 subgenus Leiradira Castelnau, 1867 alternans (Darlington, 1953), comb. nov. alticola (Darlington, 1961), comb. nov. auricollis (Castelnau, 1867), comb. nov. aurifer (Darlington, 1961), comb. nov. barrae, sp. nov. dimorphicus (Darlington, 1961) comb. nov. flos (Darlington, 1961) comb. nov. hephaestus, sp. nov. iridescens, sp. nov. jacobi (Darlington, 1961), comb. nov. latreillei (Castelnau, 1867), comb. nov. opacistriatis Sloane, 1902 puella (Tschitschérine, 1898), comb. nov. smilodon, nom. nov. soror (Darlington 1961), comb. nov. spectabilis, sp. nov. tenuis (Darlington, 1961), comb. nov. thynnefiliarum, sp. nov. vadosus, sp. nov. viridis, sp. nov. subgenus Acanthoferonia Moore, 1965 ferox (Moore, 1965), comb. nov. subgenus Loxodactylus Chaudoir, 1865 australiensis (Sloane, 1895), comb. nov. carinulatus (Chaudoir, 1865), comb. nov. subgenus Conchitella Moore, 1962 clivinoides (Moore, 1962), comb. nov. incertae sedis blackburni (Sloane, 1895), comb. nov. impar (Sloane, 1893), comb. nov. nocturnocappellus, sp. nov. parallelomorphus Chaudoir, 1878, comb. nov., replacement name for Notonomus auricollis (Castelnau, 1867: 211), synonymy by Straneo (1936), preocc. Leiradira auricollis Castelnau, 1867.

Species treatments

# Notonomus alternans (Darlington), comb. nov.

(Figs 10C, 11E, F) Leiradira (Metadira) alternans Darlington, 1953: 90.

# Material examined

Sixty-one <<, 27 , , , one < paratype (QM).

# Distribution and type locality

Specimens of this species are known from the type locality Malanda (Darlington 1953) in the north, south to Tully at elevations of 600–1300 m.

# Diagnosis

Medium- to large-sized black shiny beetles with prominent elytral striae and uneven interval widths. Superficially similar to N. opacistriatis, but easily separated from that species by the apically broadening, dull striae, which are prominent in N. opacistriatis but not found in N. alternans.

#### Description

Size. Overall length (SBL) 10.9–15.4 mm. Greatest width over elytra 3.7–5.1 mm.

Colour. Head black. Pronotum black. Elytra black. Body ventral surface piceous. Legs piceous. Mouthparts piceous. Antennae piceous.

Microsculpture. Dorsal and ventral lustre moderately shiny. Head dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Pronotum dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Elytra with microsculpture absent or not visible at  $50 \times$ magnification. Microsculpture of elytral striae slightly opaque, width not significantly widening apically, striae narrower than or, at most, of about equal width of adjacent intervals near elytral apex.

Head. Eyes medium size, slightly produced. Ocular ratio 1.40–1.50. Antennae clearly geniculate, first antennomere longer than 2+3. Frontal impressions deep, divergent, slightly recurved. Labrum with six setae on anterior margin. Labrum anterior margin moderately emarginate. Occlusal margin of right mandible with long, blade-like anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth low, broad, shallowly emarginate. Apical labial palpomere apically expanded, subsecuriform. Lacinia with a row of thick setae medially, mixed with finer setae and additional, more irregular rows of fine setae dorsally and ventrally.

Thorax. Basal pronotal seta in lateral bead near hind angle. Tarsomere 5 ventrally glabrous. Elytral intervals 3, 5 and 7 slightly wider than 2, 4 and 6. Elytral interval 3 with two setigerous punctures or with three setigerous punctures. Elytral striae all more or less impressed throughout their length. Elytral plica not externally visible, internal ridge present.

Abdomen. Ventrites 4–6 with shallow basolateral sulcus. Male aedeagus with long flagellum.

# Notonomus alticola (Darlington), comb. nov.

(Figs 12A, 13A, B) Leiradira (Metadira) alticola Darlington, 1961b: 6.

#### Material examined

Sixteen <<, 11 ,, one damaged, sex undetermined.

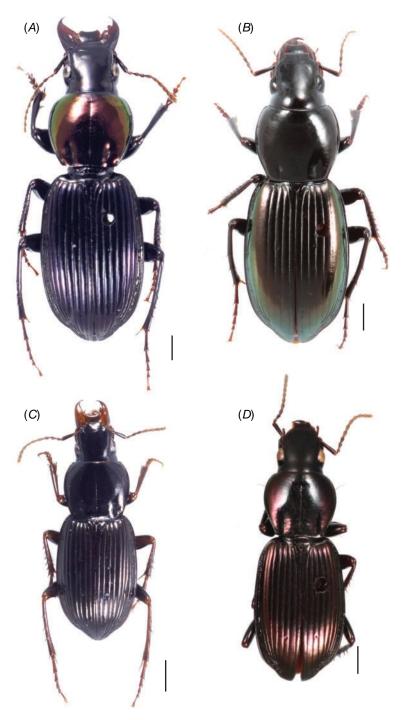


Fig. 3. Dorsal habitus, scale bars = 1.0 mm. (A) Notonomus auricollis, (B) Notonomus latreillei, (C) Notonomus puella, (D) Notonomus thynnefiliarum.

# Distribution and type locality

Darlington (1961b) established the east side of Mt Bellenden Ker as the type locality and this species is known only from Mt Bellenden and Mt Bartle Frere (Fig. 9) at elevations above 1400 m.

# Diagnosis

Large-sized beetles with relatively broader and more ovoid elytra, regularly impressed striae and subtle metallic colour on the head and pronotum that in combination readily distinguishes this species from other Notonomus species

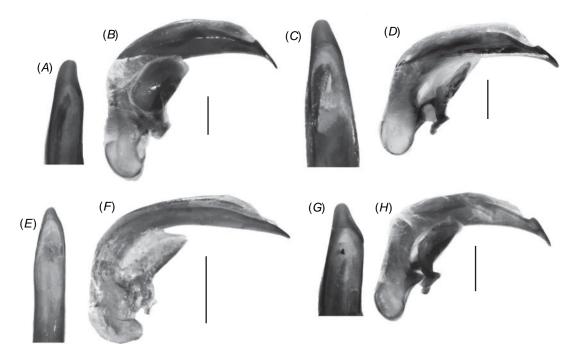


Fig. 4. Male genitalia, scale bar = 0.5 mm. Notonomus auricollis, (A) dorsal view blade of median lobe, (B) left lateral view; Notonomus latreillei, same C–D; Notonomus puella, same E–F; Notonomus thynnefiliarum, same G–H.

including N. soror, which is sympatric with it on Mt Bellenden Ker.

#### Description

Size. Overall length (SBL) 14.0–18.4 mm. Greatest width over elytra 4.8–6.3 mm.

Colour. Head black ground colour with green or metallic purple colour. Pronotum metallic green or purple. Elytra black or metallic purple along lateral margins. Body ventral surface piceous. Legs piceous. Mouthparts piceous. Antennae piceous.

Microsculpture. Dorsal and ventral lustre moderately shiny. Head dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Pronotum dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Elytra with microsculpture consisting of isodiametric sculpticells. Microsculpture of elytral striae slightly opaque, width not significantly widening apically, striae narrower than or, at most, of about equal width of adjacent intervals near elytral apex.

Head. Eyes medium size, slightly produced. Ocular ratio 1.35–1.56. Antennae clearly geniculate, first antennomere longer than 2+3. Frontal impressions shallow or not impressed. Labrum with six setae on anterior margin. Labrum anterior margin moderately emarginate. Occlusal margin of right mandible with long, blade-like anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth low, broad, shallowly emarginate. Apical labial palpomere slightly expanded apically. Lacinia with a row of thick setae medially, mixed with finer setae and additional, more irregular rows of fine setae dorsally and ventrally.

Thorax. Basal pronotal seta in lateral bead near hind angle. Tarsomere 5 ventrally glabrous. Elytral intervals all of approximately equal width. Elytral interval 3 with one setigerous puncture. Elytral striae all more or less impressed throughout their length. Elytral plica absent.

Abdomen. Ventrites 4–6 with shallow basolateral sulcus or without sulci. Male aedeagus with long flagellum.

#### Notonomus auricollis (Castelnau), comb. nov.

(Figs 3A, 4A, B, 5) Leiradira auricollis Castelnau, 1867: 159. Leiradira cupreicollis Tschitschérine, 1897: 271. Leiradira purpurascens Tschitschérine, 1897: 270. Leiradira blandula Tschitschérine, 1898: 45 new synonymy.

Material examined

One hundred <<, 115 , , , one , holotype L. blandula (ZISP).

#### Distribution and type locality

The range of this species is from as far north as southern Queensland, near Mistake Mnts and Cunningham Gap, south to Dorrigo National Park (Fig. 8). It is a rainforest species usually found at 600–1000 m elevation. Straneo (1941) selected a lectotype for this species but did not restrict the type locality (Moore et al. 1987: 163). The type locality is here restricted to the upper Clarence River, NSW in the vicinity of  $28^{\circ}42^{\circ}6^{\circ}S$   $152^{\circ}29^{\circ}21^{\circ}E$ .

# Diagnosis

Medium-sized beetles with notable metallic colours and regular, well impressed elytral striae. This species is most similar to N. latreillei, from which it differs in having more clearly impressed striae, especially laterally, and colour, and N. thynnefiliarum, which it differs from in having the

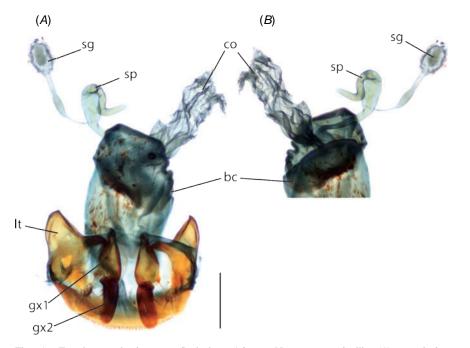


Fig. 5. Female reproductive tract. Scale bar = 1.0 mm. Notonomus auricollis, (A) ventral view, (B) dorsal view of apical portion. sg = spermatheca gland, sp = spermatheca, co = common oviduct, bc = bursa coplatrix, lt = laterotergite ix, gx1 = gonocoxite 1, gx2 = gonocoxite 2.

pronotum strongly metallic, contrasting with the head an elytral colours.

# Description

Size. Overall length (SBL) 8.9–13.2 mm. Greatest width over elytra 3.0–4.5 mm.

Colour. Head black. Pronotum black ground colour with metallic green colour or clearly metallic green, red or aeneous. Elytra metallic purple. Body ventral surface black or piceous. Legs black or piceous. Mouthparts piceous. Antennae piceous or brown and infuscated.

Microsculpture. Dorsal and ventral lustre very or moderately shiny. Head dorsally with microsculpture absent or not visible at 50× magnification. Pronotum dorsally with microsculpture absent or not visible at 50× magnification. Elytra with microsculpture consisting of isodiametric sculpticells. Microsculpture of elytral striae slightly opaque, width not significantly widening apically, striae narrower than or, at most, of about equal width of adjacent intervals near elytral apex.

