Morphology of adults and larvae and integrative taxonomy of southern hemisphere genera *Tormus* and *Afrotormus* (Coleoptera: Hydrophilidae)

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Abstract. Adult morphology of the genera *Tormus* Sharp, 1884 and *Afrotormus* Hansen, 1999, endemics of New Zealand and South Africa respectively, is examined and illustrated. The larval morphology of *Tormus* is also reviewed. Both adult and larval morphology supports the hypothesis of close relationship between these genera and *Paracymus* Thomson, 1867 of the tribe Laccobiini as shown by molecular data. The principal adult characters supporting this hypothesis are the presence of an organized stridulatory file on abdominal laterosternite 3 and the morphology of the mesofurca. The larva of *Tormus* is very similar to that of *Paracymus*, with the exception of the absence of the ligula and the presence of dense pubescence on antenna, maxilla and labium which are possible adaptations to a terrestrial lifestyle. The sister relationship of *Tormus* and *Afrotormus* seems quite probable based on several unique or rarely occurring character states shared by both genera, but needs to be confirmed by a formal phylogenetic analysis. *Tormus* inhabits moss on forest floor and *Afrotormus* was collected from under stones, and both genera hence represent previously unrecognized independent ecological transitions to terrestrial environment within Hydrophilidae. Genital morphology of *Tormus* indicated two well-defined groups

treated as species: *Tormus helmsi* Sharp, 1884 (= *Tormus nitidus* Broun, 1893a, syn. nov., = *Stygnohydrus nitidus* Broun, 1893b, syn. nov., = *Stygnohydrus femoralis* Broun, 1910, syn. nov. = *Stygnohydrus basalis* Orchymont, 1937, syn. nov.) and *Tormus posticalis* (Broun, 1917), stat. restit. Genetic data from *cox1* mitochondrial gene indicated five haplotype lineages, of which the Fiordland group is equivalent to *T. posticalis*. The more derived *T. helmsi* clade, distributed west and north of the Alpine Fault, consists of four haplotype groups that may be cryptic species with variable male genitalia. Though based on a single gene and limited sampling, our data suggest a South Island origin for *Tormus*. Evidence for isolation by distance was weak and while haplotype lineages of *T. helmsi* form a grade south to north with a monophyletic haplogroup in the North Island, environmental barriers may explain the population structure.

Introduction

The genus *Tormus* Sharp, 1884 was described and recognized as a 'peculiar endemic New Zealand form' by SHARP (1884), based on a single specimen sent to him by a New Zealand entomologist Richard Helms. First thought to be related to the Neotropical berosine genus *Derallus* Sharp, 1882 (SHARP 1884, BROUN 1893a), *Tormus* was later placed with other New Zealand endemic genera in either the Hydrobiini (ZAITZEV 1908) or Rygmodini (ORCHYMONT 1919, KNISCH 1924). In his generic revision of the Hydrophilidae, HANSEN (1991) synonymized another New Zealand endemic genus *Stygnohydrus* Broun, 1893b with *Tormus* and assigned it to the newly erected tribe Tormissini with three other New Zealand endemic genera (*Exydrus* Broun, 1886, *Hydrostygnus* Sharp, 1884, *Tormissus* Broun, 1893). Later, HANSEN (1997) examined the types of all five species of *Tormus* and *Stygnohydrus* described from New Zealand by SHARP (1844) and BROUN (1893b,c, 1910, 1917), and recognized three as valid taxa. Still, information regarding *Tormus* has remained limited, as the types (i.e., the only available specimens) were never dissected and the only available biological data were those adopted from the original descriptions.

Surprisingly, three specimens strongly resembling *Tormus* were found by HANSEN (1999a) in material of hydrophilids from the Republic of South Africa. They were assigned to a new genus, *Afrotormus* Hansen, 1999, and also placed in the tribe Tormissini.

A preliminary study of *Tormus* morphology revealed that it differs from all remaining New Zealand genera of Tormissini indicating that its tribal placement is questionable and systematic position unclear. A molecular study by SHORT & FIKÁČEK (in press), places *Tormus* near *Paracymus* Thomson, 1867 and distant from other endemic New Zealand genera. The goal of this paper is to provide detailed morphological descriptions of adults and larvae of *Tormus* which compliment larger molecular phylogenetic studies of the family (SHORT & FIKÁČEK in press) and the sphaeridiine lineage, and a revision of the New Zealand fauna

(see also Fikáček et al. 2012a). We accumulated nearly 600 specimens of *Tormus* including the DNA-grade specimens, which allowed us to address the complex species level taxonomy of the genus and provide the first insight into the intraspecific genetic diversity of the recognized species. In addition, we reexamined the known specimens of the South African genus *Afrotormus* in order to confirm its close relationship to *Tormus* as hypothesized by Hansen (1999a).

Material and methods

Depository of examined specimens. Voucher specimens are deposited in the following collections:

ANIC   Australian National Insect Collection, Canberra, Australia (A. Ślipiński);
BMNH   The Natural History Museum, London, United Kingdom (M. Barclay);
DBCP   David T. Bilton collection, Plymouth, United Kingdom;
FMNH   Field Museum of Natural History, Chicago, U.S.A. (A. Newton, M. Thayer);
LUNZ   Entomology Research Museum, Lincoln University, Christchurch, New Zealand (J. Marris);
NHMW   Naturhistorisches Museum, Wien, Austria (M. Jäch);
NMPC   National Museum, Prague, Czech Republic (M. Fikáček);
NZAC   New Zealand Arthropod Collection, Auckland, New Zealand (R. Leschen);
JNIC   John T. Nunn collection, Dunedin, New Zealand;
SEMC   Natural History Museum, University of Kansas, Lawrence, U.S.A. (A. Short);
YMC   Yûsuke Minoshina collection, Kitakyushu, Fukuoka, Japan;
TMSA   Ditsong Museum of South Africa (formerly Transvaal Museum), Pretoria, Republic of South Africa (R. Müller);
ZMUC   Zoological Museum, University of Copenhagen, Denmark (A. Solodovnikov).

Adult morphology and taxonomy. We have examined the type specimens of all five described species of *Tormus* and both described species of *Afrotormus*. In addition, 574 non-type specimens of *Tormus* from 128 localities and a single non-type specimen of *Afrotormus* were examined for this study. The male genitalia were examined for at least one specimen from each locality (except the localities with females only). The study on external morphology is based on dry mounted specimens examined using an Olympus SZ61 binocular microscope, slide mounted specimens examined using an Olympus BX41 compound microscope (mounted in Euparal and deposited in NMPC) and gold-coated specimens examined by JEOL 6380 LV electron microscope in the Laboratory of Electron Microscopy, Faculty of Science, Charles University, Prague (for *Tormus* specimens) and non-coated specimens examined by Hitachi S-3700N environmental electron microscope at the Department of Entomology, National Museum in Prague (for *Afrotormus* specimens). Habitus photographs were taken using a Canon MP-E 65 mm macro lens attached to a Canon EOS 550D camera and stacked from multiple layers using the Helicon Focus 5.1 Pro software. Drawings were prepared using a drawing tube attached to the above compound microscope. Examined specimens were databased using Mantis 2.0 (Nasrecki 2008), the faunistic districts and their abbreviations used in lists of the examined material and figures are adopted from Crosby et al. (1998).

Morphological terminology largely follows Hansen (1991), Komarek (2004) and Lawrence et al. (2010). Comparisons with other genera are based on the material deposited in the collections of the National Museum, Prague, Czech Republic (NMPC). Taxonomy and nomenclature follow Hansen (1991, 1999b) and Short & Fikáček (2011).

Larval morphology. The methods largely follow those used by MINOSHIMA & HAYASHI (2011a). The examined material is deposited in YMC, NMPC and FMNH. Larvae were preserved in vials with 99.5% ethanol or mounted on HS-slide (Higgins-Shirayama slide; SHIRAYAMA et al. 1993) (Kanto Rika Co., Ltd., Japan) with Euparal (Waldeck GmbH & Co. KG, Germany). Observations were carried out using an Olympus SZX12 binocular microscope, and an Olympus BX40 and Zeiss Axiophot compound microscopes. Photographs were taken using a Pentax K-5 digital camera attached to an Olympus SZX12 with a MeCan NY-1S digital SLR microscope adapter (MeCan Imaging Inc., Japan), and subsequently adapted in Adobe Photoshop Lightroom 4 and Photoshop CS5. Composite images were created using the focus stacking software CombineZP (HADLEY 2010).

Morphological terminology follows ARCHANGELSKY (1997) and MINOSHIMA & HAYASHI (2011a) with the exception of the antennal segments, for which we follow BEUTEL (1999) and FIKÁČEK et al. (2008); for the chaetotaxy of the larval head we refer to FIKÁČEK et al. (2008) and BYTTEBIER & TORRES (2009). Following abbreviations are used: **AN** – antenna; **FR** – frontale; **gAN** – group of antennal sensilla; **gAPP** – group of sensilla on inner appendage of maxilla; **gFR** – group of sensilla on frontale; **gLA** – group of sensilla on labium; **gMX** – group of sensilla on maxilla; **L1, L2, L3** – first, second and third larval instar; **LA** – labium; **MN** – mandible; **MX** – maxilla; **PA** – parietale; **SE** – sensorium; ■ – additional sensillum (see FIKÁČEK et al. 2008).

DNA sequencing. We used mtDNA sequences to confirm the identity of the *Tormus* larvae used for the morphological description as well as an additional source of information to understand the complex taxonomy of the genus. Specimens were collected from 13 localities throughout the known distribution of the genus in the North and South Islands of New Zealand. From each locality, a single adult specimen was used for the analysis (with the exception of Mt. Te Aroha from which the supposed larva was also analyzed). We used *Paracymus pygmaeus* (MacLeay, 1871) as an outgroup as the genus *Paracymus* Thomson, 1867 was recognized as closely related to *Tormus* by SHORT & FIKÁČEK (in press). Genomic DNA from whole specimens stored in 96% ethanol was extracted non-destructively using a Qiagen Blood and Tissue Kit, following standard protocols. We used a partial sequence of approximately 800 bp of the protein coding *cox1* gene that amplified using the primers stev_jerryF (5′-CAACATYTATTYTGATTYTTTGG-3′) and stev_patR (5′-GCACTAWT-CTGCCATATTAGA-3′). In specimens D2, D4 and D5, the sequence was amplified in two fragments, using stev_jerryF plus Tom1/R (5′-GCACTAWTCTGCCATATTAGA-3′) and Chy1/F (5′-TWGTAGCCCAYTTTCATTAYGT-3′) plus stev_patR primers. The PCR conditions used are as follows: initialization at 94°C for 3 min, denaturation at 94°C for 30 s, annealing at 47°C for 30 s, elongation at 72°C for 1 min (last three steps for 40 cycles), final elongation at 72°C for 10 min. Sequencing was done using sequencer 3130 and 3130xl Genetic Analyzer (Applied Biosystems) with BigDye®Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). Bidirectional sequences were aligned to form contigs and edited using BioEdit 7.1.9 software (HALL 1999) and were submitted to the EMBL gene database under accession numbers listed in Table 1. All voucher specimens are deposited in NMPC. We unsuccessfully attempted to isolate and amplify DNA sequences from the only available non-type specimen of *Afrotormus*.

Table 1. Data of the sequenced specimens of *Tormus* Sharp, 1884 and *Paracymus* Thomson, 1867 (as outgroup). Abbreviations of New Zealand and Australian districts: BP – Bay of Plenty, BR – Buller, FD – Fiordland, NN – Nelson, QLD – Queensland, TK – Taranaki, WD – Westland. Abbreviations of stages: A – adult, L – larva.

Code	Species (stage)	Lat / Long	Locality (event ID)	Accession #
COL127	*P. pygmaeus* (A)	26.30°S 147.08°E	Australia: QLD: Tregole NP, S of Morven day stop area	KC786888
COL1769	*T. helmsi* (A)	44.0133°S 169.0486°E	New Zealand: WD: Pleasant Flat (RL1066)	KC786889
COL1770	*T. posticalis* (A)	43.9683°S 168.6083°E	New Zealand: WD: Wharekai Te Kau walk, Jackson Bay (RL1293)	KC786890
COL1771	*T. posticalis* (A)	45.71055°S 166.6506°E	New Zealand: FD: Dusky Sound, Resolution Island, NE side of Acheron Passage (SAF044)	KC786894
COL1802	*T. helmsi* (A)	43.4383°S 169.9666°E	New Zealand: WD: Matheson Lake Track 5 km NWW of Fox Glacier village (RL1318)	KC786891
COL1805	*T. posticalis* (A)	45.7376°S 166.6087°E	New Zealand: FD: Dusky Sound, Resolution Island, 40-65 m a.s.l. (SAF048)	KC786895
COL1855	*T. helmsi* (A)	41.5843°S 172.2077°E	New Zealand: NN: 1000 Acre Plateau site 1 (TB505)	KC786892
D2	*T. posticalis* (A)	44.6650°S 167.9785°E	New Zealand: FD: Fiordland NP, Milford Sound Rd., Tutoko Track (FMHD#2005-86, ANMT site 1168)	KC786898
D4	*T. helmsi* (L)	37.5276°S 175.7447°E	New Zealand: BP: Kaimai-Mamaku Forest Park, Mt. Te Aroha, upper end Tui Mine Track near summit road (FMHD#2005-021, ANMT site 1145)	KC786897
D5	*T. helmsi* (A)	as D4	same as D4	KC786896
MF498	*T. helmsi* (A)	44.1°S 169.6083°E	New Zealand: WD: Mt. Aspiring NP, Cross Creek at Haast Pass Hwy., 18.3 km NNE of Makaroa (NZ51)	KC786882
MF499	*T. helmsi* (A)	41.135°S 172.1916°E	New Zealand: NN: Kahurangi NP, Oparara Arches 14.8 km NNE of Karamea, end of McCallum Mill Rd. at Box Canyon Cave (NZ37)	KC786883
MF500	*T. helmsi* (A)	39.2416°S 174.1133°E	New Zealand: TK: Mt. Egmont NP, Mangaoraka Walk at Egmont Road (NZ29)	KC786884
MF501	*T. helmsi* (A)	41.6033°S 171.915°E	New Zealand: NN: Charming Creek Walkway at Watsons Mill 3.3 km E of Hector (NZ35)	KC786885
MF503	*T. helmsi* (A)	42.1033°S 171.4016°E	New Zealand: BR: Paparoa NP, beginning of Cave Creek Track close to Bullock Ck. Road 5.6 km NEE of Punakaiki (NZ34)	KC786893
MF506	*T. helmsi* (A)	43.2333°S 170.1416°E	New Zealand: WD: along Three Mile Lagoon Track 1.8–3.0 km SSW of Okarito (NZ43)	KC786886
MF509	*T. helmsi* (A)	41.425°S 172.1016°E	New Zealand: NN: Hanlon Lake 5.2 km S of Te Namu at Karamea Hwy. (NZ39)	KC786887

Genetic diversity and phylogenetic analyses. Sequences were edited and aligned using the ClustalW algorithm (THOMSON et al. 1994) in BioEdit software. The best-fit model of molecular evolution for the aligned dataset was chosen using jModelTest 2.1.2 (DARRIBA et al. 2012). Phylogenetic trees were constructed under Bayesian inference with MrBayes 3.2.1 (HUELSENBECK & RONQUIST 2001), using four chains of 5,000,000 generations and sampling

the chain every 100 generations. Stationarity in MCM chains was determined using Tracer 1.5.0 (RAMBAUT & DRUMMOND 2007), and burn-in was set appropriately. Maximum likelihood analysis was conducted using RAxMLgui software (SILVESTRO & MICHALAK 2012) using the same evolutionary model as in the Bayesian analysis and running the ML+thorough bootstrap analysis with 50 runs of 1000 replicates each. As only a single specimen was sampled for each population, only a basic measurement of genetic divergence between the haplotypes and the groups of haplotypes estimated using the maximum composite likelihood model as implemented in MEGA5.1 software (TAMURA et al. 2011). Species delimitation statistics for groups of haplotypes was performed using the Species delimitation plugin (MASTERS et al. 2011) in the Geneious software package (Biomatters Ltd.). Haplotype network was constructed using Network 4.6 software (Fluxus Technology Ltd.) using the median joining (BANDELT et al. 1995) followed by maximum parsimony (POLZIN & DANESCHMAND 2003) for calculations of the network. Evidence for isolation by distance in the genetic structure of *Tormus* was examined using Isolation by Distance Web Service (JENSEN et al. 2005). A matrix of geographic distances was constructed from GPS data using Geographic distance matrix generator (ERSTS 2013). Mantel tests were used to test the correlation between genetic and geographical distance matrices and partial Mantel tests (genetics vs. geography with cluster membership as covariate, and genetics vs. cluster membership with geography as covariate, see MIERMANS 2012 for details) were used to test for possible biases associated with hierarchical structure of the data. Two parallel analyses were performed, one containing all *Tormus* populations, the other including only the populations assigned to *T. helmsi*.

Results

Tormus Sharp, 1884

Tormus Sharp, 1884: 474. Type species: *Tormus helmsi* Sharp, 1884 (by monotypy).

Tormus: BROUN (1893a: 1018, diagnosis); ZAITZEV (1908: 376, catalogue, in Hydrobiina); ORCHYMONT (1919: 106, transferred to Rygmodini); KNISCH (1924: 106, in Rygmodini); HANSEN (1991: 182, redescription, transferred to Tormissini); HANSEN (1997: 359, key to species); HANSEN (1999b: 237, catalogue); LESCHEN et al. (2003: 18, list of New Zealand genera); SHORT & FIKÁČEK (2011: 85, list of genera).

Stygnohydrus Broun, 1893b: 1018. Type species: *Stygnohydrus nitidus* Broun, 1893b (by monotypy).

Stygnohydrus: ZAITZEV (1908: 376, catalogue, in Hydrobiina); ORCHYMONT (1919: 106, transferred to Rygmodini); KNISCH (1924: 106, in Rygmodini); HANSEN (1991: 183, synonymized with *Tormus*).

Diagnosis. *Adult.* Body highly convex, compressed from sides (Fig. 1A); dorsal coloration black, without metallic reflections; clypeus without anterolateral bead (Fig. 4A); clypeus with wide anterior emargination exposing the membrane between clypeus and labrum (Fig. 4A); labrum completely exposed in dorsal view; eyes not protruding; antenna with 9 antennomeres (Fig. 3F); mandibular apex with two apical teeth (Fig. 3C); prosternum extremely short in front of procoxae, bearing longitudinal carina mesally (Fig. 4H); mesoventrite divided from mesanepisterna by distinct anapleural suture (Fig. 5A); anteromedian portion of mesoventrite with a deep pit (Figs 5B–C); posteromedian portion of mesoventrite with narrow high triangular projection (Fig. 5B); elytron with serial punctures present only posterolaterally (Figs 1A, 5K); coxae each with several strong spines ventrally (Figs 4F, 5C, 5E, 5H); femora without
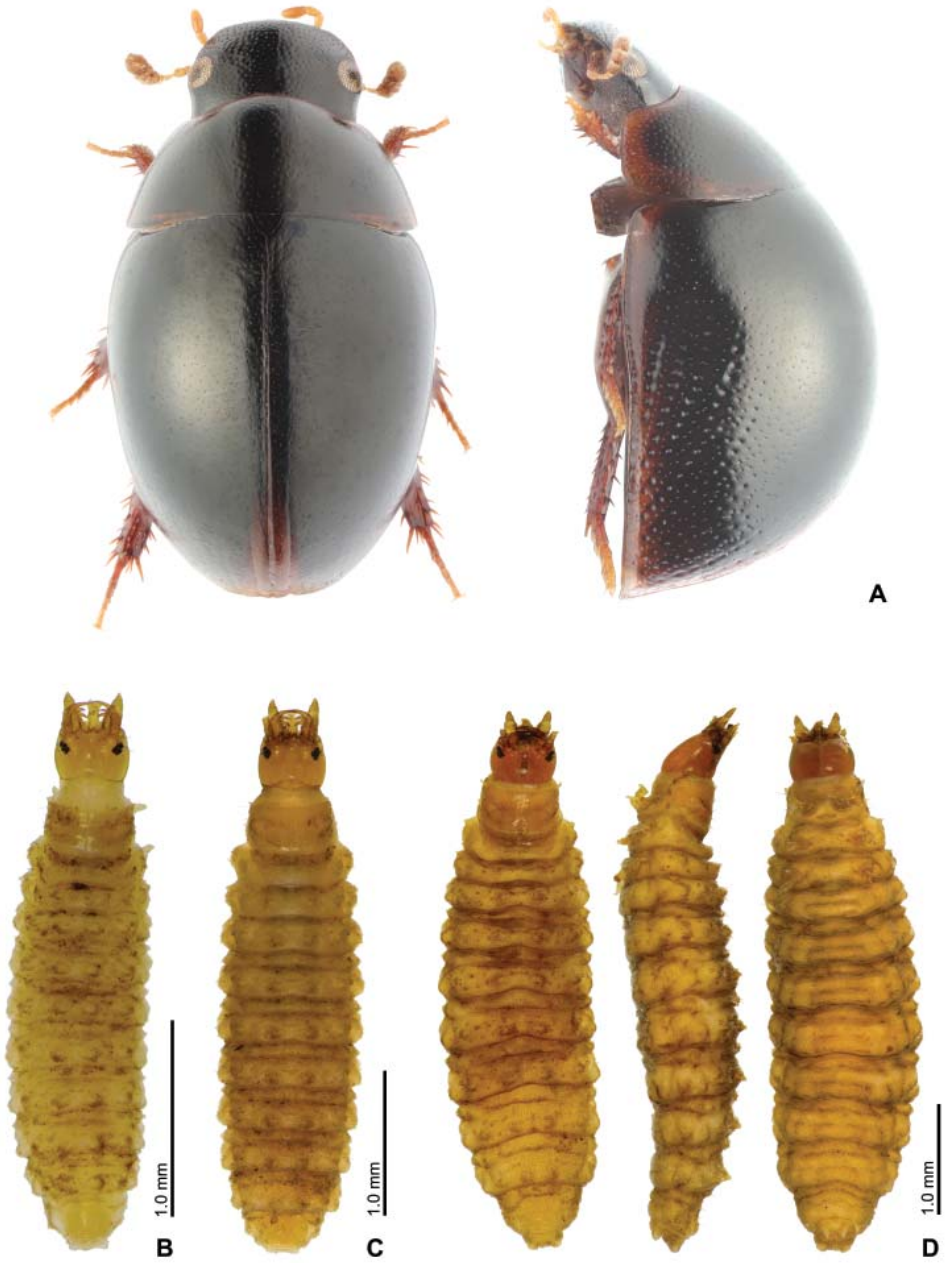
Fig. 1. Habitus of *Tormus helmsi* Sharp, 1884. A – adult; B–D – larva, first (B), second (C), and third (D) instar.
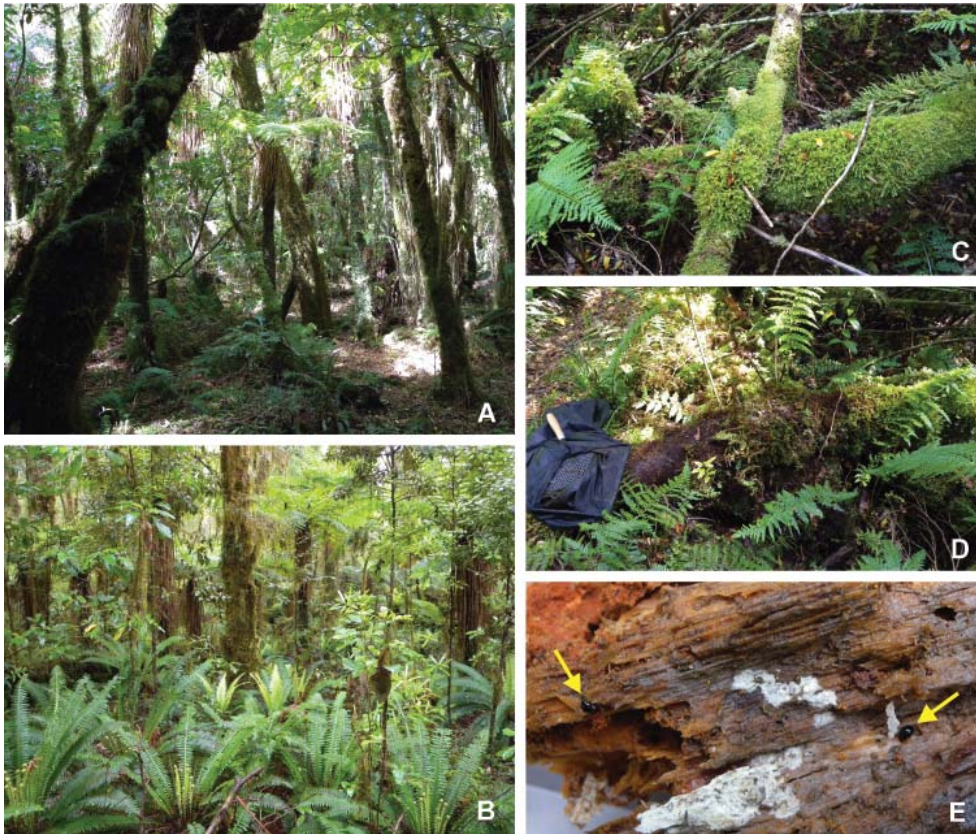
Fig. 2. Habitat of *Tormus* species. A – lower montane forest in Mt. Egmont National Park along Mangaoraka Walk, 600 m a.s.l. (Taranaki); B – *Nothofagus*-podocarp forest with rich fern and tree fern understory at Oparara Arches, 230 m a.s.l. (Nelson); C–D – moss on fallen decaying logs (Mt. Egmont NP, Mangaoraka Walk) in which numerous *Tormus* were found by moss sifting (part of the moss was already collected and sifted in Fig. D); E – the underside of a wet decaying log taken from mossy forest ground at Three Mile Lagoon Track, ca. 100 m a.s.l. (Westland), two specimens of *Tormus* are marked by arrows. All photos taken in December 2012 by M. Fikáček.

dense pubescence even basally; basal metatarsomere much shorter than metatarsomere 2 (Fig. 7C); abdomen with five ventrites; basal abdominal ventrite not carinate mesally (Fig. 6A); abdominal laterosternite 3 with organized stridulatory file (Fig. 6C); abdominal apex without apical emargination.

