Molecular phylogeny, classification, and description of new species of Australian *Nuridius* Sloane, 1890 (Carabidae: Pterostichini)

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ABSTRACT

The genus *Nuridius* Sloane is revised and expanded to 10 species including its type species *Nuridius fortis* Sloane, 1890, three newly described species: *Nuridius frickei* sp. nov., type locality Peases Lookout, Eungella National Park, QLD, *Nuridius pluto* sp. nov., type locality Jimna State Forest, QLD, and *Nuridius darlingtoni* sp. nov., type locality Bulburin National Park, QLD, and six species previously included in *Nurus* Motschulsky that are here combined in *Nuridius*: *Nuridius curtus* (Chaudoir, 1865), *Nuridius grandis* Sloane, 1910, *Nuridius nox* (Darlington, 1961), *Nuridius medius* (Darlington, 1961), *Nuridius rex* (Darlington, 1961), and *Nuridius niger* (Chaudoir, 1878). *Pachymelas* Tschitschérine, 1902 is considered a junior synonym of *Nuridius*. Bayesian analyses of a combined matrix and partitioned matrices of partial sequences from three loci (28S, COI and CAD) found support for *Nuridius* as a clade separate from *Nurus*. The comparative study of morphological features allows for recognition of the 10 species and an identification key is provided. Images of habitus and key external features, along with the aedeagus of each species are provided. All species distributions are mapped, and biogeographical implications discussed. Short notes are given on burrow-making and egg deposition into formed, two-part soil capsules by species of both *Nurus* and *Nuridius*. Conservation issues are briefly discussed.

The *Trichosternus* series is an informal group of pterostichine carabid beetles established by B.P. Moore (1965) and refined by Baehr and Will (2019). Among the genera included in this group, *Nurus* Motschulsky is notable for exceptional burrowing and brood care behaviours (Charley and Andren 2018) and critically threatened habitat in the restricted ranges of the included species (Charley and Andren 2021; Darlington 1961a; b; c; Will and Monteith 2018). Given the immediate threat *Nurus*-like species face due to habitat loss and the need for conservation efforts to protect at least some species, a robust phylogeny-based taxonomic review is required to guide conservation efforts. Recently we (Will and Monteith 2018) treated those species of *Nurus* shown to be monophyletic and grouped with the type species of the genus (*Nurus* sensu stricto). The remaining species previously attributed to *Nurus* are treated here and evidence of the non-monophyly of *Nurus* sensu lato relative to species of the genus *Trichosternus* Chaudoir is provided. These phylogenetic relationships necessitate adjusting the classification. The clade including the type species of *Nuridius* Sloane and its close relatives is recognized as constituting a distinct genus.

Based on the two type specimens of *Nuridius fortis* then available to him, Sloane (1890) reasoned that a new genus was needed to bridge the perceived gap between *Nurus* and *Paranurus* Tschitschérine (*Paranurus* then as '*Mecynognathus dilaticeps*'). He described his new species as having 'the fascies [sic] of a *Nurus*, but [it is wanting] a basal border to the elytra, and [absent the] squamulae on the lower surface of any joints of the anterior tarsi in the ♂'. Tschitschérine (1902) then proposed the *Nurus* subgenus *Pachymelas* for *N. curtus* and *N. niger*, but noted that he had not seen specimens of *Nuridius fortis* and so maintained *Nuridius* as a separate genus.

Darlington (1961b) treated both *Nuridius* and *Pachymelas* as subgenera of *Nurus*. In contrast, Moore (1965), looking across all the genera of the *Trichosternus* series, declared that the 'continued use of the groups *Pachymelas*... and *Nuridius*..., even as subgenera, seems pointless.' Subsequently, these subgenera have been treated as synonyms of *Nurus* without a specified subgeneric classification (Lorenz 2005; 2018; Moore et al. 1987).

The ongoing project of settling the genus-level issues across the *Trichosternus* series alluded to by Moore is beyond the scope of this contribution. However, given the critical need to provide an evidence-based classification of the *Nurus*-like taxa, we provide a molecular phylogeny, new classification, and descriptions of new species of *Nuridius* with the hope that this will enhance ongoing and future conservation efforts.

MATERIALS AND METHODS

Morphological methods: Morphological study and image production was conducted with the same methods used for *Nurus* species described by Will and Monteith (2018). A table of measurements and ratios is provided (Table 1). An image showing where on the specimen measurements were taken is also included. Size measurements are given as a range for all specimens, followed by the measurement of the holotype in parentheses for newly described species.

Taxon sampling

Specimens examined: A total of 632 specimens of *Nuridius* (484 of them in the QM) were examined from the following collections: AM — Australian Museum, Sydney; ANIC — Australian National Insect Collection, Canberra; CMNH — Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; EMEC — Essig Museum of Entomology, Berkeley, California; MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNHN — Muséum National d'Histoire Naturelle, Paris; QM — Queensland Museum, Brisbane.

Specimen data, mapping points and terms: Holotype label data is given verbatim and is enclosed in double quotation marks with double forward slashes used to indicate separate labels. For the new species, full label data for examined specimens is given in the species accounts and label localities are used for their distribution maps in Figs 48 and 49. For the described species, there was abundant material available. Rather than listing all specimen data in the species accounts, it is stated how many

specimens of each species were available in each museum collection. Many specimens predate the routine use of GPS and/or have various errors or inaccuracies included on labels. These errors are corrected here based on GBM's extensive personal collecting and knowledge of the region, and other sources including colloquial place names and collectors' field notes. Using this method, one entry is created for each discrete locality from which each species is known. For the described species, these are listed as a synoptic list of accurate localities derived from all specimens and arranged in order from north to south with decimal degree coordinates and altitudes for each. These points are used to generate the distribution maps in Figs 48 and 49. Our discussion of the biogeographic patterns and populations are based on this summary, and we use the term population in the colloquial sense of a series of samples of a species from a contiguous area or several adjacent areas that are thought to be potentially interbreeding.

Vegetation terminology: In the synoptic locality lists, the vegetation type is indicated by RF (rainforest) and OF (open eucalypt forest). Rainforests, sometimes referred to as 'closed canopy forests', are tree-dominated habitats where the tree canopies are contiguous, large vines (lianes) are common and ground cover is sparse. Rainforest habitats show a differentiation along precipitation gradients relative to their distance from the ocean, altitude, rain shadow effects and seasonal cyclonic rain patterns. We use the term 'wet rainforest' for the high precipitation end of the gradient where the forests are lush and taller, with a more open understorey and 'dry rainforest' for areas that are less humid, where forests are lower and with a denser shrub understorey.

DNA sequencing and phylogenetic analysis methods

Abbreviations for loci and their aligned length are as follows: 28S: 28S ribosomal DNA (1166 bases); COI: cytochrome oxidase I, (828 bases, JER-PAT primer region (COIjp), 695 bases, HCO-LCO region (COIf)); CAD2: carbamoyl phosphate synthetase domain of the rudimentary gene (831 bases).

Fragments for these genes were amplified using polymerase chain reaction, cleaned and sequenced following the same procedures and primers given by Will (2015) and Will and Monteith (2018). Assembly of multiple chromatograms for each gene fragment and initial base calls were made with Phred (Green and Ewing 2002) and Phrap (Green 1999) within the Chromaseq package in Mesquite (Maddison and Maddison 2019, 2018), with subsequent editing done based on manual inspection in Mesquite. Multiple peaks at a single position were coded using IUPAC ambiguity codes. Primary collection data for voucher specimens are deposited in the EMEC public database at https://essigdb.berkeley.edu/. The DNA sequences used include those previously used in the revision of *Nurus* (Will and Monteith 2018) and an additional 82 sequences with the following GenBank numbers: COIf, OM994356–OM994377; COIjp, OM994335–OM994354; CAD2, ON011701–ON011721; and 28S, ON015839–ON015857. The 21 *Nuridus* OTUs added here are complete for all loci with the following exceptions: *Nuridius rex* T21916 lacks COIjp, CAD2, and 28S; *Nuridius medius* EMEC347126 lacks COIjp; and *Nuridius fortis* EMEC347130 and *Nuridius frickei* EMEC347125 lack 28S.

Models of nucleotide evolution were chosen for each partition and base position for the coding sequences with the aid of mrModelTest (Nylander 2004) and PAUP* (Swofford 2002). Using the hierarchical likelihood ratio test and Akaike information criterion (Akaike 1973), the chosen models applied were GTR+I+Γ for 28S, CAD2 position 3, and COI position 3; GTR for CAD2 positions 1–2; and HKY+I+Γ for COI positions 1–2. Bayesian analyses were conducted using MrBayes ver. 3.2.7, (Ronquist et al. 2012) in parallel version (Altekar et al. 2004). Analyses were run for 5 million generations for four runs of eight chains with the sampling frequency set to 1000. The trees in a burn-in period of 50% of the generations were excluded. The average standard deviation of split frequencies (ASDSF) reached were well below 0.01 in all cases (Ronquist et al. 2009) and all ESS values viewed in Tracer (Rambaut et al. 2018) were >1000 in all analyses. The majority-rule consensus tree of post-burn-in trees was calculated to determine Bayesian posterior probabilities (pp) of clades.

RESULTS

Phylogenetic analysis results

All analyses resulted in a paraphyletic *Nurus* sensu Moore et al. (1987) relative to species of *Trichosternus* (Fig. 1), which are placed as sister to *Nurus* (taxa treated as *Nurus* s. str. by Will and Monteith (2018)), forming a clade separate from *Nuridius* species. The relationships of *Nurus* species found in the combined matrix analysis is identical to what was found in the parsimony analysis conducted by Will and Monteith (2018). The monophyly of *Nuridius* is strongly supported (pp 1.0, Fig. 1). The relationships among the taxa of *Nuridius* in the combined analysis are all strongly supported (pp 0.93–1.0) except for the sister group relationship between *N. frickei* and the remaining species, which is poorly supported (pp 0.5). The sister group relationship between *N. frickei* and the remaining species is only modestly supported by 28S and COI partitions (Figs 2, 3), while CAD2 (Fig. 4) has a basal polytomy in the genus and *N. frickei* is nested well within the clade. In all individual partition analyses, *N. fortis*, *N. grandis* and *N. pluto* are in a clade exclusive of the clade including *N. medius*, *N. niger*, and *N. rex*. Four species, *N. curtus*, *N. darlingtoni*, *N. frickei* and *N. nox*, are variable in their placement or placed as part of polytomies in the individual partition analyses. All species-level taxa represented by multiple individuals in the dataset are found to be monophyletic except for *N. fortis*, which is only supported by the COI partition (Fig. 3, pp 0.94).

Taxonomic treatment

Nuridius Sloane, 1890: 649

Type species. *Nuridius fortis* Sloane, 1890

Pachymelas Tschitschérine, 1902: 516. Type species *Feronia* (*Trichosternus*) *curta* Chaudoir, 1865, new synonymy.

Characteristics of the genus

Head relatively large; mentum deeply emarginate, sides of sinus subparallel; median tooth emarginate or bifid; paraglossae glabrous; mandibular scrobe plurisetose or (usually) glabrous; antennae filiform, with three basal segments glabrous; postocular orbits inconspicuous. Pronotum subcordate to quadrate, the margins bisetose or with basal seta only. Prosternum and mesosternum setose. Elytra fused; striae evident, very shallow and finely punctate, intervals slightly convex or nearly flat; parascutellar striole present or absent; discal pores small, confined to the apical fourth of interval 3 when present; marginal pores small; plica very narrow or not externally visible, inner ridge present but not prominent; hind wings vestigial, strap-like. Legs relatively slender; metacoxae prominent, posterior face vertically oriented; anterior tarsi of male unmodified; tarsomere 5 of all legs ventrally setose. Aedeagus (Figs 9–17, 22–33, 36–47) with orifice deflected to the right; parameres dissimilar, the left conchoid, the right longer, falcate or hooked.

Included species: *N. frickei* sp. nov., *N. curtus* (Chaudoir, 1865), *N. darlingtoni* sp. nov., *N. grandis* Sloane, 1890, *N. fortis* Sloane, 1890, *N. pluto* sp. nov., *N. nox* (Darlington, 1961), *N. medius* (Darlington, 1961), *N. rex* (Darlington, 1961), *N. niger* (Chaudoir, 1878).

New species treatments

***Nuridius frickei* sp. nov**

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(Figs 5, 9–11, 48, 51, Table 1)

Etymology: The specific epithet, *frickei*, is a Latinised version (genitive case) of the surname of Fred Fricke, an unconventional amateur beetle collector who lived in Sydney and died in 2000 (Barker 2001). His collection is now in the Australian Museum and has many specimens of both *Nurus* and *Nuridius*.

Material examined: HOLOTYPE ♂: "C.Qld. 21°07'S x 148°31'E, Pease's Lkt., Eungella, 17 Nov 1992-mid Apr 1993, D. Cook & G.B. Monteith, 900m, RF Intercept and pitfalls" (deposited in QM, Reg. No. T82377). PARATYPES (29): 15, same data as holotype (in QM); 2, same loc. as previous, 13 Jan 2008, G.B. Monteith, hand collecting (1 in QM; 1 in EMEC CARABDNA035); 5, same loc. as previous, 10 Oct 2003, G.B. Monteith, ex burrows (in QM); 1, Eungella Nat. Pk., 25 Mar 1968, E. Matthews (in ANIC); 4, Clarke Range, Qld., 3 Jan 1977, F.T. Fricke (in AM); 2, same loc. as previous, 4 Jan 1977, F.T. Fricke (in AM).

Type locality: Peases Lookout, Eungella National Park, QLD., -21.11720 S, 148.51580 E. This type locality is in continuous rainforest at about 860 m elevation and 3 km NE of Eungella township.

Diagnosis: A very distinctive species recognizable from all other *Nuridius* by the combination of smaller size, metallic green head and pronotum, the extended elytral lateral channel and the series of umbilicate setae that reach or nearly reach the elytral apex.

Description

Size: Overall length 19.9–21.9 mm (21.9 mm); greatest width of elytra 8.2–9.5 mm (9.5 mm).

Colour: Dorsal and ventral surfaces with base colour black; legs, mouthparts, and antennae dark piceous or black; head and pronotum typically with evident, metallic green reflex, sometimes lacking along margins and/or disc of pronotum; elytral black or with slight metallic green reflectance near lateral and basal margins.

Lustre: Dorsally head and pronotum somewhat to very glossy; elytral margins slightly glossy; elytral disc matte, not at all glossy; body ventrally glossy.

Head: Dorsal microsculpture with microlines not or scarcely visible at 50x magnification, when visible, forming very irregular mesh. Clypeal-ocular sulci absent or represented by very shallow, broad, nearly parallel impressions. Ocular ratio 1.37–1.41; eyes large, rounded. Mandibles very long, abruptly hooked apically, scrobe glabrous. Labrum anterior margin straight or slightly convex, medial four setae separated from each other about half to three quarters width from outermost medial seta to lateral seta. Anterior margin of clypeus very shallowly emarginate. Mentum long, deeply emarginate with parallel, prominent lateral lobes; median tooth prominent, tooth emarginated; with one pair of setae positioned at base of median tooth and a second pair of smaller setae laterad medial pair. Submentum with two lateral pairs of setae. Gula narrow, width at middle about as wide as width of mentum tooth. Antennae long, antennomeres 10–11 extended beyond pronotal base, antennomeres 5–11 elongate, apical 2/3 of 4 and entire length of 5–11 densely pubescent, 2–4 very slightly compressed at base.