Head. Eyes small, flat. Ocular ratio 1.31–1.43. Antennae clearly geniculate, first antennomere longer than 2+3. Frontal impressions shallow or not impressed. Labrum with four setae on anterior margin, median pair absent. Labrum anterior margin shallowly emarginate or entire. Occlusal margin of right mandible with long, blade-like anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth absent. Apical labial palpomere slightly expanded apically. Lacinia with a row of thick setae medially, and an irregular row of fine setae dorsally.

Thorax. Basal pronotal seta adjacent to lateral bead and about one pore's width forward of hind angle. Tarsomere 5

ventrally glabrous or setose. Elytral intervals all of approximately equal width. Elytral interval 3 with two setigerous punctures. Elytral striae all more or less impressed throughout their length. Elytral plica externally visible.

Abdomen. Ventrites 4–6 without sulci. Male aedeagus without ligula.

#### Notes on variation and synonymy

Notonomus auricollis is the only species found to be variable for ventral setation of tarsomere 5. Of 205 specimens examined for setae on tarsomere 5, 110 had no setae and 92 had at least one seta on one tarsomere (three damaged and state unknown). Of the setose individuals the number of setae was usually one, but occasionally two and setae were found on one or several legs. In this sample there was no obvious pattern related to which particular leg was setose, sex bias or specific locality. Setae were finer and shorter than what is found in other species with a pair consistently on all legs, e.g. N. latreillei. Though Tschitschérine (1896: 40) noted the difficulty of seeing the ventral setae in this species, he used this as a key identification character to separate N. auricollis and N. blandulus. Given the large series of individuals available to me and examination of the type of N. blandulus, including dissection of the male type's genitalia, it is clear that the type specimen of N. blandulus falls well within variation of N. auricollis. The type of N. blandulus is labelled 'S. Australia. Adelaide.', but this is certainly an erroneous locality. The most south-western record for N. auricollis is the vicinity of Glen Innes, NSW more than 1300 km from Adelaide. No specimens of Leiradira are known from South Australia.

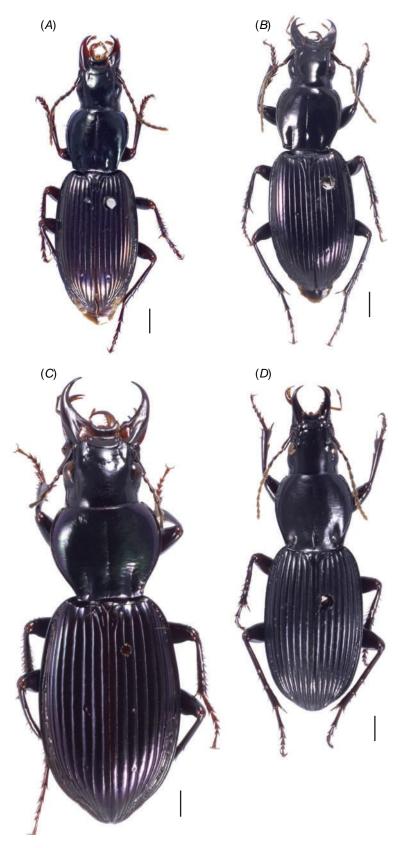


Fig. 6. Dorsal habitus. Scale bars = 1.0 mm. (A) Notonomus jacobi, (B) Notonomus tenuis, (C) Notonomus smilodon, (D) Notonomus barrae.

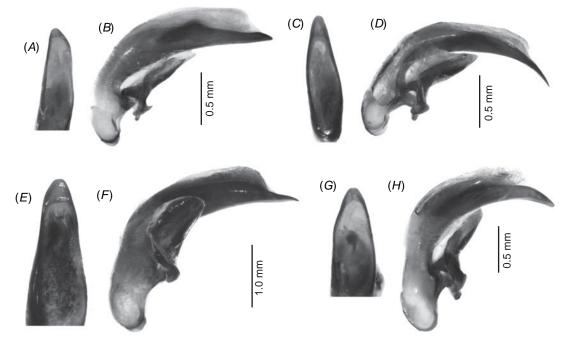


Fig. 7. Male genitalia. Notonomus jacobi, (A) dorsal view blade of median lob, (B) left lateral view median lobe with parameres; Notonomus tenuis, same C–D; Notonomus smilodon, same E–F; Notonomus barrae, same G–H.

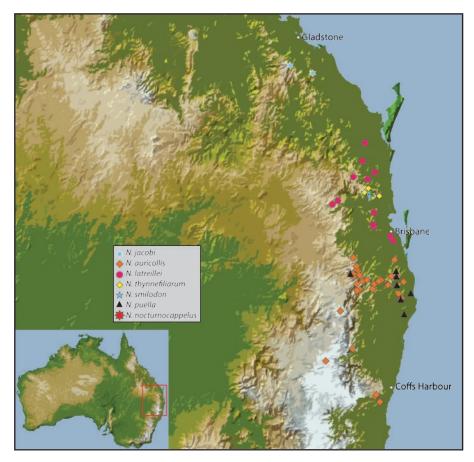


Fig. 8. Map of localities for material examined of Notonomus species.

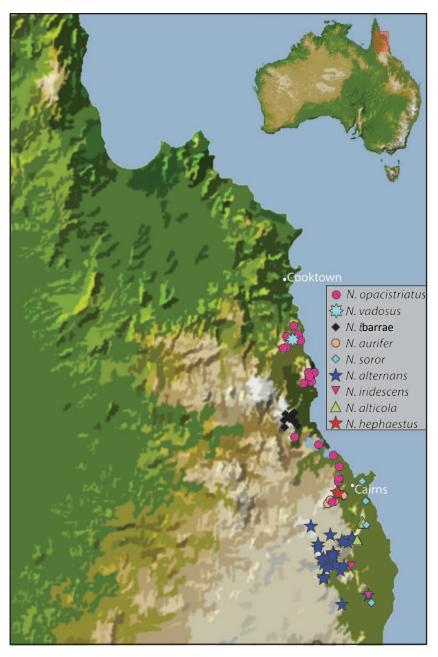


Fig. 9. Map of localities for material examined of Notonomus species.

Notonomus aurifer (Darlington) (Figs 14B, 15C, D, 17A) Leiradira (Metadira) aurifer Darlington, 1961b: 4.

# Material examined

Thirty-three <<, 18,,, paratype, (QM).

#### Distribution and type locality

Darlington (1961b) established the type locality as the 'mountains north of Kairi' and this species is known from those mountains at elevations above 900 m as far north as Lambs Head (Fig. 9).

# Diagnosis

Strikingly brilliant, shifting metallic red green beetles. Mediumto large-sized Leiradira that are very similar to N. spectabilis, but immediately separable by the dark metallic purple or blue colour of this species compared to the brilliant red in N. spectabilis. Notonomus aurifer is nearly identical to N. hephaestus in habitus and colour, but N. aurifer has the wide gula, rake-like lacinia and differs in patterns of setation generally.

# Description

Size. Overall length (SBL) 15.8–19.0 mm. Greatest width over elytra 5.3–6.6 mm.



Fig. 10. Dorsal habitus, scale bars = 1.0 mm. (A) Notonomus iridius, (B) Notonomus vadosus, (C) Notonomus alternans.

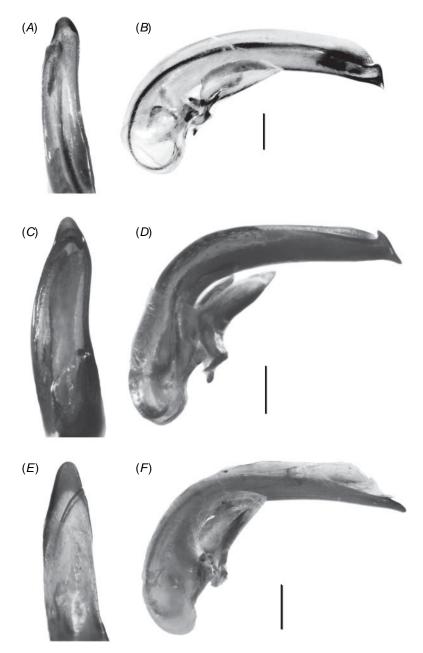


Fig. 11. Male genitalia, scale bar = 0.5 mm. Notonomus iridius, (A) dorsal view blade of median lobe, (B) left lateral view median lobe with parametes; Notonomus vadosus, same C–D; Notonomus alternans, same E–F.

Colour. Head metallic green or metallic red. Pronotum metallic green or metallic red. Elytra metallic green or metallic red. Body ventral surface black. Legs piceous. Mouthparts piceous. Antennae piceous.

Microsculpture. Dorsal and ventral lustre very or moderately shiny. Head dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Pronotum dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Elytra with microsculpture absent or not visible at  $50 \times$ magnification. Microsculpture of elytral striae strongly, obviously opaque mesh, width greatly widening and striae anastomosing apically, much wider than intervals near elytral apex.

Head. Eyes medium size, slightly produced. Ocular ratio 1.40–1.46. Antennae not geniculate, first antennomere subequal to length of 2+3. Frontal impressions deep, divergent, slightly recurved. Labrum with six setae on anterior margin. Labrum anterior margin moderately emarginate or anterior margin shallowly emarginate. Occlusal margin of right mandible with long, blade-like anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth low, broad, shallowly emarginate. Apical labial palpomere slightly expanded apically. Lacinia



Fig. 12. Dorsal habitus, scale bars = 1.0 mm. (A) Notonomus alticola, (B) Notonomus soror, (C) Notonomus viridis, (D) Notonomus opacistriatus.

with a row of thick setae medially, mixed with finer setae and additional, more irregular rows of fine setae dorsally and ventrally.

Thorax. Basal pronotal seta in lateral bead near hind angle. Tarsomere 5 ventrally glabrous. Elytral intervals 3, 5 and 7 much wider than 2, 4 and 6. Elytral interval 3 with two setigerous punctures. Elytral striae all more or less impressed throughout their length. Elytral plica flat, scarcely visible.

Abdomen. Ventrites 4–6 with shallow basolateral sulcus or without sulci. Male aedeagus with long flagellum.

# Notonomus barrae, sp. nov.

(Figs 6D, 7G, H)

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#### Material examined

Holotype. <, '55k0315418/8173573 WGS84, Mount Lewis Road, 1210 m, 23Oct-30Nov2008 K. Staunton, Pitfall CU12A2 c 688'//'QMT189878'. Deposited QM.

Paratypes. Mt Lewis, 27.xii.1972, A. and M. Walford-Huggins (< CMNH), same 7.xii.1975 (, CMNH);  $16^{\circ}32^{\circ}32.3^{\circ}S$   $145^{\circ}17^{\circ}03.7^{\circ}E$ ,

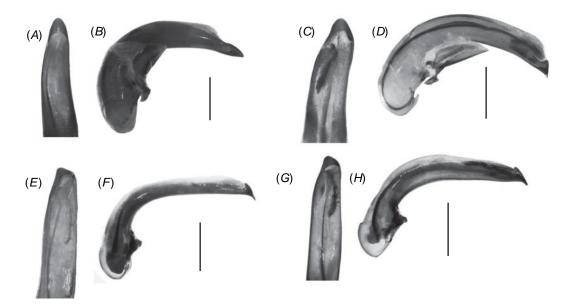


Fig. 13. Male genitalia, scale bars = 1.0 mm. Notonomus alticola, (A) dorsal view blade of median lobe, (B) left lateral view median lobe with parametes; Notonomus soror, same C–D; Notonomus viridis, same E–F; Notonomus opacistriatus, same G–H.