By the dark dorsal coloration, highly convex body and partly reduced elytral series, *Tormus* resembles some genera of the tribes Chaetarthriini (*Amphiops* Erichson, 1843 and *Micramphiops* Short, 2009: differs by completely divided eyes; *Chaetarthria* Stephens, 1835: differs by the presence of series of long setae over the abdominal ventrite 1; *Guyanobius* Spangler, 1986: differ by concealed labrum and femora with dense pubescence basally), Berosini (they

differ by 8-segmented antennae and abdominal sternite 7 which is concealed within abdomen or visible as fifth abdominal ventrite with a semicircular or rectangular emargination), Anacaenini (some *Anacaena* Thomson, 1859: differ by prosternum without median carina and femora with basal dense pubescence) and Coelostomatini (differ in entire clypeus). It may be easily distinguished from all other New Zealand hydrophilids by the combination of highly convex and laterally compressed body, black dorsal coloration, prosternum very short in front of procoxae and carinate mesally, 9-segmented antennae and abdominal ventrite 1 ecarinate mesally.

Larva. Head ca. as long as wide (Fig. 14A), stemmata very distinct and clearly divided from each other (Fig. 10A); nasale slightly asymmetrical, bearing three teeth of which two right ones are smaller than the left one (Figs 10C, 14B); epistomal lobes reaching ca. as far as nasale, nearly symmetrical; frontal lines reaching posterior margin of head (Fig. 10A, 14A), coronal line absent; submentum clearly divided from head capsule; mandibles symmetrical, each with three inner teeth (Figs 11C–D, 13C–D, 15C–D); mesal portions of antennae, maxillae and dorsal face of labium with dense and long pubescence (Figs 11, 13, 15); antennae short and stout; antennal sensorium as long as antennomere 3 (e.g., Figs 15A–B); stipes with five strong setae (MX7–11) on inner face (Fig. 11E); maxillary palpus ca. as long as stipes; inner appendage of maxillary palpomere 1 present and well sclerotized; ligula absent (Figs 11G–I, 13G–I, 15G–I); proscutum without bulges or protruding lobes (Figs 1B–D); anterior margin of proscutum with dense row of setae (Fig. 14C); meso- and metathorax with small tergites only (Fig. 14F); prosternite in form of a pair of separated transverse sclerites (Figs 12A, 14E); legs 5-segmented but short (Fig. 12B), barely visible in dorsal view; abdomen with indistinct lateral but quite distinct dorsal lobes (Figs 1B–D); median and lateral lobes of spiracular atrium fused into one lobe, bifurcate.

The larvae of *Tormus* are most similar to those of *Paracymus* (based in mandibles with three inner teeth, antennal sensorium as long as antennomere 3, frontal lines reaching posterior margin of the head, rather long maxillary palpomere 1, slightly asymmetrical nasale with distinct large teeth and rather large nearly symmetrical epistomal lobes), but differ from them by the absence of ligula, densely pubescent mouthparts and nasale with three teeth only. By the combination of the reduced ligula and frontal sulci reaching posterior margin of the head, *Tormus* may also resemble the larvae of *Berosus* Leach, 1817, *Laccobius* Erichson, 1837 and *Oocyclus* Sharp, 1882 (all with asymmetrical mandibles and left mandible with specialized comb-like structures and with highly projecting left epistomal lobe bearing a series of many stout setae on anterior margin, *Berosus* with tracheal gills on lateral sides of abdomen and reduced stigmatic atrium, and *Laccobius* and *Oocyclus* with nasale not bearing large distinct teeth) and some groups of the Sphaeridiinae (which differ by nasale without distinct teeth and mandibles always with less than three teeth).

Redescription of adult. Body elongate oval, highly convex, compressed from sides (Figs 1A). General coloration of dorsal surface piceous brown to black, margins of pronotum and lateral margins and apices of elytra pale reddish to various extent; ventral parts of prothorax brownish, meso- and metathorax blackish, epipleura pale reddish; head appendages reddish; legs with dark reddish brown coxae, femora and tibiae; tarsomeres yellowish.
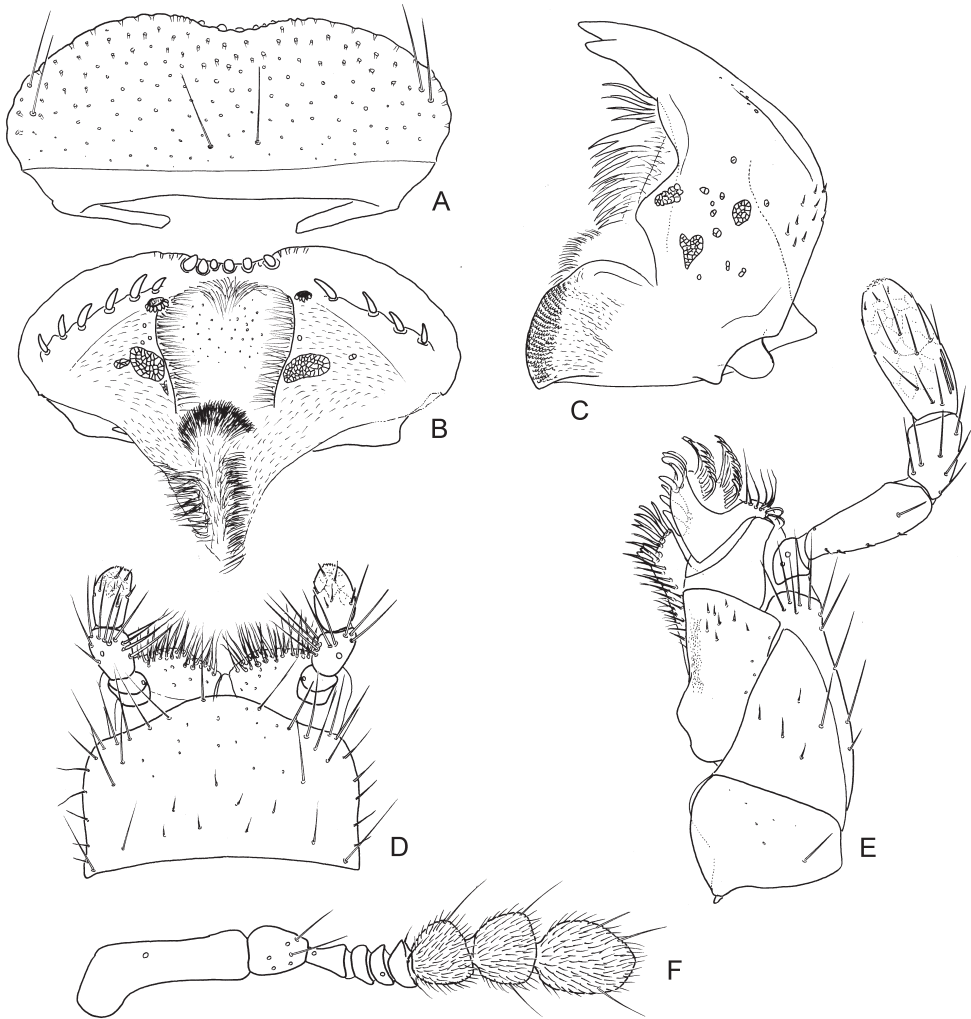
Fig. 3. Adult head appendages of *Tormus posticalis* (Broun, 1917). A – labrum in dorsal view; B – labrum in ventral view (epipharynx); C – mandible; D – labium; E – maxilla; F – antenna.

Head. *Clypeus and frons* (Fig. 4A) distinctly punctate, frons with several trichobothria (Fig. 4C), clypeus without trichobothria; frontoclypeal suture very indistinct; clypeus slightly expanded laterally, covering bases of antennae, anteromedian margin deeply excised, exposing the membrane between clypeus and labrum, lateral margins of clypeus without a bead. *Eyes* small, not protruding from outline of head, separated by 4.5× width of one eye. *Labrum* (Figs 3A–B) well sclerotized, completely exposed dorsally, widest subbasally, strongly narrowed basally and arcuately narrowing anteriad, shallowly bisinuate on anterior margin; dorsal surface bearing two pairs of long sublateral setae and one pair of submesal setae and the
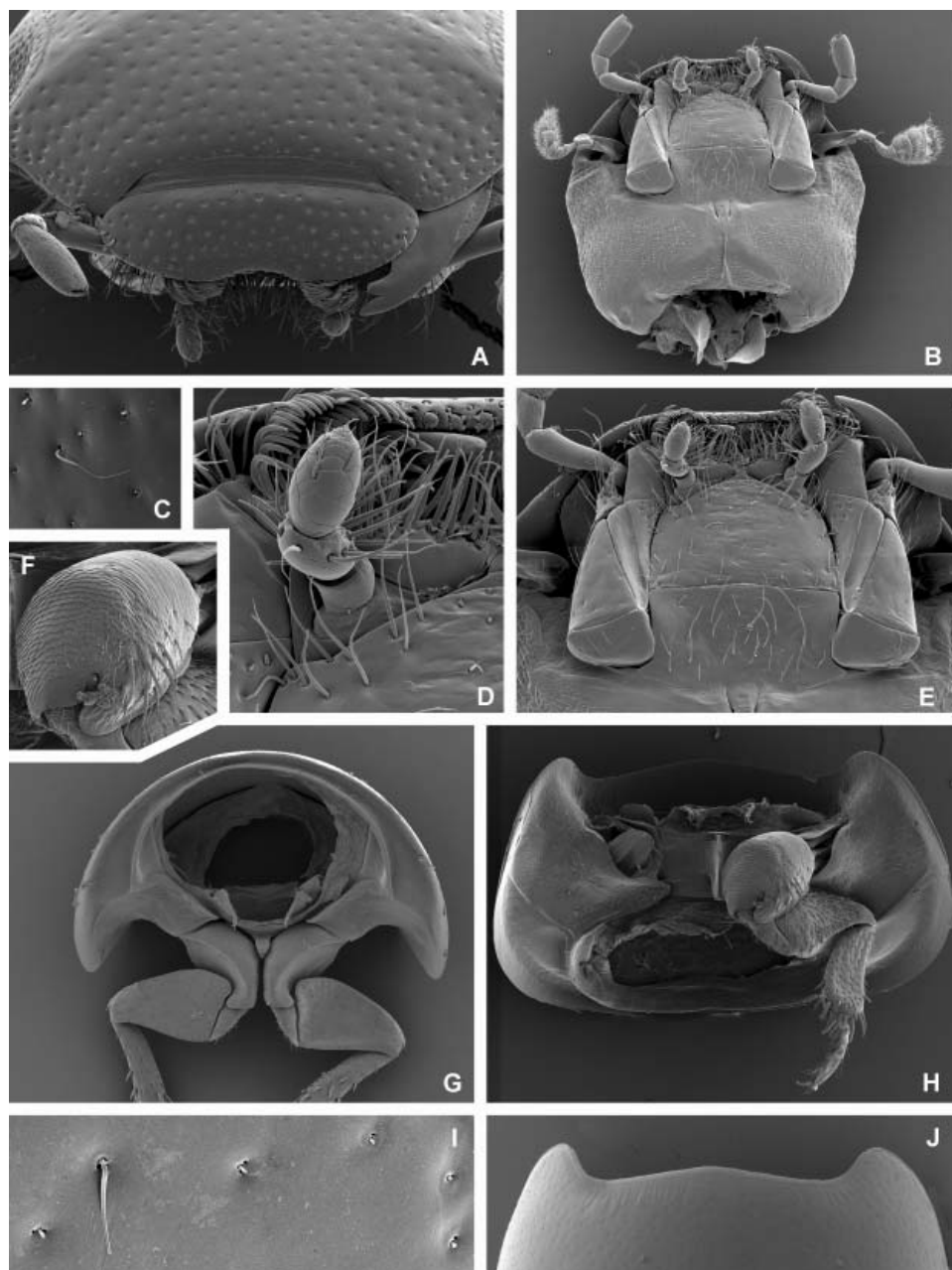
Fig. 4. Head and prothorax morphology of *T. posticalis* (Broun, 1917). A – clypeus and labrum in dorsal view; B – head in ventral view; C – trichobothrium ('systematic puncture') on frons; D – labial palpus; E – mouthparts in ventral view; G – prothorax in posterior view; H – prothorax in ventral view; I – trichobothrium on pronotum; J – anterior margin of pronotum.

ground punctation similar to that on clypeus; anterior margin mesally with a series of stout blunt spines; epipharynx with a lateral row of stout large spines on each side, median portion with two vertical rows of long cuticular spines, submesally with one pair of anterior and one pair of large posterior porose fields, basal portion with densely pubescent membranous cone. *Mandibles* (Fig. 3C) symmetrical, with arcuate lateral margin, bifid mandibular apex; mediodistal portion with a series of long cuticular projections, medioproximal portion with very fine setae, mola rather large. *Maxilla* (Fig. 3E) with a large subtriangular cardo lacking trichobothria; basistipes triangular, bearing few fine setae only; mediostipes well delimited from lacinia, lacinia moderately sclerotized, bearing stout spines and long thin cuticular projections distally and finer hair-like setae mesally; galea short, with rather stout distal setae arranged into well-defined rows; palpifer rather small, with few rather long setae; maxillary palpus with 4 palpomeres, palpomere 1 minute, palpomeres 2 and 4 subequal in length, ca. twice length of palpomere 3; base of palpomere 4 with a group of ca. three digitiform sensilla on lateral surface. *Labium* (Fig. 3D) with submentum ca. as long and wide as mentum, bearing sparsely arranged setae; mentum transverse, ca. 1.7× wider than long, with continually convex anterior margin and subparallel lateral margins, its surface bearing numerous setae along anterior margin, lateral margins with few sparsely arranged setae only; prementum subdivided into two membranous lobes bearing anteromedian group of long setae, palpifer vaguely sclerotized; labial palpus with three palpomeres, palpomere 1 minute, palpomere 2 ca. as long as palpomere 3 in both sexes, unmodified in males, bearing numerous rather long and stout setae; palpomere 3 without digitiform sensilla, bearing few minute sensilla. *Antenna* (Fig. 3F) with 9 antennomeres, scapus conical, ca. 3× as long as pedicel, pedicel widest proximally, bearing a few pore-like sensilla and two tiny setae, antennomere 3 ca. as long as antennomeres 4–6 combined, cupula small and simple, antennomeres 7–9 forming a distinct, loosely segmented and densely pubescent antennal club. *Gula* (Fig. 4B) extremely narrow, gular sutures nearly fused posteriorly of tentorial pits, the latter closely aggregated, distinct, elongate. *Temporae* without distinct ridge arising from inner margin of each eye.

Prothorax. *Pronotum* (Figs 1A, 4I–J) highly convex, widest subbasally, bearing weakly projecting anterior corners; surface smooth, without any depressions, with distinct punctation, few trichobothria present anterolaterally and posterolaterally; anterior margin slightly angulate mesally, lateral margins forming continuous curve with posterior margin; lateral margin arcuately bent to posterior margin; marginal bead present along whole anterior and lateral margins. *Hypomeron* (Fig. 4H) with rather narrow lateral glabrous portion and densely pubescent median portion, portions not divided by a ridge, hypomeral process large, bearing wide marginal bead, arcuately pointed mesally. *Prosternum* (Fig. 4H) extremely short anterior to procoxae, ca. 0.1× as long as procoxa; mesal portion largely concealed by proxocae but strongly carinate mesally, prosternal process large, nearly completely concealed by procoxae. *Coxal cavities* delimited internally by median prosternal carina, open posteriorly, coxal fissure rather long, open, notopleural suture distinct but very short. Accessory ridge below posterior pronotal margin very distinct, laterally reaching to lateral margin of hypomeron as a 'transverse fold'. *Profurca* (Fig. 4G) very short, profurcal arms widely separated, in the form of short but large slightly asymmetrical plate-like extensions directed posteriad and slightly extending of the prothoracic cavity.

Mesothorax. *Scutum* (Fig. 5G) bearing few setae mesally; scutellar shield exposed, triangular, pointed posteriorly, ca. as long as wide, bearing indistinct colon-like punctures on its surface. ***Elytron*** (Figs 1A, 5F, 5I–K) highly convex; sutural stria present, reaching ca. midlength of elytron; nine elytral series distinct only posterolaterally, obliterated anteromesally, formed by punctures of the same size but slightly more impressed than interval punctation; scutellary stria absent (not visible even in slide-mounted elytron); alternate elytral intervals
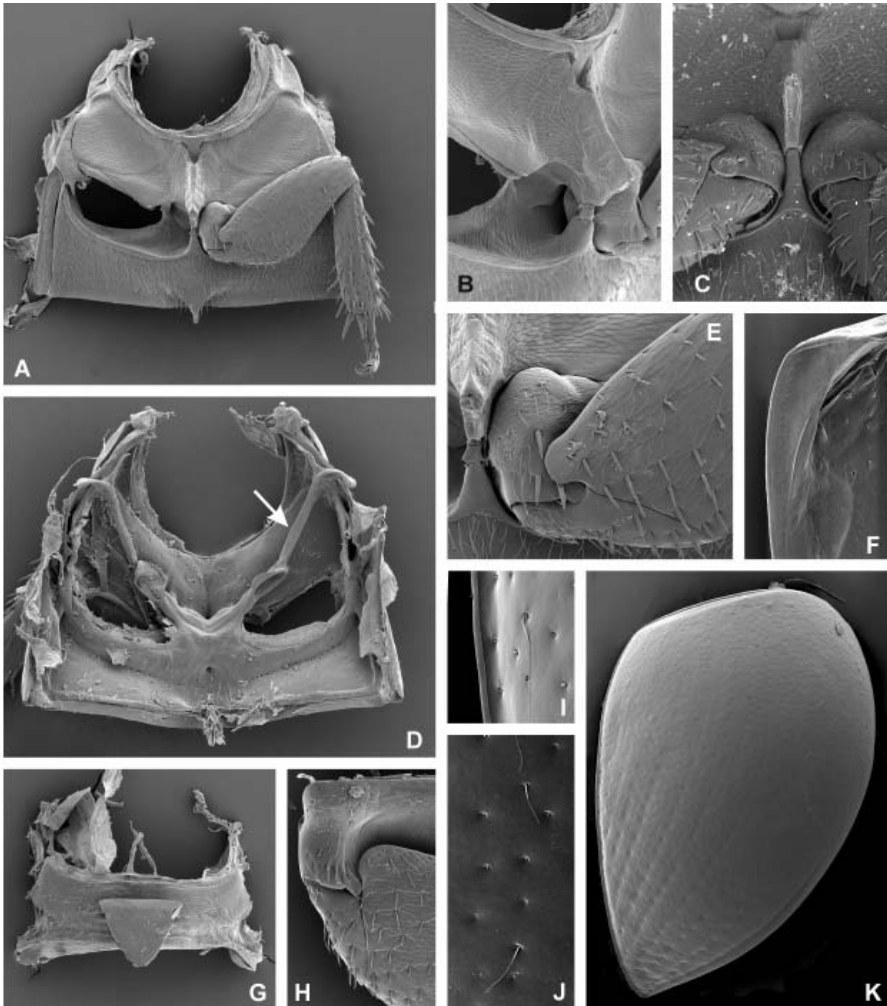