Thorax: Pronotum finely rugose throughout, shallow on disc and notably more deeply near margins. Microsculpture of pronotal disc not visible at 50x magnification, laterally and basally very distinct at low magnification, microlines form very irregular transverse mesh. Pronotum wide, rectangular, broadly reflexed laterally, lateral margins subsinuate and then straight or very slightly convergent onto base. Marginal bead thick, continuous from apex to base, interrupted near base by seta, often not or only shallowly delimited medially; basal margin broadly emarginated medially, border narrow and only impressed laterally or with an irregular medial impression, lateral region of border usually with a thickened section along its length; anterior angles prominently produced; hind angles about right-angled or slightly obtuse; base depressed across width, basal impressions very broad, shallow and not clearly delimited; anterior marginal seta set mesad of lateral channel at about 1/5 of pronotal length from front angle; seta near hind angle set in lateral bead. Prosternal process medial impression near apex broad, shallow, process apically plurisetose, 2–6 additional setae between coxae. Mesosternum medially plurisetose. Metepisternum and metepimeron very short. Elytral striae complete, very broadly and shallowly impressed. Parascutellar striole and angular base of stria 1 present, shallowly impressed. Elytral parascutellar setae absent, basal margin sharply bordered. Striae marked with dense, extremely shallow, elongate punctulae. Elytral intervals 1–7 very slightly convex. Elytral microsculpture of intervals 1–8 and in striae dense, small, granular, composed of irregular sculpticells giving a matte sheen. Interval 3 with one seta at apical ¼ or setae absent. Interval 8 laterally and marginal channel microsculpture composed of flat, very reflectant sculpticells contrasting with matte discal microsculpture. Stria 8 with 31–34 umbilicate setae, somewhat irregularly spaced, but more closely set anteriorly and posteriorly, ended apically at level of stria 2 or extended to elytral apex. Elytral humeri raised and rounded, without tooth or tubercle or with a very low, broad, rounded tubercle, sometimes unilaterally. Elytra plica very narrow, externally visible. Vestigial flight wing present as a thin strap about 2/3 elytral length. Male and female protarsi ventrally glabrous and unmodified; tarsomere 1 medially with 5–10 fine setae.

Abdomen: Abdominal ventrites smooth, 2–5 with a pair of paramedial setae and additional setae medially or laterally varying in presence and number unilaterally. Apical margin of ventrite 6 with two setae in males and four setae in females.

Male genitalia: Aedeagus (Figs 9–11) tip broadly and bluntly rounded, directed ventral and rightward; right paramere broad at base, abruptly narrowed in apical 1/3, falcate, apex hooked sharply. Dorsal ostium wide and rotated to right.

Female genitalia and reproductive tract: Laterotergite IX with 12–18 long setae along posterior margin. Gonocoxite 1 with four or five extremely short, thick setae (apparent as vestigial ensiform setae). Gonocoxite 2 elongate-falcate with one extremely short, thick medial seta and one extremely short, thick lateral seta, falcate. Elongate spermatheca ending in an oval expansion, with a short spermathecal duct digital diverticulum near base, attached at the midpoint on length of common oviduct. Spermathecal gland connected to spermathecal duct near base by long, narrow duct; glandular portion elongate, cylindrical.

Distribution: (Fig. 48) This species has a very restricted distribution within Eungella National Park in central Queensland. The accessible part of the park runs for about 25 km along the summit of the Clarke Range and has been systematically collected its full length, including use of long-term pitfall traps that reliably collected large Carabidae, over many years by Queensland Museum and other parties (Kitching 2020). Of the seven collections that have been made of the species, the four that have precise coordinates are all from Peases Lookout, and the other three unlocalized collections may well have been from the same area as it is a convenient roadside stopping place. At Peases Lookout, *Nuridius frickei* co-occurs with the much larger *N. medius*, with burrows of both being equally abundant.

***Nuridius darlingtoni* sp. nov.**

Zoobank Reg: urn:lsid:zoobank.org:act:CEEB219B-2817-4294-B6B6-1638236A4EA9

(Figs 7, 15–17, 48, Table 1)

Etymology: The specific epithet, *darlingtoni*, is a Latinised version (genitive case) of the surname of the late Philip J. Darlington Jr., carabidologist and Harvard professor, who revised *Nurus* in 1961. One of the paratypes of *Nuridius darlingtoni* sp. nov. is a specimen that is a paratype of *Nurus nox* Darlington, 1961. Given Darlington's typical thorough study of species he described, we were surprised to find that this specimen does not match the character states in the holotype of *N. nox*.

Material examined: HOLOTYPE ♂: "Bulburin S.F., via Miriamvale, Qld., 20 Dec 1983, G.B. Monteith" (deposited in QM, Reg. No. T89352). PARATYPES (33): 3, Bulburin SF, via Many Peaks, Qld., 17–19 Nov 1972, B.K. & J.A. Cantrell (in QM, Reg Nos. 89346–89348); 3, Forest Station, Bulburin SF, via Many Peaks, Qld., 2000', 2–5 Apr 1972, G.B. Monteith (2 in QM, Reg. Nos. T.89337–89338; 1 in ANIC); 2, same loc. as previous, 12–15 Apr 1974, G.B. Monteith (in QM); 1, 24°32'S, 151°28, Bulburin Barracks, 7–8 Oct 1999, Monteith, Burwell, Cook & Evans, rainforest, 580 m, 7817 (in QM); 4, Australia, Bulburin SF, Q., 14 Apr 1974, B.P. Moore (2 in ANIC; 2 in CMNH); 1, Bulburin SF, 15 Jan 2008, GBM (in EMEC); 3, Bulburin, Jan 2008, K. Will (in EMEC); 2, Kroombit Tops, 65 km SW of Gladstone, 1000–1100 m, 22–26 Feb 1982, rainforest, Monteith, Thompson & Yeates (in QM, Reg. Nos. 89361–89362); 7, Kroombit Tops (Three Moon Creek), 45 km SW of Calliope, 9–19 Dec 1983, rainforest, G. Monteith & G. Thompson (in QM, Reg. Nos. T89363–89369); 4, -24.413°S, 151.039°E, Kroombit Tops NP, Munholme Ck, 858 m, 28–29 Nov 2009, hand coll., Monteith & Turco, 18666 (in QM); 1, Mt Jacob, 45 m S of Gladstone, 2000', Mar 1958, P.J. Darlington (in MCZ); 1, Bulburin NP, Bobby Range Rd, 190 m, -24.569°S, 151.531°S, 7 Nov 2020, dug from burrow, M. Rix (in QM, Reg. No. 266602); 1, Bulburin NP, Dawes Range Rd, 660 m, -24.598°S, 151.511°S, rainforest, 6 Nov 2020, M. Rix, dug from burrow (in QM).

Type locality: Bulburin National Park, QLD. Approximate area near -24.527 S, 151.471 E. The type locality is in high quality rainforest on red basalt soil at 600 m elevation. This is thought to be the same locality where P.J. Darlington collected both this species and *Nuridius nox* in 1957 (Darlington 1960).

Diagnosis: Recognizable from all other *Nuridius* species by the combination of being entirely black beetles, with narrow pronotal margins, pronotum with the anterior marginal setae absent, and the elytra humeri with a distinct tubercle.

Description

Size: Overall length 22.1–27.8 mm (23.3 mm); greatest width of elytra 12.4–10.0 mm (10.8 mm).

Colour: Dorsal and ventral surfaces black; legs, mouthparts, and antennae dark piceous or black.

Lustre: Dorsally head, pronotum, and elytral margins very glossy; elytral disc more matte in striae with intervals dorsally contrastingly slightly glossier; body ventrally moderately glossy.

Head: Dorsal microsculpture with microlines not visible at 50x magnification. Clypeal-ocular sulci very shallow and broadly impressed. Ocular ratio 1.32–1.39; eyes moderately large, rounded. Mandibles long, abruptly hooked apically, scrobe glabrous. Labrum anterior margin convex with more or less prominent medial lobe, medial four setae separated from each other about half to three quarters width from outermost medial seta to lateral seta. Anterior margin of clypeus moderately to shallowly emarginate. Mentum long, deeply emarginate with parallel, prominent lateral lobes; median tooth prominent, tooth emarginated; with one pair of setae positioned at base of median tooth and a second pair of smaller setae laterad medial pair. Submentum with two lateral pairs of setae. Gula narrow, width at middle about as wide as width of mentum tooth. Antennae long, antennomere 11 extended beyond pronotal base, antennomeres 5–11 elongate, apical 3/4 of 4 and entire length of 5–11 densely pubescent, 2–4 slightly compressed at base.

Thorax: Microsculpture of pronotal disc not visible at 50x magnification except near base laterally, where microlines form very irregular dense mesh. Pronotum transverse, quadrate, sides subsinuate and then straight onto base. Marginal bead thick, continuous from apex to base, slightly wider near base, constricted and sometimes interrupted at the level of hind seta; with or without crenulations in the anterior half; basal margin not bordered or with a poorly defined border only in the lateral ¼; margin concave; anterior angles prominently produced; hind angles right-angled or slightly acute, rounded and not denticulate; base deeply depressed, basal impressions very broad, shallow and not clearly delimited posteriorly, more sharply and deeply impressed anterior of lateral convexity; anterior marginal seta absent. Seta near hind angle set in lateral bead. Prosternal process medial impression near apex shallow or moderately deep, process apically plurisetose, medially along entire length with 10–14 long, scattered setae. Mesosternum medially plurisetose. Metepisternum and metepimeron very short. Elytral striae complete, very broadly and shallowly impressed. Parascutellar striole and angular base of stria 1 present as shallow punctulae, striae not impressed or entirely absent. Elytral parascutellar setae absent, basal margin sharply bordered. Striae marked with very sparse, shallow, elongate punctulae or punctulae absent. Elytra intervals 1–7 low, convex. Elytral microsculpture small, granular, composed of irregular sculpticells giving a matte sheen. Interval 3 with zero or one seta (sometimes only unilaterally). Marginal channel microsculpture composed of flat, slightly reflectant sculpticells, somewhat contrasting with matte discal microsculpture. Stria 8 with 30–36 umbilicate setae, somewhat irregularly spaced, but more closely set anteriorly and posteriorly, ended apically at level of interval 4. Stria 7 variably impressed apically, apparent or anastomosed with stria 8. Elytral humeri raised and rounded, without tooth or tubercle or with a very low, broad, rounded rearward-facing thickening, sometimes unilaterally. Elytra lacking externally visible plica, apiocolaterally internal ridge scarcely apparent. Vestigial flight wing present as a thin strap about ¾ elytral length. Male and female protarsi ventrally glabrous and unmodified; tarsomere 1 medially with 6–8 fine setae.

Abdomen: Abdominal ventrites smooth, 2–5 with a row of paramedial setae. Apical margin of ventrite 6 typically with two setae in males, four setae in females and a variable number, up to four, irregularly placed setae.

Male genitalia: Aedeagus (Figs 15–17) right paramere long, very broad at base and tapering apically and sharply curved at apex; left paramere broadly rounded at apex, conchiferous. Tip of median lobe blunt, subtruncate, tip apical of ostium very elongate and bent ventrally (Fig. 16). Dorsal ostium wide and rotated to right.

Female genitalia and reproductive tract: Laterotergite IX with more than 25 long setae along posterior margin. Gonocoxite 1 with three

or four extremely short, thick setae (apparent as vestigial ensiform setae). Gonocoxite 2 elongate, paddle-shaped, with one extremely short, thick medial seta, lateral setae absent. Elongate spermatheca ending in an oval expansion, with a short spermathecal duct digitiform diverticulum near base, attached at the midpoint on length of common oviduct. Spermathecal gland connected to spermathecal duct near base by long, narrow duct; glandular portion small, short, falcate, slightly expanded near base.

Distribution: (Fig. 48) The species occurs widely in rainforests on the Bulburin Plateau, including lower elevations on both the Dawes and Bobby Ranges that flank the south-flowing valley of Granite Creek. At several sites it co-occurs with the slightly larger *N. nox*. An outlier population of *N. darlingtoni* occurs in rainforests along creek lines at altitudes above 800 m on the wet eastern rim of the Kroombit Tops, 50 km NW of Bulburin. Its occurrence there was detected during surveys in the 1980s (Monteith 1986) and it was recorded as *Nurus nox*. The species was targeted as *Nurus* sp. nov. in a post-bushfire survey of Bulburin in 2020–21 (Gynther et al. 2023).

***Nuridius pluto* sp. nov**

Zoobank Reg: urn:lsid:zoobank.org:act:8C10BFE8-20E2-4E5D-91A7-380A0AC0F4A2

(Figs 19, 25–27, 49, 62, Table 1)

Etymology: The specific epithet, *pluto*, is based on the god of the underworld from Greek mythology and is an allusion to life in an underground burrow and the sombre colour of this *Nuridius* species. The epithet is treated as a noun in the genitive case.

Material examined: HOLOTYPE ♂: "Aust: SEQ, 26.39°S, 152.27°E, Jimna, 640m, 7 Jan- 2 Mar 1992, D.J. Cook, RF pitfall" (deposited in QM, Reg. No. T259434). PARATYPES (20): 1, same data as holotype, but date 29 Nov 1991–7 Jan 1992 (in QM); 7, Tungi Creek, Jimna, SE Qld, 8 Sept 1974, G. Monteith, ex burrows (in QM); 2, Peach Trees, via Jimna, -26.635°, 152.444°E, 25 Jun 2017, 520 m, G.B. Monteith, ex burrow, RF (1 in QM; 1 in EMEC); 2, Peach Trees, via Jimna, -26.639°S, 152.448°E, 1 June, 1997, 496 m, G.B. Monteith, ex burrows with double entrances (in QM); 3, Deer Reserve, Kilcoy, -29.985°S, 152.478°E, 10 Mar 2009, G. Monteith & F. Turco, ex burrows, (1 in QM; 2 in EMEC); 4, same loc. as previous, 11 Jan 1975, G.B. & S.R. Monteith, ex burrows (3 in QM; 1 in EMEC); 1, same loc. as previous, 11 Jan–29 Mar 1975, Pitfall 30, G.B. & S.R. Monteith (in QM).

Type locality: The corrected type locality for the species is -26.658 S, 152.453 E, which is in intact rainforest opposite the present Jimna Fire Tower Picnic Area at 680 m elevation.

Diagnosis: Recognizable from all other *Nuridius* species by the combination of being entirely black beetles, with narrow pronotal margins, pronotum with the anterior marginal setae present, the elytral basal margin sharply bordered, and meso- and metatibia dorsally smooth.

Description

Size: Overall length 26.6–24.3 mm (23.8 mm); greatest width of elytra 10.1–11.3 mm (10.1 mm).

Colour: Dorsal and ventral surfaces black; legs, mouthparts, and antennae dark piceous or black.

Lustre: Dorsally head, pronotum, and elytral margins very glossy, interval 1 often somewhat glossy; elytral disc matte; body ventrally moderately glossy.

Head: Dorsal microsculpture with microlines forming evident, nearly isodiametric mesh throughout. Clypeal-ocular sulci very broadly impressed, parallel, with 2 (0–3) short setae at anterior end. Ocular ratio 1.37–1.40; eyes large, rounded. Mandibles long, abruptly hooked apically, scrobe glabrous or with up to six very fine, short setae. Labrum anterior margin nearly straight or convex, medial four setae separated from each other about half to three quarters width from outermost medial seta to lateral seta. Anterior margin of clypeus emarginate. Mentum long, deeply emarginate with parallel, prominent lateral lobes; median tooth prominent, tooth emarginated; constantly with one pair of setae positioned at base of median tooth and usually with a second pair of smaller setae laterad medial pair and a few, scattered small setae. Submentum with two lateral pairs of setae. Gula narrow, width at middle about as wide as width of mentum tooth. Antennae long, antennomere 11 extended beyond pronotal base, antennomeres 5–11 elongate, apical 2/3 of 4 and entire length of 5–11 densely pubescent, 2–4 slightly compressed at base.