974 m, headlamp search, 19.xii.2010, K. Will (AUS2010.xii.19.2) (EMEC208703<, EMEC209820 <, EMEC209819 ,, EMEC); Mount Lewis Road, 1160 m, 23.x-30.xi.2008 K. Staunton, pitfall (T193500, T193501, << QM), same 3Sep-23Oct (T193502, QM); Mt Lewis Rd, 29 km from Highway, 14. vii. 97, G. Monteith, 1200 m, (T65725, QM). 16.511°S.145.209°E, Mt Lewis Rd hut, 12 km NW Julatten. 1187 m. 22.xi.2009. Hand. 18632 G.B. Monteith and F. Turco, kww884, EMEC209812 (< EMEC). Devils Thumb area, 10 km NW Mossman, -16.394167°/145.289167°, 1000-1180 m, Monteith, D. Yeates, G. Thompson, 09-10.x.1982 (T20255, OM); same, 16 23Sx145 16E, 1160 m, 30.vi−1.vii.1997, D.J. Cook (T193503 < QM). 16°23<sup>0</sup>48<sup>th</sup>S 145°17<sup>0</sup>38<sup>0</sup>E, Devils Thumb, above Fern Patch, Carbine Tableland, 26-27.xi.1990, G. Monteith, H. Janetzki, pitfall trap, 1050 m, (T20266 < QM); (16°24°27°S 145°16°20°E), Devils Thumb-Plane Crash, 27.xi.90, G. Monteith, G. Thompson, D. Cook, R. Sheridan, H. Janetzki, 1300 m (T20267 < QM);  $(16^{\circ}26^{\circ}54^{\circ}S \ 145^{\circ}16^{\circ}53^{\circ}E),$  Mossman Bluff Summit, 10 km W Mossman, 21.xii.89, G. Monteith, G. Thompson, ANZSES, 1300 m (T20264 , QM); (16°27°52<sup>®</sup>S 145°17°12<sup>®</sup>E), Mossman Bluff Track, 10 km W Mossman, 17-19.xii.1988, G. Monteith, G. Thompson, pitfall trap, 1000 m (T20261 < QM); (16°28°S 145°18°E), Mossman Bluff Track, 5-10 km W Mossman, 01-17.i.1989, G. Monteith, G. Thompson, ANZSES, pitfall trap, 1260 m (T20263 < QM); (16°29°54<sup>0</sup>S 145°19°13<sup>0</sup>E), Mt Demi summit, 16-17.xii.1995, G. Monteith, G. Thompson, 1000 m (T25804, QM); (16°29°54<sup>®</sup>S 145°19°13<sup>®</sup>E), Mt Demi, 7 km SW Mossman, 29.x.1983, D. Yeates, G. Thompson, 1100 m (T20256, T20257, , , QM); ( $16^{\circ}6^{0}44^{\circ}S$ 145°24°58°E), Mt Hemmant, 25-27.xi.1993, G. Monteith, D. Cook, H. Janetzki, L. Roberts, 1050 m (T20270 <, T20271 ,, QM); (16°27°17°S 145°12°26°E), Mt Spurgeon, 2 km SE, via Mt Carbine, 20.xii.88, G. Monteith, G. Thompson, 1100 m (T20262, , QM); (16°26<sup>0</sup>27<sup>(0</sup>S 145°15<sup>0</sup>8<sup>(0)</sup>E), Pauls Luck, Platypus Ck, 13 km W Mossman, 01-16.i.1990, ANZSES, pitfall trap, 1100 m (T20265, , QM); (16°24<sup>0</sup>19<sup>0</sup> S 145°13<sup>0</sup>1<sup>0</sup> E), Stewart Ck, 4 km NNE Mt Spurgeon (camp 1), 15-20.x.1991, G. Monteith, H. Janetzki, D. Cook, L. Roberts, 1250-1300 m (T20268, T20269, ,, QM); (16°27°52°S 145°17°12°E), The Bluff, 11 km W Mossman, 2.xi.1983, G. Monteith, D. Yeates, G. Thompson, 800–1300 m (T20258, T20259, T20260 <, QM).

Distribution and type locality

The type locality is Mount Lewis, Queensland, S  $16^{\circ}30^{0}45^{\%}E$   $145^{\circ}16^{0}13^{\%}$ . The species is known from as far north as Mt Hemmant, just south of Cape Tribulation, through the Daintree and Carbine Tableland to just south of the level of Mossman and Mt Lewis (Fig. 9). It is a rainforest species found at 1000–1300m elevation. Reported as 'Leiradira NQ2' by Yeates et al. (2002).

# Diagnosis

Fairly small, very narrowly-built beetles with notably elongate narrow head and mandibles, no anterior retinacular tooth on the right mandible and a very wide gula.

#### Description

Size. Overall length (SBL) 9.9–12.2 mm. Greatest width over elytra 3.1–4.2 mm.

Colour. Head black. Pronotum black. Elytra black with spectral iridescence. Body ventral surface black or piceous. Legs piceous. Mouthparts piceous or rufobrunneous, paler than head. Antennae rufobrunneous, paler than head.

Microsculpture. Dorsal and ventral lustre very or moderately shiny. Head dorsally with microsculpture consisting of isodiametric sculpticells. Pronotum dorsally with microsculpture consisting of isodiametric sculpticells. Elytra with microsculpture consisting of isodiametric sculpticells. Microsculpture of elytral striae slightly opaque, width not significantly widening apically, striae narrower than or, at most, of about equal width of adjacent intervals near elytral apex.

Head. Eyes small, flat. Ocular ratio 1.39–1.53. Antennae clearly geniculate, first antennomere longer than 2+3. Frontal impressions deep, divergent, straight. Labrum with six setae on

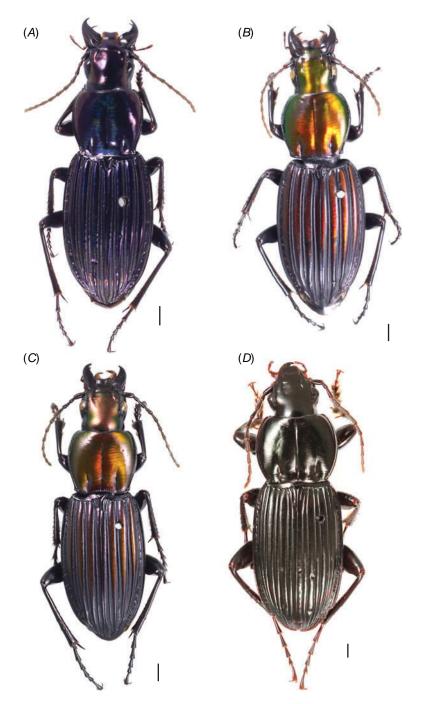


Fig. 14. Dorsal habitus, scale bars = 1.0 mm. (A) Notonomus spectabilis, (B) Notonomus aurifer, (C) Notonomus hephaestus, (D) Notonomus nocturnocappelus.

anterior margin. Labrum anterior margin deeply emarginate. Occlusal margin of right mandible without anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth moderately prominent, bilobed. Apical labial palpomere slightly expanded apically. Lacinia with a row of thick setae medially, mixed with finer setae and additional, more irregular rows of fine setae dorsally and ventrally.

Thorax. Basal pronotal seta adjacent to lateral bead and near hind angle. Tarsomere 5 ventrally glabrous. Elytral intervals all of approximately equal width. Elytral interval 3 without setigerous punctures. Elytral striae all more or less impressed throughout their length. Elytral plica absent.

Abdomen. Ventrites 4–6 without sulci. Male aedeagus without ligula.

# Etymology

Honours Cheryl Barr, Museum Scientist/Collection Manager Emeritus, EMEC, whose efforts contributed to this and

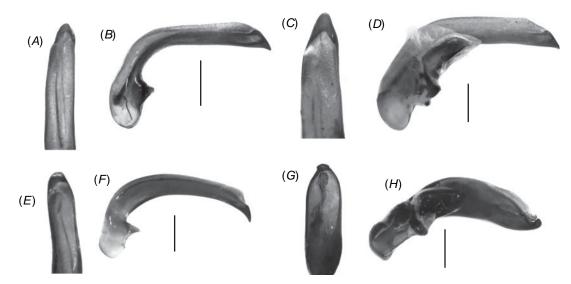


Fig. 15. Male genitalia, scale bars = 1.0 mm. Notonomus spectabilis, (A) dorsal view blade of median lobe, (B) left lateral view median lobe with parameres; Notonomus aurifer, same C–D; Notonomus hephaestus, same E–F; Notonomus nocturnocappellus, same G–H.

many other entomological studies during her time at the EMEC.

#### Notonomus iridescens, sp. nov.

(Figs 10A, 11A, B) urn:lsid:zoobank.org:act:251A39E8-9450-41A2-8D31-7D95A8E5 A8F9

#### Material examined

Holotype. <, 'Upper Boulder Creek, via Tully, 500–600 m 24-27 Oct 1983 Monteith, Yeates & Thompson, QM Reg. No. T20250'. Deposited QM.

Paratypes. Upper Boulder Creek, 11 km NNW Tully, 16–19.xi.1984 D. Cook, G. Monteith, G. Thompson, 850 m, QM reg. No. T20251, (, QM); Upper Boulder Creek, 11 km N Tully 05–07.xii.1989, G. Monteith, G. Thompson, H. Janetzki, pitfall trap rainforest, 1000 m, QM Reg. No. T20252, (< QM);  $17^{\circ}36^{\circ}$ S  $145^{\circ}45^{\circ}$ E, Henrietta Ck, Palmerston NP, 30. xi.1992–15.iv.1993, R. Raven et al. 380 m, rainforest pitfall, 9761 T110058 (< QM).

### Distribution and type locality

The type locality is Upper Boulder Creek, Queensland,  $17^{\circ}49^{0}44^{\circ}S$   $145^{\circ}54^{0}2^{\circ}E$ . The specimens in the type series represent the only known localities (Fig. 9).

#### Diagnosis

Black, somewhat shiny beetles with deeply impressed pronotal basal impressions and dull elytral striae that are very similar to N. soror, but with four setae on the margin of the labrum and typically more broadly built.

# Description

Size. Overall length (SBL) 10.9–11.7 mm. Greatest width over elytra 3.7–3.8 mm.

Colour. Head black. Pronotum black. Elytra black with spectral iridescence. Body ventral surface piceous. Legs piceous. Mouthparts piceous. Antennae piceous.

Microsculpture. Dorsal and ventral lustre moderately shiny or dull. Head dorsally with microsculpture absent or not visible at 50× magnification. Pronotum dorsally with microsculpture absent or not visible at 50× magnification. Elytra with microsculpture absent or not visible at 50× magnification. Microsculpture of elytral striae strongly, obviously opaque mesh, width slightly widening apically, width less than intervals near elytral apex.