Fig. 5. Morphology of *Tormus posticalis* (Broun, 1917). A – meso- and metathorax in ventral view; B – mesoventral process in ventrolateral view; C – mesoventral process in ventral view; D – internal view of meso- and metathorax with mesofurca; E – coxa, trochanter and basal portion of femur of mesothoracic leg; F – basal portion of epipleuron; G – scutellum; H – coxa, trochanter and basal portion of femur of metathoracic leg; I – detail of lateral margin of elytron with trichobothrium; J – detail of elytra punctuation with distinct trichobothria; K – elytron in dorsal view.
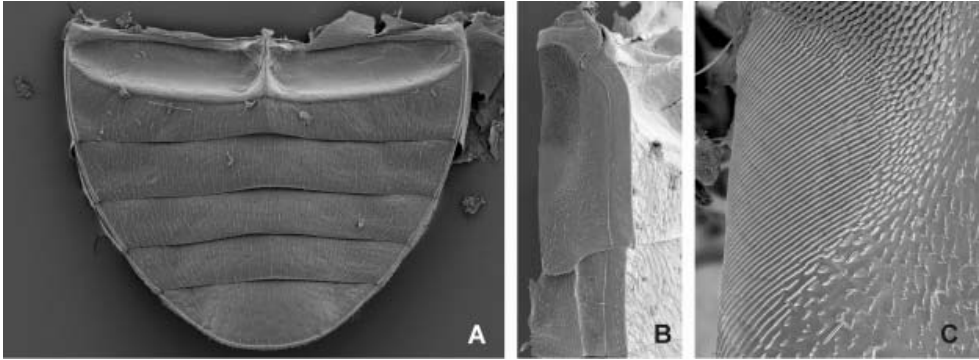
Fig. 6. Morphology of *Tormus posticalis* (Broun, 1917). A – abdomen in ventral view; B – abdominal laterosternites 3–4; C – details of organized stridulation file on laterosternites 3.
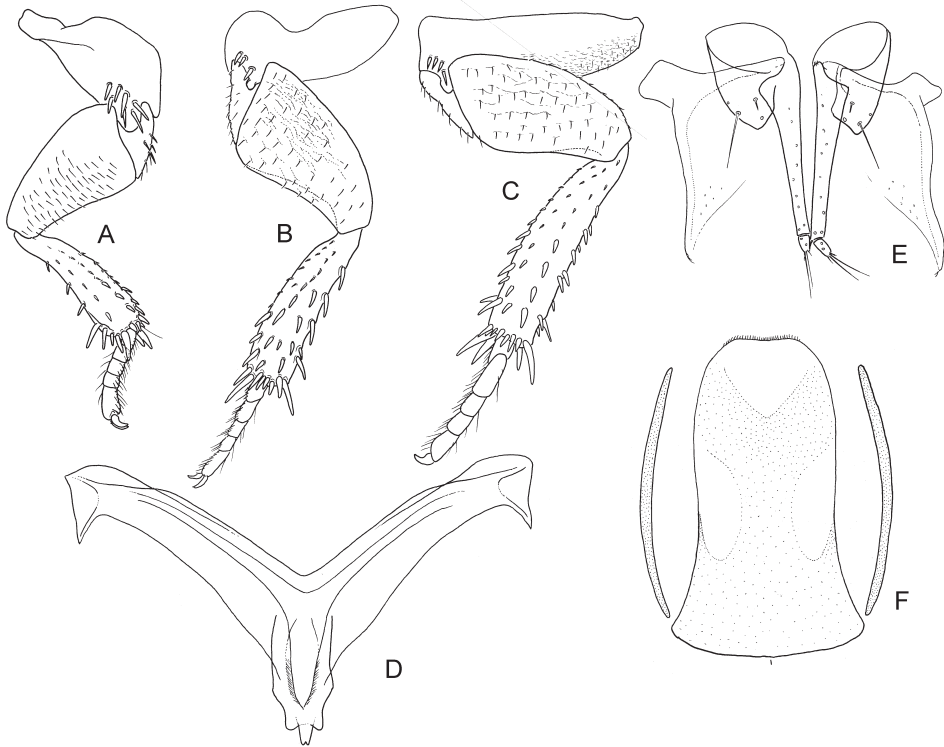

Fig. 7. Morphology of *Tormus helmsi* Sharp, 1884. A – prothoracic leg; B – mesothoracic leg; C – metathoracic leg; D – metafurca; E– female genitalia; F – male sternite 9.

each with numerous trichobothria, punctures of elytral intervals colon-like, each bearing a short club-like seta; lateral edge with a narrow bead; epipleuron moderately wide anteriorly, gradually narrowing to elytra midlength, indistinct more posteriad, its median pubescent portion delimited from lateral narrow bare one by a straight fine line or ridge; ventral elytral surface without any elevated ridges, only with a narrow longitudinal field of fine spines situated sublaterally between anterior fourth and midlength. *Mesoventrite* (Figs 5A–C) divided from mesanepisternum by distinct anapleural suture; mesoventrite subtriangular in shape, widely extending laterad posteriorly, lateral extensions bearing distinct coxal lobes; median portion of mesoventrite elevated into a narrow median crest, the crest strongly angulate in lateral view, bearing few stiff setae apically; mesoventral process narrow; anteromesal portion of mesoventrite with a deep pit; whole surface with scale-like microsculpture, mesally bearing sparsely arranged setae; trochantin well divided from mesoventrite, transverse, long and narrow. *Mesanepisterna* not meeting anteromesally, narrowly divided by anterior portion of mesoventrite; anterior collar well-defined, moderately wide; mesal portion of each mesanepisternum with few setae, large lateral portions bare. *Mesepimeron* with large ventral portion, not reaching anterior collar of mesanepisternum anteriorly, forming lateral margin of coxal cavity; its surface with few setae only. *Coxal cavities* obliquely transverse, ca. 3× wider than long, very narrowly separated from each other by mesoventral and metaventral processes; internal postcoxal wall moderately wide mesally and posteriorly. *Mesofurca* (Fig. 5D) well-developed, long, arising as two basally fused arms from posterior wall of coxal cavities, bearing plate-like extensions at midlength and reaching to dorsolateral body walls.

   Metathorax. *Metanotum* very short, weakly sclerotized, ca. 5.5× wider than long, with nearly totally reduced anterior membranous area, alacristae widely separated, slightly diverging anteriad. *Metaventrite* (Fig. 5A) short, ca. as long as mesoventrite, evenly convex, with slightly elevated median portion well defined posteriorly by a blunt ridge with slightly stouter setae, whole surface (except for a small posterior area) bearing rather dense pubescence; metacoxal process rather long and distinctly exposed. Postcoxal ridge very narrow but well-defined. *Metanepisternum* ca. 7.5× longer than wide, without an obliquely transverse strengthened ridge anteriorly; whole surface sparsely pubescent. *Metepimeron* without distinct ventral portion. *Metafurca* (Figs 7D) rather large, Y-shaped; stalk very short, without basal extensions; lateral arms rather long, without anterobasal extensions, apical portions widened. *Hind wing* absent.

   Legs (Figs 7A–C). *Coxae* with numerous (procoxae) or few (meso- and metacoxae) large spines ventrally close to trochanter articulation, otherwise bare; procoxae subglobular, slightly transverse; mesocoxae transverse, rather robust mesally, narrowly separated; metacoxae narrowly transverse, subrectangular in ventral view. *Trochanters* with proximal parts concealed by coxae, distal subtriangular parts exposed ventrally, bearing sparsely arranged setae. *Femora* attached to trochanters by their posteromesal (in meso- and metafemora) or anteromesal (on profemora) portions only, anteromesal (in meso- and metafemora) or posteromesal bases (in profemora) free, rounded; profemora sparsely pubescent ventrally (except for bare posterobasal portion), meso- and metafemora with short sparsely arranged spines; tibial grooves present, deep, defined by a high ridge ventrally and low ridge dorsally. *Tibiae* slightly longer than femora, abruptly widening subproximally, slightly widening distad;

each tibia with three dorsal, three outer lateral, and irregular ventral and inner lateral series of spines; ventral, outer lateral and distally situated inner lateral spines stout and long. ***Tarsi*** with 5 tarsomeres, basal pro- and mesotarsomere subequal in length to tarsomere 2, basal metatarsomere distinctly shorter than metatarsomere 2; pro- and mesotarsomere 5 nearly as long as tarsomeres 3–4 combined, metatarsomeres 4 and 5 subequal in length. All tarsomeres with numerous moderately long setae ventrally and few setae of same length dorsally; claws arcuate, without subbasal tooth; tarsi and claws not sexually dimorphic.

Abdomen (Figs 6A–B) with five exposed ventrites; ventrite 1 with moderately large bare coxal grooves, remaining portion sparsely pubescent, median portion without longitudinal carina; ventrites 2–4 subequal in length, sparsely pubescent on whole surface; ventrite 5 slightly longer than preceding ones, its posterior margin without median emargination or group of enlarged setae; lateral margins of ventrites 1–4 and lateral and posterior margin of ventrite 5 with narrow but distinct bead. Laterosternite 3 simple, dorsal portion not divided from ventral by a ridge, bearing an area of goose-head-shaped cuticular projections which is posteriorly organized into a stridulatory file consisting of obliquely arranged uninterrupted lamellae; laterosternites 4–6 step-like, subdivided into elevated ventral and depressed dorsal portion, nearly without cuticular projections; tergites 1–6 membranous, bearing very fine cuticular asperities posteriorly, tergite 7 moderately sclerotized.

Genitalia. *Male genitalia* (Figs 7F, 9). Aedeagus of simply trilobed type; parameres ca. as long as phallobase, wide basally, narrowing apicad, apices species-specific in shape; whole paramere bearing numerous pore-like sensilla; median lobe slightly shorter than parameres, widely subrectangular in apical portion, slightly angulate on apex, apodemes rather long and reaching into phallobase, gonoporus apical; phallobase with moderately large but rather indistinctly detached manubrium. Sternite 9 widely tongue-like, with long subbasal lateral struts. Sternite 8 crescent-like without distinct anterior projection. ***Female genitalia*** (Fig. 7E). Coxostyli 9 very long, cylindrical, gonostyli 9 very short, ca. 0.1× as long as coxostyli 9; each mediotergite 8 with two setae and two pores posteriorly.

Description of larva. See under *Tormus helmsi*.

Biology. Both adults and larvae are terrestrial, inhabiting moss on the ground and on fallen decaying trunks (Figs 2C–D) in forests (e.g., Figs 2A–B) or closely above tree line in the lower alpine zone. Most specimens collected by us were found by sifting moss, less frequently singletons were found in samples of forest leaf litter. Infrequently, adults were also found on the underside of wet rotting logs on forest floor, especially when these are lying next or on the moss (Fig. 2E). Label data also indicate that adults are sometimes found on moss and tree trunks at night. Immature stages were collected together with adults in all known cases, the larvae have three larval instars, typical for the Hydrophilidae.

Distribution. The genus is endemic to the two main islands of New Zealand (Fig. 16).

Status of *Stygnohydrus*. Broun (1893b) erected *Stygnohydrus* based on a single teneral specimen (type of *S. nitidus* Broun, 1893) and mentioned that it is closely related to *Tormus* which he knew from Sharp's (1884) original description. Broun (1893b) mentions the ecarinate prosternum and the carinate abdominal ventrite 1 in the description of *S. nitidus* (type species of *Stygnohydrus*), which are characters he likely considered diagnostic of *Tormus*. Both characters were

apparently misinterpreted by Broun (1893b, 1910, 1917) as he overlooked the prosternal carina concealed by the procoxae and considered the ridge between the metacoxal grooves of abdominal ventrite 1 as a median carina (see also Hansen 1991: 183). All species of *Tormus* described subsequently by Broun (1893c, 1910, 1917) were already found congeneric by Broun himself, i.e. described as *Stygnohydrus* or transferred there after the description (see the note about the letter of Broun to d'Orchymont in Orchymont (1937: 155)). As Broun never examined the types of *Tormus helmsi*, he did not realize they were congeneric with *Stygnohydrus* and that the supposed differences in prosternal and abdominal morphology do not exist. For that reason, *Tormus* and *Stygnohydrus* were maintained as separate genera until Hansen (1991) compared their type species.

Genetic and morphological diversity. Each locality sampled exhibited unique haplotype, which may be related to the small sample sizes sequenced. The only exception is Mt. Te Aroha where one larva and one adult, both from the same sample, were sequenced, and shared the same haplotype (also, confirming the identity of the larvae used for the morphological description below).

TIM2 with invariable sites (+I) and rate variation among sites (+G) following the gamma distribution was selected as the optimal nucleotide substitution model for our *cox1* data under the Aikake and corrected Aikake information criterion as implemented in jModeltest.

Table 2. Genetic divergence between sequences (in %) estimated using the maximum composite likelihood model as implemented in MEGA5. Given locality data correspond with those given in Fig. 8. Specimens of *T. posticalis* (Broun, 1917) are marked by an asterisk (*), specimens of *T. helmsi* Sharp, 1884 are given without any symbol.

|		1*	2*	3*	4*	5	6	7	8	9	10	11	12	13	14	15
WD: Jackson Bay	1*															
FD: Resolution Is.	2*	3.3														
FD: Resolution Is.	3*	3.6	0.3													
FD: Milford Sound	4*	3.6	0.5	0.8												
WD: Matheson Lake	5	5.2	5.6	5.9	5.6											
WD: Pleasant Flat	6	5.5	6.0	6.3	5.9	0.7										
WD: Cross Creek	7	5.6	6.1	6.4	6.1	0.8	0.1									
WD: 3 Mile Lagoon	8	5.7	5.8	6.2	6.1	4.2	4.2	4.3								
TK: Mt. Egmont NP	9	6.3	7.0	7.4	7.4	4.9	5.1	5.2	7.2							
BP: Mt. Te Aroha (A)	10	6.1	7.1	7.4	7.1	4.0	4.5	4.6	6.3	2.1						
BP: Mt. Te Aroha (L)	11	6.1	7.1	7.4	7.1	4.0	4.5	4.6	6.3	2.1	0.0					
NN: Oparara Arches	12	7.3	8.3	8.6	8.3	6.3	6.6	6.7	8.1	8.6	8.0	8.0				
NN: Charming Creek	13	8.9	9.3	9.6	9.3	8.0	8.2	8.0	9.3	10.0	9.5	9.5	4.5			
BR: Paparoa NP	14	7.2	9.3	9.6	9.4	6.9	7.0	6.9	8.6	8.9	8.9	8.9	2.9	4.6		
NN: Hanlon Lake	15	7.7	9.3	9.6	9.3	6.9	7.1	6.9	8.6	8.8	7.8	7.8	3.4	5.5	3.3	
NN: 1000 Acre Plat.	16	8.0	9.8	10.1	10.1	7.6	8.1	8.0	8.8	9.3	9.6	9.6	3.6	5.6	1.9	3.7
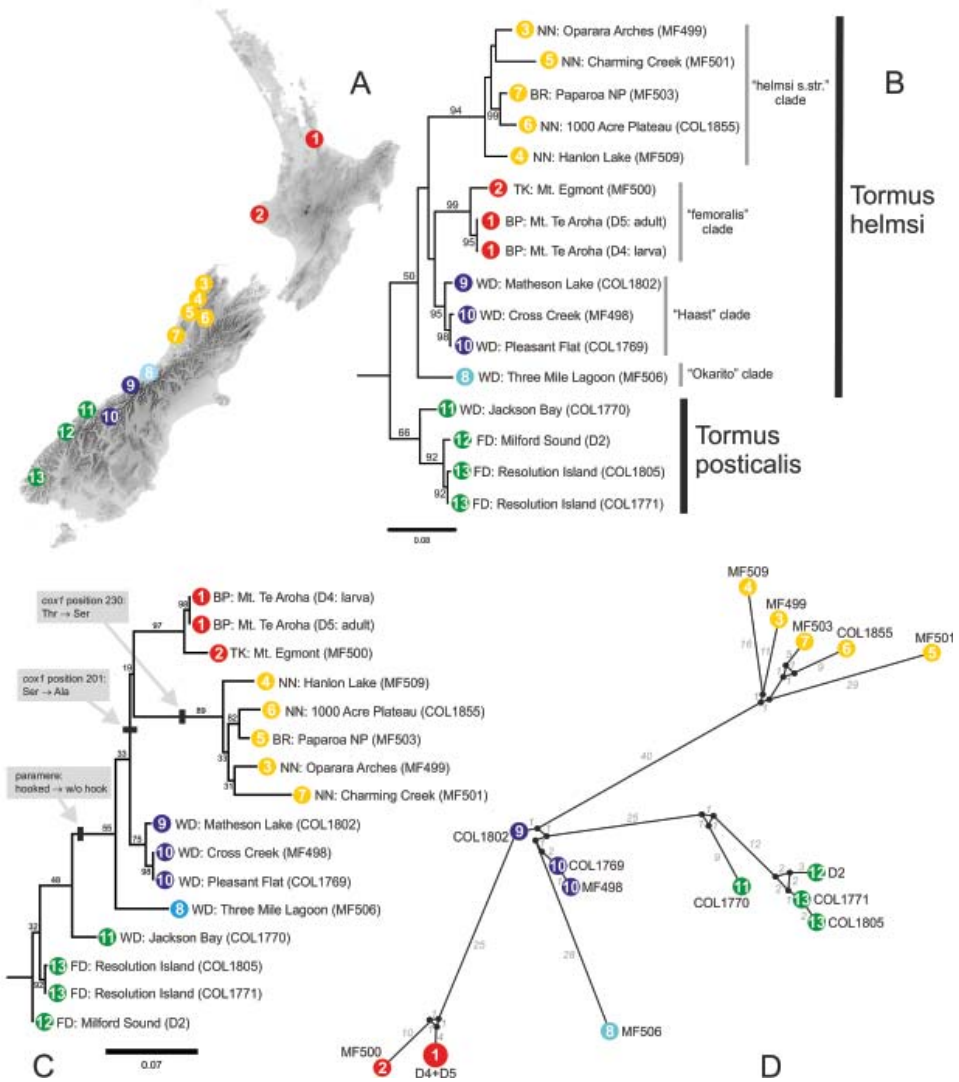
Fig. 8. Results of phylogenetic analyses of *Tormus* Sharp, 1884 and its genetic diversity. A – map of localities of the sequenced specimens. B – Bayesian analysis with posterior probabilities above/below branches (outgroup and values lower than 50 omitted). C – maximum likelihood analysis with bootstrap support values above/below branches (outgroup and values below 50 omitted) and mapped clade specific morphological character and conserved amino acid changes. D – haplotype network with grey numbers indicating the number of substitutions on each branch. Color marking indicates the clades/clusters, numbers in color circles indicate different localities.
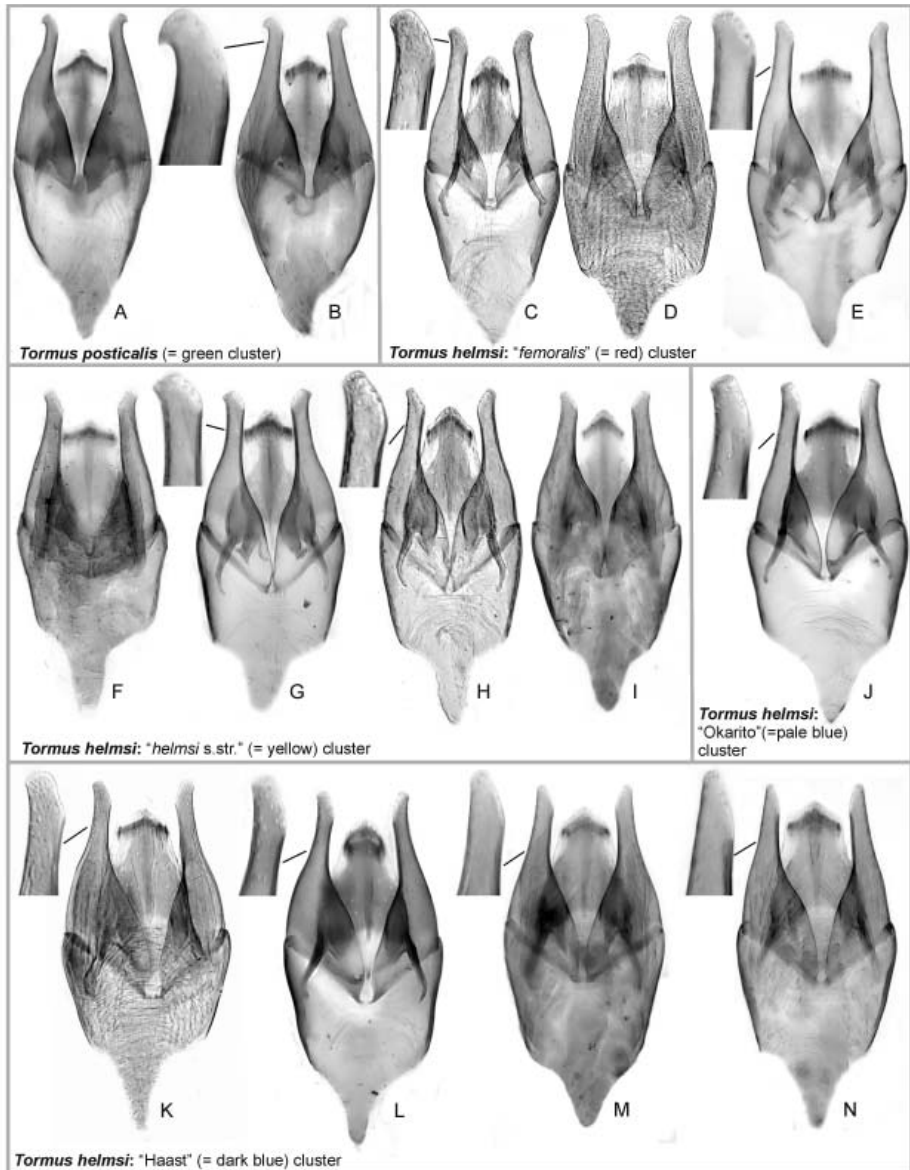
Fig. 9. Variability of the aedeagus morphology in *Tormus posticalis* (Broun, 1917) (A–B) and *T. helmsi* Sharp, 1884 (C–N). Data on the specimens: A – Westland, Jackson Bay (voucher COL1770); B – Fiordland: Milford Sound (voucher D2); C – Taranaki, Mt. Egmont NP (voucher MF500); D – Bay of Plenty, Mt. Te Aroha (voucher D5); E – Waikato, Mt. Pirongia; F – Buller, Bullock Creek; G – Nelson, Oparara Arches (voucher MF499); H – Buller, Paparoa NP (voucher MF503); I – Buller, Italians Creek; J – Westland, Three Mile Lagoon (voucher MF506); K – Westland, Pleasant Flat; L – Westland, Cross Creek (voucher MF498); M – Westland, Gillespies; N – Westland, Matheson Lake (voucher COL1802).

Bayesian analysis recognized five monophyletic clades which are geographically limited and allopatric (Fig. 8B), the same groups were also recognized as distinct clusters in the haplotype network analysis (Fig. 8D), resulting in the network with the 'Haast' group in the centre. Maximum likelihood analysis also recognized the same groups as other analyses (Fig. 8C) but placed the root of the tree (i.e. *Paracymus pygmaeus* used as an outgroup) within the southernmost (green) cluster, making it therefore paraphyletic. The overall generic diversity of *Tormus* was found very high (6.5 %) with the mean divergences ranging between 0.5–3.9 % within each group, and between 4.2–9.0 % between groups. The highest within-group diversity was found in the yellow ('*helmsi* s. str.') clade from northern South Island which was however represented by the highest number of specimens (n = 5). Two conserved group-specific amino acid changes were found (Fig. 8C): Ser-Ala at position 201 (alanine in red and yellow groups, serine in remaining groups of *Tormus*) and Thr-Ser at position 230 (serine in the yellow group, threonine in all remaining *Tormus* groups). The Ser-Ala change indicates that the sister relationship of the red ('*femoralis*') and yellow ('*helmsi* s. str.') clades as recognized by the ML analysis is more likely than the topology revealed by the Bayesian analysis.