Thorax: Microsculpture of pronotal disc not visible at 50x magnification except near base, especially near basal angle, where microlines form very irregular transverse mesh. Pronotum quadrate, wider than long, sides sinuate in basal ⅓ and then straight or very slightly divergent onto base. Marginal bead thick, continuous from apex to base, wider near base, often abruptly narrowed and/or with a small notch level of basal seta; basal margin not bordered or with poorly defined border near basal impressions, emarginated medially; anterior angles only slightly produced; hind angles broadly obtuse or more narrowly so, nearly right-angled; base depressed, entire base at edge turned ventrally; basal impressions very broad, shallow and not clearly delimited or deeply impressed; deep to shallow, transverse sulci distant from anterior margin, very shallowly impressed medially or not evident. Anterior marginal seta set mesad of lateral channel; seta near hind angle set against lateral bead. Prosternal process medial impression near apex moderately deep, process apically plurisetose, medially along entire length with 6–20 long, scattered setae. Mesosternum medially plurisetose. Metepisternum and metepimeron very short. Elytral striae complete, broadly and very shallowly impressed and marked with shallow, elongate punctulae. Parascutellar striole and angular base of stria 1 present, impressed or not evident. Elytral parascutellar setae absent, basal margin sharply bordered from level of interval 3. Elytra with intervals 1–7 very slightly convex; microsculpture on intervals 1–7 and in striae dense, small, granular, composed of irregular sculpticells giving a matte sheen, contrasting with interval 8 to marginal region that has a glossy lustre due to microsculpture composed of flat, very reflectant sculpticells. Interval 3 with one seta at apical 1/4. Stria 8 with 34–39 umbilicate setae, somewhat irregularly spaced, but more closely set anteriorly and posteriorly, ended apically at level of interval 6. Elytra lacking externally visible plica, apiocolaterally internal ridge scarcely apparent. Vestigial flight wing present as a thin strap 1/5 to 1/2 elytral length. Male and female protarsi ventrally glabrous and unmodified; tarsomere 1 medially with 2–6 fine setae.

Abdomen: Abdominal ventrites smooth, 2–5 with numerous, scattered setae forming an irregular row of setae, more densely and irregularly placed medially. Apical margin of ventrite 6 typically with two setae in males and four setae in females, number varies ±1, often unilaterally.

Male genitalia: Aedeagus (Figs 25–27) with apex of median lobe with rounded tip asymmetrically produced to the right of the midline and directed ventrally; right paramere elongate, falcate, tapering to point without sharp hook. Dorsal ostium wide and slightly rotated to right.

Female genitalia and reproductive tract: Laterotergite IX with more than 20 long setae along posterior margin. Gonocoxites 1 and 2 without setae. Gonocoxite 2 elongate, paddle shaped. Elongate spermatheca ending in an oval expansion, with a small spermathecal duct digital diverticulum near base, attached at the midpoint on length of common oviduct. Spermathecal gland connected to spermathecal duct near base by long, narrow duct; glandular portion elongate, slightly expanded near base and expanded ovoid at apex.

Distribution: (Fig. 49) The species lives in burrows in hard clay soils in poor rainforest within a radius of 3 km around the township of Jimna and in similar habitats in the higher parts of Deer Reserve State Forest, 35 km south of Jimna. Much of the original rainforest in both areas has been cleared for plantations of pine, and *N. pluto* is now confined to remnant rainforest patches. The habitat of *N. pluto* contrasts with *N. fortis*, whose habitat is in the friable red basalt soils of the better-quality rainforests 45 km further NW along the Jimna Range.

Previously described species

***Nuridius curtus* (Chaudoir, 1865) new combination**
(Figs 6, 12–14, 49, 54, 61, Table 1)

Feronia curta Chaudoir, 1865: 78

Type: Chaudoir (1865) described the species from a single female in the Paris Museum (MNHN) labelled 'Northern Australia' (Moore et al. 1987).

Type locality: It is not possible to determine the precise type locality. Given that the hinterland of Mackay, where most populations currently exist, was still being tentatively explored by Europeans in the 1860s, the original collections may have come from

much further south, perhaps near Eidsvold (settled 1848) or inland from Gladstone (settled 1850) where outlier southern populations occur.

Material examined: 90 specimens in the following collections: AM, 14; ANIC, 11 ; EMEC, 3; QM, 62. Synoptic localities, north to south: Broken River, Fern Flat campground, 730 m, OF, -21.170S, 148.499E; Broken River, Sth of, 770 m, OF, -21.175S, 148.506E; Eungella Barracks, 1.5 km S., 800 m, OF, -21.180S, 148.512E; Eungella, 2 km SE of Broken River, 840 m, OF, -21.181S, 148.519E; Crediton, 850 m, OF, -21.198S, 148.513E; Mt Bryden, 0.2 km S., 800 m, OF, -21.344S, 148.567E; Upper East Funnel Ck, Black Mtn (creek), 250 m, RF, 21.572S, 149.185E; Upper East Funnel Ck, Black Mtn (ridge), 450 m, RF, -21.578S 149.179E; Blue Mtn, 0.6 km SE, 930 m, RF,-21.605S, 148.974E; Blue Mountain, 1 km S, 680 m, RF, -21.612S, 148.971E; Stoney Creek, track crossing, 280 m, RF, -21.623S, 148.978E; Pine Mountain, summit, 600 m, RF, -21.743S, 148.839E; Pine Mountain, 0.6 km S, 420 m, RF, -21.748S, 148.842E; Upper Hall Ck, NW of Carmila, 350 m, RF, -21.867S, 149.301E; Kroombit Tops, behind barracks, 805 m, OF, -24.357S, 150.960E; 'Eidsvold, Thomas Bancroft, 1913', -25.375S, 151.123E.

Distribution: (Fig. 49) This is the only species of *Nuridius* that regularly occurs in open eucalypt forests. At its northern limit at the southern end of the Clarke Range, it overlaps with the rainforest-restricted *N. medius* in different habitats, with populations only a few hundred metres apart at Broken River. Other northern populations are in rainforest habitat that caps mountains closer to the coast (Pine, Blue and Black Mts). Isolated southern populations have been identified recently, 350–450 km further south, at Kroombit Tops by Monteith (1986) (also open forest) and Eidsvold (1913 specimen in AM, habitat unknown), which may indicate that there are uncollected intervening populations.

Nuridius fortis Sloane, 1890 combination revised

(Figs 18, 28–33, 49, 58, 60, 64, Table 1)

Nuridius fortis Sloane, 1890: 649

Types: Sloane described the species from a male and female without indicating a holotype. The two specimens are in AM and are labelled as syntypes. The female bears AM Reg. Nos K14456 (old) and K205619 (new) plus Sloane's label '*Nuridius fortis* Sloane ♀, Wide Bay, Type'. Darlington has added a label on red card in his writing stating 'HOLOTYPE, *N. fortis* Sl. Det. Darlington', however this action was not published and has no validity. We now select this specimen as the lectotype and have labelled it as such. The male specimen bears AM Reg. No K205620 and Sloane's label '*Nuridius fortis* Sloane, ♂, Wide Bay, Type'. We now select this as Paralectotype and have labelled it as such.

Type locality: 'Wide Bay' was used in the late 1800s for the broad district around the port of Maryborough, extending 100 km inland as far as Gayndah. George Masters made very large Coleoptera collections for both the Australian Museum and the Macleay Museum during lengthy stays between Maryborough and Gayndah in 1867 and 1870 (Monteith 2001). Much of this material is labelled 'Wide Bay', including the holotype, negating the possibility of fixing a type locality. Two old Masters specimens in ANIC (ex Macleay Museum (Stanbury and Britton 1981)) labelled 'Queensland' have an old Macleay Museum drawer label pinned beside them that reads 'Maryborough, *Nuridius fortis* Sl.' Intensive modern collecting near Maryborough has failed to locate the species. The nearest recent collection is from Stockhaven, 75 km WSW of Maryborough, and this would have been within Masters' travelling range in 1870.

Material examined: 25 specimens in the following collections: AM, 2; ANIC, 2; EMEC, 3; QM, 18. Synoptic localities, north to south: 2.5 km SE of Stockhaven, 500 m, RF, -25.802S, 151.988E; Oakview NP, summit, 620 m, RF, -26.155S, 152.330E; 3.7 km N of Wrattens Camp, 630 m, RF, -26.261S, 152.317E; 1.5 km ENE of Wrattens Camp, 600 m, RF, -26.286S, 152.343E; Wrattens Camp, 700 m, RF, -26.293S, 152.331E; Mt Kandanga, 490 m, RF, -26.451S, 152.580E;.

Distribution: (Fig. 49) The species occurs on the rainforest summits of several subcoastal mountains in southern Queensland between 25.8°S and 26.3°S. These all have small summit areas except for Wratten NP, where good populations exist in several well-developed rainforest patches on basalt soil across an extensive plateau.

***Nuridius grandis* Sloane, 1910 combination revised**
(Figs 8, 22–24, 49, 52, 59, 63, Table 1)

Nuridius grandis Sloane, 1910: 388

Type: In ANIC with labels: "Blackall Range 11/06 [white paper]"// "*N. grandis* Sl., Holotype p.10 [pink paper]"// "*Nuridius grandis* Sl, Type, Id by T.G. Sloane"// "[white paper, bordered in red]//" "ANIC Database No. 25-164229 [green paper]". Sloane does not indicate the sex of the 'single specimen' sent to him by Henry Hacker. Its internal structures are completely hollowed out by dermestid damage, and the sex is not determinable.

Type locality: Given as 'Blackall Range', which is a low (max. 400 m), mostly rainforest, subcoastal range that extends for 35 km north from Landsborough in southern Queensland. An extensive area is now cleared for agriculture and urban development. Significant collecting effort and searching for burrowing carabids has been done recently in the area but this species has not been found.

Material examined: 28 specimens in the following collections: ANIC, 3; CMNH, 1; EMEC, 3; QM, 21. Synoptic localities, north to south: Cooran Tableland, hotspot, 445 m, RF, -26.274S, 152.836E; Cooran Tableland, BS68, 450 m, RF, -26.281S, 152.835E; Cooran Tableland, old barracks site, 465 m, RF, -26.283S, 152.833E; 'Eumundi', -26.477S, 152.949E; 'Blackall Range', -26.600S, 152.850E.

Distribution: (Fig. 49) An old specimen in QM labelled with only 'Eumundi', which is at the northern base of the Blackall Range, may support the veracity of the type locality but recent searches for these beetles near the town were not successful. The only population currently known is on Cooran Tableland, in Woondum National Park, which is 25 km north of Blackall Range. The tableland is ca. 400 m in altitude, mostly open forest, but with rainforest along many of the higher gullies, in most of which *N. grandis* is present.

***Nuridius medius* (Darlington, 1961) new combination**
(Figs 21, 39–41, 49, 50, Table 1)

Nurus medius Darlington, 1961: 12

Types: Holotype: Male. "M.C.Z. Type 30353"// "Eungella Rge. W. of Mackay, Q 2-3000' Nov 57 Darlingtons"// "Nurus medius. Darl.".

Type locality: The parts of the Eungella Range accessible to Darlington by road at the time of his 1957 visit stretch north-south for 20 km, from Broken River to Dalrymple Heights. Since his diary in the MCZ indicates that he camped at the southern end of Broken River, his collecting was probably in that area.

Material examined: 224 specimens in the following collections: AM, 31; ANIC, 18; CMNH, 1; EMEC, 10; QM, 164. Synoptic localities, north to south: Mt Macartney, summit, 950 m, RF, -20.833S, 148.555E; Mt Macartney, 850 m, RF, -20.843S, 148.557E; Mt William, 0.9 km E, 1160 m, RF, -21.016S, 148.608E; Mt William, summit, 1240 m, RF, -21.017S, 148.599E; Mt David, summit, 1230 m, RF, -21.018S, 148.626E; Mt William, 1100 m, RF, -21.023S, 148.608E; Upper Cattle Creek, 900 m, RF, -21.028S, 148.603E; Mt Dalrymple, summit, 1200 m, RF, -21.028S, 148.640E; Eungella QCAS (Queensland and Chinese Academy of Sciences), 1000 m, RF, -21.035S, 148.600E; Dalrymple Road, 950 m, RF, -21.036S, 148.596E; Eungella QCAS, 600 m, RF, -21.056S, 148.635E; Eungella QCAS, 400 m, RF, -21.061S, 148.637E; Pease's Lookout, Eungella NP, 880 m, RF, -21.117S, 148.516E; Eungella schoolhouse, 720 m, RF, -21.135S, 148.492E; Eungella, Sky Window, 780 m, RF, -21.145S, 148.499E; Diggings Road, 870 m, RF, -21.149S, 148.466E; Eungella QCAS, 800 m, RF, -21.149S, 148.503E; Broken River, 725 m, RF, -21.168S, 148.507E; Crediton Creek, 850 m, RF, -21.187S, 148.524E; Crediton SF, 700 m, RF, -21.297S, 148.578E.

Distribution: (Fig. 49) *Nuridius medius* is extremely common at Eungella and restricted to the rich, wet rainforests in the area from the summits of the higher peaks (Williams, David and Dalrymple) around 1250 m down to 400 m in the upper parts of Finch Hatton Gorge. It occurs 20 km further north of Eungella at Mt Macartney and probably throughout the highlands of the intervening Clarke Range that are yet to be surveyed. Though a burrow maker, *N. medius* is often taken by casual collectors because it usually rests at the burrow entrance in the daytime and is exposed by casual rock- and log-turning.

***Nuridius niger* (Chaudoir, 1878) new combination**
(Figs 34, 42–44, 48, 53, 56, Table 1)

Nurus niger Chaudoir, 1878: 37

Types: Female. "Cape York". Although Chaudoir (1878) mentions a single female in his description Moore et al. (1987) cite possible syntypes in MNHN.

Type locality: The species does not occur at Cape York but in the hinterland of Bowen and on nearby islands. Bowen was the earliest port in the northern half of Queensland, established in 1861. The type may have been collected by Eduard Dämel who collected insects widely in Queensland for European museums between 1862 and 1875, including at both Bowen and Cape York, (Bieler and Petit 2012; Monteith 1987). Some of his specimens may have become confused between the two localities. A very old specimen in QM labelled simply 'Bowen' indicates that the species was available to early collectors near that port.

Material examined: 73 specimens in the following collections: AM, 3; ANIC, 1; EMEC, 2; QM, 67. Synoptic localities, north to south: Cape Upstart, 5 km N. of Station Hill, 550 m, OF, -19.732S, 147.812E; 'Bowen', 20 m, -20.012S, 148.245E; Hayman Island, -20.053S, 148.888E; Mt Abbot, summit, 1000 m, -20.101S, 147.743E; Mt Abbot, RF gully, 750 m, -20.102S, 147.749E; Mt Abbot, campsite, 800 m, -20.102S, 147.756E; Mt Abbot, sthn. slopes, 100–500 m, OF, -20.106S, 147.770E; Mt Aberdeen, nth. summit, 850 m, RF, -20.198S, 147.920E; Mt Aberdeen, summit saddle, 800 m, RF, -20.201S, 147.919E; Mt Aberdeen, sth. summit, 900 m, RF, -20.205S, 147.919E; Mt Aberdeen, east slopes, 500 m, RF, -20.205S, 147.927E; Mt Hayward, 350 m, RF, -20.315S, 148.759E; Lindeman Island, -20.444S, 149.042E; 5–8 km N. of Mt Macartney, RF, -20.801S, 148.498E; Cathu SF, lookout, 800 m, -20.823S, 148.533E.

Distribution: (Fig. 48) *Nuridius niger* occurs in dry rainforests and sometimes in open forest at higher altitudes. At its southern limit, it abuts the northern limit of *N. medius* at Mt Macartney, with *N. medius* found in the wetter rainforests near the summit above 900 m and *N. niger* in drier, lower rainforests on the northern flank. From Mt Macartney, it is known from a string of mainland mountain summits (Hayward, Aberdeen, Abbott, Upstart) stretching 150 km north. On both Mt Abbott and Cape Upstart, it occurs in both rainforest and open forest habitats. Old specimens from the 1920s were taken on the offshore Hayman and Lindeman Islands in the Whitsunday Group, both of which have dry rainforests on low mountains. These islands would have been part of the mainland at periods of low sea level as recently as 7,000 years ago (Blair et al. 2014).