Head. Eyes small, flat. Ocular ratio 1.38–1.45. Antennae clearly geniculate, first antennomere longer than 2+3. Frontal impressions deep, divergent, slightly recurved. Labrum with four setae on anterior margin, median pair absent. Labrum entire. Occlusal margin of right mandible with long, blade-like anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth low, broad, shallowly emarginate. Apical labial palpomere slightly expanded apically. Lacinia with a row of thick setae medially, and an irregular row of fine setae dorsally.

Thorax. Basal pronotal seta in lateral bead near hind angle. Tarsomere 5 ventrally glabrous. Elytral intervals all of approximately equal width. Elytral interval 3 with one setigerous puncture. Elytral striae all more or less impressed throughout their length. Elytral plica absent.

Abdomen. Ventrites 4–6 with shallow basolateral sulcus. Male aedeagus with long flagellum.

# Etymology

The specific epithet draws attention to the spectral iridescence of the beetle.

Notonomus jacobi (Darlington), comb. nov.

# (Figs 6A, 7A, B)

Leiradira (Stomimorphus) jacobi Darlington, 1961b: 9.

#### Material examined

Six <<, 8 ,,.

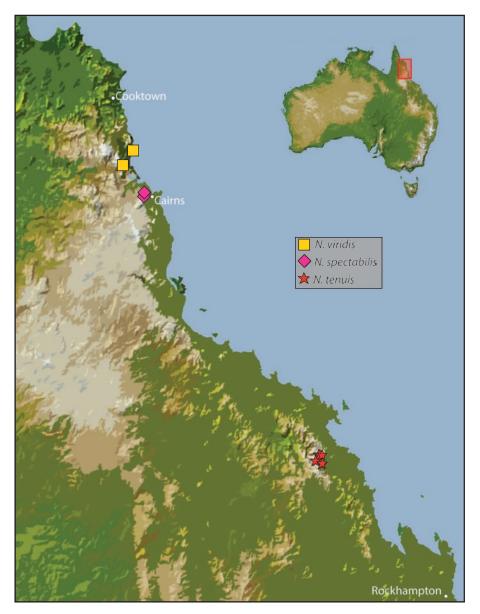


Fig. 16. Map of localities for material examined of Notonomus species.

# Distribution and type locality

Darlington (1961b: 10) established the type locality as 'Mt Jacob, c. 45 miles south of Gladstone, South Queensland'. However, Mt Jacob is not an official name that appears on any maps and, as deduced by Monteith (1986), the locality referred to by Darlington corresponds to Bulburin National Park. The type locality can be refined to there, in the vicinity of  $24^{\circ}30^{\circ}58^{\circ}S$   $151^{\circ}27^{\circ}42^{\circ}E$ . The species is only known from the type locality and the plateau to the west, Kroombit Tops (Monteith 1986) Fig. 8.

# Diagnosis

Similar to N. thynnefiliarum and N. auricollis but with the pronotal margins more sinuate near the base and a subtle green to blue metallic colour on the pronotum.

#### Description

Size. Overall length (SBL) 9.7–11.0 mm. Greatest width over elytra 3.5–4.1 mm.

Colour. Head black. Pronotum black. Elytra black. Body ventral surface black or piceous. Legs piceous. Mouthparts piceous or rufobrunneous, paler than head. Antennae piceous or rufobrunneous, paler than head.

Microsculpture. Dorsal and ventral lustre moderately shiny or dull. Head dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Elytra with microsculpture consisting of a mesh of slightly transversely stretched sculpticells. Microsculpture of elytral striae slightly opaque, width not significantly widening apically, striae narrower than or, at most, of about equal width of adjacent intervals near elytral apex.

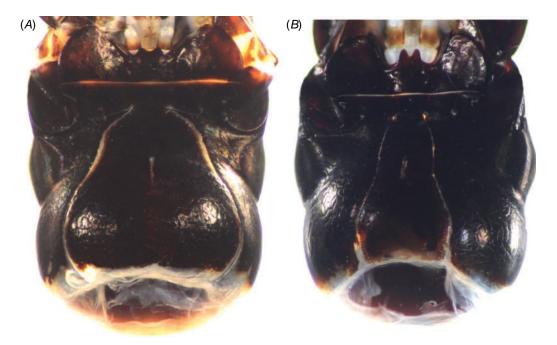


Fig. 17. Ventral view of head capsule. (A) Notonomus aurifer, wide gula, (B) Notonomus hephaestus, typical narrower gula.

Head. Eyes medium-sized, flat. Ocular ratio 1.36–1.41. Antennae clearly geniculate, first antennomere longer than 2 +3. Frontal impressions short, shallow, recurved. Labrum with six setae on anterior margin. Labrum anterior margin deeply emarginate. Occlusal margin of right mandible with a sharp, narrow anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth low, broad, shallowly emarginate. Apical labial palpomere slightly expanded apically. Lacinia with a row of thick setae medially, and an irregular row of fine setae dorsally.

Thorax. Basal pronotal seta adjacent to lateral bead and near hind angle. Tarsomere 5 ventrally glabrous. Elytral intervals all of approximately equal width. Elytral interval 3 with two setigerous punctures. Elytral striae all more or less impressed throughout their length. Elytral plica flat, scarcely visible.

Abdomen. Ventrites 4–6 without sulci. Male aedeagus without ligula.

#### Notonomus latreillei (Castelnau), comb. nov.

#### (Figs 3B, 4C, D)

Leiradira latreillei latreillei Castelnau, 1867: 158. Leiradira liopleura Chaudoir, 1868: 163. Leiradira latreillei chaudoiri Straneo, 1941: 91.

Leiradira latreillei Chaudoir, 1868: 162 [non Castelnau 1867].

#### Material examined

Fifteen <<, 17 ,,.

# Distribution

The range of this species is from just south and west of Brisbane, e.g. Pine Mt, to the north as far as Yabba Creek (Fig. 8). It has been

collected in a variety of forest types including rainforest, vine forest and eucalypt forest, at elevations of 50–470 m.

#### Diagnosis

A medium- to small-sized beetle, somewhat convex in form. Frequently with the outer elytral striae wanting. Most similar to N. auricollis, though distinctly differently coloured as discussed under that species.

# Description

Size. Overall length (SBL) 9.5–11.5 mm. Greatest width over elytra 3.3–3.9 mm.

Colour. Head black. Pronotum black. Elytra black ground colour with metallic green or bronze reflex. Body ventral surface black or piceous. Legs black or piceous. Mouthparts piceous. Antennae piceous.

Microsculpture. Dorsal and ventral lustre moderately shiny. Head dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Pronotum dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Elytra with microsculpture consisting of isodiametric sculpticells. Microsculpture of elytral striae slightly opaque, width not significantly widening apically, striae narrower than or, at most, of about equal width of adjacent intervals near elytral apex.

Head. Eyes medium size, slightly produced. Ocular ratio 1.35–1.42. Antennae clearly geniculate, first antennomere longer than 2+3. Frontal impressions shallow or not impressed. Labrum with four setae on anterior margin, median pair absent. Labrum anterior margin shallowly emarginate. Occlusal margin of right mandible with long, blade-like anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth absent. Apical labial palpomere slightly expanded apically. Lacinia with a row of thick setae medially, and an irregular row of fine setae dorsally.

Thorax. Basal pronotal seta adjacent to lateral bead, near hind angle or about one pore's width forward of hind angle. Tarsomere 5 setose. Elytral intervals all of approximately equal width. Elytral interval 3 with two setigerous punctures. Elytral striae 5–7 more shallowly impressed in basal third than striae 1–4 or 5–7 very shallow or absent in middle half. Elytral plica externally visible.

Abdomen. Ventrites 4-6 without sulci. Male aedeagus without ligula.

# Notes on variation and synonymy

The sample of specimens available for study for this species is small, eight specimens from five localities, and there is significant variation in size and the level of impression of striae 5–7. I am unable to assess Straneo's subspecies.

### Notonomus opacistriatis Sloane

(Figs 12D, 13G, H) Notonomus opacistriatis Sloane 1902: 319.

# Material examined

Thirty-one <<, 27 , , , four damaged, sex undetermined.

#### Distribution and type locality

Specimens are known from as far north as Big Tableland and south to Chujeba Peak (Fig. 9). Darlington (1961b) doubted Cairns was the correct locality as given for the syntypes collected by Froggatt, or provided by Froggatt to Sloane (Sloane 1902). Darlington treated specimens he collected 'near Davies Creek road on the northern Atherton Tableland near Black Mt about 20 miles north of Kuranda' as 'virtual topotypes'. Black Mt is ~20 miles north of Kuranda; however, Davies Creek Road is 20 km (12.5 miles) south-west of Kuranda. In Darlington's list of localities (1960) he correctly places the Davies Creek locality on his map but does not list a Black Mt site. Given the ambiguity of the exact type locality, I select  $16^{\circ}38^{\circ}55^{\circ}S$  145°29°29°29°E, Black Mt, 17 km ESE Julatten, the locality data on an extensive series of N. opacistriatis specimens in the QM, as the type locality.

# Diagnosis

Medium- to large-sized, black shiny beetles with prominent elytral striae. Superficially similar to N. alternans but easily separated from that species, which has regularly impressed, narrow striae.

# Description

Size. Overall length (SBL) 10.9–13.7 mm. Greatest width over elytra 3.4–4.9 mm.

Colour. Head black. Pronotum black with spectral iridescence. Elytra black with spectral iridescence. Body ventral surface black. Legs piceous. Mouthparts piceous. Antennae piceous.

Microsculpture. Dorsal and ventral lustre very shiny. Head dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Pronotum dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Elytra with microsculpture

absent or not visible at  $50 \times$  magnification. Microsculpture of elytral striae strongly, obviously opaque mesh, width greatly widening and striae anastomosing apically, much wider than intervals near elytral apex.

Head. Eyes medium size, slightly produced. Ocular ratio 1.46–1.52. Antennae not geniculate, first antennomere subequal to length of 2+3. Frontal impressions deep, divergent, slightly recurved. Labrum with six setae on anterior margin. Labrum anterior margin shallowly emarginate. Occlusal margin of right mandible with long, blade-like anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth low, broad, shallowly emarginate. Apical labial palpomere slightly expanded apically. Lacinia with a row of thick setae medially, mixed with finer setae and additional, more irregular rows of fine setae dorsally and ventrally.

Thorax. Basal pronotal seta in lateral bead near hind angle. Tarsomere 5 ventrally glabrous. Elytral intervals 3, 5 and 7 slightly wider than 2, 4 and 6. Elytral interval 3 with two setigerous punctures. Elytral striae all more or less impressed throughout their length. Elytral plica flat, scarcely visible.

Abdomen. Ventrites 4–6 with shallow basolateral sulcus or without sulci. Male aedeagus with long flagellum.

#### Notes of variation

Notonomus (Leiradira) opacistriatis and N. (L.) viridis (see below) are the only species of Leiradira in which there is variation in the female protarsomere ventral setation. In all other species females lack the two rows of squamose setae found in males. Of the 21 female specimens of N. opacistriatis examined 11 had squamose setae on the ventral surface of tarsomeres 1 and 2, and 10 did not. Females of both states were taken from across the entire range of the species.