All examined specimens of *Tormus* are very uniform in morphology, with variation only detected in the male genitalia (shape of the paramere apex), strength of dorsal punctuation of elytra, and the declivity of the posterior portion of elytra in lateral view. The highest diversity of aedeagal morphology was found in the specimens from central and southern Westland ('Haast' clade) which genitalia resemble those from the North Island and northern South Island, plus contain the morphotypes without widened apex of parameres unique for the clade. Specimens from northern South Island are also quite variable with aedeagi resembling those of North Island and 'Okarito' groups, but without any unique morphotypes. The North Island populations have all rather uniform and only slightly variable aedeagus. The same is true for the southern South Island clade, in which only a slight intraspecific variation was observed and which are easily distinguishable from remaining clades by the parameral hooks. Dorsal punctuation of anterior portion of the elytra and the declivity of elytra in lateral view are rather uniform only in the North Island specimens (with coarse elytral punctation and steep posterior portion of elytra) whereas the South Island ones vary in these characters (elytral punctuation very fine to strong, posterior portion of elytra oblique to nearly vertical). The variation of the non-genital characters is continuous and was unreliable for sorting material into distinct morphotypes.

Species-level taxonomy. The morphological study revealed that the species-level taxonomy of *Tormus* is a complex issue. Five species were originally described, of which only three were considered valid based on study of the type material by HANSEN (1997). The characters HANSEN (1997) used for delimiting species (coloration and strength of the dorsal punctation) were unreliable to distinguish specimens with clear differences in aedeagal morphology and are moreover slightly variable in specimens from the same locality. No additional external characters corresponding with the differences of genital morphology were found even by a detailed study using SEM. A study of genital morphology of specimens from all localities from which males were available showed three facts: (1) the Fiordland and southernmost Westland specimens have a very distinct aedeagus with hooks on paramere apices and vary only very slightly in genital morphology; (2) the specimens from North Island all have rather

Table 3. Divergence within and between groups (in %) recognized in phylogenetic analyses. Betw Group Div – between group divergence (MEGA5); Intra Dist – average pairwise tree distance among members of the clade (Geneious); Inter Dist – average pairwise tree distance between the clade and the closest clade (indicated in parentheses) (Geneious).

Betw Group Div					Species (clade)	Intra Dist	Inter Dist
2	**3**	**4**	**5**				
5.9	6.0	9.0	6.9	**1**	*Tormus posticalis*	2.2	5.4 ('Haast')
	4.2	7.3	4.6	**2**	*T. helmsi* ('Haast' clade)	0.9	4.7 ('Okarito')
		8.7	6.6	**3**	*T. helmsi* ('Okarito' clade)	–	4.7 ('Haast')
			8.9	**4**	*T. helmsi* ('*helmsi* s.str.' clade)	4.2	7.5 ('Haast')
				5	*T. helmsi* ('*femoralis*' clade)	1.4	4.8 ('Haast')

uniformly shaped genitalia, but the same genital morphology is also found in some South Island specimens; and (3) the specimens from northern half of South Island (Nelson, Buller and central and nothern Westland) have very variable genitalia and no clear correlation with geography may be observed. Morphology was therefore found as insufficient to resolve species-level taxonomy of *Tormus,* assuming that multiple species exist, which is the reason why the sequence data of the *cox1* fragment were examined.

Although the precise pattern of the basal branching was in conflict between Bayesian and ML analyses and the support of the clades was low in both cases, both analyses agree in reconstructing the southernmost (green) cluster on the base of the tree and grouping the remaining groups into a weakly supported but monophyletic clade. This division is in agreement to morphology of the aedeagus, namely with the presence (in green group) or absence (in remaining groups) of the apical hook of the paramere. The green group, therfore, fulfills traditional criteria of species delimitation and can unambiguously be identified as a separate species, *T. posticalis*.

Representatives of the remaining clusters show deep genetic divergences correlated with geography but cannot be reliably recognized by means of genital morphology. Still, their distances to the closest group vary between 4.7–7.5 % that corresponds or is even higher than minimum distance delimiting *T. posticalis* (i.e. the only clade which separate species status is unambiguous). The dark blue ('Haast'), pale blue ('Okarito') and red ('*femoralis*') clades are moreover genetically more similar to *T. posticalis* than to the yellow ('*helmsi* s. str.') clade. Combined with the reciprocal allopatry of all clades these results indicate that the four clades may represent four separate geographically limited cryptic species or distinct populations of a single variable species, but additional genetic studies are required. For practical taxonomic purposes, we distinguish two morphologically distinct taxa below: *Tormus posticalis* characterized by the hook-like apices of parameres, and *T. helmsi* (understood here as a complex of four haplotype lineages) characterized by the absence of the parameral hooks.

Full Mantel tests for isolation by distance showed weak to moderate correlation between genetic and geographic distance for complete data as well as for populations of *T. helmsi*. Partial Mantel tests show moderate partial correlation between genetic distance and cluster membership controlled for geography in both cases, and very weak or no correlation between

Table 4. Results of full and partial Maltel tests for isolation by distance (numbers: Pearson's coefficient of correlation, r).

Matrix A	Matrix B	Covariate	all haplogroups		haplogroups of *T. helmsi*	
			gen + geo	gen + log(geo)	gen + geo	gen + log(geo)
Genetics	geography	–	0.43	0.59	0.32	0.51
genetics	geography	clusters	0.08	0.19	-0.24	-0.09
genetics	clusters	geography	-0.67	-0.58	-0.72	-0.61

genetics and geography when controlled for cluster membership. These results (Table 4) indicate that isolation by distance does not explain the observed genetic variation of *Tormus* and that some environmental (or geographic) barriers limiting dispersal are, or were, present to structure current populations.

Key to *Tormus* species

Morphologically, the species of *Tormus* may be reliably identified only by the examination of the male genitalia, but both species were never found in sympatry and locality data may therefore be useful for quick identification. See above for details on genetically distinct haplotypes here considered as belonging to *T. helmsi*.

1   Parameres with apical hook (Figs 9A–B). Fiordland and southernmost Westland. ....
....***T. posticalis*** (Broun, 1917)
–   Parameres without apical hook (Figs 9C–N). North Island and central and northern parts of South Island. .... ***T. helmsi*** Sharp, 1884

Tormus helmsi Sharp, 1884
(Figs 1, 7, 9C–N, 10–16)

Tormus helmsi Sharp, 1884: 474. Type locality: New Zealand, Buller, Greymouth.
= *Stygnohydrus nitidus* Broun, 1893b, **syn. nov.** Type locality: New Zealand, Westland, Boatmans. Trasferred to *Tormus* by Hansen (1991: 183).
= *Tormus nitidus* Broun, 1893c: 1402, **syn. nov.** Secondary homonym of *Stygnohydrus nitidus*. Type locality: New Zealand, Westland, Capleston. Synonymized with *Stygnohydrus nitidus* by Hansen (1997: 360).
= *Stygnohydrus basalis* Orchymont, 1937: 155, **syn. nov.** Replacement name for *Tormus nitidus* Broun, 1893. Synonymized with *Stygnohydrus nitidus* by Hansen (1997: 360).
= *Stygnohydrus femoralis* Broun, 1910: 12, **syn. nov.** Type locality: New Zealand, Taupo, Raurimu.

Type material examined. *Tormus helmsi*: Holotype: unsexed specimen (BMNH): 'Tornus [sic!] / helmsi / Type D.S. / Greymouth N. Zd / Helms [handwritten on the label with the specimen] // Type / H. T. [rounded label with red margin] // Greymouth / New Zealand / Helms // Sharp Coll. / 1905-313.'
    Stygnohydrus nitidus: Holotype: unsexed teneral specimen (BMNH): 'Syn- / type [rounded label with blue margin] // Type [rounded label with red margin] // New Zealand / Broun Coll. / Brit. Mus. / 1922-482 // Westland // 2343 // Stygnohydrus nitidus'
    Tormus nitidus: Lectotype (designated by Hansen (1997)): unsexed specimen (BMNH): 'Type [round label with red margin] // 2445 // Capleston / Westland // New Zealand / Broun Coll. / Brit. Mus. / 1922-482 // Tormus / nitidus // LECTOTYPE / Tormus nitidus Broun / M. Hansen des. 1996'

Stygnohydrus femoralis: HOLOTYPE: 1 ♀ (BMNH):   [female symbol] // Type [round label with red margin] // Raurimu / Jany. 1909 // 3032. // Stygnohydrus / femoralis. // New Zealand / Broun Coll. / Brit. Mus. / 1922-482.'

Additional adult specimens examined (445 specimens). **NEW ZEALAND: North Island: COROMANDEL:** 1 ♀ (NZAC): Maumaupaki Track, 36°58.2′S 175°34.6′E, 17.xi.2004, lgt. A. C. Eyles & J. I. Townsend. **BAY OF PLENTY:** 4 spec. (NZAC): Horohoro state forest, Mamaku Plat, elev. 550 m [38°16′23″S 176°7′45″E], 24.vii.1976, lgt. J. S. Dugdale (76/43); 26 spec. (FMNH, NMPC, YMC): Kaimai-Mamaku Forest , Mount Te Aroha, upper end of Tui Mine Track near summit road , elev. 775 m, 37°31.658′S 175°44.684′E, 19.xi.2005, lgt. Newton & Thayer (FMHD#2005-021); 3 spec. (NZAC): Mount Te Aroha [37°32′29″S 175°42′39″E], 21.x.1967, lgt. J. C. Watt; 1 ♀ (NZAC): Mount Te Aroha 37°32.5′S 175°42.7′E, 27.ii.1992, lgt. J. S. Dugdale (92/6); 1 ♀ (NZAC): same locality, 12.xii.2004, lgt. R. Leschen & S. Williford (RL890). **TARANAKI:** 1 spec. (LUNZ): Mount Egmont National Park, North Egmont Road [ca. 39°16.2′S 174°5.1′E], 24.v.1986, lgt. C. L. Lyal (CL479); 6 spec. (LUNZ): Mount Egmont National Park, Potaema picnic area, elev. 650 m [39°18.8′S 174°8.8′E], 24.xii.1985, lgt. R. M. Emberson & P. T. Syrett; 4 spec. (LUNZ): Mt. Egmont, elev. 823 m [ca. 39°17′S 174°7′E], 29.xi.1970, lgt. A. W. Don; 9 spec. (NMPC, NZAC): Mt. Egmont NP, Mangaroaka Walk at Egmont road, elev. 600 m, 39°14.5′S 174°6.8′E, 1.xii.2012, lgt. Fikáček (NZ29); 15 spec. (NMPC, DBCP, NHMW, NZAC, ZMUC): Mt. Egmont NP, Potaema Walk 6.8 km W of Pembroke, elev. 650 m, 39°21.3′S 174°8.8′E, 28.xi.2012, lgt. Becker, Fikáček & Hájek (NZ16); 1 spec. (NMPC): Mt. Egmont NP, walk from The Plateau to Manganui Lodge, elev. 1230 m, 39°18.4′S 174°5.5′E, 28.xi.2012, lgt. Becker, Fikáček & Hájek (NZ18); 2 spec. (LUNZ): North Egmont, Holly Hut, elev. 950 m [39°15.9′S 174°2.8′E], 27.xi.1975, lgt. A. K. Walker; 1 spec. (LUNZ): Pouakai Range [39°14.5′S 174°1.2′E], 9.–13.i.1978, lgt. J. C. Watt; 2 spec. (LUNZ): Pouakai Road, Ahukawakawa Track, elev. 1067 m [39°15.3′S 174°2.5′E], 11.i.1978, lgt. J. C. Watt (78/10). **TAUPO:** 1 spec. (NZAC): Ohakune Mount Rd. Tk. [39°25.1′S 175°24′E], 24.xi.1965, lgt. J. I. Townsend; 2 spec. (NZAC): same locality, 27.xi.1985, lgt. R. C. Craw (85/65); 2 ♀♀ (BMNH): Waimarino [39°26′S 175°8′E], i.1910, without collector; Taranaki, 1 ♀ (JNIC): Mt. Egmont, Patea walk, 39°18.5′S 174°6.8′E, 10.xii.1995, lgt. J. T. Nunn. **WAIKATO:** 2 spec. (NZAC): Mt. Pirongia, Track 2 to Wharauroa [37°59.5′S 175°5.9′E], 16.i.1977, lgt. A. K. Walker (77/2); 1 ♂ (NZAC): same locality, 9.vi.1977, lgt. B. A. Holloway (77/61). **WELLINGTON:** 1 ♀ (NZAC): Mt. Holdsworth Track [40°52.4′S 175°25′E], 3.ix.1965, lgt. J. I. Townsend.

South Island: NELSON: 1 ♀ (NMPC): 1000 acre Plateau, site 1, elev. 1022 m, 41°35.0′S 172°12.4′E, 8.ii.2011, lgt. L. Dunning & L. Shield (TB505); 1 spec. (NZAC): Blue Duck Creek, Gouland Downs, elev. 762 m [41°50′S 172°21.9′E], 5.ii.1966, lgt. J. I. Townsend; 1 ♀ (NMPC): Charming Creek walkway at Watsons Mill, 3.3 km E of Hector, elev. 70 m, 41°36.2′S 171°54.9′E, 5.xii.2012, lgt. Fikáček, Hájek & Leschen (NZ35); 1 ♀ (NZAC): Frazer Stream, S. Paturad [42°18.7′S 172°16.6′E], 22.viii.1967, lgt. F. Alack; 1 ♂ (NZAC): Glen Hope [41°21.3′S 173°9.3′E], 20.vi.1915, lgt. T. Hall; 23 spec. (NZAC): Gourland Downs [= Gouland Downs, 40°53.5′S 172°21.2′E], 5.ii.1965, lgt. J. I. Townsend; 1 ♀ (NMPC): Hanlon Lake, 5.2 km S of Te Namu on Karamea Highway, elev. 80 m, 41°25.5′S 172°6.1′E, 6.xii.2012, lgt. Fikáček, Hájek & Leschen (NZ39); 1 spec. (NZAC): Hope [41°21.3′S 173°9.3′E], 21.xii.1915, lgt. T. Brookes; 1 ♀ (NZAC): Lake Rotoiti [41°50.5′S 172°50.6′E], iii.1949, lgt. A. E. Brookes; 1 ♀ (NZAC): Mt. Arthur [41°13.1′S 172°40.9′E], 19.xi.1969, lgt. J. I. Townsend; 2 spec. (NZAC): Mt. Augustus, Granity, elev. 853 m [41°40.5′S 171°51.4′E], 4.iii.1970, lgt. J. S. Dugdale; 3 spec. (NZAC, NMPC): Oparara Arches, 14.8 km NNE of Karamea, end of McCallum Mill Road at Box Canyon Cave, elev. 230 m [41°8.1′S 172°11.5′E], 6.xii.2012, lgt. Fikáček, Hájek & Leschen (NZ37); 2 spec. (NZAC): Punakaiki, Bullock Creek [42°12.1′S 171°24.5′E], 12.x.1970, lgt. J. I. Townsend; 1 ♀ (NZAC): Surveyors Creek, Karamea Saddle, elev. 609 m [41°18.3′S 173°24.8′E], 13.x.1970, lgt. J. I. Townsend. **BULLER:** 1 ♂ (NZAC): Bullock Creek, elev. 20 m [ca. 42°6′S, 171°22″E], 6.xii.1982, lgt. C. A. Muir; 5 spec. (NZAC): E of Mt. Dewar, elev. 1127 m [ca. 42°4.9′S, 171°32.7′E], 12.xii.1969, lgt. J. S. Dugdale; 1 ♂ (NZAC): Flagstaff Biological Reserve, Hochstetter [ca. 42°26.9′S 171°39.3′E], 20.ix.1972, lgt. J. S. Dugdale (72/174); 2 spec. (NZAC): Lake Roto-roa near camp ground [ca. 41°51.9′S 172°38.8′E], 9.i.1993, lgt. J. W. M. Marris; 9 spec. (NZAC): Mawhera state forest [42°29.5′S 171°31′E], 10.xi.1971, lgt. J. McBurney (71/144); 1 spec. (NZAC): Mawhera state forest, S of Ngahere [42°23.7′S 171°26.8′E], 27.i.1972, lgt. J. S. Dugdale (72/98); 5 spec. (NZAC, ANIC, NMPC): Mawhera state forest, Kangaroo Creek, 5 km SE of Ngahere [42°25.4′S 171°29.6′E], 27.i.1972, lgt. J. S. Dugdale (72/86); 3 spec. (NZAC): Mount Dewar, elev. 1000 m [42°4.9′S 171°32.7′E], xii.1969, lgt. J. I. Townsend (69/234); 1 spec. (NZAC): same locality, xii.1969, lgt. J. I. Townsend (69/239); 2 spec. (NZAC): same locality, xii.1969, lgt. J. I. Townsend; 4 spec. (NZAC, NMPC): same locality, 2.xii.1969, lgt. J. G. McBurney; 3 spec. (NZAC): same locality, 2.xii.1969, lgt. J. I. Townsend; 1 ♂ (NZAC): same locality, 5.xii.1969, lgt. J. C. Watt; 5 spec. (NZAC): same locality, 10.xii.1969, lgt. J.

C. Watt; 1 ♂ (NZAC): Paparoa National Park, Mt. Bovis Tarn, elev. 1000 m [42°6.9′S 171°29.3′E], 9.xi.1990, lgt. P. Syrett & R. M. Emberson; 3 spec. (NZAC): Paparoa Range, Croesus Track, elev. 850 m [42°15.6′S 171°21.8′E], 19.i.1982, lgt. R. M. Emberson & J. W. Early; 2 spec. (NZAC): Punakaiki Scenic Reserve, Porarari River, elev. 20 m [42°6.5′S 171°19.6′E], 9.vi.1985, lgt. J. W. Early (LCNZ 85/7); 6 spec. (NZAC, ANIC, NMPC): Stoney Creek, Inangahua valley [ca. 41°51.5′S 171°56.9′E], 19.ix.1972, lgt. J. S. Dugdale (72/182); 6 spec. (NZAC): 6 km SW of Rotokohu [42°0.7′S 171°51.1′E], 25.i.1972, lgt. J. S. Dugdale (72/99); 2 spec. (NZAC): 9 miles E of Reefton [42°6.9′S 172°2.4′E], 10.ii.1965, lgt. N. A. Walker; 5 spec. (LUNZ): Ananui Creek, Charleston state forest [41°56.9′S 171°30.3′E], 7.viii.1977, lgt. R. M. Emberson; 6 spec. (NZAC, NMPC): Boatmans Creek [42°2.6′S 171°53.7′E], 4.x.1971, lgt. G. Kuschel (71/117); 5 spec. (NZAC): Capleston [42°4′S 171°54.9′], 8.iii.1972, lgt. J. C. Watt (72/111); 12 spec. (NZAC): Capleston env., Beetle reserve, (42°4′3.69″S, 171°54′57.66″E), 6.iv.1973, lgt. J. C. Watt; 1 ♀ (NZAC): Cave Creek Monument, 42°6′S 171°24′E, 20.i.2005, lgt. R. Leschen, T. Buckley, P. Lambert (RL928); 20 spec. (NZAC, ANIC, NMPC): Central Val, 4.5 km SE of Cronadun [42°2′S 171°53′E], 28.i.1972, lgt. J. C. Watt; 1 ♂ (NZAC): Inangahua [41°51.3′S 171°56.9′E], 23.i.1957, lgt. E. S.Gourlay; 1 spec. (NZAC): Inangahua state forest, Fletcher Creek [41°59.3′S 171°50.6′E], xi.1971, lgt. J. G. McBurney; 4 spec. (NZAC): same locality, 25.i.1971, lgt. J. S. Dugdale; 10 spec. (NZAC): same locality, 9.xi.1971, lgt. J. S. Dugdale; 1 spec. (NZAC): same locality, 26.i.1972, lgt. J. S. Dugdale; 16 spec. (NZAC): same locality, 19.ix.1972, lgt. J. S. Dugdale; 1 ♂ (NZAC): Maruia Saddle, Murchinson district [42°2.1′S 172°17.5′E], 2.vi.1965, lgt. J. I. Townsend (65/338); 1 ♂ (NZAC): Matiri Tops [41°38′S 172°14.9′E], 17.ii.1964, lgt. J. I. Townsend; 1 ♂ (NZAC): Mt. Murchinson, Buller valley, elev. 1341–1432 m [41°43.8′S 172°29.9′E], 21.xi.1971, lgt. J. S. Dugdale; 3 spec. (NZAC, NMPC): N of Capleston, Italian Creek [42°2.9′S 171°55.3′E], 21.iv.1972, lgt. J. S. Dugdale; 5 spec. (NZAC): same locality, 12.i.1973, lgt. J. C. Watt; 1 ♂ (NMPC): Paparoa NP, beginning of Cave Creek Track close to Bullock Creek Road, 5.6 km NEE of Punakaiki, elev. 115 m, 42°6.2′S 171°24.1′E, 4.xii.2012, lgt. Fikáček, Hájek & Leschen (NZ34); 3 spec. (LUNZ): Paparoa range, Buckland Peaks, elev. 1250 m [41°53.3′S 171°38.3′E], 15.xi.1987, lgt. R. M. Emberson & P. T. Syrett; 3 spec. (NZAC): Rahu saddle, elev. 600–670 m [42°18.8′S 172°7′E], 1.vi.1965, lgt. J. I. Townsend (65/334); 1 (LUNZ): same locality, 16.x.1984, lgt. J. W. Early (LCNZ 84/7); 10 spec. (NZAC): Redman Creek, Capleston [42°3.6′S 171°52.8′E], 10.i.1973, lgt. J. C. Watt (73/6); 1 spec. (NZAC): Tawhai state forest [42°9′S 171°47′E], x.1972, without collector (72/190A); 24 spec. (NZAC): Tawhai state forest, 3 km S of Reefton [42°9′S 171°47′E], 9.xi.1971, lgt. J. S. Dugdale (71/128); 1 ♂ (NZAC): Tutaki valley, saddle near Rotoroa, Braeburn Track [41°51′S 172°27.9′E], 9.iii.1965, lgt. J. I. Townsend & G. Kuschel. **North Cantenbury:** 1 ♀ (NZAC): Lewis Pass [42°22.7′S 172°23.9′E], 19.iii.1965, lgt. G. W. Ramsay & J. I. Townsend (65/265). **Westland:** 1 spec. (NZAC): Mt. Greenland, elev. 228 m [42°57.2′S 170°49.8′E], i.–ii.1940, lgt. E. S. Gourlay; 2 ♂♂ (NZAC): same locality, 10.vi.1983, lgt. H. P. McColl (8/83); 1 ♂ (NZAC): Mt. Tuhua, E. side of lake Kaniere [42°49.3′S 171°11.4′E], 20.xi.1984, lgt. C. F. Butcher (84/74); 1 spec. (NMPC): Pleasant Flat, elev. 120 m, 44°0.8′S 169°2.9′E, 13.i.2006, lgt. R. Leschen, T. Buckley, R. Hoare (RL1066); 25 spec. (NMPC, DBCP, NZAC, NHMW, ZMUC): same locality, 11.xii.2012, lgt. Fikáček, Hájek & Leschen (NZ49); 4 spec. (NMPC, NZAC): along Three Mile Lagoon Track, 1.8–3.0 km SWW of Okarito, elev. 100–140 m, 43°14′S 170°8.5′E, 8.xii.2012, lgt. Fikáček, Hájek & Leschen (NZ43); 1 ♂ (NMPC): Cross Creek on Haast Pass Highway, 18.3 NNE of Makarora, elev. 500 m, 44°6′S 169°36.5′E, 11.xii.2012, lgt. Fikáček, Hájek & Leschen (NZ51); 1 spec. (NZAC): Denniston [41°44.2′S 171°47.7′E], i.–ii.1965, lgt. J. I. Townsend; 1 spec. (NZAC): same locality, i.–ii.1965, lgt. J. I. Townsend; 4 spec. (NZAC): same locality, 7.x.1969, lgt. J. I. Townsend; 2 ♀♀ (NZAC): Haast Pass [44°6.4′S 169°21.3′E], 20.iii.1968, lgt. R. A. Cumber; 2 spec. (NMPC): same locality, 19.i.2010, lgt. Jäger & Nunn; 12 spec. (NZAC): Nile river valley [42°1.4′S 171°30.9′E], 1.ix.1971, lgt. R. M. Emberson; 4 spec. (LUNZ): Okuku state forest, 10 km E of Kumara [42°37.8′S 171°18.5′E], 28.viii.1977, lgt. R. M. Emberson; 1 spec. (NZAC): Paparoa Range, Lochnagar Ridge, camp area, elev. 1060 m [42°6.5′S 171°33.1′E], xii.1969, lgt. J. S. Dugdale; 2 spec. (NZAC): same locality, xii.1969, lgt. J. I. Townsend; 4 spec. (NZAC): Ross Mikonui Track, 43°S 170°51′E, 9.xi.2005, lgt. R. Leschen & S. Nomura (RL1015); 2 spec. (NZAC): 2 miles S of Fox Glacier [43°29.5′S 180°1.5′E], 8.ii.1965, lgt. N. A. Walker; 2 spec. (NZAC): Alex Knob [43°25.6′S 170°9.1′E], 3.xi.1965, lgt. A. C. Eyles; 3 spec. (NZAC): same locality, 23.ii.1966, lgt. J. I. Townsend; 1 ♂ (LUNZ): Canavans Knob env. [43°22.9′S 170°9.8′E], 4.ii.1982, lgt. A. B. Miller; 2 spec. (NZAC): Fox Glacier [43°28′S 170°1.2′E], 17.ii.1965, lgt. T. Wood; 1 spec. (NZAC): same locality, 11.xi.1965, lgt. J. I. Townsend; 1 spec. (NZAC): same locality, 12.xi.1965, lgt. J. I. Townsend; 1 spec. (NZAC): Fox Glacier, Minnehaha Track, [43°28′S 170°1.2′E], 8.ii.1965, lgt. N. A. Walker; 2 spec. (NZAC): Franz Josef [43°23.3′S 170°11′E], 2.xi.1960, lgt. J. I. Townsend; 1 ♂ (LUNZ): same locality, 1.iv.1988, lgt. R. M. Emberson & P. T. Syrett; 3 spec. (NZAC): Gillespies Beach [43°25′S 169°49.3′E], 12.xi.1968, lgt. J. I. Townsend (68/173); 2