Nuridius nox (Darlington, 1961) new combination

(Figs 20, 36–38, 49, 55, Table 1)

Nurus nox Darlington, 1961: 11

Types: Holotype: Male. "M.C.Z. Type 30352"// "Mt. Jacob SQ c45 mi. S. of Gladstone c2000' Mar58 Darlingtons"// "Nurus nox Darl."

Type locality: Darlington's locality 'Mt Jacob' is an old name used by early foresters for an extensive plateau of rainforest, later called 'Bulburin' and now entirely within the Bulburin National Park (Monteith, 1986). Darlington's unpublished diary (held in the MCZ) describes collecting in the first rainforest he encountered on the road up to the plateau from the township of Builyan, which places him at -24.527S, 151.471E, just before the old Forest Station clearing that is now the park picnic area.

Material examined: 35 specimens in the following collections: AM, 1; ANIC, 5; EMEC, 1; QM, 28. Synoptic localities, north to south: Forest Station site, Bulburin NP, 600 m, RF, -24.527S, 151.471E; Bobby Range Rd 3, Bulburin NP, 620 m, RF, -24.547S, 151.546E; Bobby Range Rd 4, Bulburin NP, 625 m, RF, -24.547S, 151.545E; Top of Range, Bulburin NP, Pitfall 33, 610 m, RF, -24.552S, 151.546E; Bobby Range Rd 2, Bulburin NP, 600 m, RF, -24.555S, 151.555E; Granite Creek, Bulburin NP, 200 m, RF, -24.570S, 151.531E; Dawes Range Rd 2, Bulburin NP, 690 m, RF, -24.577S, 151.514E; Dawes Range Rd 3, Bulburin NP, 610 m, RF, -24.612S, 151.537E; Mt Fort William, via Kalpowar, 695 m, RF, -24.647S, 151.339E.

Distribution: (Fig. 49) *Nuridius nox* is restricted to rainforest and occurs throughout the Bulburin Plateau, with an outlier population at Mt Fort William, 20 km SW of Bulburin. At Bulburin, *Nuridius nox* co-occurs with the slightly smaller *N. darlingtoni*; both species are sometimes found in identical-looking burrows within meters of each other. The species was targeted in a post-bushfire survey of Bulburin in 2020–21 (Gynther et al. 2023).

***Nuridius rex* (Darlington, 1961) new combination**
(Figs 35, 45–47, 48, 57, Table 1)

Nurus rex Darlington, 1961: 9

Types: Holotype: Male. "M.C.Z. Type 30351"// "Elliot Range, Townsville Q c 3000 ' Mar58 Darlingtons"// "Fig. Todd 1961"// "Nurus rex Darl."

Type locality: Although Darlington's specimens are labelled only with 'Elliot Range', his published list of localities (Darlington 1960) states that he collected on Sharp Elliot, a discrete peak a little south of the main summit. His unpublished diary (held in the MCZ) states that he followed Double Creek to slightly below the summit of Sharp Elliot at -19.550S, 146.991E, which can be taken as the precise type locality.

Material examined: 77 specimens in the following collections: ANIC, 7; EMEC, 6; QM, 64. Synoptic localities, north to south: Mt Elliot, North Ck., 1000 m, RF, -19.490S, 146.963E; Mt Elliot, Upper North Ck., 1100 m, RF, -19.494S, 146.965E; Mt Elliot, west of summit (Stuart Lay), 1200 m, RF, -19.494S, 146.970E; Mt Elliot, summit, 1210 m, RF,- 19.498S, 146.976E; Mt Elliot, Upper St Margarets Creek, 900 m, RF, -19.500S,146.983E; Sharp Elliot (Darlington), 1000 m, RF, -19.550S, 146.991E.

Distribution: (Fig. 48) This is the northmost *Nuridius* species and is restricted to rainforests above ca. 900 m on Mt Elliot where it is still very common in burrows, often exposed by turning rocks, as Darlington found during his collecting. All modern samples are from the main summit, accessed by either North or St Margarets Creeks.

Key to adults of *Nuridius* species

1. Elytral basal border evident from humeri to at least stria 1 (Figs 50, 51) **2**
1'. Elytra lacking basal border (Fig. 52) **5**

2. Pronotum lacking anterior marginal setae **3**
2'. Pronotum with anterior marginal setae present **7**

3. Meso- and metatibia dorsally very rugose-striate (Fig. 53) **4**
3'. Meso- and metatibia dorsally smooth (Fig. 54) ..... *Nuridius darlingtoni*

4. Pronotum with large, prominently convex basolateral tubercles, lateral margins straight or subsinuate to the hind angles (Fig. 55) ..... *Nuridius nox*
4'. Pronotum with scarcely convex basolateral tubercles, lateral margins nearly evenly arcuate to the hind angles (Fig. 56) ..... *Nuridius niger*

5. Pronotum lateral margin throughout its length with a very broad, sharply delimited, reflexed region, area near hind angles projecting posteriorly far beyond posterior seta (Fig. 57). Size very large (41–45 mm) and body form broadly robust (Fig. 35); distribution restricted to Mt Elliot ..... *Nuridius rex*
5'. Pronotum lateral margin not broadly reflexed, lateral channel not sharply delimited medially (Fig. 58), area near hind angles little projecting posteriorly beyond posterior seta (Fig. 58). Size 33–25 mm and body form somewhat elongate; distribution in southern Queensland **6**

6. Large (31–33 mm); male aedeagus (Figs. 22–24); range restricted to coastal ranges east of the north-south valley of the Mary River; transverse impression of the anterior third of the pronotum marked with deep, paramedial depressions, not or very little impressed medially (Fig. 59). All elytral intervals with a notably glossy media area contrasting with the matte area in the striae (Fig. 63) and laterally on the interval ..... *Nuridius grandis*
6'. Small (25–29 mm); male aedeagus (Figs. 28–33); range restricted to inland ranges west of the Mary River valley; transverse impression of the anterior third of the pronotum shallowly, but more or less uniformly impressed throughout, not marked with deep, paramedial depressions (Fig. 60). Elytral interval 1 glossy, all other intervals uniformly matte with the same microsculpture in the striae and laterally on the interval or only very slightly glossier (Fig. 64) ..... *Nuridius fortis*

7. Metallic green colour on head and pronotum, usually also on elytra at least along the margins ... **8**
7'. Entirely black without metallic colour **9**

8. Large (29–37 mm). Elytral humeri narrow, not at all reflexed, humeral tooth evident, bluntly pointed (Fig. 50) ..... *Nuridius medius*

8'. Small (19–20 mm). Elytral humeri widely reflexed, humeri with a very low, thick tubercle (Fig. 51) ..... *Nuridius frickei*

9. Pronotum clearly sinuate in the basal third, lateral bead interrupted at the level of the hind seta, forming a notch in the bead (Fig. 62). Elytral humeri with a prominent, but very blunt tooth .... *Nuridius pluto*

9'. Pronotum not sinuate in the basal third or with only the slightest suggestion of a sinuation, lateral bead entire, not interrupted at the level of the hind seta and lacking a notch in the bead (Fig. 61). Elytral humeri rounded and lacking a tubercle .... *Nuridius curtus*

DISCUSSION

Phylogeny

The clade consisting of *N. fortis*, *N. grandis*, and *N. pluto* is supported in the combined and all single partition analyses. However, there is no consistently supported relationship among the three. The combined data and COI analyses resulted in (*N. fortis* (*N. grandis* + *N. pluto*)), the 28S analysis (*N. grandis* (*N. fortis* + *N. pluto*)), and CAD2 (*N. pluto* (*N. grandis* + *N. fortis*)) (Figs 1–4). While lack of agreement between the different sequence partitions makes their relationships uncertain, the morphological features presented in the key, diagnosis, and description readily distinguish between these three species and their distributions are allopatric, leaving little doubt of their separation. However, unlike other species of the genus, specimens we assigned to *Nuridius fortis* do not form a distinctly supported clade except in the COI-only analysis. Additionally, a single male from Wrattens Camp had a unique form of the aedeagus and paramere (Figs 31–33) that suggests the possibility of yet another species. However, we could not find any other morphological differences between this specimen and other specimens considered typical *N. fortis*. The sequence data also does not support an additional species within our *N. fortis* sample, as none of the analyses resulted in a monophyletic set of samples from Wrattens Camp (Figs 1–4). The lack of monophyly, apparently driven by the 28S and CAD2 data (Figs. 2, 4), implies that expanding the sample of specimens, localities, and loci for this species would be useful to develop a better understanding of its potentially complex population structure.

The distinctive dorsally rugose-striate meso- and metatibia found in *N. nox* and *N. niger* was initially suspected to be a synapomorphy for these two species. However, none of the analyses identified these two as sister species. This suggests that the tibial rugosity either evolved twice in these species or was independently lost in the related *N. rex* and *N. medius* (Fig. 1). Similarly, characteristics useful for species identification, such as the presence or absence of the basal border of the elytra and form of the elytral humeral tooth, are not recovered as synapomorphic.

Biology

Like all species of genus *Nurus* (Charley and Andren 2018, 2021), adults of *Nuridius* species live singly in permanent burrows with a widened entrance opening beneath the downslope edge of a stone, log or exposed root. In front of the entrance, a 'stage' is kept clear of fallen leaves where passing prey, particularly millipedes, are ambushed by the carabid resting at its burrow entrance. Further observations by GBM on field and captive specimens are as follows. Burrows are 25–50 cm in length, slope gradually downwards in a wide spiral and have a turning chamber at the end. Burrows are excavated with the elongate mandibles, without use of forelegs. 'Mouthfuls' of soil are carried, sometimes backwards, to the entrance and spread over the 'stage' area. Females of both genera lay batches of ca. 6–12 large, elongate eggs in individual, compressed soil capsules (Figs 65C, 66) stored in the burrow and carried by the female in the mandibles when necessary. Each soil capsule comprises two parts: a larger, ovate, hollowed-out shell opening dorsally and a smaller, slightly domed 'lid' that closes the aperture of the shell (Fig. 66). The egg rests loosely in the central chamber. The method of oviposition and construction of the capsules has not been observed. Hatched batches of first instar larvae (Fig. 65B) are sometimes found in the burrow with the female and clearly do not disperse immediately on hatching. Whether they receive initial food from prey brought in by the female is not known and needs investigation. Later instars are not found in

the burrows and details of larval life outside the burrow are not known.

The egg capsules recorded here for *Nurus* and *Nuridius* are like the two-part soil capsules recorded and illustrated for the pterostichine genus *Abax* in Italy by Brandmayr (1977). Kavanaugh (1998) records capsules in *Percus* and reviews the literature on the topic, with some speculation on whether retention of the larvae in the brood chamber after hatching is accompanied by some 'feeding' by the female. Parallel behaviour in Australian *Nurus* and *Nuridius* needs further study in this respect.

Habitat and distribution

Like *Nurus* species (Will and Monteith 2018), *Nuridius* species are almost entirely restricted to rainforest, where the moist ground floor surface, free of dense herbaceous layer, favours their burrow-living habits while the supply of slowly decaying wood provides their predominantly millipede diet. (Charley and Andren 2018, 2021). For those *Nuridius* species that sometimes occur in open eucalypt forests those sites are at relatively high altitude (southern Clarke Range and Kroombit Tops for *N. curtus* and Mt Abbott and Cape Upstart for *N. niger*), where the cooler, moister environment and clearer ground layer tends to resemble that of rainforests. Further, it can be predicted that rainforest was previously present at those sites.

Mesic habitats, exemplified by modern rainforest, are ancestral in Australia and once covered much of the continent but have shrunk in modern times due to the gradual onset of aridity over the last 30 million years. The result of this process, summarised by Byrne et al. (2011), is that rainforest in eastern Australia now occupies a disjunct series of often small, favourable, higher-rainfall, usually elevated sites along the eastern margin of the continent. This habitat disjunction has been a driver of allopatric speciation in the rainforest biota and Bryant and Krosch (2016) summarise the major barriers between the biogeographic regions proposed by Ebach et al. (2015) along the eastern Australian coast. Within this biogeographic framework, all *Nurus* species fall within the southern, high-rainfall NE New South Wales region, while all *Nuridius* species fall within the northern, much drier Eastern Queensland region. The barrier between the regions is the Brisbane Valley Barrier (Fig. 49), across which Bryant and Krosch (2016) summarise times of molecular divergence as far back as 25 million years.

Within the Eastern Queensland region, the 10 *Nuridius* species occur on a series of disjunct mountains, ranges and plateaus stretching in a narrow subcoastal band for 1000 km from 27°S to 19.5°S, none of them more than 150 km inland (Figs 48–49). This chain of habitats is broken by a dry corridor about midway (ca 22–23°S) termed the St Lawrence Gap (Figs. 48–49) by Bryant and Krosch (2016) and is terminated at the north by their Burdekin Gap (ca. 20.2S-19.5S; Fig. 48). Two major foci of rainforest habitats occur south of the St Lawrence Gap and two north of the gap. Those to the south of the gap are the southern complex of ranges (D'Aguilar, Blackall, Conondale, Jimna and Cooran Ranges) at 26-27°S between Brisbane and Gympie and the northern complex of Bulburin and Kroombit (24.3-24.8°S) southwest of Gladstone. North of the St Lawrence Gap, there is the major rainforest system centred on the Clarke Range (20.2-21.7°S) between Proserpine and Sarina and the isolated rainforest system on Mt Elliot (19.5°S) at the northern limit of *Nuridius* distribution and the region.

The phylogeny of *Nuridius* (Figs 1–4) shows considerable congruence with the arrangement of habitat distribution outlined above. The three species forming the most consistent clade (*N. grandis*, *N. fortis* and *N. pluto*) are all closely allopatric within the southernmost rainforest system (Fig. 49) with the large *N. grandis* on the subcoastal Blackall and Cooran Ranges, separated by the Mary River Valley from the more inland *N. fortis* and *N. pluto*, which have their central populations on the Jimna-Wrattens Range. *Nuridius fortis* has disjunct occurrences to the north of the Jimna Range (Stockhaven and Oakview), while *N. pluto* has a disjunct occurrence to the south (Deer Reserve), both presumably a product of the past aridity-driven disjunction of rainforest habitats. *Nuridius darlingtoni*, allied to this clade, occurs in the next major rainforest complex north (Kroombit/Bulburin), so all four related species occur to the south of the St Lawrence Gap.

The next most consistent clade is that of *N. medius*, *N. niger* and *N. rex*. These three have adjacent but allopatric distributions north of the St Lawrence Gap. *Nuridius medius* is extremely abundant and appears to form a continuous population throughout the wet rainforests of the Clarke Range. At the northern end of the Clarke Range, where the habitat suddenly becomes drier with falling altitude, *Nuridius niger* replaces *N. medius* with which it is contiguous along a line that separates wet rainforests from dry rainforests. Further highly disjunct occurrences of *N. niger* occur 100 km further north on summits of three well-separated mountains (Aberdeen, Abbot and Upstart) that rise abruptly from low hot plains in the middle of the low rainfall biogeographic barrier designated the Burdekin Gap by Bryant and Krosch (2016). Another 100 km further north across the hot lowland delta of the Burdekin River, the sister species of *N. niger* has differentiated on the isolated 1100 m, rainforest summit area of Mt Elliot as *Nuridius rex*, the largest member of *Nurus* or *Nuridius*.