# Notonomus puella (Tschitschérine), comb. nov.

(Figs 3C, 4E, F)

Leiradira puella Tschitschérine, 1898: 41.

#### Material examined

Five <<, nine , , , one , holotype and two << (ZISP).

# Distribution and type locality

The holotype is labelled with only NSW and no further locality data is provided with the description. The species ranges from Victoria Park, NSW to Numinbah Arch, QLD, west to Springbrook (Fig. 8). It has been repeatedly collected in the Nightcap Ranges National Park and the type locality is here established as the vicinity of the Big Scrub Loop, Nightcap Ranges National Park, 28°38°11<sup>®</sup>S 153°20<sup>°</sup>6<sup>®</sup>E.

# Diagnosis

Very small-sized beetles, distinct from all other species though most similar to N. tenuis, from which it can be separated by the combination of the black colour with an iridescent shine, pronotum flat and slightly reflexed at the hind angles, basal setae of the pronotum forward of hind angle at least one pore's width or more and complete elytral striae.

# Description

Size. Overall length (SBL) 7.3–8.2 mm. Greatest width over elytra 2.5–3.0 mm.

Colour. Head black. Pronotum black. Elytra black. Body ventral surface piceous. Legs piceous. Mouthparts rufobrunneous, paler than head. Antennae brown and infuscated.

Microsculpture. Dorsal and ventral lustre very. Head dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Pronotum dorsally with microsculpture absent or not visible at  $50 \times$  magnification or with microsculpture consisting of isodiametric sculpticells just visible. Elytra with microsculpture absent or not visible at  $50 \times$  magnification or with microsculpture absent or not visible at  $50 \times$  magnification or with microsculpture strate states of a mesh of slightly transversely stretched sculpticells. Microsculpture of elytral striae slightly opaque, width not significantly widening apically, striae narrower than or, at most, of about equal width of adjacent intervals near elytral apex.

Head. Eyes small, flat. Ocular ratio 1.38–1.42. Antennae clearly geniculate, first antennomere longer than 2+3. Frontal impressions shallow or not impressed. Labrum with four setae on anterior margin, median pair absent. Labrum anterior margin moderately emarginate. Occlusal margin of right mandible with long, blade-like anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth absent. Apical labial palpomere slightly expanded apically. Lacinia with a row of thick setae medially, and an irregular row of fine setae dorsally.

Thorax. Basal pronotal seta adjacent to lateral bead and forward of hind angle at least one pore's width or more distance. Tarsomere 5 ventrally glabrous. Elytral intervals all of approximately equal width or 3, 5 and 7 very slightly wider. Elytral interval 3 with two setigerous punctures. Elytral striae all more or less impressed throughout their length. Elytral plica externally visible.

Abdomen. Ventrites 4–6 without sulci. Male aedeagus with long flagellum.

#### Notonomus smilodon, nom. nov.

(Figs 6C, 7E, F)

Stomimorphus violaceus Straneo, 1953: 2. preocc. by Notonomus violaceus (Castelnau, 1834: 76).

urn:lsid:zoobank.org:act:781B3A50-6AE7-4F32-A4AA-8E83E4D 1E898

Material examined

Four <<, four ,,.

# Distribution and type locality

The original descriptions only state that the unique type was from 'Australia, Queensland'. Type locality is designated here as the Mary Cairncross Park, Queensland,  $26^{\circ}46^{0}47^{\circ}S$  $152^{\circ}52^{\circ}51^{\circ}E$ . The species is only known from the Blackall Range in the vicinity of Maleny, Qld (Darlington 1961b), west to Mt Cabinet and south to the Bellthorpe State Forest in the Conondale Range (Fig. 8).

# Diagnosis

Large, easily recognised beetles with distinct falcate mandibles and cordiform pronotum.

#### Description

Size. Overall length (SBL) 16.4–16.7 mm. Greatest width over elytra 5.4–6.0 mm.

Colour. Head black. Pronotum black ground colour with or without metallic purple or green reflex. Elytra black ground colour with metallic green or purple colour and slight iridescence. Body ventral surface black or piceous. Legs piceous. Mouthparts piceous. Antennae piceous.

Microsculpture. Dorsal and ventral lustre very or moderately shiny. Head dorsally with microsculpture absent or not visible at 50× magnification or with microsculpture consisting of isodiametric sculpticells. Pronotum dorsally with microsculpture absent or not visible at 50× magnification. Elytra with microsculpture absent or not visible at 50× magnification or with microsculpture consisting of transversely stretched sculpticells. Microsculpture of elytral striae slightly opaque, width not significantly widening apically, striae narrower than or, at most, of about equal width of adjacent intervals near elytral apex.

Head. Eyes medium size, slightly produced. Ocular ratio 1.38–1.49. Antennae clearly geniculate, first antennomere longer than 2+3. Frontal impressions short, shallow, recurved or shallow or not impressed. Labrum with six setae on anterior margin. Labrum anterior margin deeply emarginate. Occlusal margin of right mandible with a sharp, narrow anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth low, broad, shallowly emarginate. Apical labial palpomere slightly expanded apically. Lacinia with a row of thick setae medially, and an irregular row of fine setae dorsally.

Thorax. Basal pronotal seta adjacent to lateral bead and near hind angle. Tarsomere 5 setose. Elytral intervals all of approximately equal width. Elytral interval 3 with two setigerous punctures. Elytral striae all more or less impressed throughout their length. Elytral plica externally visible.

Abdomen. Ventrites 4-6 without sulci. Male aedeagus without ligula.

Notonomus soror (Darlington), comb. nov.

(Figs 12B, 13C, D)

Leiradira (Metadira) soror Darlington, 1961b: 7.

Material examined

Four <<, five ,,.

#### Distribution and type locality

Darlington (1961b) established the east side of Mt Bellenden Ker as the type locality. Additionally it is known from Boulder Creek, Mt Murray Prior and North Bell Peak (Fig. 9) at 500–100 m elevation.

#### Diagnosis

Elongate, parallel-sided, medium- to small-sized, black beetles. Nearly identical externally to N. iridescence but with six setae on the anterior margin of the labrum.

# Description

Size. Overall length (SBL) 10.1–12.5 mm. Greatest width over elytra 3.2–3.9 mm.

Colour. Head black or metallic purple. Pronotum black. Elytra black with spectral iridescence. Body ventral surface piceous. Legs piceous. Mouthparts piceous. Antennae piceous.

Microsculpture. Dorsal and ventral lustre very or moderately shiny. Head dorsally with microsculpture absent or not visible at 50× magnification. Pronotum dorsally with microsculpture absent or not visible at 50× magnification. Elytra with microsculpture absent or not visible at 50× magnification. Microsculpture of elytral striae slightly opaque, width not significantly widening apically, striae narrower than or, at most, of about equal width of adjacent intervals near elytral apex.

Head. Eyes small, flat. Ocular ratio 1.31–1.48. Antennae clearly geniculate, first antennomere longer than 2+3. Frontal impressions deep, divergent, slightly recurved. Labrum with six setae on anterior margin. Labrum anterior margin moderately emarginate. Occlusal margin of right mandible with long, blade-like anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth low, broad, shallowly emarginate. Apical labial palpomere slightly expanded apically. Lacinia with a row of thick setae medially, and an irregular row of fine setae dorsally.

Thorax. Basal pronotal seta in lateral bead near hind angle. Tarsomere 5 ventrally glabrous. Elytral intervals all of approximately equal width. Elytral interval 3 with one setigerous puncture. Elytral striae all more or less impressed throughout their length. Elytral plica absent.

Abdomen. Ventrites 4–6 with shallow basolateral sulcus. Male aedeagus with long flagellum.

#### Notonomus spectabilis, sp. nov.

# (Figs 14A, 15A, B)

urn:lsid:zoobank.org:act:E1669D0C-5452-44F6-B119-95A409A AFD78

#### Material examined

Holotype. <, 'NEQ: 16°55<sup>6</sup>S 145°40<sup>6</sup>E, Mt Williams, 900–1000 m, 2-3 Dec 1993, Cook, Monteith & Janetzki'//'QM Reg. No. T20305'. Deposited QM.

Paratypes. Mt Williams,  $(16^{\circ}54^{\circ}53^{\circ}S 145^{\circ}39'43^{\circ}E)$ , 02-03.xii.1993, D. Cook, G. Monteith, H. Janetzki, 900–1000 m (T20304, , QM) Mt Williams summit,  $(16^{\circ}54^{\circ}53^{\circ}S 145^{\circ}39^{\circ}43^{\circ}E)$ , 27-28.xi.1997, G. Monteith, D. Cook, 1000 m (T65732 T128384, T128385, , QM) Mt Williams, 0.8 km W,  $(16^{\circ}54^{\circ}52^{\circ}S 145^{\circ}39^{\circ}16^{\circ}E)$ , 27-10.ii.1998, G. Monteith, D. Cook, pitfall trap, rainforest, 820 m (T65727, T65728, T65729, T65730, T65731, << QM); Chujeba Peak summit  $(16^{\circ}56^{\circ}14^{\circ}S 145^{\circ}39^{\circ}19^{\circ}E)$ , 14-16.xii.1989, G. Monteith, G. Thompson, 1000 m, (T20293 , T20294 <, T20296 , T20297, T20298, T20299, T20300, T20301, T20302, T20303, << QM).

# Distribution and type locality

Type locality is Mt Williams, Queensland,  $16^{\circ}55^{\circ}S$   $145^{\circ}40^{\circ}E$ . This species is only known from the two localities

in the type material (Fig. 16) at elevations from 800 m to 1000 m. Reported as 'Leiradira NQ4' by Yeates et al. (2002).

# Diagnosis

Medium- to large-sized Leiradira that are very similar to N. aurifer, but immediately separable by the dark metallic purple or blue colour of this species compared with the brilliant red in N. aurifer.

# Description

Size. Overall length (SBL) 15.8 mm. Greatest width over elytra 5.5–6.3 mm.

Colour. Head metallic purple. Pronotum metallic purple or metallic blue. Elytra metallic purple or metallic blue. Body ventral surface black or piceous. Legs piceous. Mouthparts piceous. Antennae piceous.

Microsculpture. Dorsal and ventral lustre very or moderately shiny. Head dorsally with microsculpture absent or not visible at 50× magnification. Pronotum dorsally with microsculpture absent or not visible at 50× magnification. Elytra with microsculpture absent or not visible at 50× magnification. Microsculpture of elytral striae strongly, obviously opaque mesh, width greatly widening and striae anastomosing apically, much wider than intervals near elytral apex.

Head. Eyes medium size, slightly produced. Ocular ratio 1.28–1.44. Antennae not geniculate, first antennomere subequal to length of 2+3. Frontal impressions deep, divergent, slightly recurved. Labrum with six setae on anterior margin. Labrum anterior margin shallowly emarginate. Occlusal margin of right mandible with long, blade-like anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth low, broad, shallowly emarginate. Apical labial palpomere slightly expanded apically. Lacinia with a row of thick setae medially, mixed with finer setae and additional, more irregular rows of fine setae dorsally and ventrally.