spec. (LUNZ): Lake Moeraki [43°43.7′S 169°16.3′E], 12.xii.1994, lgt. C. J. Vink; 2 spec. (NZAC): Lake Paringa, southern end [43°43.2′S 169°24.4′E], 7.ii.1960, lgt. N. A. Walker; 12 spec. (LUNZ, NMPC): Lake Wombat Track [43°24.2′S 170°10.1′E], 13.i.1986, lgt. J. W. Early; 1 ♂ (NZAC): Matheson Lake track, 5 km NWW of Fox Glacier village, elev. 120 m, 43°26.3′S 169°58′E, 9.xi.2007, lgt. R. Leschen & C. Carlton (RL1318); 1 spec. (NMPC): same locality, 9.xii.2012, lgt. Fikáček, Hájek & Leschen (NZ45); 2 spec. (LUNZ): Mt. Aspiring National Park, Haast Pass highway, Depot Creek [43°57.9′S 169°14.6′E], 11.xi.1995, lgt. R. M. Emberson & P. T. Syrett; 2 spec. (NZAC): Upper Callery [43°25.4′S 170°12.4′E], 2.xi.1965, lgt. J. I. Townsend & A. C. Eyles; 5 spec. (LUNZ, NMPC): Westland National Park, Gillespies, Cook River road, elev. 120 m [43°28.9′S 169°56.3′E], 20.x.1981, lgt. R. M. Emberson (LCZN 81/16). Otago Lakes: 1 ♂ (LUNZ): Mt. Aspiring National Park, Cameron Flat, Makarora river [44°9.5′S 169°18′E], 2.i.1985, lgt. R. M. Emberson & P. T. Syrett.

Larval specimens examined. NEW ZEALAND: North Island: Bay of Plenty: 19 L1, 23 L2, 20 L3 (FMNH, YMC, NMPC): Kaimai-Mamaku Forest, Mount Te Aroha, upper end of Tui Mine Track near summit road, elev. 775 m, 37°31.658′S 175°44.684′E, 19.xi.2005, lgt. Newton & Thayer (FMHD#2005-021). Larvae were associated with adults using the *cox1* molecular markers, see the Genetic and morphological diversity above and the results of the phylogenetic analyses in Fig. 8.

Redescription of adults. Body length 2.7–3.9 mm (holotype 3.5 mm), body width 1.8–2.2 mm (holotype 2.1 mm). Head and pronotum with sparsely arranged but rather coarse punctures, without microsculpture on interstices; elytra anteriorly with sparse punctuation consisting of punctures ca. as large as on pronotum or distinctly smaller., interstices smooth or with very weak microsculpture. Elytra more or less evenly convex, oblique to nearly vertical posteriorly in lateral view. Parameres of aedeagus variable in shape, but never with hook-like apices (Figs 9C–N).

Description of larvae. General morphology. *Third instar.* Body moderately thick, nearly parallel-sided, widest between abdominal segments 2–4 (Fig. 1D). Color yellowish brown, sclerotized parts slightly darker (Fig. 1D).

Head. Head capsule (Fig. 14A) semicircular; cervical sclerites small. Frontal lines visible in basal two-thirds, almost straight and divergent anteriad, reaching base of head capsule without fusing; coronal line absent. Surface of head capsule smooth. Six stemmata on each anterolateral corner of head capsule; each stemma more or less protuberant. Clypeolabrum (Fig. 14B) somewhat asymmetrical. Nasale asymmetrical with three teeth; right two teeth closely aggregated. Epistomal lobes slightly asymmetrical, projecting as far as or slightly further than nasale; right lobe projecting slightly further than left one. Lateral margin of each epistomal lobe membranous; inner margin with fringe of short, trichoid cuticular projections.

Antenna (Fig. 15A–B) 3-segmented, short, rather stout. Antennomere 1 as long as antennomeres 2 and 3 combined, anterior two-thirds of inner face including intersegmental membrane between antennomeres 1 and 2 and large portion of ventral surface bearing cuticular projections; projections on inner face trichoid, long on apical part, short on basal part; projections on ventral surface fine, rather densely arranged. Antennomere 2 narrower than antennomere 1, bearing rather short, trichoid cuticular projections on basal part and lateral half of dorsal and lateral surfaces; intersegmental membrane between antennomeres 2 and 3 with few rather short, trichoid cuticular projections on inner face. Antennomere 3 the narrowest and shortest, as long as antennal sensorium SE1.

Mandibles (Figs 15C–D) moderately wide, symmetrical, with three inner teeth each. Distal two inner teeth large, basal one small, distal one shorter than middle one.
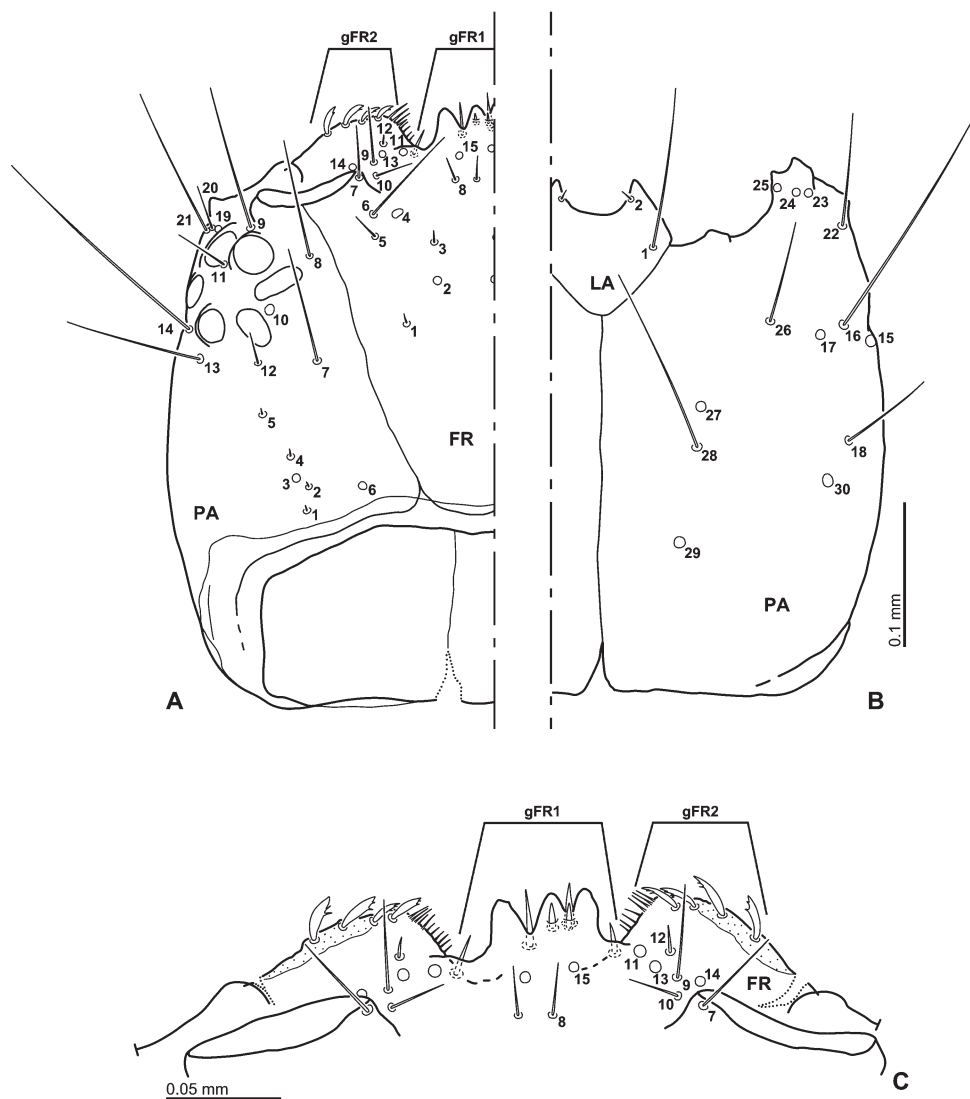
Fig. 10. First instar larva of *Tormus helmsi* Sharp, 1884. A–B – head capsule, dorsal (A) and ventral (B) view; C – detail of anterior margin of head capsule, dorsal view.

Maxilla (Figs 15E–F) 6-segmented, longer than antenna. Cardo moderate in size, irregularly shaped. Stipes the longest, longer than palpomeres 1–4 combined; dorsal surface bearing densely arranged, short, trichoid cuticular projections on inner and outer parts; apical part of outer face including intersegmental membrane between stipes and palpomere 1 bearing rather long, trichoid cuticular projections. Maxillary palpus rather stout, 4-segmented. Palpomere 1
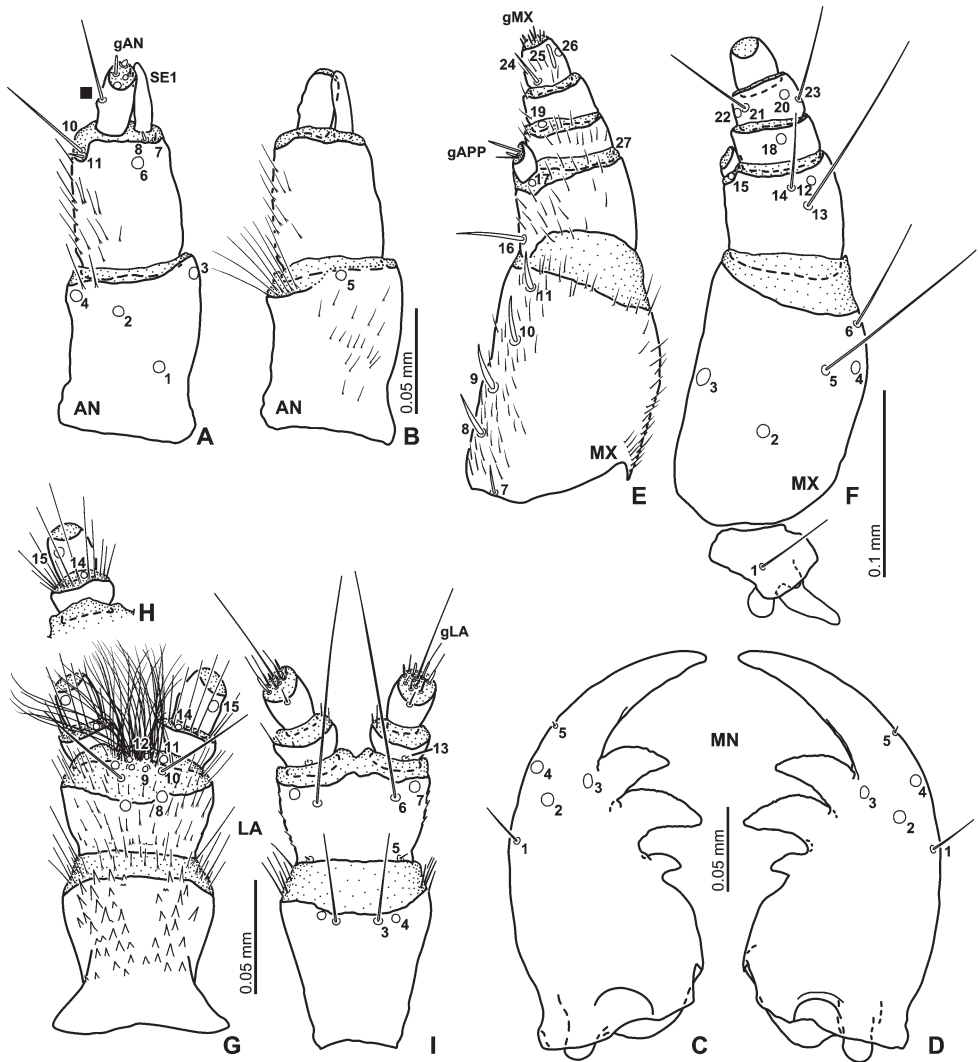
Fig. 11. Head appendages of *Tormus helmsi* Sharp, 1884 first instar larva. A–B – antenna, dorsal (A) and ventral (B) view; C–D – mandibles, dorsal view; E–F – maxilla, dorsal (E) and ventral (F) view; G–I – labium, dorsal view (G), detail of dorsal surface of labial palpus (H) and ventral view (I).

widest and longest, completely cylindrically sclerotized, bearing densely arranged, short, trichoid cuticular projections on median part of dorsal surface to lateral surface, including intersegmental membrane between palpomeres 1 and 2. Palpomere 2 narrower than palpomere 1 but wider than palpomere 3, as long as or slightly longer than palpomere 3, bearing densely arranged, short, trichoid cuticular projections on apical part of inner face including

intersegmental membrane between palpomeres 2 and 3 and median part of dorsal surface to lateral face including intersegmental membrane; fine cuticular projections present ventrally on basal part. Palpomere 3 much wider than and as long as or slightly shorter than palpomere 4, bearing densely arranged, short, trichoid cuticular projections on median part of dorsal surface to lateral surface, including intersegmental membrane between palpomeres 3 and 4. Palpomere 4 bearing short, trichoid cuticular projections dorsally; inner process sclerotized, slightly shorter than palpomere 1.

Labium (Figs 15G–J) well developed but ligula reduced. Submentum (see Fig. 10B) fused to head capsule, rather small, subpentagonal, wider than mentum. Mentum subquadrate in dorsal view (Fig. 15G), subtrapezoidal in lateral view (Fig. 15H). Dorsal surface with rather densely arranged, strong cuticular teeth; lateral face of apical part including intersegmental membrane between mentum and prementum bearing densely arranged short to long trichoid cuticular projections; remaining part of dorsal surface of intersegmental membrane bearing short, trichoid cuticular projections. Prementum subrectangular, slightly transverse, apical part wider than basal part; dorsal and lateral surfaces including membranous area of prementum bearing densely arranged short and narrow trichoid cuticular projections; median part of membrane (on place of the missing ligula) bearing very densely arranged, very long, trichoid cuticular projections; ventral surface of membrane bearing a few short to rather long, trichoid cuticular projections. Labial palpi moderately short, palpomere 1 larger than palpomere 2, bearing a few short, trichoid cuticular projections laterally; dorsal and lateral face of intersegmental membrane between palpomere 1 and 2 bearing a transverse row of very long to rather long, trichoid cuticular projections.

Thorax. Prothorax wider than head capsule (Fig. 1D). Proscutum (Figs 1D, 14C–D) formed by one large plate subdivided by fine sagittal line, anterior part rather weakly sclerotised; median part weakly convex transversely on each side, this part bare except few setae; anterolateral portion weakly convex; whole sclerite bearing densely arranged small, conical cuticular projections and sparsely arranged rather short lanceolate setae and a few long trichoid setae; anterior margin of sclerite bearing fringe of stout, lanceolate setae (Fig. 14D); setae composing a transverse row. Prosternal sclerite divided into two plates, bearing setae along anterior margin (Fig. 14E). Mesonotum with two sclerites on each side (Fig. 14F); anterior ones small, transverse, subtriangular, bearing fine cuticular projections; posterior ones large, subtriangular, bearing a few rather short, lanceolate, rod-like or spiniform setae of variable length, without cuticular projections; posterior mesonotal sclerites narrowly touching each medially, whereas anterior ones not. Two pairs of weakly convex tubercles present dorsolaterally; median ones posterolaterally to posterior mesonotal sclerite, lateral ones behind spiracles; tubercles bearing a few rod-like setae; lateroventral surface with two weakly convex projections. Metanotum with one sclerite on each side (e.g., Fig. 14F); metanotal sclerites transverse, oval, bare but with a few setae of variable length and shape; sclerites not touching each other medially. Six rather large setiferous tubercles bearing a few rather short, rod-like setae (e.g., Fig. 12C) present dorsally on posterior part, composing a transverse row; median two pairs behind metanotal sclerites, remaining ones more laterally; lateroventral surface with two weakly convex projections. Legs (see Fig. 12B) short, stout, slightly or not visible in dorsal view, 5-segmented; all three pairs similar in shape.

Abdomen. Abdomen 10-segmented, tapering posteriad, covered with fine cuticular projections densely arranged, with tubercles bearing several rather short, rod-like setae (e.g., Fig. 12C); dorsal sclerites on segments 1–7 absent. Segments 1 to 6 similar in shape and size, segment 7 smaller than others. Segments 1–6 with two transverse rows of tubercles dorsally to laterally; transverse fold subdividing segment, present between rows of tubercles. Anterior row composed of six large tubercles, spiracle present between lateral two tubercles, close to second one from the outest, lateral pair present on lateral face; posterior row composed of five small tubercles, mesal one slightly transverse, lateral pair on lateral face; lateroventral surface with two weakly convex projections; lateral part of ventral surface with closely aggregated four weakly convex projections. Segment 7 similar to segment 1–6 but posterior row of tubercles composed of three tubercles smaller and more weakly projected; projections of ventral surface indistinct, with a pair of weakly convex areas laterally.

Spiracular atrium modified (Fig. 14G). Segment 8 with irregularly shaped, oval dorsal plate, and with two pairs of tubercles on posterolateral part; dorsal plate bearing densely arranged, small cuticular projections and sparsely arranged, rather short rod-like or slightly lanceolate setae; posterior margin of segment 8 with two rather short and four long trichoid setae. One pair of membranous procerci present on lateral part of posterior margin of segment 8, bearing two rather short setae and one long seta. Segment 9 unilobed and bifurcated (see also Discussion); median lobe and each lateral lobe of spiracular atrium fused into one lobe, median part of dorsal surface weakly sclerotised, margin of sclerite unclear; urogomphi small, sclerotized, one segmented. Acrocercus and prostyli absent. Ventral surface of spiracular atrium with two projections.

Second instar. Very similar to third instar larva (Fig. 1C).

Head. Frontal lines clearly visible, almost straight and divergent anteriad, very slightly lyriform, reaching base of head capsule without fusing (as in Fig. 10B).
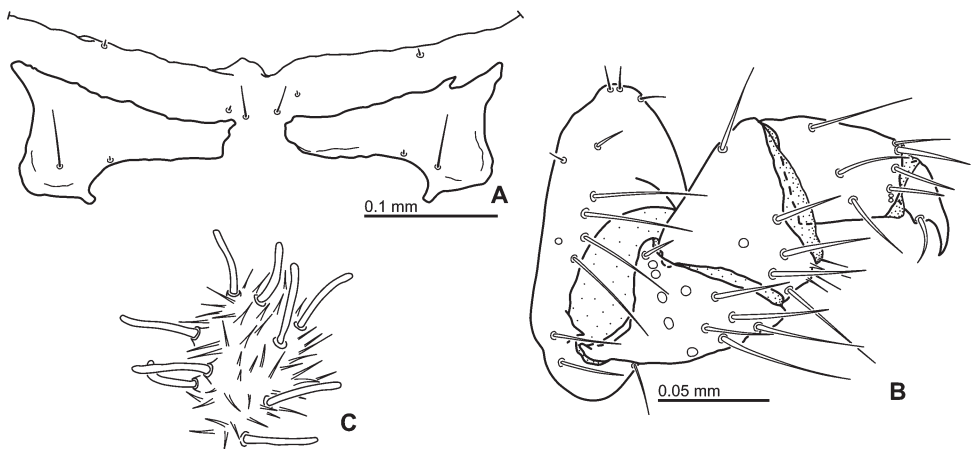

Fig. 12. First instar larva of *Tormus helmsi* Sharp, 1884. A – prosternum, ventral view; B – mesothoracic leg, anterior view; C – tubercle on dorsal surface of abdomen.

Antenna, maxilla and labium proportionally slightly stouter than in third instar (Fig. 13).
Thorax and abdomen. Cuticular projections on membrane finer and narrower than in third instar.

First instar. Very similar to second instar (Fig. 1B).

Head. Antenna, maxilla and labium proportionally slightly stouter than in second instar (Fig. 11).

Thorax and abdomen. Cuticular projections on membrane slightly narrower than in second instar, but the size of projection similar to second instar, thus proportionally longer than in second instar; arrangements of cuticular projections sparser than in third instar.