The remaining three species (*N. curtus*, *N. nox* and *N. frickei*) have no strongly supported sister relationships with other congeners. *Nurus curtus* has the longest north-south range (540 km) in the genus and is the only species that occurs on both sides of the St Lawrence Gap. Its habitat preference varies throughout that range. At its northern limit, it occupies open forest where it is contiguous with the range of the rainforest *N. medius*. A little further south, it occupies rainforest on several mountain summits (Pine, Blue, Black) that rise from dry eucalypt surroundings, while at the southern end of its range it occupies open forest on Kroombit Tops adjacent to the rainforest occurrence of *N. darlingoni*. *Nuridius nox* occupies a small north-south range of less than 20 km in rainforest of the Bulburin Range, south of the St Lawrence Gap and is placed as sister to the clade of *N. medius*, *N. niger* and *N. rex*, all distributed north of the St Lawrence Gap. *Nuridius nox* co-occurs with *N. darlingtoni* at Bulburin. The rather enigmatic *Nurus frickei* is the smallest member of the genus, placed as sister to all other species, and is known from a single small area in the Clarke Range, north of the St Lawrence Gap, where it is common and co-occurs with the equally common *N. medius*.

Conservation aspects

Species of *Nuridius* and *Nurus* are flightless, so these beetles have low dispersal powers. They also occupy restricted ranges in habitat types that have contracted over recent geological time (Byrne et al. 2011). This qualifies them to be regarded as 'short-range endemics' as defined by Harvey (2002) and worthy of conservation concern. Following our taxonomic review of *Nurus* (Will and Monteith 2018) the New South Wales Government, under whose jurisdiction all species of that genus fall, instigated surveys of *N. atlas* (Laporte, 1867) and *N. brevis* Motschulsky, 1865 using the novel and effective survey method of counting active burrows to gain density and distribution data (Charley and Andren 2018, 2021). This led to assessment under the NSW Biodiversity Conservation Act 2016 and recent listing under that Act of 'Critically endangered' for *Nurus atlas* (NSW Threatened Species Scientific Committee 2023a) and 'Vulnerable' for *Nurus brevis* (NSW Threatened Species Scientific Committee 2023b).

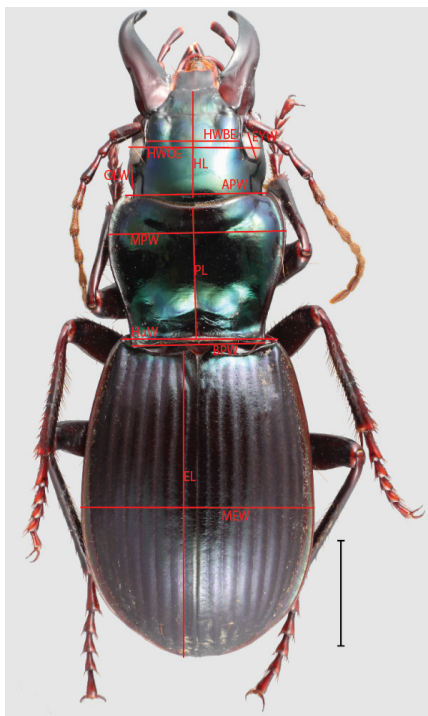
All species of *Nuridius* fall under the jurisdiction of the Queensland Government, which administers a Threatened Species Program under the QLD *Nature Conservation Act 1992*. Under that program, two species occurring at Bulburin National Park, *N. nox* and *N. darlingtoni* (as *N.* sp. nov.), were used as 'short-range endemic' indicator species in a recent post-bushfire survey of that area by Gynther et al. (2023). Some of the data we present here may allow for other *Nuridius* species to be assessed under that legislation. The northern species, *Nuridius frickei* and *N. rex*, have narrowly restricted, high-altitude distributions but show no indications of change. On the other hand, species accounts for *N. fortis*, *N. grandis*, and *N. pluto* indicate populations of some of the more southern, low-altitude species have clearly retreated from sites where they were readily collected in earlier times. This may reflect habitat clearing for agriculture and forestry purposes in some areas. Another potential factor, flagged by Charley and Andren (2018, 2023) as a threatening process for *Nurus atlas* and *N. brevis* in NSW, is predation by the Cane Toad, *Rhinella marina* (Linnaeus, 1758) that was introduced in 1935 in an attempt to control sugar cane pests. Cane Toads are

now widespread in Australia and cause significant ecological damage (Shine 2010). The toad is an efficient predator of ground dwelling Carabidae, despite the beetles' chemical defences (Moore 1979), as indicated by numerous *Nuridius* elytra in gut contents of toads from Bulburin pictured by Turvey (2013).

ACKNOWLEDGEMENTS

We thank Elise Rappel (undergraduate UC, Berkeley) for help with PCR and sequencing efforts, Stuart Lay (CSIRO) for providing some essential samples for sequencing, Karin Koch (QM) for specimen databasing, Vivian Sandoval for photographs in Figs. 65 and 66, Derek Smith (AM) for assistance with loans from Australian Museum, and the reviewers for their helpful comments that allowed us to improve the manuscript.

TABLES AND FIGURES



HL	Head length — from base of labrum to base of occiput
PL	Pronotal length along middle line
EL	Elytron length from basal margin to apex of the left elytron
HWOE	Head width over eyes
HWBE	Head width between eyes at the level of the anterior supraocular setae
MPW	Maximum pronotal width
APW	Anterior pronotum width
BPW	Basal pronotum width
MEW	Maximum elytral width
HuW	Humeral width
EYW	Eye width
OLW	Ocular lobe width
mettar1	Metatarsomere 1 length
mettib	Metatibia length
metepimL	Metepimeron length along lateral edge
metepiW	Metepimeron width along anterior edge
D.61	min or max from Darlington 1961, if beyond range of measured specimens

Supplementary table figure. An image of *Nuridius medius* showing measurement locations.

Table 1. Measurements of *Nuridius* species. Measurements are in ocular units except holotypes, which are in mm.

	Measurement			Ratio							
	HL	**PL**	**EL**	**HWOE**	**HWBE**	**MPW**	**APW**	**BPW**	**MEW**	**HuW**	**EYW**
N. pluto sp. nov.	90	90	245	105	75	130	105	105	180	120	25
N. pluto sp. nov.	92	82	217	99	71	120	99	99	170	106	20
N. pluto sp. nov.	85	82	222	96	70	125	99	99	161	110	20
N. pluto HT (mm)	5.2	5.2	13.39	6	4.5	7.6	6.4	6.16	10.14	7.41	1.41
N. medius	105	115	311	134	100	170	140	126	225	150	25
N. medius	102	104	263	112	84	152	117	117	204	126	21
N. medius	106	116	296	125	93	167	137	130	207	143	24
N. medius (D. 61)											
N. rex	150	140	367	140	107	227	160	150	282	192	25
N. rex	125	121	317	121	92	190	135	124	225	171	23
N. rex (D. 61)											
N. grandis	115	111	297	129	95	157	124	112	225	154	27
N. grandis	126	110	285	129	95	165	130	125	217	156	27
N. grandis	106	106	290	122	91	151	123	118	215	139	28
N. fortis (Oak.)	90	88	225	98	72	130	101	94	172	122	23
N. fortis (Oak.)	104	91	240	107	80	137	107	101	191	124	25
N. fortis (Stock.)	109	104	255	119	90	155	127	121	195	135	27
N. fortis (Wratt.)	105	104	255	116	82	150	120	115	202	145	27
N. fortis (Wratt.)	95	97	244	112	83	140	115	109	192	125	24
N. fortis (Wratt.)	91	91	235	104	78	135	107	105	186	125	24
N. frickei sp. nov.	70	75	188	85	62	121	87	107	147	112	18
N. frickei sp. nov.	70	72	176	79	56	117	79	97	131	102	20
N. frickei HT (mm)	4.65	4.9	12.35	5.2	3.85	8	5.6	7.12	9.49	7.8	1.35
N. nox	120	91	280	125	82	160	144	128	220	147	25
N. nox	125	110	310	134	97	190	134	153	255	164	29
N. nox (D. 61)											
N. niger	122	125	336	132	100	204	142	166	275	171	29
N. niger	81	100	249	103	72	162	109	123	218	132	27
N. curtus	110	97	253	114	88	171	123	138	214	164	23
N. curtus	70	77	180	79	58	119	80	92	137	105	18
N. curtus	90	88	220	95	71	142	100	116	160	116	20
N. darlingtoni sp. nov.	104	95	246	110	79	155	115	128	198	140	28
N. darlingtoni sp. nov.	81	77	195	91	69	120	91	100	160	114	19
N. darlingtoni HT (mm)	4.4	5.2	13.65	6.16	4.65	8.84	7.15	7.15	10.79	8.45	1.3

Table 1 (cont.) Measurements of *Nuridius* species.

	Measurement			Ratio							
	TL	**PW**	**EW**	**OR**	**MPW/ BPW**	**MPW/ PL**	**APW/ BPW**	**MEW/ HuW**	**MEW/ MPW**	**MEW/ HWOE**	**EYW/ HL**
N. pluto sp. nov.	26.56	8.13	11.25	1.40	1.24	1.44	1.00	1.50	1.38	1.71	0.28
N. pluto sp. nov.	24.44	7.50	10.63	1.39	1.21	1.46	1.00	1.60	1.42	1.72	0.22
N. pluto sp. nov.	24.31	7.81	10.06	1.37	1.26	1.52	1.00	1.46	1.29	1.68	0.24
N. pluto HT (mm)	23.79	7.6	10.14	1.33	1.23	1.46	1.04	1.37	1.33	1.69	0.27
N. medius	33.19	10.63	14.06	1.34	1.35	1.48	1.11	1.50	1.32	1.68	0.24
N. medius	29.31	9.50	12.75	1.33	1.30	1.46	1.00	1.62	1.34	1.82	0.21
N. medius	32.38	10.44	12.94	1.34	1.28	1.44	1.05	1.45	1.24	1.66	0.23
N. medius (D. 61)	37.00		11.50								
N. rex	41.06	14.19	17.63	1.31	1.51	1.62	1.07	1.47	1.24	2.01	0.17
N. rex	35.19	11.88	14.06	1.32	1.53	1.57	1.09	1.32	1.18	1.86	0.18
N. rex (D. 61)	45.00										
N. grandis	32.69	9.81	14.06	1.36	1.40	1.41	1.11	1.46	1.43	1.74	0.23
N. grandis	32.56	10.31	13.56	1.36	1.32	1.50	1.04	1.39	1.32	1.68	0.21
N. grandis	31.38	9.44	13.44	1.34	1.28	1.42	1.04	1.55	1.42	1.76	0.26
N. fortis (Oak.)	25.19	8.13	10.75	1.36	1.38	1.48	1.07	1.41	1.32	1.76	0.26
N. fortis (Oak.)	27.19	8.56	11.94	1.34	1.36	1.51	1.06	1.54	1.39	1.79	0.24
N. fortis (Stock.)	29.25	9.69	12.19	1.32	1.28	1.49	1.05	1.44	1.26	1.64	0.25
N. fortis (Wratt.)	29.00	9.38	12.63	1.41	1.30	1.44	1.04	1.39	1.35	1.74	0.26
N. fortis (Wratt.)	27.25	8.75	12.00	1.35	1.28	1.44	1.06	1.54	1.37	1.71	0.25
N. fortis (Wratt.)	26.06	8.44	11.63	1.33	1.29	1.48	1.02	1.49	1.38	1.79	0.26
N. frickei sp. nov.	20.81	7.56	9.19	1.37	1.13	1.61	0.81	1.31	1.21	1.73	0.26
N. frickei sp. nov.	19.88	7.31	8.19	1.41	1.21	1.63	0.81	1.28	1.12	1.66	0.29
N. frickei HT (mm)	21.90	8.00	9.49	1.35	1.12	1.63	0.79	1.22	1.19	1.83	0.29
N. nox	30.69	10.00	13.75	1.52	1.25	1.76	1.13	1.50	1.38	1.76	0.21
N. nox	34.06	11.88	15.94	1.38	1.24	1.73	0.88	1.55	1.34	1.90	0.23
N. nox (D. 61)	37.00		11.50								
N. niger	36.44	12.75	17.19	1.32	1.23	1.63	0.86	1.61	1.35	2.08	0.24
N. niger	26.88	10.13	13.63	1.43	1.32	1.62	0.89	1.65	1.35	2.12	0.33
N. curtus	28.75	10.69	13.38	1.30	1.24	1.76	0.89	1.30	1.25	1.88	0.21
N. curtus	20.44	7.44	8.56	1.36	1.29	1.55	0.87	1.30	1.15	1.73	0.26
N. curtus	24.88	8.88	10.00	1.34	1.22	1.61	0.86	1.38	1.13	1.68	0.22
N. darlingtoni sp. nov.	27.81	9.69	12.38	1.39	1.21	1.63	0.90	1.41	1.28	1.80	0.27
N. darlingtoni sp. nov.	22.06	7.50	10.00	1.32	1.20	1.56	0.91	1.40	1.33	1.76	0.23
N. darlingtoni HT (mm)	23.25	8.84	10.79	1.32	1.24	1.70	1.00	1.28	1.22	1.75	0.30