Thorax. Basal pronotal seta in lateral bead near hind angle. Tarsomere 5 ventrally glabrous. Elytral intervals 3, 5 and 7 much wider than 2, 4 and 6. Elytral interval 3 with two setigerous punctures. Elytral striae all more or less impressed throughout their length. Elytral plica flat, scarcely visible.

Abdomen. Ventrites 4–6 with shallow basolateral sulcus or without sulci. Male aedeagus with long flagellum.

#### Etymology

The specific epithet is the Latin word for outstanding or noteworthy and reflects the notably attractive purple colour of the dorsal surface of this species.

# Notonomus tenuis (Darlington), comb. nov.

# (Figs 6B, 7C, D)

Leiradira (Stomimorphus) tenuis Darlington, 1961: 10.

Material examined

Eight <<, two ,,.

Distribution and type locality

Only known from the type locality, Eungella Range, Qld (Fig. 16).

# Diagnosis

Fairly small, black and non-metallic beetles similar to N. puella but distinguished from that species as noted under its diagnosis.

#### Description

Size. Overall length (SBL) 9.3–9.8 mm. Greatest width over elytra 3.3–3.4 mm.

Colour. Head black. Pronotum black. Elytra black. Body ventral surface black or piceous. Legs piceous. Mouthparts piceous. Antennae piceous.

Microsculpture. Dorsal and ventral lustre moderately shiny or dull. Head dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Pronotum dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Elytra with microsculpture consisting of transversely stretched sculpticells. Microsculpture of elytral striae slightly opaque, width not significantly widening apically, striae narrower than or, at most, of about equal width of adjacent intervals near elytral apex.

Head. Eyes medium-sized, flat. Ocular ratio 1.36–1.42. Antennae clearly geniculate, first antennomere longer than 2+3. Frontal impressions short, shallow, recurved. Labrum with six setae on anterior margin. Labrum anterior margin deeply emarginate. Occlusal margin of right mandible with a sharp, narrow anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth low, broad, shallowly emarginate. Apical labial palpomere slightly expanded apically. Lacinia with a row of thick setae medially, and an irregular row of fine setae dorsally.

Thorax. Basal pronotal seta adjacent to lateral bead and near hind angle. Tarsomere 5 ventrally glabrous. Elytral intervals all of approximately equal width. Elytral interval 3 with two setigerous punctures. Elytral striae all more or less impressed throughout their length. Elytral plica externally visible.

Abdomen. Ventrites 4–6 without sulci. Male aedeagus without ligula.

#### Notonomus thynnefiliarum, sp. nov.

# (Figs 3D, 4G, H)

urn:lsid:zoobank.org:act:150D7569-D051-4C4F-AC56-1CF27054AECD

#### Material examined

Holotype. <, 'Pitfall 1 A/1 <, Mary Cairncross Park, via Maleny, S.E. Qld, G.B. & S.R. Monteith'//'QMT189877'. Deposited QM.

Paratypes. Same data as holotype (T196019, QM). T197245, T197246 << QM; T197247, T197248, , QM. Cairncross NP via Maleny, SE Qld, 17.iv.1966. B. Cantrell (T197249, T197250, , QM; T197251 < QM). Rainforest pitfall 1 Mary Cairncross Park, via Maleny, SE Qld, 1974–1975. 488 m. G.B. and S.R. Monteith B3 (T197254, T197255, , QM). Pitfall 13 Bouloumba Ck Conondale, SE Qld. G. Maywald A/3 (T197252 < QM). Pitfall 13 Bouloumba Ck Conondale, SE Qld. G. Maywald A/3 (T197258 < QM). Pitfall 29 Mt Cabinet, via Jimna, Qld. G.B. and S.R. Monteith B/3 (T197253, QM). Site 29, Mt Cabinet, via Jimna, SE Qld. 8.ix.1974 G.B. Monteith Rainforest (T197256, QM). Rainforest pitfall 29B Mt Cabinet, via Conondale, SE Qld. 1974–1975, 792 m G.B. and S.R. Monteith 9T197257, QM). Distribution and type locality

The type locality is Mary Cairneross Park, Queensland. Estimated coordinates  $26^{\circ}46^{\circ}47^{\circ}$ S  $152^{\circ}52^{\circ}51^{\circ}$ E. Only known from the type locality and the two additional sites in the type series (Fig. 8).

# Diagnosis

Fairly small-sized beetles typically with distinct metallic, coppery colour on the pronotum and elytra (see variation below). The elytral striae are completely impressed and the fifth tarsomere is ventrally setose. This combination of features and its distribution separate it from the most similar species, N. latreillei and N. auricollis.

#### Description

Size. Overall length (SBL) 9.5–10.0 mm. Greatest width over elytra 3.4–3.5 mm.

Colour. Head black. Pronotum black ground colour with copper colour reflex, especially near margins. Elytra black ground colour with more or less prominent copper colour. Body ventral surface piceous. Legs piceous. Mouthparts rufobrunneous, paler than head. Antennae brown and infuscated.

Microsculpture. Dorsal and ventral lustre moderately shiny or dull. Head dorsally with microsculpture absent or not visible at 50× magnification. Pronotum dorsally with microsculpture absent or not visible at 50× magnification or with microsculpture consisting of isodiametric sculpticells just visible. Elytra with microsculpture absent or not visible at 50× magnification or with microsculpture consisting of a mesh of slightly transversely stretched sculpticells. Microsculpture of elytral striae slightly opaque, width not significantly widening apically, striae narrower than or, at most, of about equal width of adjacent intervals near elytral apex.

Head. Eyes small, flat. Ocular ratio 1.37. Antennae clearly geniculate, first antennomere longer than 2+3. Frontal impressions shallow or not impressed. Labrum with four setae on anterior margin, median pair absent. Labrum anterior margin moderately emarginate. Occlusal margin of right mandible with long, blade-like anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth absent. Apical labial palpomere slightly expanded apically. Lacinia with a row of thick setae medially, mixed with finer setae and additional, more irregular rows of fine setae dorsally and ventrally.

Thorax. Basal pronotal seta adjacent to lateral bead, near hind angle or about one pore's width forward of hind angle. Tarsomere 5 setose. Elytral intervals all of approximately equal width. Elytral interval 3 with two setigerous punctures. Elytral striae all more or less impressed throughout their length. Elytral plica externally visible.

Abdomen. Ventrites 4–6 without sulci. Male aedeagus without ligula.

#### Variation

Two specimens from Bouloumba are on the large end of the size range and have a very subdued metallic colour, almost black. It is not clear if this is due to an artefact of preservation or this is a natural colour.

# Etymology

The specific epithet honours the three Thynne sisters who donated the land for the Mary Cairneross Reserve, which is the type locality for this species.

# Notonomus vadosus, sp. nov.

# (Figs 10B, 11C, D)

urn:lsid:zoobank.org:act:555F0F30-9CFD-4E31-A8F2-04C 605043A83

# Material examined

Holotype. <, 'Mt Finnigan summit, via Helenvale, N. Qld. 28-30 Nov 1985, 1100 m, G. Monteith and D. Cook, Pitfall traps, rainforest'//'QM Reg. No. T20253'. Deposited QM.

Paratype. Same as holotype, 3–5 Dec 1990, 1050 m, Monteith, Thomas, Cook, Sheridan and Roberts, QM Reg. No. T20254 (, QM).

# Distribution and type locality

The type locality is Mount Finnigan, Queensland. Estimated coordinates  $15^{\circ}49^{0}6^{\circ}S$   $145^{\circ}16^{0}45^{\circ}E$ . Only known from the type locality (Fig. 9). Reported as 'Leiradira NQ1' by Yeates et al. (2002).

#### Diagnosis

Unique among Notonomus (Leiradira) species in having all elytral striae very shallowly impressed or absent.

# Description

Size. Overall length (SBL) 12.4–13.7 mm. Greatest width over elytra 4.2–4.5 mm.

Colour. Head black. Pronotum black. Elytra metallic green or copper colour. Body ventral surface piceous. Legs piceous. Mouthparts piceous. Antennae piceous.

Microsculpture. Dorsal and ventral lustre very or moderately shiny. Head dorsally with microsculpture absent or not visible at 50× magnification. Pronotum dorsally with microsculpture absent or not visible at 50× magnification. Elytra with microsculpture absent or not visible at 50× magnification.

Head. Eyes medium size, slightly produced. Ocular ratio 1.44–1.46. Antennae clearly geniculate, first antennomere longer than 2+3. Frontal impressions deep, divergent, slightly recurved. Labrum with six setae on anterior margin. Labrum entire. Occlusal margin of right mandible with long, blade-like anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth low, broad, shallowly emarginate. Apical labial palpomere slightly expanded apically. Lacinia with a row of thick setae medially, and an irregular row of fine setae dorsally.

Thorax. Basal pronotal seta in lateral bead, adjacent to lateral bead near hind angle. Tarsomere 5 ventrally glabrous. Elytral intervals all of approximately equal width. Elytral interval 3 with one setigerous puncture. Elytral striae scarcely impressed or absent. Elytral plica absent.

Abdomen. Ventrites 4–6 with shallow basolateral sulcus. Male aedeagus with long flagellum.

# Etymology

From the Latin for shallow, drawing attention to the shallowly impressed elytral striae.

#### Notonomus viridis, sp. nov.

#### (Figs 12C, 13E, F)

urn:lsid:zoobank.org:act:68A2B2D3-02B1-45FF-8ED2-DFC93E9 AD813

# Material examined

Holotype. <, 'Mossman Bluff Track, 5–10 km W. Mossman, N. QLD, 20 Dec 1989 – 15 Jan 1990, Monteith, Thompson & ANZSES, site 6A, 810 m, Pitfall'//'QM Reg. No. T20286'. Deposited QM.

Paratypes. Same as holotype, 16–30.xii.1988, G. Monteith, G. Thompson, ANZSES, pitfall trap, 480 m (T20272, , QM), 600 m (T20274, ,~ QM), 860 m (T20275, < QM), 1000 m (T20276, < QM); 01–17.i.1989, 1000 m (T20277, < QM); 20–15.i.1990 480 m (T20278, , QM), 760 m (T20279, T20280, T20281, << QM), 810 m (T20285, ,~ QM), 860 m (T20282 <, T20283, ~, T20284 <, QM), 930 m (T20289 <, T20290 ,~, T20291 <, T20292 ,~, QM), 1000 m (T20287, T20288, << QM).

#### Distribution and type locality

The type locality is Mossman Bluff Track, Queensland. Estimated coordinates  $16^{\circ}28^{\circ}30^{\circ}$ S  $145^{\circ}18^{\circ}30^{\circ}$ E. Only known from the vicinity of the type locality (Fig. 16). Reported as 'Leiradira NQ3<sup>°</sup> by Yeates et al. (2002).

#### Diagnosis

Distinctive medium-sized Leiradira with vividly metallic green pronotum and purple to blue-black elytra.

# Description

Size. Overall length (SBL) 12.3–14.8 mm. Greatest width over elytra 4.3–5.1 mm.

Colour. Head black ground colour with very slight metallic green colour in some. Pronotum metallic green. Elytra black with spectral iridescence. Body ventral surface black. Legs piceous. Mouthparts piceous. Antennae piceous.