Chaetotaxy of head. *First instar. Frontale* (Figs 10A, C). Central part with three pairs of sensilla (FR1–3) divergent posteriad; FR1 short seta, rather close to frontal line; FR2 pore-like, situated more anteriorly and more mesally to FR1; FR3 short seta, situated anteriorly to FR2. Pore-like sensillum FR4 and setae FR5–6 situated posteromesally to antennal socket, forming triangular group, FR5 rather short seta, FR6 moderately long seta; FR4 mesally to FR5–6, FR5 posteriorly to FR6; FR6 laterally to FR4. FR7 rather long seta situated on inner face of antennal socket. Pore-like sensillum FR15 and moderately short seta FR8 situated on mesal part of clypeolabrum, behind nasale; FR15 anteriorly to FR8. FR9–14 forming oblique group on basal and inner part of epistome anteromesally to antennal socket, FR11 and FR13–14 pore-like, FR9–10 rather long setae, FR9 longer than FR10, FR12 short and slightly stout seta; FR11 situated mesally to remaining sensilla, close to lateral-most seta of gFR1; FR12–13 close to FR11, between FR11 and FR9 or anteriorly to line connecting FR11 and FR9; FR10 and FR14 close to antennal socket, FR14 laterally to remaining sensilla, FR10 posteromesally to FR14; FR9 between FR14 and FR13. Nasale with a group of six stout and moderately short setae and with two minute setae (gFR1); lateral-most stout ones on emargination between nasale and epistomal lobe, remaining stout ones on median part of nasale; minute ones present ventrally on median tooth of nasale (not seen in Fig. 10C, see Fig. 14B). Each epistomal lobe with a group of four stout setae on median part of anterior margin (gFR2), each seta bearing two subapical teeth on inner face; all setae nearly equidistant.

Parietale (Figs 10A–B). Dorsal surface with a group of five sensilla (PA1–5) forming irregularly longitudinal row in posterior part of parietale; PA1–2 and PA4–5 very short setae, PA3 pore-like. PA6 pore-like, located posteromesally, moderately close to posterior end of frontal lines. Two long setae PA7–8 situated along frontal line, PA7 more distant from frontal line than PA8; PA8 behind antennal socket, close and anterolaterally to mesal-most stemma of anterior low of stemmata; PA7 between PA6 and PA8, at ca. midlength between PA6 and PA8. Long seta PA9 situated very close and posterolaterally to antennal socket. Pore-like sensillum PA10 situated between mesal-most stemmata of anterior and posterior rows; rather long seta PA11 between lateral two stemmata of anterior row, slightly posteriorly to these. PA12 rather short seta close to and behind mesal-most stemma of posterior row, at midlength between PA7 and PA13; PA13 long seta, behind median stemma of posterior row. PA14–17 and PA26 forming irregular transverse row on anterior third of lateral surface ordered as follows from dorsal to ventral: PA14, PA15, PA16, PA17, PA26; PA26 more distant from PA17 than PA16; PA14 very long seta, PA15 and PA17 pore-like, PA26 long seta. PA18 long seta situated on

median part of lateroventral surface, posteriorly to PA15–17, close and anterolaterally to PA30. PA19–22 closely aggregated, forming slightly irregular transverse row on anterior corner of head capsule, order from dorsal to ventral: PA19, PA20, PA21, PA22; PA19 pore-like, PA20 rather short seta, PA21 very long seta, PA22 long seta. Pore-like sensilla PA23–25 situated close to ventral mandibular articulation; PA23 laterally to PA24–25, PA25 on inner margin, PA24 between PA23 and PA25. PA27–28 situated mesal third of ventral surface, at ca. midlength of ventral parietale; PA27 pore-like, anteriorly to PA28; PA28 very long seta. Pore-like sensillum PA29 situated posteriorly to PA28, on basal third of ventral parietale; pore-like sensillum PA30 on posterior two-fifths of lateroventral surface, behind PA18.

Antenna (Figs 11A–B). Antennomere 1 with five pore-like sensilla (AN1–5); AN1 situated dorsally on posterior two-fifths, in lateral part of dorsal surface; AN2 dorsally on anterior fifth of sclerite, between AN1 and AN4 more distant from AN1 than AN4; AN3 subapically on dorsal part of lateral face, AN4 on subapically on dorsal part of inner face, AN5 ventrally on median portion of anterior margin of sclerite. Antennomere 2 with one pore-like sensillum (AN6) situated dorsally on subapical part of sclerite, laterally to midwidth of antennomere 2; setae AN7–8 and AN10–11 and sensorium SE1 on intersegmental membrane between antennomeres 2 and 3, AN9 absent; AN7–8 and SE1 on lateral face, AN7–8 minute, behind SE1, SE1 long and moderately stout, rounded apically, about as long as antennomere 3; AN10–11 on inner face, AN10 long, AN11 short, both setae close to each other. Antennomere 3 with one long additional seta situated on midlength of inner face, with apical sensilla (gAN) in apical membranous area.

Mandibles (Figs 11C–D). Mandible with two setae (MN1 and MN5) and three pore-like sensilla (MN2–4) situated apically to midlength; MN6 probably absent. MN1 rather short, situated laterally on mandibular midlength. MN2–4 situated anteriorly to MN1 and posteriorly to MN5, laterally to apical inner tooth; MN3 close to base of apical inner tooth, MN2 on ca. at midlength between MN1 and MN3, MN3 anterolaterally to MN2; MN5 minute, on apical fifth of lateral mandibular face.

Maxilla (Figs 11E–F). Cardo with one rather long ventral seta (MX1). Stipes with an irregular row of five setae (MX7–11) situated dorsally along inner face; MX7 rather short and stout but shorter and narrower than MX8–11, situated on basal margin of sclerite; MX8–11 rather short, stout, almost equidistant from each other; MX8 more distant from MX7 than from MX9. Pore-like sensilla MX2–3 situated ventrally, MX2 on midlength of inner face, MX2 medially on posterior two-fifth; MX4–6 ventrally on subapical part of lateral face of sclerite, MX4 pore-like, MX5 very long seta, MX6 long seta; MX4 basally to MX6; MX5 mesally to MX4; MX6 close to borderline between sclerite and intersegmental membrane. Dorsal surface of palpomere 1 with one rather long, stout seta (MX16) situated basally on inner face. Three sensilla (MX12–14) situated on median to lateral part of ventral surface; MX12 pore-like, MX13 very long seta, MX14 rather long seta; MX12 and MX14 close to distal margin of sclerite, MX14 mesally to MX12; MX13 on ca. anterior one-third, behind MX12 and MX14. Pore-like sensilla MX15 and MX17 situated on membrane below inner appendage, MX17 dorsally, MX15 ventrally. Inner appendage with a few short setae apically (gAPP). Palpomere 2 with two pore-like sensilla (MX18 and MX19) and one minute seta (MX27); MX18 situated ventrally on median and anterior part of sclerite; MX19 dorsally on
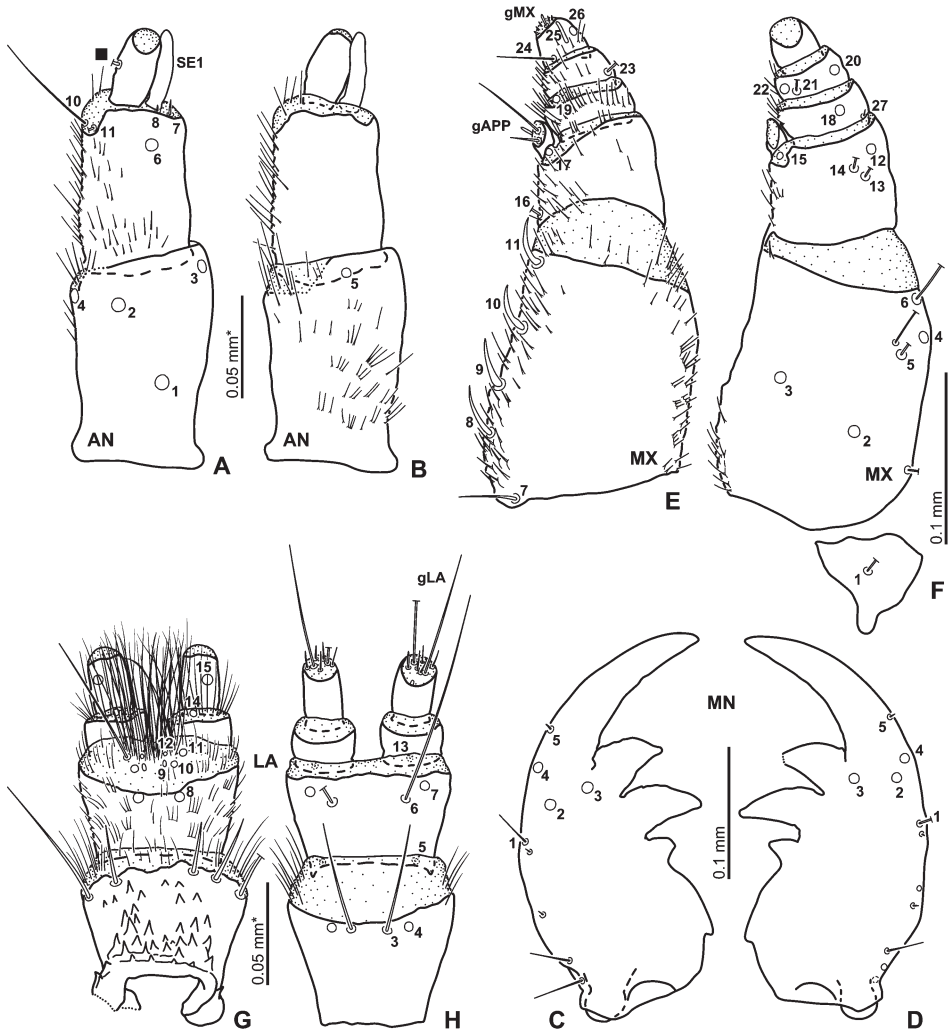
Fig. 13. Head appendages of *Tormus helmsi* Sharp, 1884, second instar larva. A–B – antenna, dorsal (A) and ventral (B) view; C–D – mandibles, dorsal view; E–F – maxilla, dorsal (E) and ventral (F) view; G–H – labium, dorsal (G) and ventral (H) view.

inner part of intersegmental membrane between palpomeres 2 and 3; MX27 basally on lateral face. Palpomere 3 with two long setae (MX21 and MX23) and two pore-like sensilla (MX20 and MX22) situated on or slightly anteriorly to midlength of sclerite; MX21 and MX22 closely aggregated, situated on inner face, MX22 dorsally to MX21; MX20 on lateral part of ventral surface, close to MX23; MX23 on lateral face. Palpomere 4 with one rather short and slightly stout seta (MX24) situated basally on inner face, and with digitiform sensillum (MX25) and
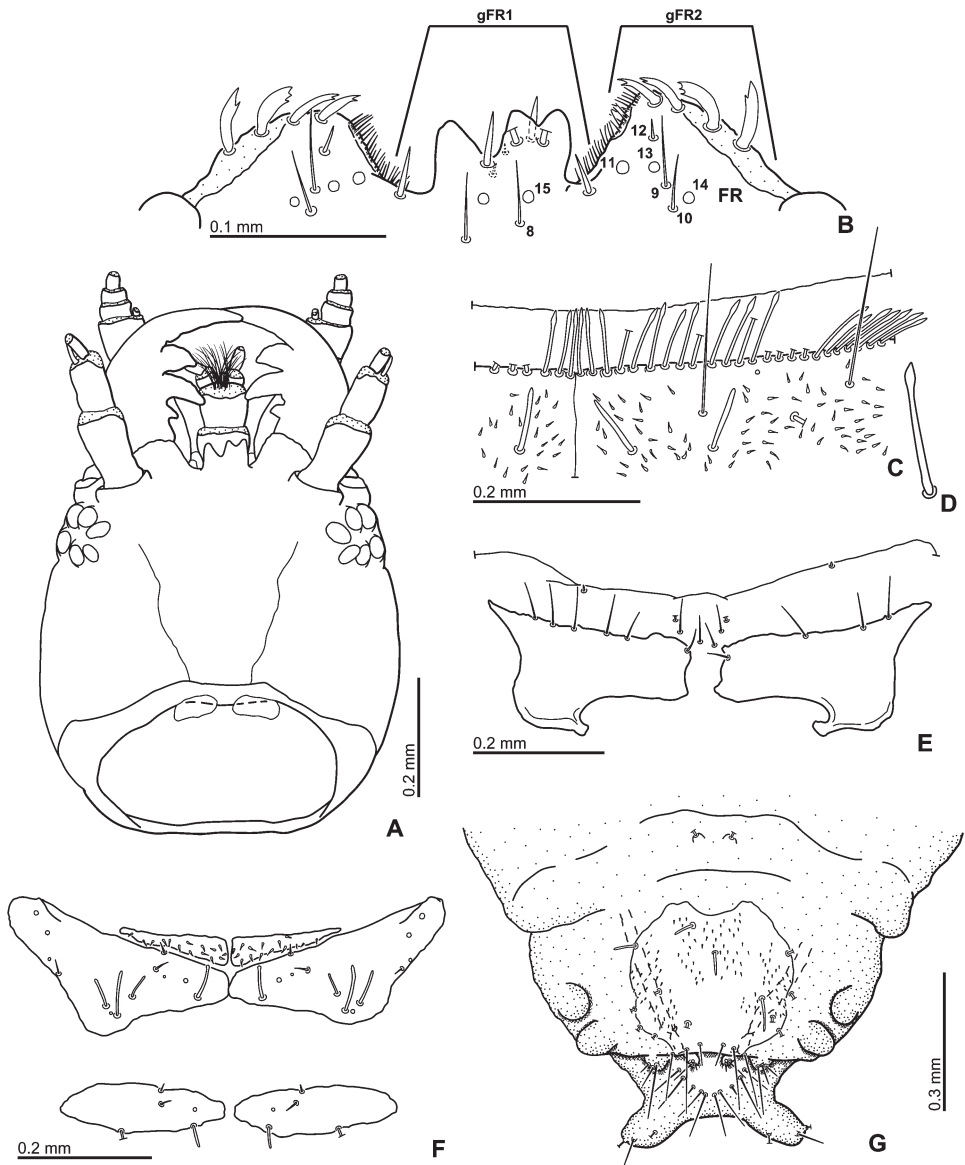
Fig. 14. *Tormus helmsi* Sharp, 1884, second (F) and third (A–E, G) instar larva. A – head, dorsal view; B – detail of anterior margin of head capsule, dorsal view; C – anterior part of dorsal surface of pronotum; D – detail of seta on anterior margin of pronotum; E – prosternum, ventral view; F – meso- and metanotal sclerites, dorsal view; G – spiracular atrium, dorsal view.
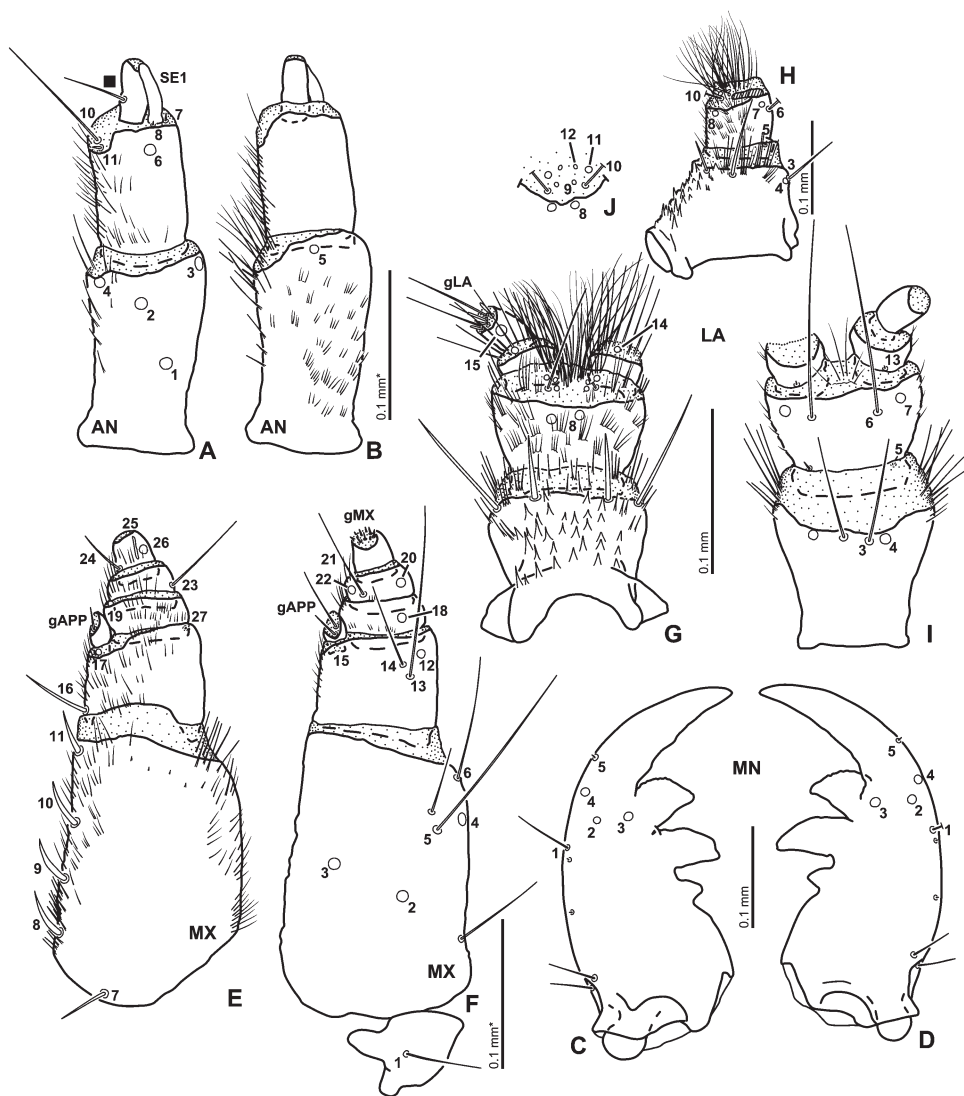
Fig. 15. Head appendages of *Tormus helmsi* Sharp, 1884, third instar larva. A–B – antenna, dorsal (A) and ventral (B) view; C–D – mandibles, dorsal view; E–F – maxilla, dorsal (E) and ventral (F) view; G–J – labium, dorsal (G), lateral (palpus omitted) (H), ventral (I) view, and detail of anteromedian surface of prementum, anterior view (J) (palpomere 2 of right palpus missing).

pore-like sensillum (MX26) apically on outer face of sclerite; MX25 dorsally, MX26 ventrally. Apical membranous area of palpomere 4 with several minute setae (gMX).

Labium (Figs 10B, 11G–I). Submentum with two pairs of setae (LA1–2) on anterolateral portion; LA1 very long situated posteriorly to LA2, LA2 short. Ventral surface of mentum with one pair of long setae (LA3) and one pair of pore-like sensilla (LA4) situated medially close to distal margin of sclerite; LA3 mesally to LA4. Prementum and its anterior membranous area with five pairs of sensilla (LA8–12) on dorsal surface and with three pairs of sensilla (LA5–7) on ventral surface. LA5–7 situated on lateral part of sclerite, LA5 very short seta, LA6 very long seta, LA7 pore-like; LA5 basally, LA6–7 apically close to distal margin of sclerite, LA7 laterally to LA6. Pore-like sensilla LA8 situated medially on borderline between sclerite and membrane; LA9–12 close to each other, on anterior membranous area of premen-tum, LA9 and LA11–12 pore-like, LA10 long seta; LA9–10 behind LA11–12, LA10 laterally to LA9; LA12 mesally to LA11. Palpomere 1 with two sensilla (LA13–14); LA13 minute seta, situated ventrally on basal part; LA14 pore-like, dorsally on intersegmental membrane between palpomeres 1 and 2. Palpomere 2 with pore-like sensillum LA15 situated subapically on outer face. Apical membranous area of palpomere 2 with several setae of variable length and shape (gLA).

Second instar. Primary sensilla of second instar larva similar to that of first instar; secon-dary chaetotaxy of second instar similar to third instar.

Parietale with five secondary sensilla. Two rather short secondary setae situated close to PA8; one posteriorly to PA8, one anteriorly to PA8; one rather short seta and one pore-like sensillum between PA9 and PA19, seta close to PA9, pore-like one close to PA19; one rather short seta between PA14 and PA15.

Mandible and maxilla (Figs 13C–F). See mandible and maxilla of third instar (some setae are missing from examined specimen, but judging from the arrangements of secondary sensilla, secondary chaetotaxy of second instar larva almost same as that in third instar).

Labium (Figs 13G–H). Dorsal surface of mentum with two or three stout secondary setae on each side, situated on distal margin of sclerite; lateral-most ones very long, median one or ones rather short.

Third instar. Very similar to second instar.

Mandible (Fig. 15C–D) with four to six secondary setae situated on outer face posteriorly to MN1; one minute close to MN1, one to two minute posteriorly to MN1, two to three rather short on basal part.

Maxilla (Figs 15E–F). Stipes bearing two secondary setae situated on ventral part of outer face; rather short one close to MX5, remaining rather long one on basal part.

Comments on the synonymy. As we explain above in the Species-level taxonomy section, we adopt here the conservative approach and distinguish only two reciprocally allopatric species of *Tormus* which are both diagnosable morphologically. The reciprocal allopatry allows us to establish synonymies of *T. helmsi* on the basis of the position of type localities of the respective species within the known range of *T. helmsi* (Fig. 16). Three species de-scribed by Broun (1893b,c, 1910), *Tormus nitidus*, *Stygnohydrus nitidus* and *Stygnohydrus femoralis*, hence become synonyms of *T. helmsi*. Of these, *T. nitidus* and *S. nitidus* belong to

the same genetically distinct clade as *T. helmsi* (which is here hence called the '*helmsi* s.str.' clade), whereas *S. femoralis* represents the North Island clade called here for that reason the '*femoralis*' clade. Remaining two clades of *T. helmsi* do not correspond to any of the original species described by historical authors, and are therefore called 'Okarito' and 'Haast' clades following their known geographic ranges.

Distribution. The species occurs in the central and southern part of the North Island (but is likely absent from the northern and eastern parts of the island) and along the western coast and in the Southern Alps Mts. of the South Island, reaching southwards to southern Westland (Haast). We have found a single male specimen localized   Reef Point, Antipodes Is., 28.ii.1969, lgt. G. Kuschel (69/70)' in the collection of NZAC. As Antipodes Islands are however more or less bare rocks without vegetation ca. 700 km southeast from New Zealand (whereas *Tormus* is shown here to inhabit forests) and as *Tormus* was never recorded from these islands before (ORDISH 1974, MARRIS 2000), we consider this specimen as mislabeled and do not list it in the material examined above.

Tormus posticalis (Broun, 1917) stat. restit.
(Figs 3–6, 9A–B)

Stygnohydrus posticalis Broun, 1917: 371. Type locality: New Zealand, Fiordland, Hollyford. Transferred to *Tormus* by HANSEN (1991: 183). Synonymized with *T. helmsi* by HANSEN (1997: 360).

Type material examined. LECTOTYPE (designated by HANSEN (1997)): unsexed specimen (BMNH):   Type [round label with red margin] // 3819 // New Zealand / Broun Coll. / Brit. Mus. / 1922-482. // Hollyford / 19.2.1914. // Stygnohydrus / posticalis // LECTOTYPE / Stygnohydrus posticalis Broun // M. Hansen des. 1995'. PARALECTOTYPES: 1 ♂, 4 unsexed spec. (BMNH):   3819. // New Zealand / Broun Coll. / Brit. Mus. / 1922-482. // Hollyford / 19.2.1914. // PARALECTOTYPE / Stygnohydrus posticalis Broun / M. Hansen des. 1995"; 1 ♂, 3 spec. (NZAC):   Coll. / T. Hall. / 19.2.1914 // Hollyford / Southland / South Island // 3819. // Stygnohydrus / posticalis / Broun. // T. Broun / Collection // A. E. Brookes / Collection // PARALECTOTYPE / Stygnohydrus / posticalis Broun, 1917 / des. M. Fikáček 2012'. [Note. The four specimens deposited in NZAC are not mentioned by HANSEN (1997) who designated the lectotype of *S. posticalis*. However, their labels correspond precisely with the original description in which T. Hall is even mentioned as the collector of the type specimens. For that reason, the specimens are clearly a part of the original type series and must be considered as paralectotypes. They were labelled accordingly by us].