FIGURES

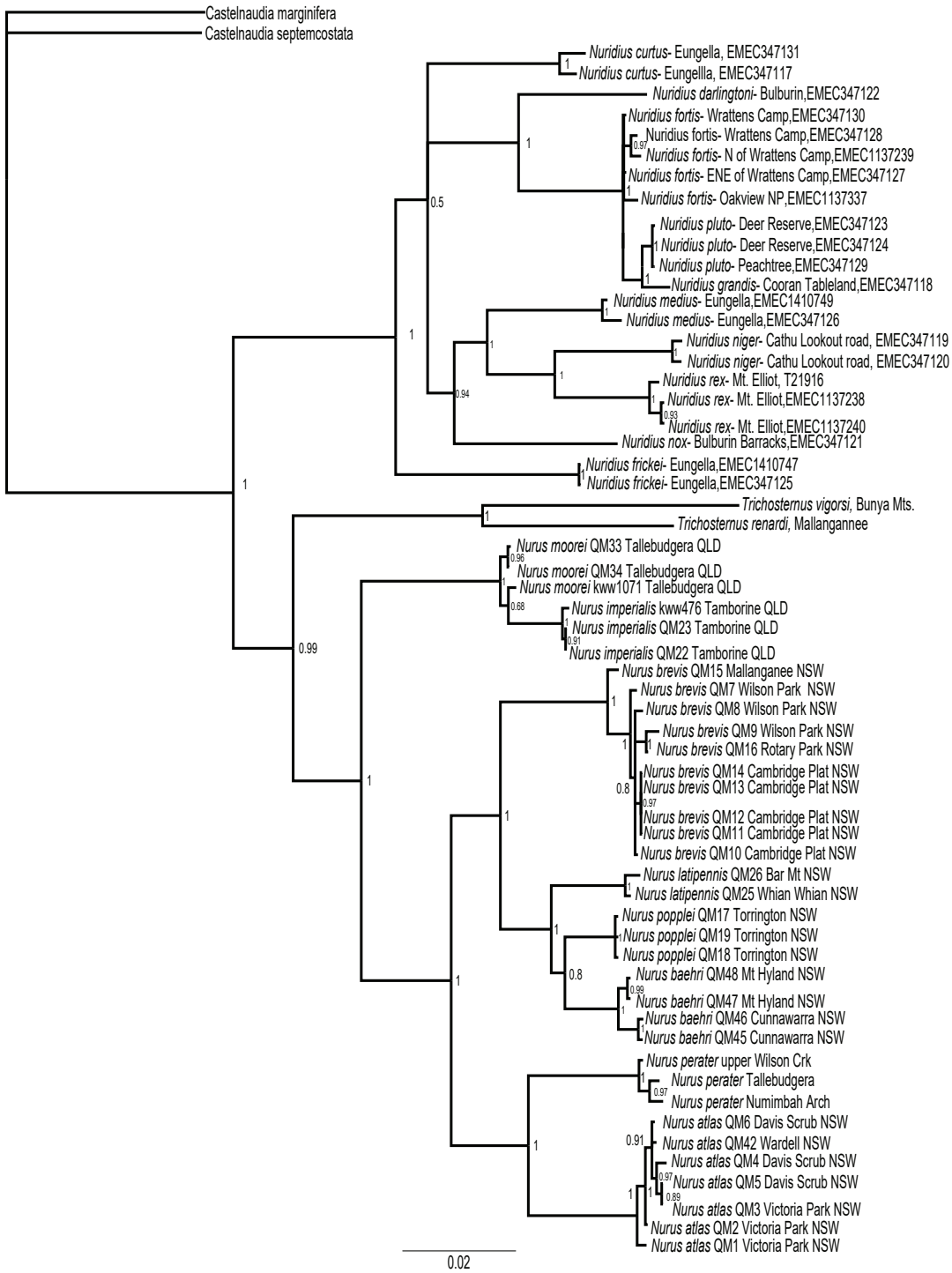
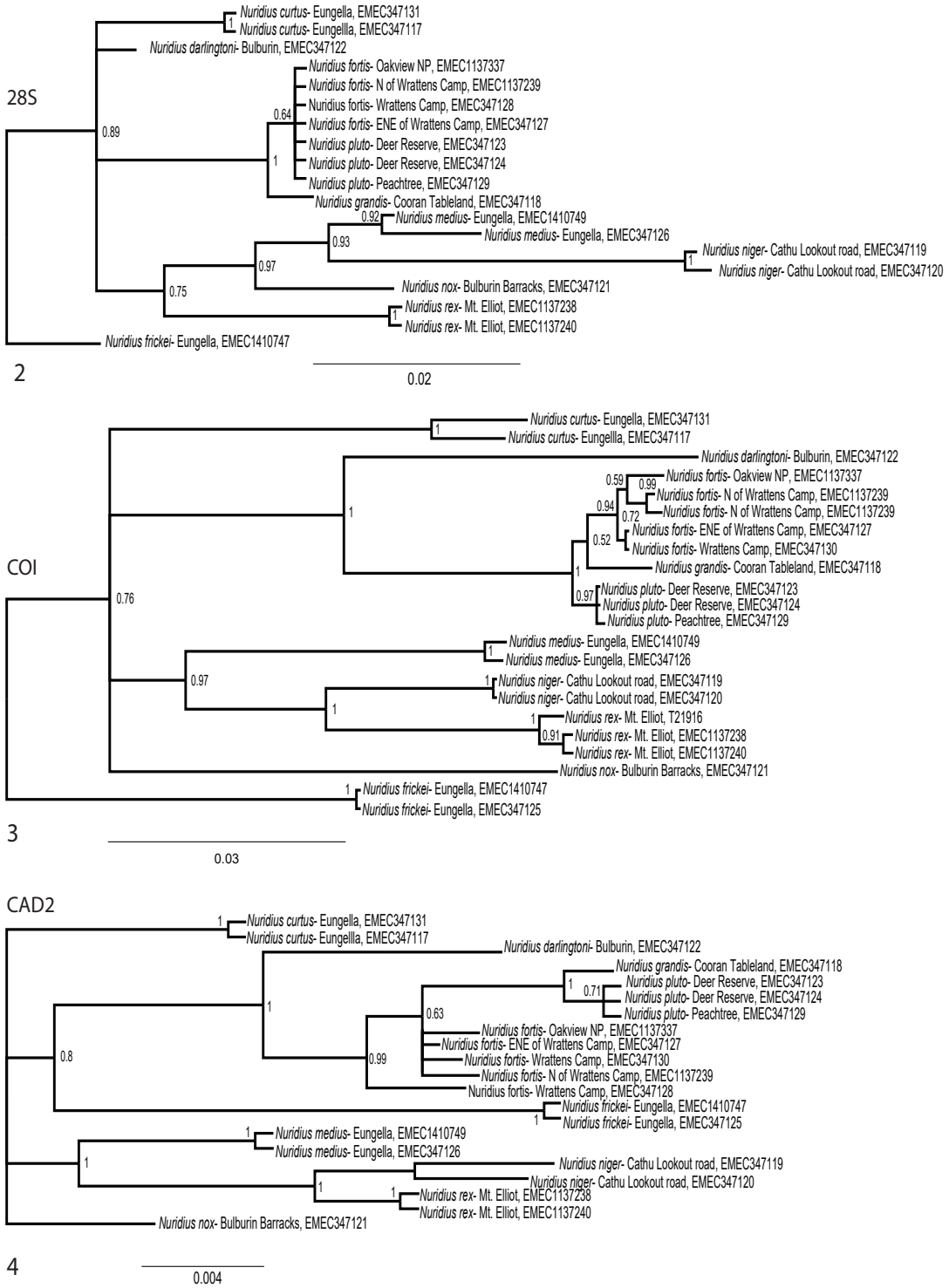
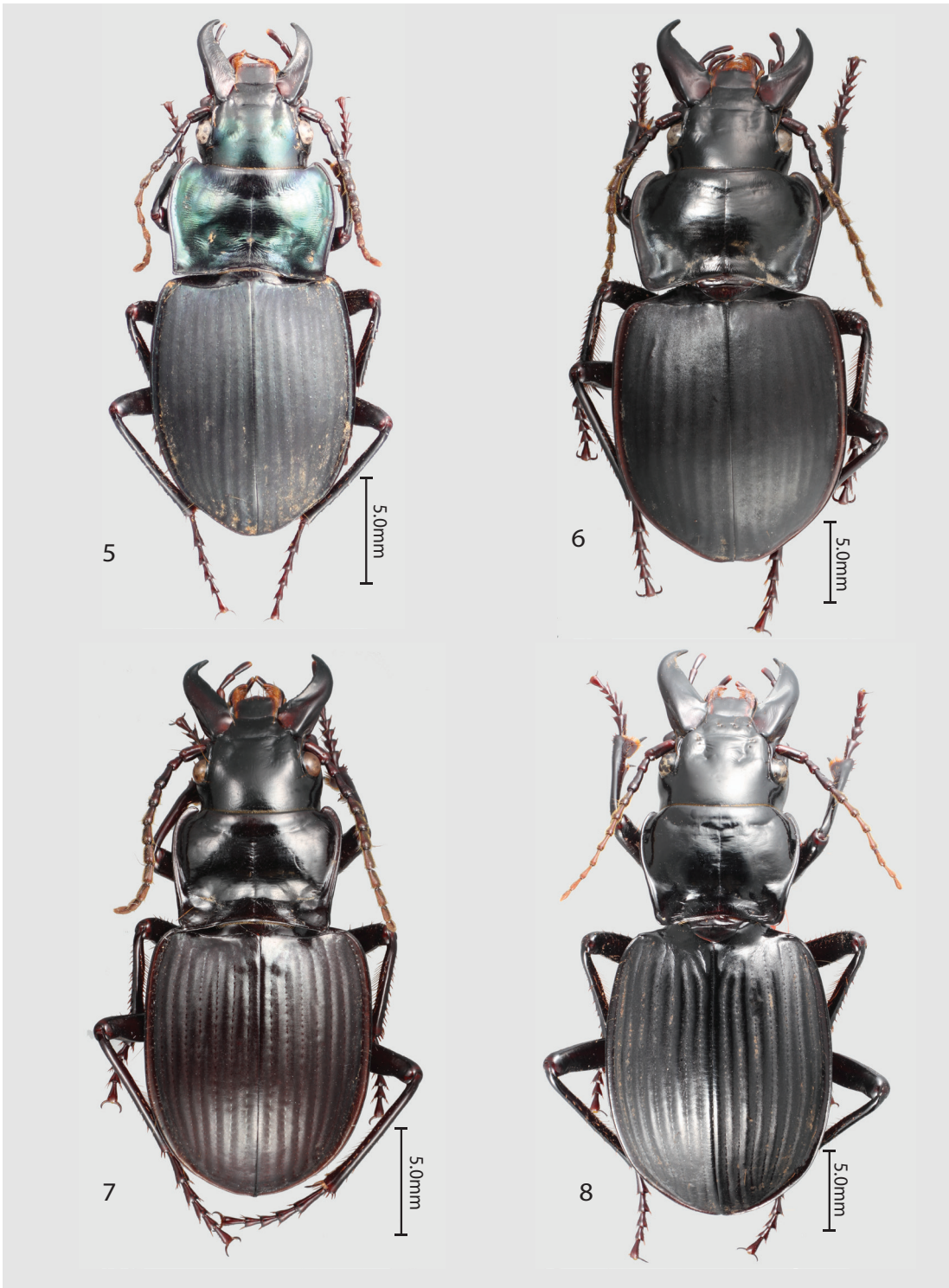


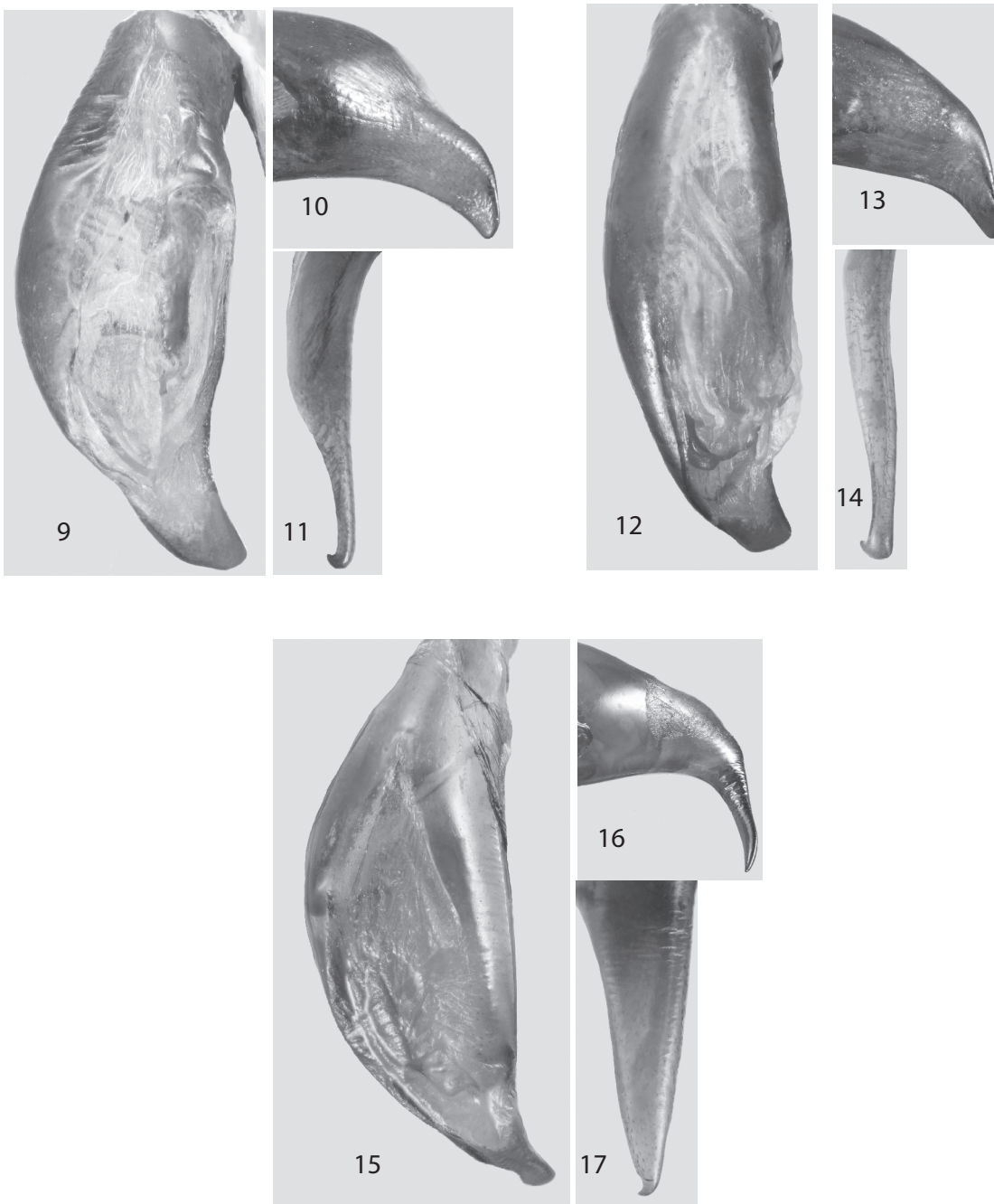
Figure 1. Phylogeny of included taxa based on the Bayesian analyses of a combined data matrix.



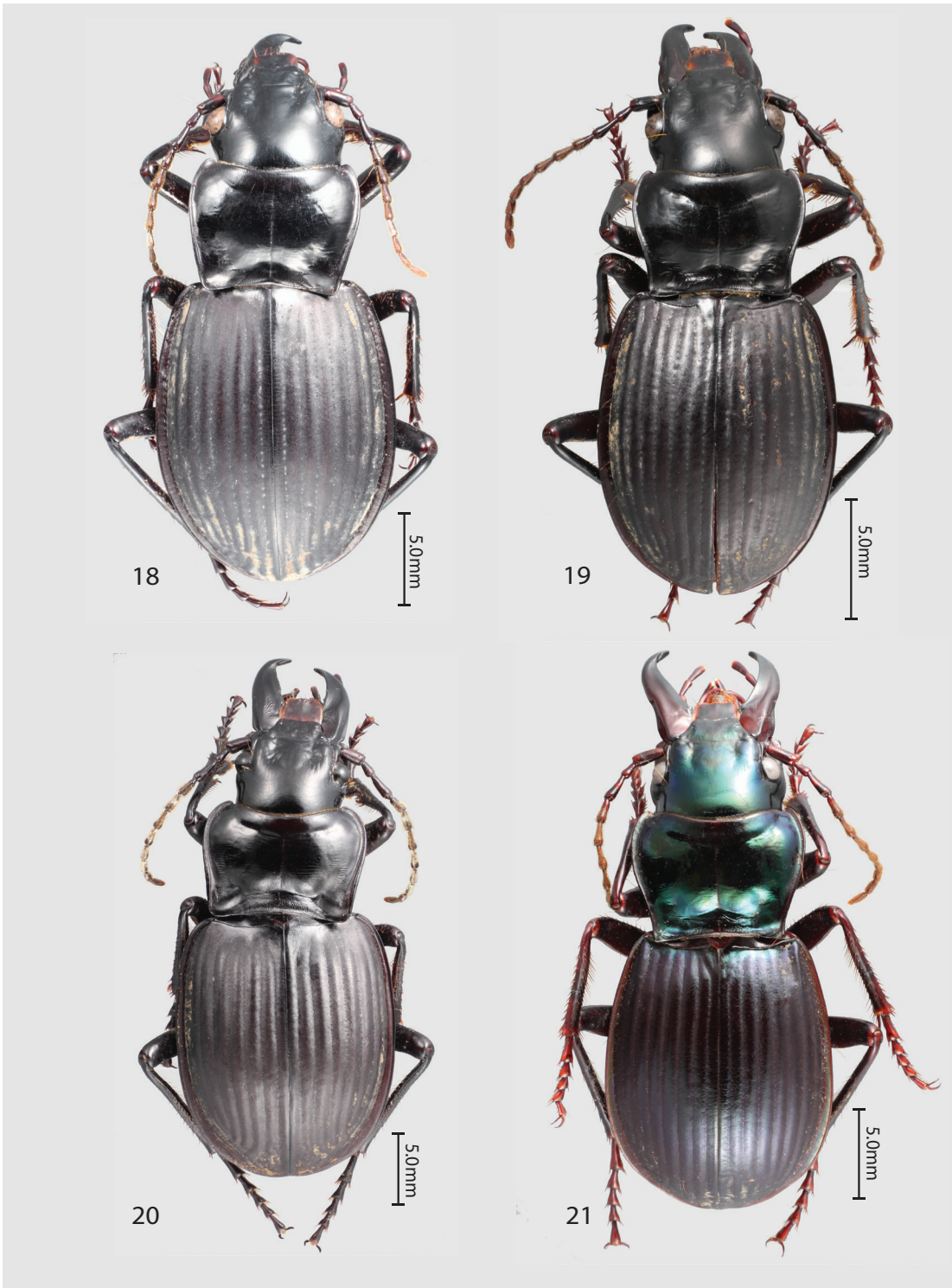
Figures 2-4. *Nuridius* species subtree based on the Bayesian analyses partitioned matrices of partial sequences from three loci: 2. 28S, 3. COI and 4. CAD2.