Microsculpture. Dorsal and ventral lustre moderately shiny. Head dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Pronotum dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Elytra with microsculpture absent or not visible at  $50 \times$  magnification. Microsculpture of elytral striae strongly, obviously opaque mesh, width greatly widening and striae anastomosing apically, much wider than intervals near elytral apex.

Head. Eyes medium size, slightly produced. Ocular ratio 1.39–1.54. Antennae not geniculate, first antennomere subequal to length of 2+3. Frontal impressions deep, divergent, slightly recurved. Labrum with six setae on anterior margin. Labrum anterior margin shallowly emarginate. Occlusal margin of right mandible with long, blade-like anterior retinacular tooth. Gula very wide, nearly width of head. Mentum tooth low, broad, shallowly emarginate. Apical labial palpomere slightly expanded apically. Lacinia with a row of thick setae medially, mixed with finer setae and additional, more irregular rows of fine setae dorsally and ventrally.

Thorax. Basal pronotal seta in lateral bead near hind angle. Tarsomere 5 ventrally glabrous. Elytral intervals 3, 5 and 7 slightly wider than 2, 4 and 6. Elytral interval 3 with one setigerous puncture. Elytral striae all more or less impressed throughout their length. Elytral plica flat, scarcely visible.

Abdomen. Ventrites 4–6 with shallow basolateral sulcus or without sulci. Male aedeagus with long flagellum.

# Variation

Of the seven females in the series of paratypes, five have protarosomere 1 with a ventral vestiture of expanded, squamous setae as in males, while two have typical unadorned female tarsomeres. Those with the additional setae are designated in the type material list above with a tilde sign next to the ,. The only other species to show variation of the female tarsal vestiture is N. (L.) opacistriatis (see above).

#### Etymology

The specific epithet draws attention to the green metallic head and pronotum in this beetle.

#### Notonomus hephaestus, sp. nov.

# (Figs 14C, 15E, F, 17B)

urn:lsid:zoobank.org:act:D07C8B21-F7E8-4000-9B8E-57C3BF2 50186

# Material examined

Holotype. <, 'Lambs head, 10 km W. Edmonton N. Qld. 10-12 Dec 1989, 1200 m, Monteith, Thomson, Janetski'//'QM Reg. No. 20088'. Deposited QM.

Paratypes. Same as holotype QM Reg. Nos T20083, <, T20084, <, T20089, , (QM). East Lambs Head (east end),  $17^{010}46^{10}$ S  $145^{0}39^{0}20^{10}$ E, 29. xi.93, G. Monteith, H. Janetzki, D. Cook, 1180 m (T20102, < QM).

#### Distribution and type locality

The type locality is Lambs Head, Queensland. Estimated coordinates  $17^{\circ}123^{\circ}$ S  $145^{\circ}38^{\circ}33^{\circ}$ E. Only known from the type locality (Fig. 9).

# Diagnosis

Strikingly brilliant, shifting red to green metallicbeetles. Notonomus hephaestus is nearly identical to N. aurifer in habitus and colour, but N. hephaestus has the typical, narrow gula, brush-like lacinia and differs in patterns of setation as described below.

#### Description

Size. Overall length (SBL) 20.0–22.6 mm. Greatest width over elytra 6.8–7.8 mm.

Colour. Head metallic green or metallic red. Pronotum metallic green or metallic red. Elytra metallic green or metallic red. Body ventral surface black. Legs piceous. Mouthparts piceous. Antennae piceous.

Microsculpture. Dorsal and ventral lustre very or moderately shiny. Head dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Pronotum dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Elytra with microsculpture absent or not visible at  $50 \times$  magnification. Microsculpture of elytral striae strongly, obviously opaque mesh, width greatly widening and striae anastomosing apically, much wider than intervals near elytral apex.

Head. Eyes medium size, slightly produced. Ocular ratio 1.32–1.38. Antennae not geniculate, first antennomere subequal to length of 2+3. Frontal impressions short, shallow, recurved. Labrum with six setae on anterior margin. Labrum anterior margin shallowly emarginate. Occlusal margin of right mandible with moderately long, thick anterior retinacular tooth. Gula narrow, much narrower than width across mentum. Mentum tooth prominent, bilobed. Apical labial palpomere slightly expanded apically. Lacinia multiple rows of moderately heavy and fine setae forming a brush.

Thorax. Basal pronotal seta in lateral bead near hind angle. Tarsomere 5 ventrally glabrous. Elytral intervals 3, 5 and 7 much wider than 2, 4 and 6. Elytral interval 3 without setigerous punctures. Elytral striae all more or less impressed throughout their length. Elytral plica externally visible.

Abdomen. Ventrites 4–6 with shallow basolateral sulcus or without sulci. Male aedeagus with long flagellum.

#### Etymology

Named for the Greek god of fire and metallurgy. This is an allusion to the fiery red metallic colours of this beetle.

#### Notonomus nocturnocappellus, sp. nov.

#### (Figs 14D, 15G, H)

urn:lsid:zoobank.org:act:E3477C81-BAF5-420F-A221-375 63F7E2C70

#### Material examined

Holotype. <, '28°36<sup>1</sup>39.0<sup>®</sup>S 153°21<sup>®</sup>46.8<sup>®</sup>E, AUSTRALIA: New South Wales, Whian Whian Conservation Area, 379 m, 2.i.2011, K. Will, vine/ palm scrub, pitfall/B.mori extract [AUS2011.i.2.4]'//'U.C Berkeley EMEC 2008, 469'. Deposited ANIC.

Paratypes. '28°35<sup>6</sup>31.3<sup>\overlines</sup> 153°22<sup>\overlines</sup> 50.7<sup>\overlines</sup>, AUSTRALIA: New South Wales Nightcap Ranges National Park, Eucalyptus 2nd growth, 396 m. 2.i.2011 K. Will [AUS2011.i.2.5]', (EMEC 208467 , ANIC); same data (EMEC 208466 < EMEC, EMEC 208468 < QM), same data with DNA voucher number kww870 (EMEC208657 < EMEC).

### Distribution and type locality

The type locality is Whian Conservation Area, New South Wales,  $28^{\circ}36^{\circ}39^{\circ}S$   $153^{\circ}21^{\circ}47^{\circ}E$ . Only known from the type locality (Fig. 8).

# Diagnosis

The large size and relatively wide, depressed body form in combination with wider elytral intervals 3, 5 and 7 and the placement of the hind setae of the pronotum in the marginal bead separates this species from all other Notonomus.

#### Description

Size. Overall length (SBL) 19.0–21.3 mm. Greatest width over elytra 6.5–7.4 mm.

Colour. Head black. Pronotum black. Elytra black. Body ventral surface black. Legs piceous. Mouthparts piceous. Antennae piceous.

Microsculpture. Dorsal and ventral lustre dull. Head dorsally with microsculpture consisting of isodiametric sculpticells. Pronotum dorsally with microsculpture absent or not visible at  $50 \times$  magnification. Elytra with microsculpture consisting of isodiametric sculpticells. Microsculpture of elytral striae slightly opaque, width not significantly widening apically, striae narrower than or, at most, of about equal width of adjacent intervals near elytral apex.

Head. Eyes prominent. Ocular ratio 1.32–1.59. Antennae not geniculate, first antennomere subequal to length of 2+3. Frontal impressions short, straight. Labrum with four setae on anterior margin, median pair absent. Labrum anterior margin shallowly emarginate. Occlusal margin of right mandible with moderately long, thick anterior retinacular tooth. Gula narrow, much narrower than width across mentum. Mentum tooth prominent, bilobed. Apical labial palpomere apically expanded, subsecuriform. Lacinia multiple rows of moderately heavy and fine setae forming a brush.

Thorax. Basal pronotal seta adjacent to lateral bead near hind angle. Tarsomere 5 ventrally glabrous. Elytral intervals 3, 5 and 7 slightly wider than 2, 4 and 6. Elytral interval 3 with two setigerous punctures. Elytral striae all more or less impressed throughout their length. Elytral plica externally visible.

Abdomen. Ventrites 4–6 without sulci. Male aedeagus without ligula.

# Etymology

The specific epithet is a Latin form of the type locality, Nightcap Range.

# Notonomus impar (Sloane), comb. nov.

# Sarticus impar Sloane, 1903: 614.

Sloane noted in his treatment of this species that, like N. blackburni, it deviated from the typical characteristics of Sarticus species (Sloane 1903: 610). The holotype is now highly damaged and is missing both the prothorax and head. Fortunately, features noted by Sloane such as the uneven widths of the intervals and ventral punctation allow for confident identification of intact, associated specimens in the ANIC collection that appear to have been studied and identified as this species by Sloane. Based on this series of specimens, it is clear that Sloane's initial hesitation to place this species in Sarticus was justified. Though the pronotum is rounded at the hind angles the lateral margins are not explanate as is typical of Sarticus. Ventral punctation is common among Sarticus, but this varies between species (Lutshnik 1916) and the pronotal form falls well within variation found in Notonomus.

Key to subgenera and species

1. Gula very wide (Fig. 17A), reaching or surpassing the buccal fissure laterally, sutures often very lightly marked
Leiradira sensu Darlington 2
Gula narrow (Fig. 17B), not as wide or up to just a little wider than
the apices of the mental epilobes, sutures usually clearly
evidentOther Notonomus spp. 19
2. Mentum tooth absent
Mentum tooth present, usually broad and little produced7

prominent setae. Questionable specimens of N. auricollis covered by
both couplets
Tarsomere 5 glabrous ventrally or, at most, some (one to two) legs with one
fine seta on the tarsus, or with a pair of fine setae
4. Abdominal ventrites with minute punctulae laterally
Abdominal ventrites without minute punctulae laterallyNotonomus
thynnefiliarum
5. Pronotum black or with a very slight tint of metallic colour near the
margins. Elytral striae 5-7 more shallowly impressed in the basal
third than 1-4. Often 5-7 are very shallow or absent in the middle
half. When impressed basally 5-7 are frequently interrupted or
crenulated Notonomus latreillei
Pronotum prominently a metallic cupreous or green colour. All elytral
striae more or less equally impressed along their length Notonomus
auricollis (in part)
6. Dorsal surface black with spectral iridescence. SBL < 9.0 mm
Leiradira puella
Pronotum with distinct green or cupreous metallic sheen, elytra
black with a slight violaceous colour. SBL>9.0 mmNotonomus
auricollis (in part)
7. Right mandible with sharp, prominent anterior retinacular tooth (Fig. 18A)
or no retinacular teeth
Right mandible with a large, broad blade-like tooth (Fig. 18B)
8. Right mandible with sharp, prominent anterior retinacular tooth (Fig. 18A).
Elytral plica present
Right mandible without retinacular teeth. Elytral plica absent
9. Tarsomere 5 glabrous ventrally
Tarsomere 5 setose ventrally
10. Head and pronotum with slight green metallic sheen and obvious, irregular
mesh of microsculpture. Elytra with noticeable purpurescent or bronze
colourNotonomus jacobi
Head and pronotum without microsculpture. Colour black, with slight
iridescence throughout
11. Anterior margin of the labrum with six setae
Anterior margin of the labrum with four setaeNotonomus iridescens
12. Striae deeply impressed throughout their length
Striae scarcely impressed or absentNotonomus vadosus
13. Elytral striae without or with slightly opaque microsculpture, not
significantly widening apically, narrower or, at most, of about equal
width of the intervals near the apex
Elytral striae with strongly opaque microsculpture, greatly widening and
anastomosing apically, wider than the intervals near the apex
14. Elytral intervals nearly of equal width. Elytral interval 3 with one
setigerous puncture
with two setigerous puncturesNotonomus alternans
15. Elytra broad, elongate ovoid. Slight metallic sheen throughout. Head
and pronotum, particularly the pronotum near the base, cuprous.
Elytra purpurescent with distinct blue to purple margins. Mesh
microsculpture evident on elytra Notonomus alticola
Body form narrow, elytra parallel-sided. Black and more or less iridescent
throughout. Transversely stretched microsculpture scarcely visible on
throughout. Transversely stretched microsculpture scarcely visible on
throughout. Transversely stretched microsculpture scarcely visible on elytra
throughout. Transversely stretched microsculpture scarcely visible on elytraNotonomus soror 16. Elytral intervals 3, 5 and 7 about twice as wide as adjacent intervals 1, 2,
<ul> <li>throughout. Transversely stretched microsculpture scarcely visible on elytra</li></ul>
throughout. Transversely stretched microsculpture scarcely visible on elytraNotonomus soror 16. Elytral intervals 3, 5 and 7 about twice as wide as adjacent intervals 1, 2, 4 and 6 in the basal third of the elytra
throughout. Transversely stretched microsculpture scarcely visible on elytra