Additional adult specimens examined (129 specimens). **NEW ZEALAND: WESTLAND:** 3 spec. (LUNZ): Cascade State Forest, Jackson River, elev. 30 m [44°4.99′S 168°39.117′E], 12.iv.1982, lgt. J. W. Early (LCNZ82/113; 1 ♀ (NZAC): Jackson Bay [43°58.1′S 168°36.5′E], 23.ix.1979, lgt. A. K. Walker (79/90); 1 ♀ (NMPC): Wharekai Te Kau walk, Jackson Bay, elev. 25 m, 43°58.1′S 168°36.5′E, 5.xi.2007, lgt. R. Leschen & C. Carlton (RL1293); 7 spec. (NMPC, NZAC): same locality, 12.xii.2012, lgt. Fikáček, Hájek & Leschen (NZ54). **FIORDLAND:** 1 spec. (NZAC): 2 mi. below Hollyford camp [44°44′S, 168°8′E], 10.xii.1966, lgt. A. K. Walker; 2 spec. (NZAC): 4 miles E of Milford, elev. 220 m [44°39′S, 167°59′E], 20.ii.1965, lgt. N. A. Walker; 3 spec. (NZAC): 7 miles into Hollyford valley [44°43′S 168°7′E], 20.ii.1965, lgt. N. A. Walker; 1 spec. (NZAC): Bauza Island [45°17′24″S 166°54′55″E], 27.xi.1981, lgt. C. F. Butcher (81/187); 1 ♀ (NZAC): Cascade Creek, Eglinton valley [ca. 44°53′45″S 168°5′3″E], 30.x.1966, without collector; 2 spec. (NZAC): Cleddau Valley, 44°42.9′S 167°57.4′, 2005, lgt. T. Jewell; 1 ♀ (NZAC): Dashwood Stream, Spey River, elev. 230 m [45°31′50″S 167°12′17″E], i.1970, lgt. A. C. Eyles; 2 spec. (NZAC): Deep Cove, Lydia river, elev. 213 m [45°30′21″S 167°7′49″E], i.1970, lgt. I. Townsend; 2 ♀♀ (NZAC): E slope of Mt. Lyttle, above Motoi camp, elev. 914 m [44°46′32″S 168°5′35″E], 15.xii.1966, lgt. A. K. Walker; 2 spec. (NZAC): Fiordland National Park, Deep Cove [45°26′43″S 167°8′32″E], i.1970, lgt. I. Townsend; 1 spec. (LUNZ): same locality, 3.ii.1983, lgt. D. R. Penman; 2 spec. (LUNZ): same locality, 1.ii.1988, lgt. J. W. Early; 13 spec. (LUNZ, NMPC): Fiordland National Park, Grebe valley neat NZED base, elev. 270 m [45°39′S 167°22′E],
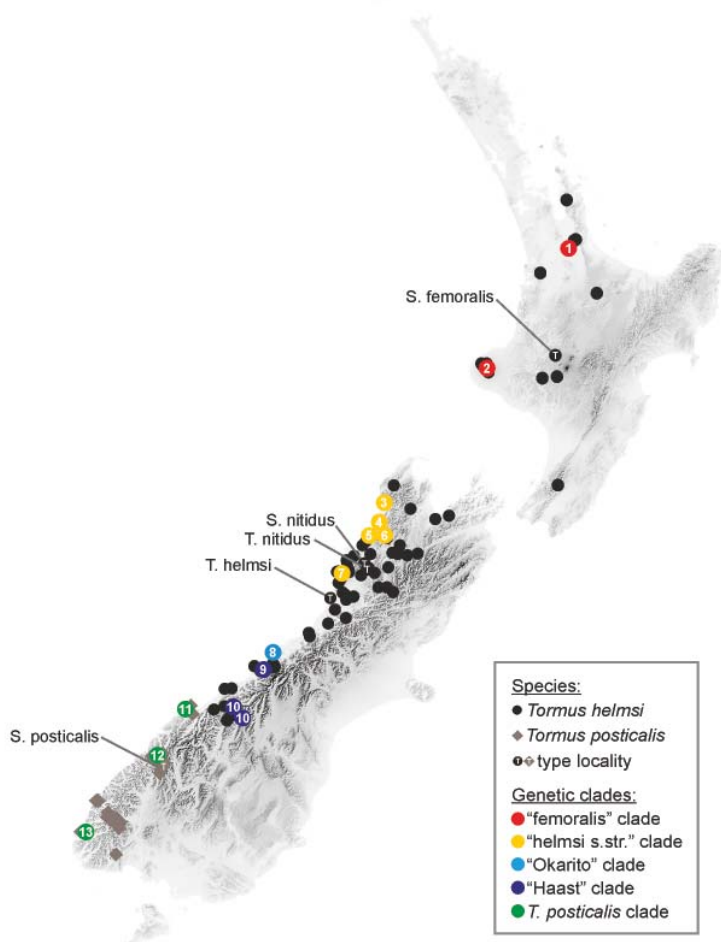
Fig. 16. Summary of known distribution of *Tormus* Sharp, 1884, combining the distribution data of the museum specimens (black and grey symbols), known distribution of genetically distict clades based on sequenced specimens (color symbols: colors and locality numbers correspond to those in Fig. 8) and the position of the type localities of all five described species of *Tormus* and *Stygnohydrus* Broun, 1893.

4.ii.1982, lgt. R. M. Emberson & P. T. Syrett; 3 spec. (LUNZ, NMPC): Fiordland National Park, S arm of Lake Manapouri [45°34′S 167°23′E], 4.ii.1982, lgt. S. P. Worner; 1 ♂, 2 ♀♀, 8 spec. (FMNH, KSEM, NMPC): Fiordland NP, Milford Sound road, Tutoko Track, elev. 70 m [40°39.5′S 167°58.7′E], 9.xii.2005, lgt. A. Newton & M. Thayer (FMHD#2005-86); 1 ♀ (JNIC): First Bay, Lake Hauroko [46°0′S 167°19.7′E], 6.i.1996, lgt. J. T. Nunn; 1 spec. (NZAC): Gut Bay [45°17.71′S 166°57.46′E], 23.xi.1981, lgt. C. F. Butcher (81/177); 5 spec. (NZAC, NHMW, ZMUC): same locality, 24.xi.1981, lgt. C. F. Butcher (81/180); 1 spec. (NZAC): same locality, 26.xi.1981, lgt. C. F. Butcher; 3 spec. (NZAC): Hollyford [44°45′34″S 168°8′26″E], 20.ii.1965, lgt. N. A. Walker; 3 spec. (NZAC): Hollyford valley, below Hidden Falls, [44°37′49″S 168°7′20″E], without date and collector; 1 spec. (NZAC): Hollyford
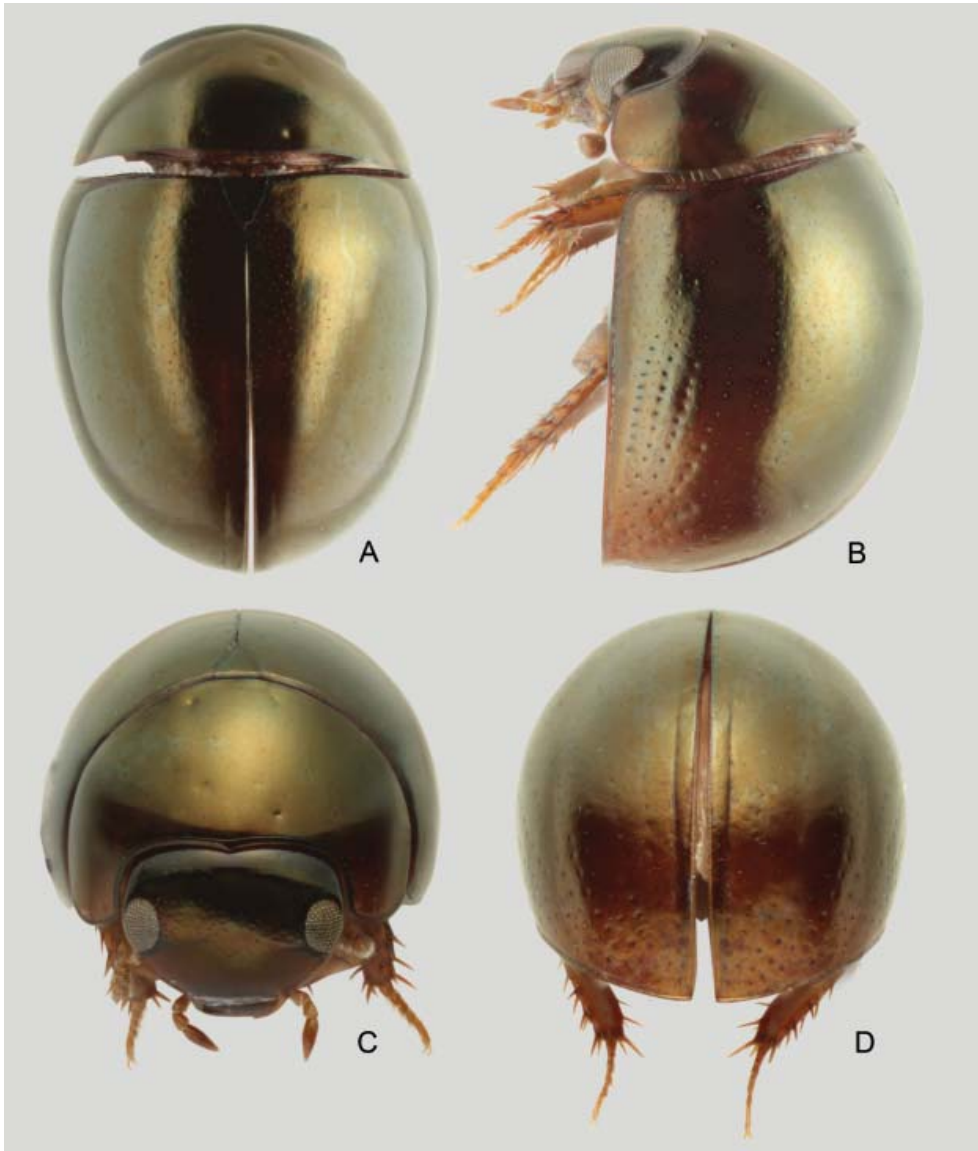
Fig. 17. Habitus of *Afrotormus minutus* Hansen, 1999 from Knysna, Diepwalle. A – dorsal view; B – lateral view; C – frontal view; D – posterior view.

valley, Hidden Falls [44°37′49″S 168°7′20″E], 6.i.1967, lgt. A. K. Walker; 1 spec. (NZAC): Key Summit, elev. 450 m [44°48′54″S 168°7′38″E], 14.xii.1966, lgt. A. K. Walker; 1 ♂ (NZAC): Lake Manapouri env., Mica Burn et West Arm, elev. 180–230 m [45°29′49″S 167°13′54″E], i.1970, lgt. G. W. Ramsay; 1 ♀ (NZAC): Lake Manapouri, Tyrret Range, Wolfe Flat, elev. 600–680 m [45°32′S, 167°18′E], i.1970, lgt. G. W. Ramsay; 29 spec. (NZAC, ANIC, DBCP, NMPC): Lake Manapouri, West Arm [45°30′43″S 167°18′22″E], i.1970, lgt. I. Townsend; 6 spec. (NZAC): Milford Road 20 mi. [44°51′S 168°6′E], 1.xi.1966, lgt. J. I. Townsend; 2 spec., 1 ♂ (NZAC): Milfourd Sound, [44°40′22″S 167°55′30″E], 1.xi.1966, lgt. J. I. Townsend; 1 ♂ (NZAC): Mt. Christina forest, elev. 320 m [44°48′S 168°6′E], 22.xii.1947, lgt. J. T. Salmon; 5 spec. (NZAC): Percy stream, Tyrret range, elev. 460 m [45°33′22″S 167°16′16″E], i.1970, lgt. I. Townsend; 1 spec. (NZAC): same locality, 11.i.1970, lgt. J. McBurney; 1 ♀ (LUNZ): Spey valley, elev. 180 m [45°32′57″S 167°12′51″E], 5.ii.1983, lgt. J. W. Early & C. A. Muir (LCNZ83/5); 1 ♂ (NMPC): Resolution Island, Acheron Passage (NE side), Dusky Sound, elev. 5 m, 45°42′37″S 166°39′2″E, 22.i.2011, lgt. S. A. Forgie (SAF044); 5 spec. (NZAC, NMPC): Secretary Island, Grono Bay Track [45°16.933′S 166°56.67′E], 1.xii.1981, lgt. C. F. Butcher (81/190).

Larval specimens examined (not described here). NEW ZEALAND: Fiordland: 2 L1, 6 L2, 5 L3 (FMNH, YMC, NMPC): Fiordland NP, Milford Sound road, Tutoko Track, elev. 70 m [40°39.5′S 167°58.7′E], 9.xii.2005, lgt. A. Newton & M. Thayer (FMHD#2005-86).

Redescription of adults. Body length 3.0–3.6 mm (holotype 3.5 mm), body width 1.9–2.2 mm (holotype 2.1 mm). Head and pronotum with sparsely arranged but rather coarse punctures, without microsculpture on interstices; elytra anteriorly with sparse punctuation consisting of punctures slightly smaller than those on pronotum, interstices smooth. Elytra evenly convex, oblique posteriorly in lateral view. Parameres of aedeagus with distinct apical hook directed laterad (Figs 9A–B).

Larvae. Larvae of this species were not examined in detail, but the basic study did not reveal any characters distinguishing them from those of *T. helmsi* described above.

Afrotormus Hansen, 1999

Afrotormus Hansen, 1999a: 146. Type species: *Afrotormus metallescens* Hansen, 1999 (by original designation).
Afrotormus: Hansen (1999b: 238, catalogue); Short & Fikáček (2011: 85, list of genera).

Diagnosis of adult. Body highly convex, not compressed from sides (Fig. 17); dorsal coloration metallic, dark but never black (Fig. 17); clypeus with anterolateral bead (Fig. 18B); clypeus with wide anterior emargination exposing the membrane between clypeus and labrum (Fig. 18B); labrum completely exposed in dorsal view (Fig. 17C); eyes not protruding; antenna with 8 antennomeres (Fig. 18H); mandibular apex with three apical teeth (Fig. 18E); prosternum extremely short in front of procoxae, bearing longitudinal carina mesally (Fig. 18G); mesoventrite divided from mesanepisterna of partly fused to them, anapleural suture indistinct to absent; anteromedian portion of mesoventrite without deep pit (Figs 19B–C); posteromedian portion of mesoventrite with narrow high triangular projection; elytron with punctural series present only posterolaterally (Fig. 17B); pro- and mesocoxae each with several strong spines ventrally, metacoxae without spines (Figs 18G, 19B–D); femora without dense pubescence even basally (Fig. 19A); basal metatarsomere ca. as long as metatarsomere 2 (Fig. 19D); abdomen with five ventrites; basal abdominal ventrite carinate mesally (Fig. 19F); abdominal laterosternite 3 with organized stridulation file (Fig. 19E); abdominal apex without apical emargination.

Afrotormus is superficially rather similar to *Tormus* and therefore also resembles some genera of the Chaetarthriini, Berosini, Anacaenini and Coelostomatini. The characters diagnosing *Afrotormus* from these groups are the same as for *Tormus* (see above), with the only exception of the number of antennomeres (8 both in *Afrotormus* and the highly globular representatives of the Berosini). *Afrotormus* further differs from all these taxa by the completely metallic dorsal coloration, which is otherwise rather rare in the Hydrophilidae (it is found in some *Paracymus* which differ from *Afrotormus* by body never highly convex, and pro- and mesofemora with dense pubescence basally, and in some *Tropisternus* Solier, 1834 which are large-sized aquatic beetles restricted to New World and having legs with swimming hairs). In South Africa, *Afrotormus* is superficially most similar to the *Grodum*-group of the genus *Anacaena* (see Hansen 1999 and Komarek & Beutel 2004 for details) with which it may even co-occur. Species of *Grodum*-group of *Anacaena* may be easily distinguished from *Afrotormus* by elytra series developed even mesally, absence of exposed membrane between anterior margin of clypeus and labrum, flat median portion of the mesoventrite and femora with dense basal pubescence.

Redescription of adult (characters in which *Afrotormus* differs from *Tormus* are marked by an asterisk). Body widely oval, highly convex* (Figs 17A–B); general coloration of dorsal surface metallic*, brown to bronze.

Head. ***Clypeus and frons*** (Figs 17C, 18B) distinctly punctate, frons and clypeus without trichobothria*, frontoclypeal suture indistinct; clypeus slightly expanded laterally, covering bases of antennae, anteromedian margin deeply excised, exposing the membrane between clypeus and labrum, lateral margins of clypeus with a bead*. ***Eyes*** small, not protruding from outline of head, separated by 3.5× width of one eye. ***Labrum*** (Fig. 18B) well sclerotized, completely exposed dorsally, widest subbasally, strongly narrowed basally and arcuately narrowing anteriad, shallowly bisinuate on anterior margin; dorsal surface without any setae*, ground punctation slightly stronger than on clypeus*; anterior margin mesally with a series of stout blunt spines; epipharynx not examined. ***Mandibles*** (Fig. 18E) with trifid mandibular apex*, otherwise not examined. ***Maxilla*** (Fig. 18F) with a large subtriangular cardo lacking trichobothria; basistipes triangular, bearing few fine setae only; mediostipes and lacinia not examined; galea with rather stout distal setae arranged into well-defined rows; maxillary palpus with 4 palpomeres, palpomere 1 minute, palpomeres 2 and 4 subequal in length, ca. 3× the length of palpomere 3; base of palpomere 4 with a group of ca. six digitiform sensilla on lateral surface*. ***Labium*** (Figs 18C–D, F) with submentum ca. half as long* and as wide as mentum, bearing sparsely arranged setae; mentum transverse, ca. 1.7× wider than long, with triangular anterior margin* and subparallel lateral margins, its surface bearing sparsely arranged setae on whole surface*, lateral margins without setae*; prementum subdivided into two membranous lobes bearing anteromedian group of long setae; labial palpus with three palpomeres, palpomere 1 minute, palpomere 2 much longer* than palpomere 3 in both sexes, modified or unmodified in males*, bearing numerous rather long and stout setae; palpomere 3 minute* without digitiform sensilla. ***Antenna*** (Figs 18H) with 8 antennomeres*, scapus conical, ca. 4× as long as pedicel*, pedicel bulbose*, antennomeres 3–5 short, subequal in length, antennomeres 6–8 forming a distinct, rather compact* and densely pubescent antennal club. ***Gula*** (Fig. 18G) narrow*, gular sutures distinctly separated*, tentorial pits rather
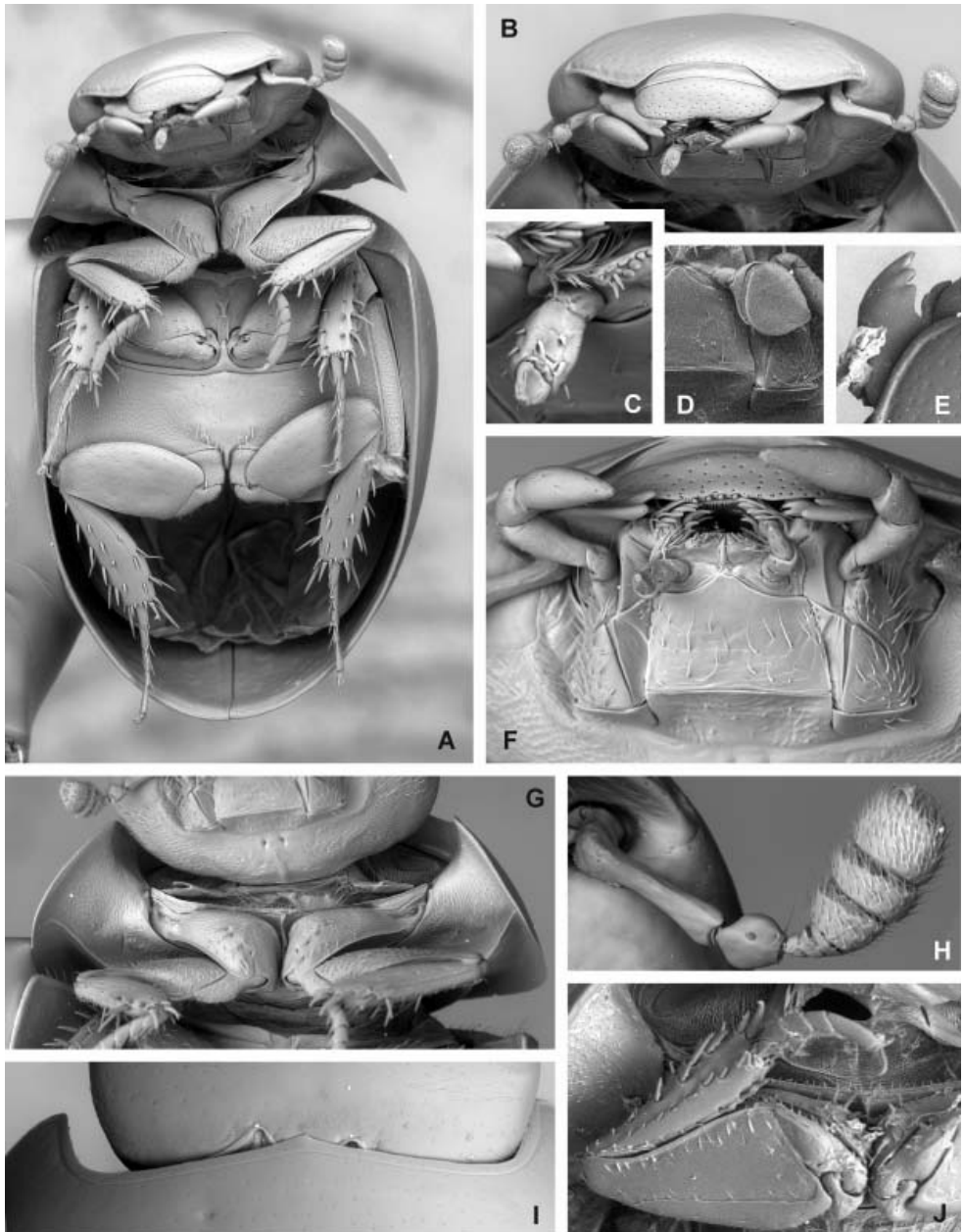
Fig. 18. Morphology of *Afrotormus minutus* Hansen, 1999 (A–D, F–J) and *A. metallescens* Hansen, 1999 (E). A – ventral view of the body; B – head in frontal view; C – male labial palpus; D – punctation of frons; E – mandible; F – ventral view of mouthparts; G – prothorax in ventral view; H – antenna; I – anterior margin of pronotum; J – prothoracic leg in ventral view.

closely aggregated, distinct, pit-like*. *Temporae* with very distinct long ridge arising from inner margin of each eye*.