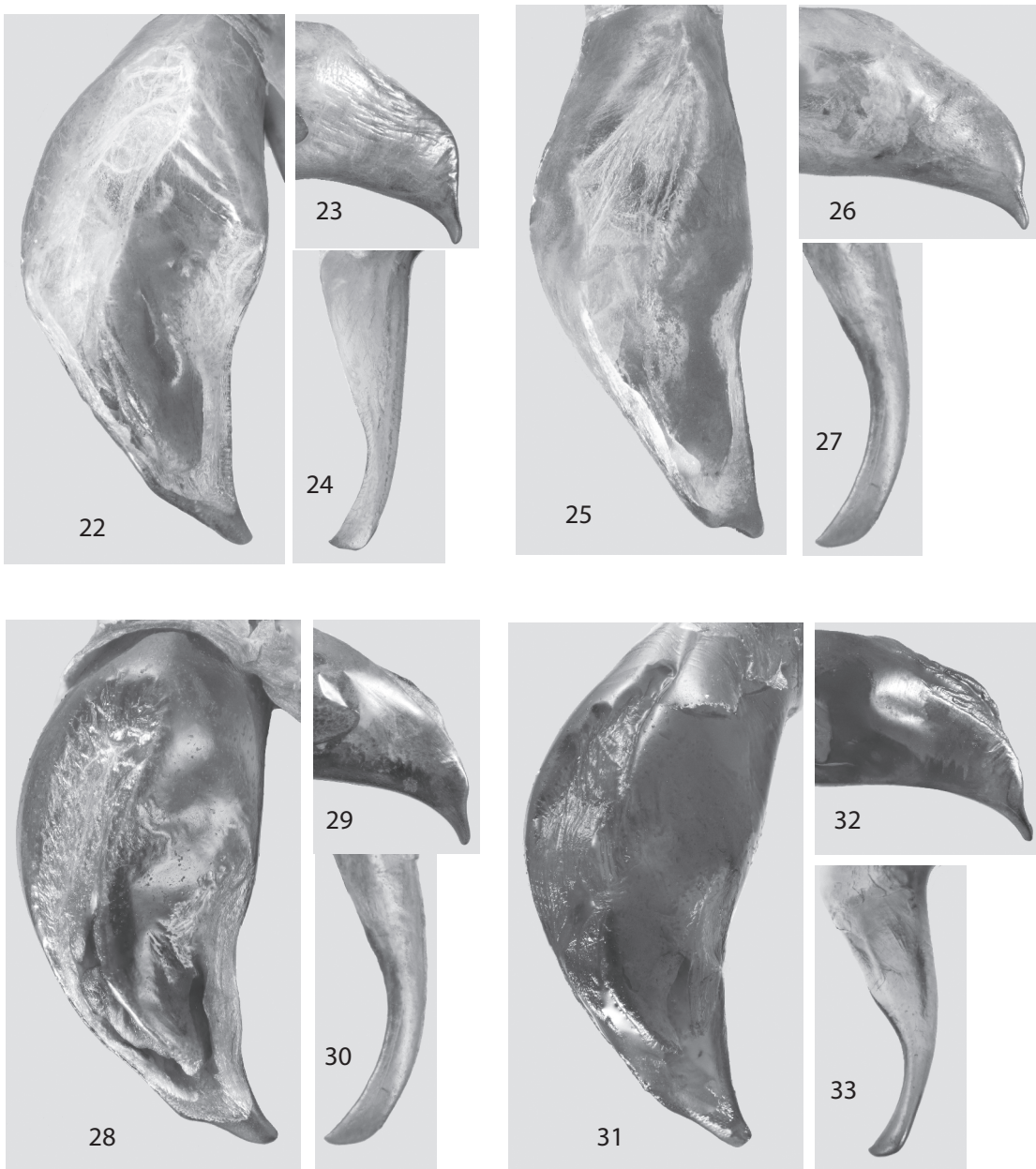
Figures 5-8. Habitus images of **5** *Nuridius frickei* **6** *N. curtus* **7** *N. darlingtoni* and **8** *N. grandis*.



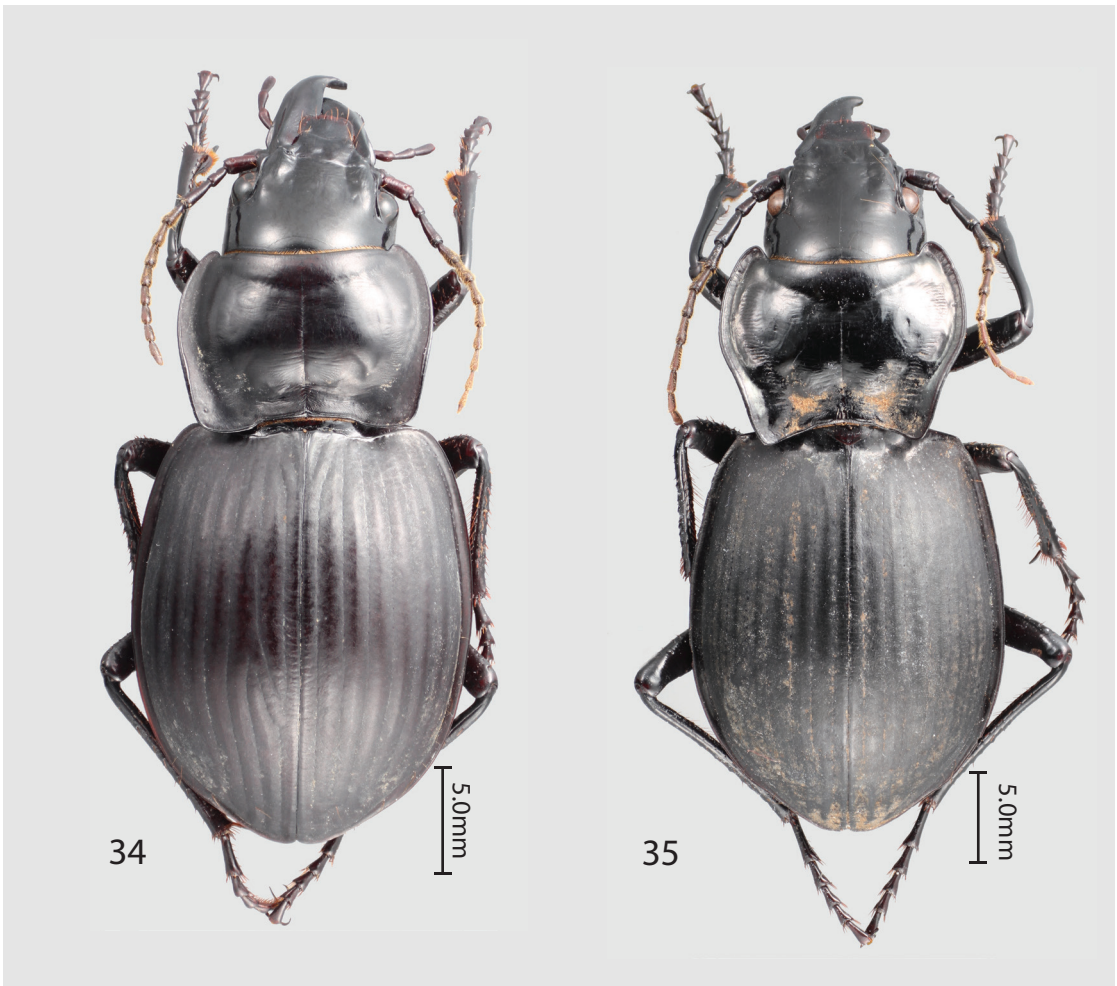
Figures 9-17. Male aedeagus. Clockwise in each set: dorsal, left lateral tip, and apical portion of left paramere. **9–11**. *Nuridius frickei* **12–14** *N. curtus* **15–17** *N. darlingtoni*.



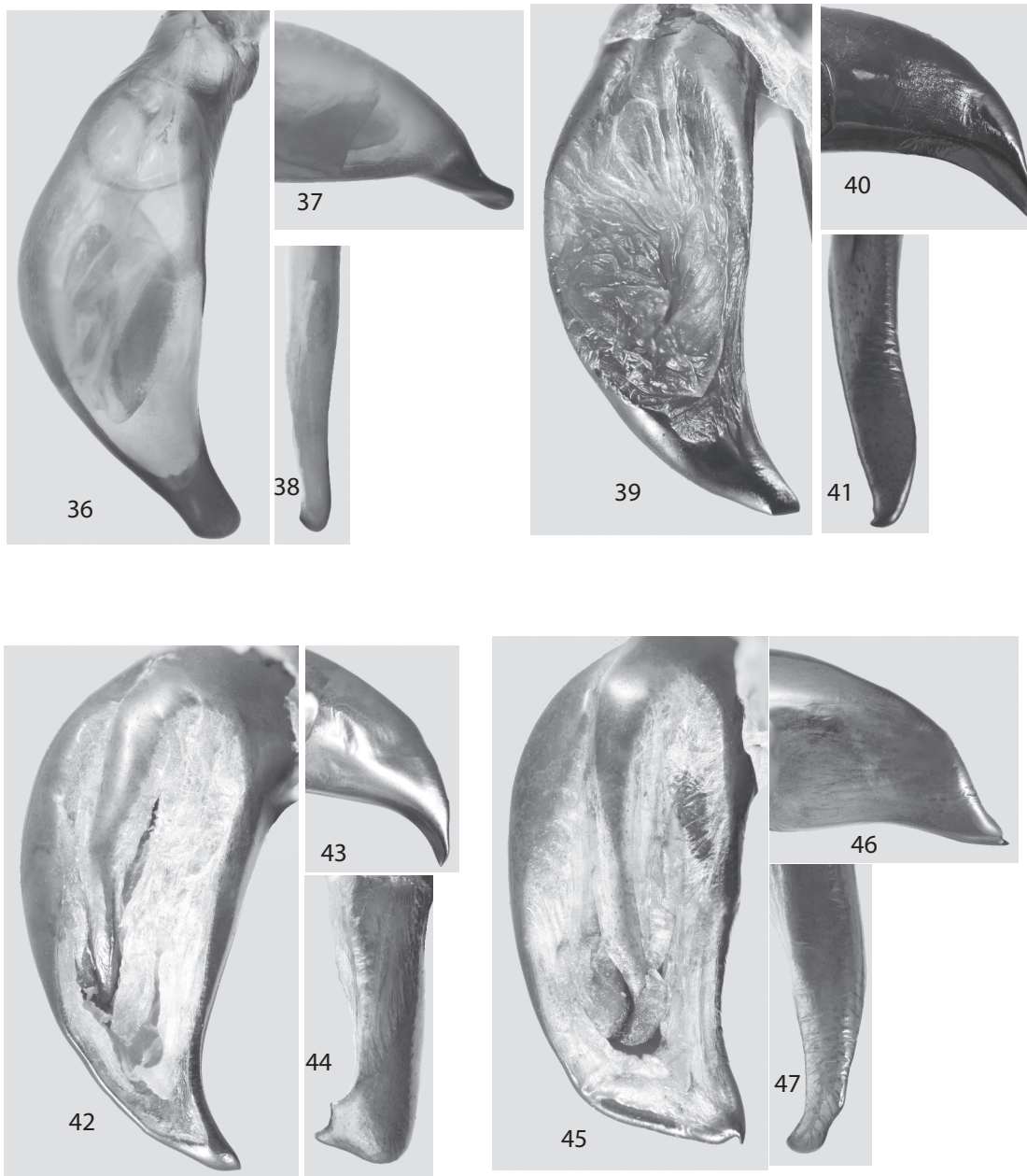
Figures 18-21. Habitus images of **18** *Nuridius fortis* **19** *N. pluto* **20** *N. nox* and **21** *N. medius*.



Figures 22-33. Male aedeagus. Clockwise in each set: dorsal, left lateral tip, and apical portion of left paramere. **22–24** *Nuridius grandis* **25–27** *N. pluto* **28–30** *N. fortis* typical form **31–33** *N. fortis* Wrattens Camp variant form.



Figures 34-35. Habitus images of **34** *Nuridius niger* **35** *N. rex*.



Figures 36-47. Male aedeagus. Clockwise in each set: dorsal, left lateral tip, and apical portion of left paramere. **36–38** *Nuridius nox* **39–41** *N. medius* **42–44** *N. niger* **45–47** *N. rex*.

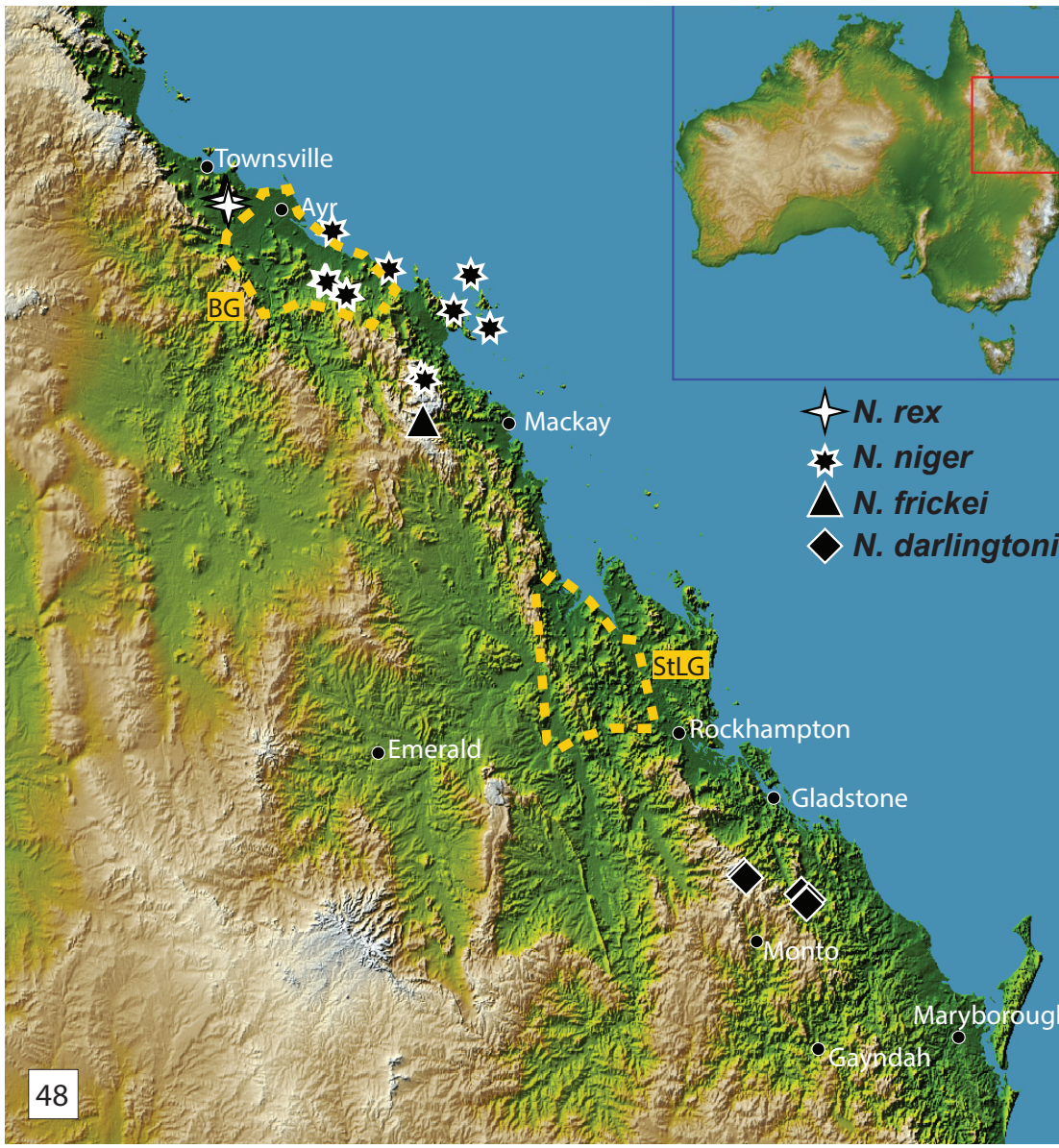


Figure 48. Map showing localities for *Nuridius* species and locations of hypothesized habitat disjunctions of Bryant and Krosch (2016): St Lawrence Gap (StLG) and Burdekin Gap (BG).