3. Tarsomere 5 setose ventrally on all legs, with two or rarely three pairs of

Pronotum with shallowly arcuate margins, somewhat constricted at the base, slightly narrower than elytral width. Dorsally black iridescent throughout......Notonomus opacistriatis

- Dorsally vivid red-green metallic .....Notonomus aurifer Dorsally deep blue-purple metallic....Notonomus spectabilis
- - Eyes and postocular region greatly enlarged and very prominent. Metatrochanters very long and pointed.....Notonomus (Acanthoferonia) ferox
- 21.Body form exceptionally elongate cylindrical (Fig. 1E). Elytra with internal ridge and no external plica...... Notonomus (Conchitella) clivinoides Body form various, but not elongate cylindrical. Elytral plica usually

22 22. Tropical species. See Darlington's key to the doddi-group that includes

- N. flos and N. dimorphicus. In that key Notonomus hephaestus will key to couplet 7 where the following can be inserted:
- Odd numbered elytral intervals much wider than even intervals. Dorsally vivid red-green metallic ......Notonomus hephaestus
- Species from outside the tropics. No key includes all of the other currently described Notonomus species. For informal groups and species use Sloane's (1913) key. Notonomus nocturnocappelus will key to couplet 20(24) there, but fail to fit character combinations of the remaining groups. Refer to the diagnosis provided herein. For species published after 1913 consult works by Sloane (1913, 1916, 1923) and Moore (1960, 1961, 1963).

# Discussion

Morphology and implied relationships

The genus Notonomus has over 120 described species and a diversity of morphological character states. Based on material I have collected and studied, at least 40 species, probably more, remain to be described and many of the currently recognised species need a thorough study to test their status. Morphology needs to be comprehensively studied among Notonomus species and near relatives to summarise the full diversity in the group and discover morphological diagnostic and synapomorphic features. Here I focus on Leiradira species (sensu Darlington) and limit discussion to prominent character systems and similarities across taxa that may prove to be synapomorphies once comparatively analysed.

Many species of Leiradira are recognised at a glance by gross features of the head, including somewhat elongate mandibles and more or less geniculate antennae, though both of these vary enough to include states also found in most Notonomus species. At a finer scale the details of the mouthparts are also sometimes, but not in all cases, distinctive in species traditionally included in Leiradira. Among those characters are the presence of a very transverse mentum (Moore 1965) and the lacinia having a medial row of thick, almost tooth-like setae (Darlington 1961b). These features led to some authors grouping Leiradira species with Delinius (e.g. Tschitschérine 190; Moore 1965) or place them near Lesticus in a broadly defined 'Trigonotomides' (Chaudoir 1868). Darlington (1961b), however, preferred a closer relationship of Leiradira and Notonomus based on variation he saw, but

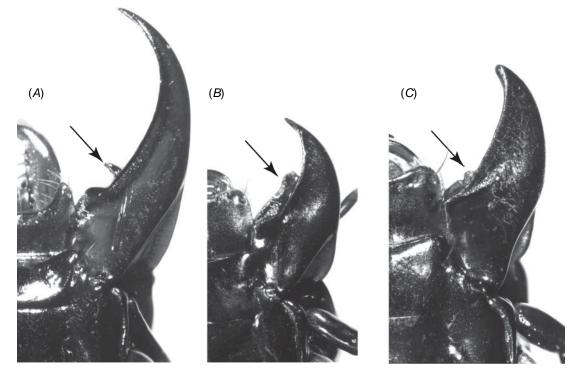


Fig. 18. Right mandible, dorsal view. Arrow indicates retinacular tooth. (A) Notonomus smilodon, (B) Notonomus viridis, (C) Notonomus hephaestus.

postulated a recent common ancestor of Leiradira. Delinius and Notonomus. Darlington's assessment of variation was at least partly on track and he correctly noted that his Metadira species and species in the doddi-group were most similar and that the widened and opaque striae of the elytra are most likely synapomorphies. The position of the pronotal setae and mouthpart characters he used are more problematic. All mouthparts features vary between species traditionally placed in Leiradira such that no character state is found exclusively and uniformly in all Leiradira that is not also found in some Notonomus species. The only possible exceptions are the extremely wide gula (Fig. 17A) and tooth-like lacinial setae. The vestiture of the lacinia varies in Leiradira from having almost no other setae in addition to the prominent medial row of heavy tooth-like setae, to having a larger and heavier row medially but also having numerous additional ventral and dorsal setae. The difference between this latter state and the typical Notonomus lacinial brush is a matter of the density of the setae and not obviously significant. The exceptionally wide gula is quite distinct from the much narrower form found in other Notonomus. The difference between N. aurifer and N. hephaestus (Fig. 17), for example, is clear and remarkable. The suite of character states - transverse mentum, low or absent mentum tooth, rake-like lacinia and very wide gula - is found in Delinius, some Lesticus species, Paraloma, some Platycaelus species (K. Will, unpubl. data) and Leiradira. The suite of features appears to co-vary. This is likely a syndrome related to a feeding adaptation that has evolved in these various groups independently. Forsythe (1982, 1983) noted the relationship of gular width and musculature and feeding in carabids. In species with large mandibular adductors, gular width decreases to accommodate these large muscles that drive mastication with the mandibles. Gular width is expanded for larger stipital retractor muscles that drive the maxillae, which includes the lacinia. Heavily built, rake-like laciniae are associated with a wide gula and a lack of extra-oral digestion. In the few species included in Forsythe's study no specific diet type was identified for beetles with mouthparts of this type. Both fragmentary and 'mush' contents were seen in the crop. The inclusion of N. dimorphicus, N. hephaestus, N. flos, and probably other doddi-group species, in Leiradira suggests that evolution of this mouthpart syndrome and its reversal has occurred within Notonomus.

The typical species of Notonomus have the occlusal margin of the right mandible with a moderately long to short, thick triangular anterior retinacular tooth (Fig. 18C). Within Leiradira species four different forms of the right mandible are known. Notonomus flos, N. dimorphicus and N. hephaestus all have the typical Notonomus triangular tooth (Fig. 18C). Notonomus barrae has no tooth. Notonomus Jacobi, N. tenuis and N. smilodon (i.e. Stomimorphus sensu Darlington) have a very narrow, elongate tooth (Fig. 18A). All other species of Leiradira have a broad, thin blade-like tooth (Fig. 18B). These very distinctive mandibular types suggest that there may be feeding specialisations in Leiradira and that these may prove to be synapomorphies for clades within the genus Notonomus.

The female reproductive tract is frequently an important source of phylogenetic characters in carabids (Liebherr and Will 1998). Many species of Notonomus have not yet been examined; however, for all taxa I have studied this system is surprisingly uniform and unadorned (Fig. 5) across species of Notonomus, Parhypates and Sarticus. The male aedeagus median lobe and paramere form is also not exceptional or notably varied. However, the structures of the endophallus does show promise for phylogenetic characters. Some species have an elongate flagellum (e.g. Fig. 13D), which is linear and the length of the median lobe as in many Leiradira species, or it is much longer than the median lobe and coiled as in some Parhypates species. Possibly homologous to one or both of these are short, broader ligula found in many species of Notonomus and some Sarticus. A flagellum that is linear and the length of the median lobe is found in all species of Darlington's Metadira, N. puella, N. dimorphicus, N. flos and N. hephaestus. This feature is consistent with the placement of N. dimorphicus and N. flos in Leiradira, and may prove to be synapomorphic for the clade.

# Possible local mimicry

In terms of size, colour, general body form and modifications of the elytral striae N. aurifer and N. hephaestus are nearly identical (Fig. 14B, C). However, close examination of the pattern of setation, genitalia and especially head and mouthparts (Fig. 17) reveals significant differences that have typically been considered generic-level distinctions. The phylogenetic relationships of N. hephaestus are not known, but if similarity of colour and elytral modifications were to prove synapomorphic and place this species sister to N. aurifer, then this would represent a case of very divergent and likely very rapid mouthpart evolution. If N. hephaestus is more closely related to other Notonomus with unmodified mouthparts, e.g. N. dimorphicus and N. flos (Fig. 2), then this is a case of morphological structure and colour mimicry.

The ranges of N. aurifer and N. hephaestus are sympatric on Lambs Head in Queensland. In addition to these two metallic red species, an undescribed red-bronze Trichosternus species and the red-bronze form of Notonomus montorum Darlington are also sympatric there. To the north of Lambs Head there is an apparent distributional break coincident with the lowlands along the Clohesy River. North-east of the river in the highlands on and near Mt Williams and Chujebu Peak, the red-coloured species are not found, but rather there occurs a suite of black, metallic blue or purple species, including N. spectabilis, and a blue colour form of N. montorum, which are both restricted to the area, and the widespread N. opacistriatis. Outside the Lamb Range, black, blue, green and iridescent-coloured Notonomus and Trichosternus predominate. The coincident distribution of red beetles at Lambs Head seems unlikely to be a random pattern and it implies predation pressure by a visual predator. However, there is no obvious candidate predator of these large, flightless and largely nocturnally active beetles currently known to be restricted to the Lamb Range. Resemblance of form, colour and in some cases behaviour that can be attributed to mimicry is well documented in carabids. This includes mimicry with cockroaches (Schmied et al. 2013), mutillid wasps (Mawdsley et al. 2012), chrysomelid

beetles (Lindroth 1971) and within complexes of associated carabid beetles (Bonacci et al. 2011). As all the species involved have pygidial glands, and so are presumably chemically defended, this may be a case of Müllerian mimicry, but more information on the distribution, phylogeny and behaviour is needed to fully understand the underlying cause of this pattern.

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