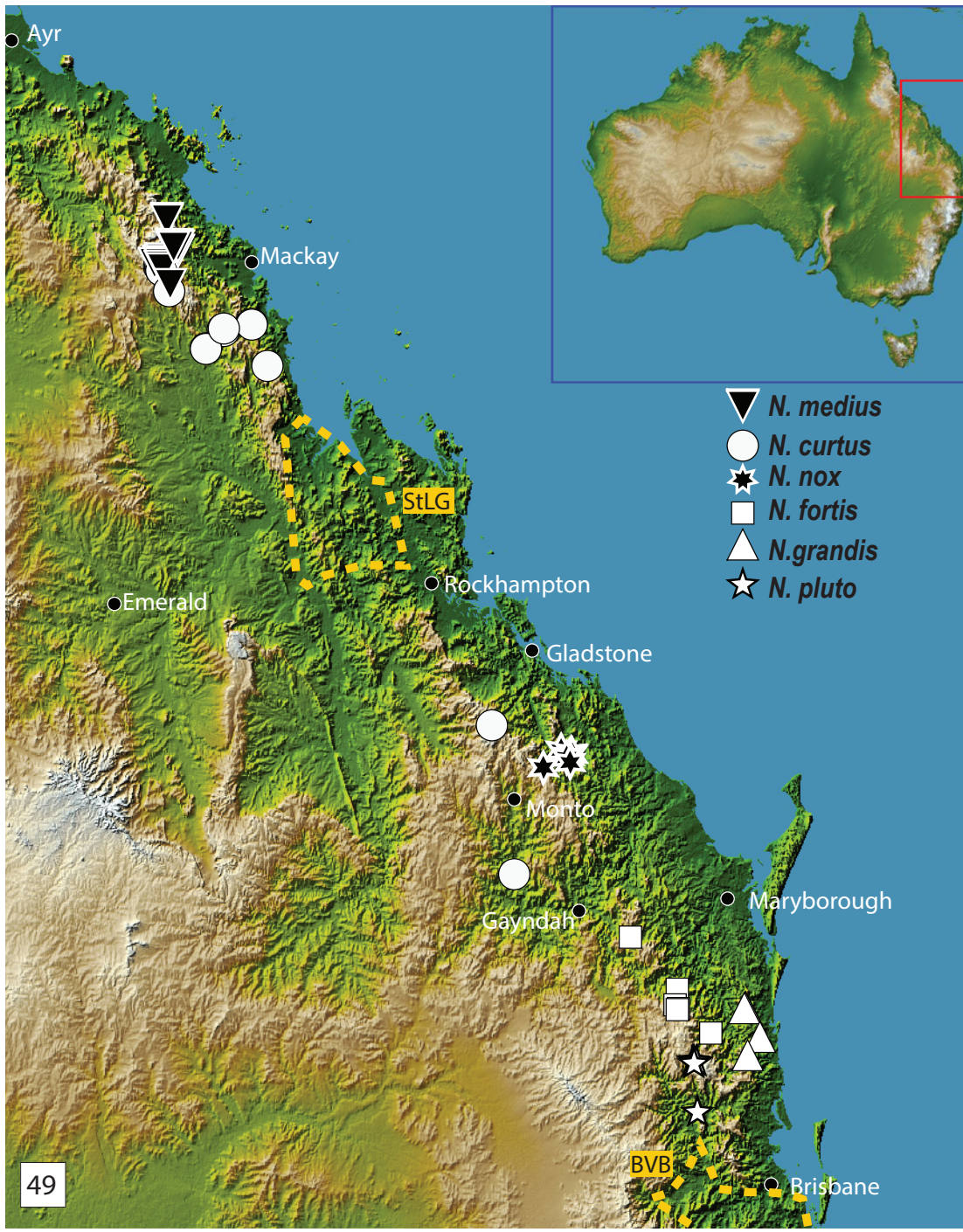
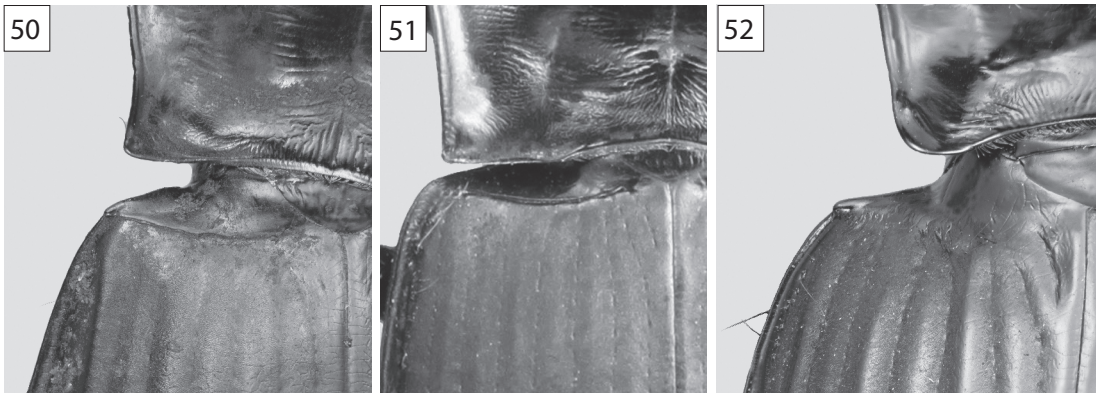
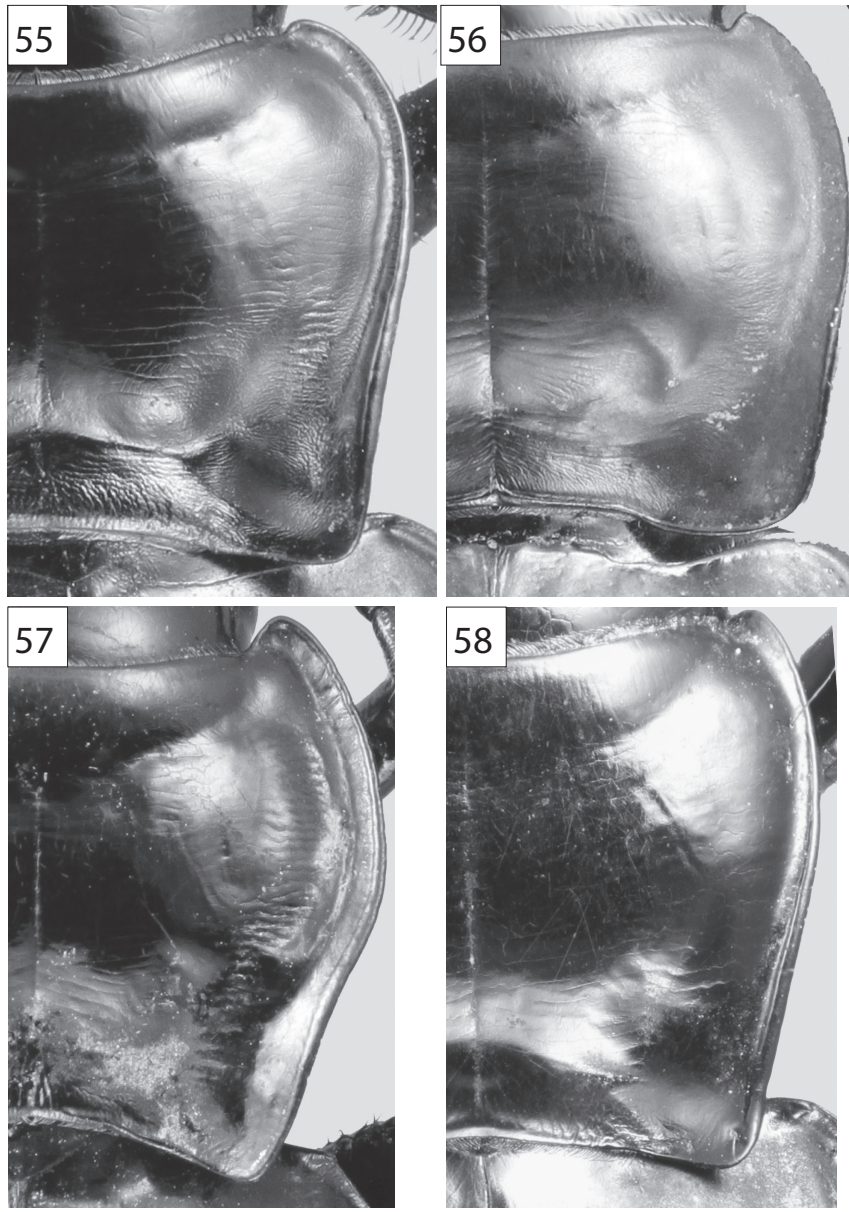


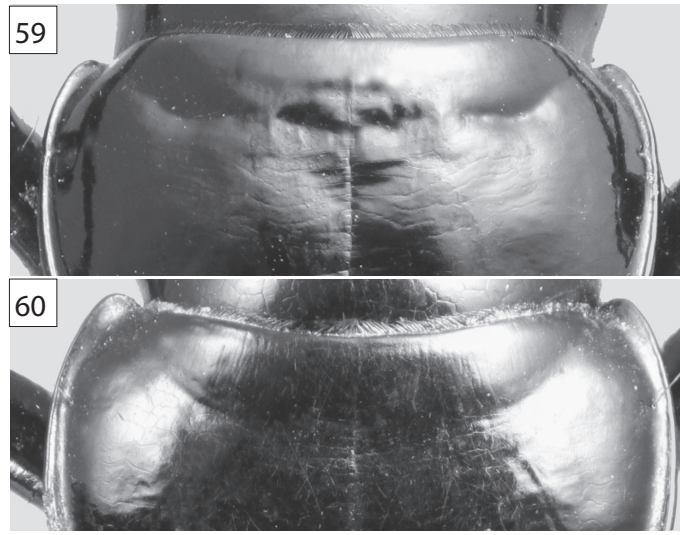
Figure 49. Map showing localities for *Nuridius* species and locations of hypothesized habitat disjunctions of Bryant and Krosch (2016): St Lawrence Gap (StLG) and Brisbane Valley Barrier (BVB).

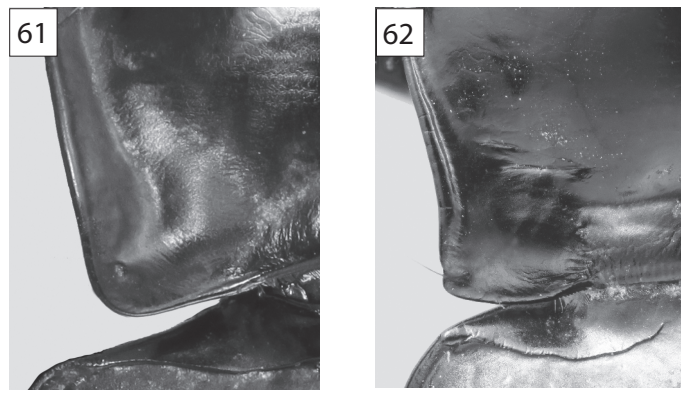


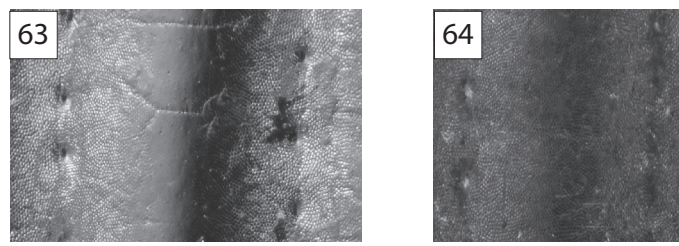
Figures 50-52. Left elytral humeral and pronotal basal angle region of **50** *Nuridius medius* **51** *N. frickei* and **52** *N. grandis*.
Figures 53–54. Dorsal view of right metatibia of **53** *Nuridius niger* and **54** *N. curtus*.



Figures 55-58. Right side of pronotum of **55** *Nuridius nox* **56** *N. niger* **57** *N. rex* **58** *N. fortis*.



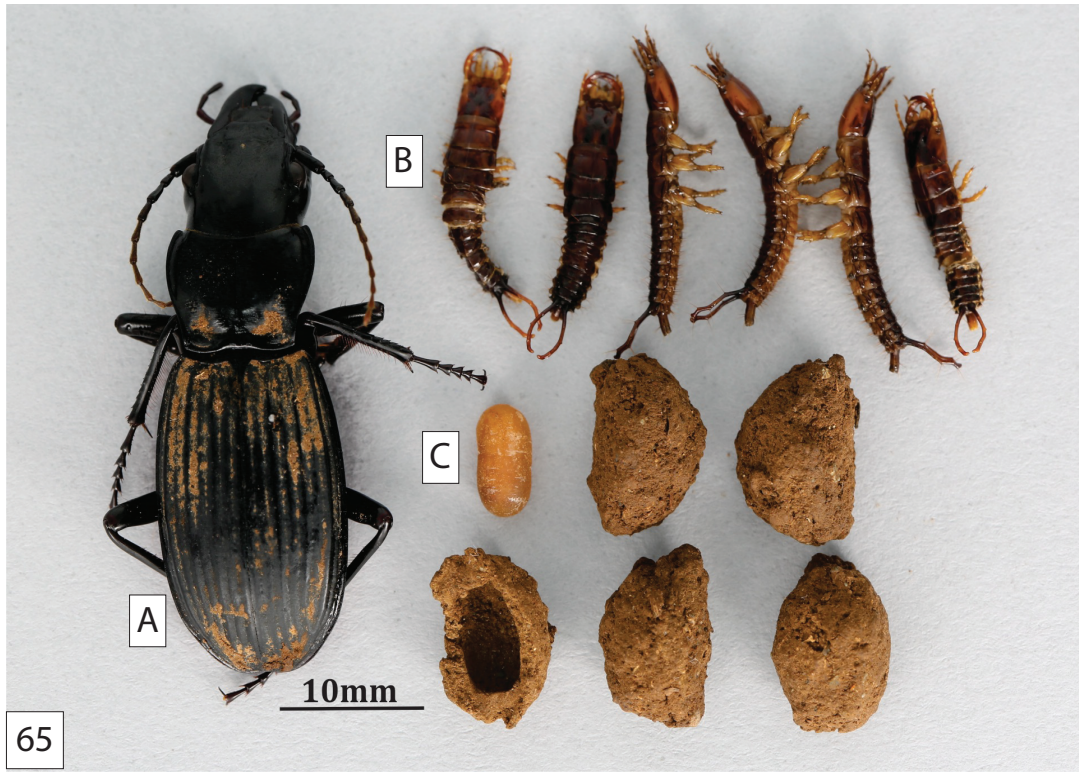




Figures 59–60. Anterior third of the pronotum of **59** *Nuridius grandis* and **60** *N. fortis*.

Figures 61–62. Pronotal left hind angle of **61** *Nuridius curtus* and **62** *N. pluto*.

Figures 63–64. Close-up of elytral discal region of interval 3 of **63** *Nuridius grandis* and **64** *N. fortis*.



Figures 65–66. Life stages typical of *Nurus* and *Nuridius* species represented by *Nurus perater* (Sloane, 1923). **65A** Adult female **B** 1st instar larvae **C** eggs and egg capsules **66** An egg and closeup of the soil capsule halves**.** Photographs by Vivian Sandoval.

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