Prothorax. ***Pronotum*** (Figs 17A–C, 18I) highly convex, widest subbasally, bearing weakly projecting anterior corners; surface smooth, without depressions, with distinct punctation, without trichobothria*; anterior margin sharply* angulate mesally, lateral margins forming continuous curve with posterior margin; lateral margin arcuately bent to posterior margin; marginal bead present along whole anterior and lateral margins. ***Hypomeron*** (Fig. 18G) with rather narrow lateral glabrous portion and densely pubescent median portion, portions not divided by a ridge, hypomeral process not examined. ***Prosternum*** (Fig. 18G) extremely short anterior to procoxae, ca. 0.1× as long as procoxa; mesal portion largely concealed by procoxae but strongly carinate mesally, prosternal process large, nearly completely concealed by procoxae. ***Coxal cavities*** delimited internally by median prosternal carina, open posteriorly, coxal fissure rather long, widely* open, notopleural suture distinct but very short. Accessory ridge below posterior pronotal margin very distinct, laterally reaching to lateral margin of hypomeron as a 'transverse fold'. ***Profurca*** not examined.

Mesothorax. ***Scutum*** with scutellar shield exposed, triangular, pointed posteriorly, ca. as long as wide. ***Elytron*** (Figs 17A–B) highly convex; sutural stria present, reaching ca. midlength of elytron; nine elytral series distinct only posterolaterally, obliterated anteromesally, formed of the punctures of the same size but slightly more impressed as interval punctation; scutellary stria absent; elytral trichobothria absent*, punctures of elytral intervals very fine, each bearing very fine seta; lateral edge with a narrow bead; epipleuron moderately wide anteriorly, gradually narrowing to elytra midlength, indistinct more posteriad, not subdivided into pubescent and bare portions*; ventral elytral surface not examined. ***Mesoventrite*** (Figs 19A–C) divided from mesanepisternum by distinct anapleural suture or fused, with reduced anapleural sutures; mesoventrite subtriangular in shape, widely extending laterad posteriorly; median portion of mesoventrite elevated into a narrow median crest, the crest strongly angulate in lateral view, bearing few stiff setae apically; mesoventral process narrow; anteromesal portion of mesoventrite without deep pit*; whole surface with scale-like microsculpture; trochantin not examined. ***Mesanepisterna*** not meeting anteromesally, narrowly divided by anterior portion of mesoventrite; anterior collar well-defined, moderately wide. ***Mesepimeron*** not examined. ***Coxal cavities*** obliquely transverse, not examined in detail. ***Mesofurca*** not examined.

Metathorax. ***Metanotum*** not examined. ***Metaventrite*** (Fig. 19A) slightly longer than mesoventrite*, evenly convex, with slightly elevated median portion well defined posteriorly by a blunt ridge with spines, whole surface bearing very sparse* pubescence. Postcoxal ridge very distinct. ***Metanepisternum*** ca. 8× longer than wide, without an obliquely transverse strengthened ridge anteriorly; whole surface sparsely pubescent. ***Metepimeron*** without distinct ventral portion. ***Metafurca*** not examined. ***Hind wings*** well developed or absent, not examined in detail.

Legs (Figs 18AJ, 19A, D). ***Coxae*** with few* (pro- and mesocoxae) large spines ventrally close to trochanter articulation, metacoxae bare; procoxae subtriangular*, transverse; mesocoxae transverse, rather robust mesally, narrowly separated; metacoxae narrowly transverse, subrectangular in ventral view. ***Trochanters*** with proximal parts concealed by coxae, distal subtriangular parts exposed ventrally, bearing sparsely arranged setae. ***Femora*** attached to

trochanters by their posteromesal (in meso- and metafemora) or anteromesal (on profemora) portions only, anteromesal (in meso- and metafemora) or posteromesal bases (in profemora) free, rounded or angulate; profemora sparsely pubescent ventrally (except for bare postero-basal portion), with shallow but distinct depression dorsally*, meso- and metafemora with short sparsely arranged spines; tibial grooves present, deep, defined by a high ridge ventrally and low ridge dorsally. **Tibiae** slightly longer than femora, abruptly widening subproximally, slightly widening distad; each tibia with large spines along outer face, with longest spines mesodistally. **Tarsi** with 5 tarsomeres, tarsomeres 1–4* subequal in length. All tarsomeres
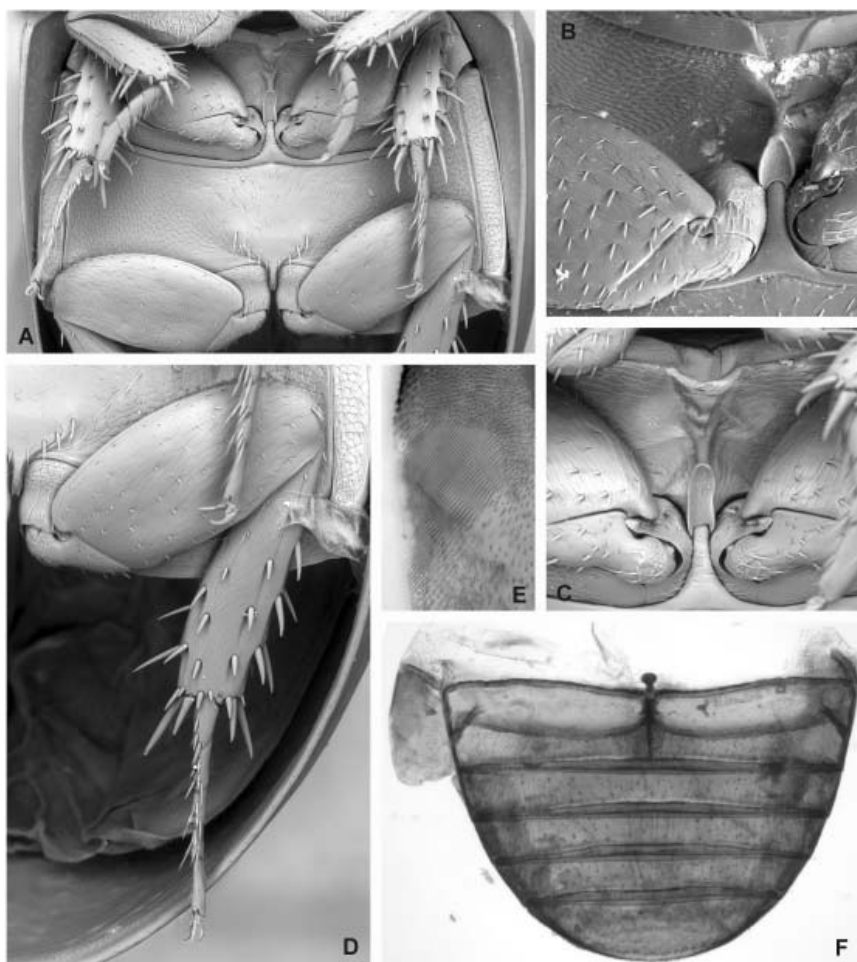

Fig. 19. Morphology of *Afrotormus minutus* Hansen, 1999 (A, C–F) and *A. metallescens* Hansen, 1999 (B). A – meso- and metathorax in ventral view; B–C – detail of mesoventrite and mesoventral process in ventral view; D – metathoracic leg; E – detail of stridulation file on abdominal laterosternite 3; F – abdomen in ventral view, with exposed left laterosternite 3.

with numerous moderately long setae ventrally and few setae of same length dorsally; claws arcuate, without subbasal tooth; tarsi and claws not sexually dimorphic.

Abdomen (Figs 19E–F) with five exposed ventrites; ventrite 1 with moderately large bare coxal grooves, remaining portion sparsely pubescent, median portion with longitudinal carina throughout*; ventrites 2–5 subequal in length, sparsely pubescent on whole surface; ventrite 5 without median emargination or group of enlarged setae posteromesally. Laterosternite 3 simple, dorsal portion not divided from ventral by a ridge, bearing an area of goose-head-shaped cuticular projections which is posteriorly organized into a stridulatory file consisting of obliquely arranged uninterrupted lamellae.

Genitalia. *Male genitalia* (Figs 20A–D). Aedeagus of simply trilobed type; parameres slightly longer* than phallobase, wide basally, widely subparallel basally*, suddenly narrowing subapically*, apices species-specific in shape; whole paramere bearing numerous pore-like sensilla; median lobe slightly shorter than parameres, widely subrectangular in apical portion, slightly angulate on apex, apodemes rather long and reaching into phallobase, gonoporus apical; phallobase with moderately large but rather indistinctly detached manubrium. Sternite 9 wide basally, strongly narrowing apicad into a narrow long projection*, with long subbasal lateral struts. Sternite 8 not examined. *Female genitalia* not examined.

Biology. Terrestrial. Based on label data of known specimens, they were sifted from forest leaf litter and fynbos litter, or found under stones. Larvae are unknown.

Distribution. The genus is endemic to the Western Cape Province, Republic of South Africa (Fig. 20I).

Key to *Afrotormus* species

1   Body larger, 2.8–3.0 mm long. Anapleural sutures of mesothorax distinct (Fig. 19B). Mesoventral plate wider (19B). Male labial palpi modified, bearing widened palpomeres 2–3 and a large membranous lobe on palpomere 3 (Figs 18D, 20E–F). Hind wings absent. Apical portion of parameres very narrow (Fig. 20A). ..... *A. metallescens* Hansen, 1999
–   Body smaller, 1.8–2.0 mm long. Anapleural sutures completely reduced (Fig. 19C). Meso-ventral plate narrow, parallel-sided (Fig. 19C). Male labial palpi not modified, similar to that of female (Figs 18C, 20G–H). Hind wings present. Apical portion of parameres widely rectangular (Figs 20G–H). .... *A. minutus* Hansen, 1999

Afrotormus metallescens Hansen, 1999
(Figs 18D–E, 18J, 19B)

Afrotormus metallescens Hansen, 1999a: 147. Type locality. Republic of South Africa, Western Cape Province, Heuningnes River, 34.42°S 20.02°E.

Type material examined. HOLOTYPE: ♂ (TMSA): 'S. Afr., S. W. Cape / Heuningnes Riv. / 34.42 S – 20.02 E // 28.10.1983; E-Y: 2030 / from under stones / leg. Endrödy-Younga // HOLOTYPE / Afrotormus metallescens / M. Hansen'. PARATYPE: ♀ (ZMUC): same locality data, but with type label 'PARATYPE / Afrotormus / metallescens / M. Hansen'.
Additional material examined. None.

Diagnosis. Dorsal coloration brown to dark brown, with bronze metallic reflections; sides of pronotum and elytra and whole ventral portion and appendages reddish. Head and pronotum

with rather distinct punctuation consisting of simple punctures; elytral punctures slightly smaller but still distinct. Male labial palpi modified, widened, palpomere 3 with large transparent disc; female labial palpi simple. Mesoventrite divided from anepisterna by distinct anapleural suture; mesoventral plate ca. 1.6× longer than wide, with weakly convex lateral margins. Hind wings not developed. Aedeagus with phallobase slightly shorter than parameres, parameres subangulate in apical fourth of outer margin, apex narrowed into a hook-like apex. Male sternite 9 wide basally, projecting as a narrow median projection mesally.

Distribution. Republic of South Africa: Western Cape. Known only from the type locality.
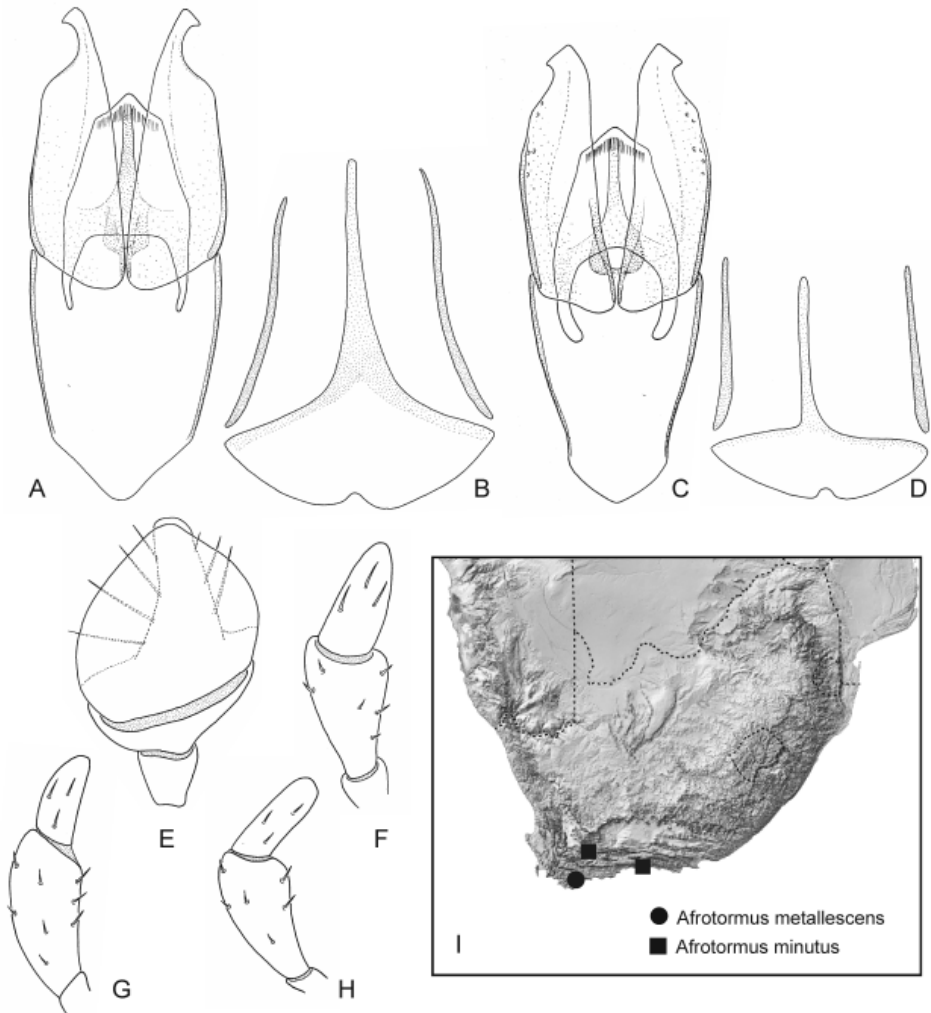

Fig. 20. Morphology (A–H) and distribution (I) of *Afrotormus* species. A–D – male genitalia (A, C – aedeagus; B, D – male sternite 9): A–B – *A. metallescens* Hansen, 1999; C–D – *A. minutus* Hansen, 1999. E–H – labial palpus (E, G – male; F, H – female): E–F – *A. metallescens*; G–H – *A. minutus*.

Afrotormus minutus Hansen, 1999

(Figs 18A–C, 18F–I, 19A, 19C–F)

Afrotormus minutus Hansen, 1999: 148. Type locality: Republic of South Africa, Western Cape Province, Langeberge Mts., Bossmansbos, 1050 m a.s.l., 33.56°S 20.53°E.

Type material examined. Holotype: ♀ (TMSA): 'S. Afr., Langeberge / Bossmansbos, 1050m / 33.56S – 20.53E // 9.3.1979, E-Y: 1563 / sift. forest litter / leg. Endrödy-Younga // Holotype / Afrotormus minutus / M. Hansen'.
Additional material examined. SOUTH AFRICA: Western Cape: 1 ♂ (FMNH): Knysna, Diepwalle, fynbos litter, 18.xii.1981, leg. S. Peck (FMHD#81-722).

Diagnosis. Dorsal coloration metallic bronze; sides of pronotum and elytra and whole ventral portion and appendages reddish. Head and pronotum with very fine punctuation, that of clypeus and pronotum with colon-like punctures, that of elytra simple. Male labial palpi not modified, similar to that of female. Mesoventrite not divided from anepisterna, anapleural suture reduced; mesoventral plate ca. 2.6× longer than wide, with parallel lateral margins. Hind wings well developed, but not examined in detail. Aedeagus with phallobase slightly shorter than parameres, parameres arcuate on outer margin, apex widely rectangular. Male sternite 9 wide basally, projecting as a narrow median projection mesally.
Distribution. Known only from two localities in the Western Cape Province which are ca. 240 km from each other.

Discussion

Phylogenetic position of *Tormus* and *Afrotormus*. In his revision of hydrophilid genera, Hansen (1991) placed *Tormus*, together with several other New Zealand endemic genera, in the new sphaeridiine tribe Tormissini. The Tormissini was considered monophyletic based on the following shared characters: (1) labrum well sclerotized and exposed, (2) antennal club compact, (3) mesoventrite with the anteromedian pit, (4) antennal pedicel not conical, (5) accessory ridge behind posterior pronotal margin reaching posterolateral corners, (6) anteriorly shortened elytral stria 10, and (7) elytral stria 10 diverting from lateral margin. Later, in assigning the newly described *Afrotormus* to the Tormissini, Hansen (1999a) remarked the genus was rather similar to *Tormus* and has   all diagnostic features of Tormissini … except that the antennae are 8-segmented'.

Tormus substantially differs from the rest of the Tormissini in its head morphology (particularly the mouthparts), which is extremely modified in all tormissine genera but *Tormus*. Moreover, some of the above tormissine diagnostic characters are in fact only present in *Tormus* or *Afrotormus* but not in remaining Tormissini: antennal pedicel globose (elongate in other Tormissini) and elytral stria 10 shortened anteriad and diverging from lateral elytral margin (slightly shortened and divergent only in *Exydrus* Broun, 1886, complete and not divergent in *Hydrostygnus* Sharp, 1884 and *Tormissus* Broun, 1893). These differences suggested that *Tormus* was not closely related to other Tormissini. This was subsequently confirmed by a multigene phylogenetic analysis of the Hydrophilidae performed by Short & Fikáček (in press) in which *Tormus* was revealed as related to the genus *Paracymus* within the tribe Laccobiini. Two morphological characters of phylogenetic importance support this placement of *Tormus*: (1) the presence of the organized stridulatory file on laterosternite 3, and (2) the morphology of mesofurca. An organized stridulatory file (i.e. with parallel lamelae,

Figs 6C, 19E) is only known in three groups of the Hydrophilidae: Berosini, Laccobiini and a subclade of the Hydrobiusini (see SHORT & LIEBHERR (2007) for the details on the latter). Long mesofurcal arms reaching lateral body wall (as in *Tormus*) are present in the Laccobiini, Berosini, Hydrobiusini, Hydrophilini and *Amphiops* Erichson, 1843 (and are absent from all remaining groups of Hydrophilidae). Moreover, the morphology of mesofurcal arms (i.e. directed dorsolaterad and bearing disc-like widening at midlength) corresponds with the morphology found in *Paracymus relaxus* (whereas in *Laccobius* the arms are directed rather dorsad, and in *Laccobius*, *Berosus* and *Hydrobius* Leach, 1815 they lack disc-like widenings at midlength). In addition, the position within the Laccobiini is supported by the combination of the following adult characters: (1) labrum well sclerotized and exposed (present in more groups of Hydrophilidae); (2) labrum excised anteriorly with exposed membrane between clypeus and labrum (present in *Paracymus*, some Hydrophilini and some *Enochrus* Thomson, 1859), (3) coxae with strong spines ventrally (present in many *Paracymus* and *Oocyclus*), and (4) basal metatarsomere only slightly shorter than metatarsomere 2 (also found in many *Paracymus*; the basal metatarsomere is usually much shorter than metatarsomere 2 in the Hydrophilidae except most Sphaeridiinae).

Larvae of *Tormus* are very similar to those of *Paracymus* in many characters (see ARCHANGELSKY (1997, 1999a) for details on morphology of *Paracymus* larvae): (1) mandible with three inner teeth; (2) antennal sensorium as long as antennomere 3; (3) frontal lines reaching posterior margin of the head; (4) maxillary palpomere 1 rather long; (5) slightly asymmetrical nasale with distinct large teeth; and (6) rather large nearly symmetrical epistomal lobes. ARCHANGELSKY (2004) listed the presence of the cuticular spines on inner face of the stipes as a synapomorphy for *Oocyclus + Laccobius + Paracymus* clade. The larva of *Tormus* corresponds with the above genera in this character, but the cuticular projections are hair-like instead of spine-like. On the other hand, larvae of both *Tormus* and *Paracymus* strongly differ from those of *Laccobius* and *Oocyclus* in head morphology (the latter two genera have strongly asymmetrical mandibles and clypeolabrum, rather short first maxillary palpomere, antennal sensorium shorter than antennomere 3, see ARCHANGELSKY (1997) for details). These differences correspond to the inner topology of the Laccobiini revealed by molecular data (SHORT & FIKÁČEK, in press), in which two main clades (*Laccobius*-group containing both *Laccobius* and *Oocyclus*, and *Paracymus*-group containing both *Tormus* and *Paracymus*) were recognized.

Colonization of terrestrial habitats by *Tormus* and *Afrotormus*. The sister-group relationship of *Tormus* and *Afrotormus* proposed by HANSEN (1999a) is supported by several characters including one unique feature: (1) prosternum is extremely reduced and nearly completely concealed by procoxae (unique within Laccobiini, similar morphology is only known in some Chaetarthriini), (2) anterior margin of pronotum angulate (unique within Hydrophilidae), (3) elytra with striae preserved only posterolaterally (present only in some genera of the Chaetarthriini and Anacaenini), and (4) femora without dense basal pubescence. The morphology of the aedeagus is also similar in both genera, and the presence of the hook on the parameral apex is shared by both *Afrotormus* species and the basalmost species of *Tormus* (*T. posticalis*). This may indicate that the presence of the apical hook on the paramere may also be a synapomorphy of both genera. Additionally, the morphology of the median process of the mesoventrite is very similar in both genera and clearly differs from the state present in most Laccobiini in which the mesoventral process is very distinctly arrow-shaped.

Based on these shared characters, it seems likely that *Afrotormus* + *Tormus* form a clade and represents an independent transition to terrestrial habitats within the Hydrophilidae. On the other hand, some of the characters in which *Afrotormus* and *Tormus* differ from each other vary also within *Paracymus* (e.g., number of antennomeres, presence/absence of median carina on the abdominal ventrite 1, presence/absence of the median pit on the mesoventrite). An alternative scenario is that *Tormus* and *Afrotormus* are solely morphologically unusual terrestrial representatives of *Paracymus* (much in the way the anacaenine genera *Grodum* Hansen, 1999 and *Enigmata* Hansen, 1999 are derived lineages of *Anacaena* Thomson, 1859, see KOMAREK & BEUTEL 2007) and characters listed above as synapomorphies would then be interpreted as convergences associated with terrestrial life style. The sister-group relationship of *Tormus* and *Afrotormus* and their relationship to *Paracymus* need to be tested by a formal phylogenetic analysis which would include a wide sampling of *Paracymus* species.

Two morphological trends known from other hydrophilid terrestrial groups are observed in *Tormus* and *Afrotormus*: (1) the reduction and loss of trichobothria, and (2) the tendency of the mesoventrite to fuse with the mesanepisterna. The sequential loss of the trichobothria was shown recently to be correlated with the habitat shift to terrestrial habitats in the Hydrophilidae and Helophoridae and trichobothria were hypothesized as primarily functional in aquatic environment only (FIKÁČEK et al. 2012b). In *Tormus*, the trichobothria are present but their basal sockets are retracted below the surface of the body, even though the socket morphology is doughnut-shape as in most aquatic Hydrophilidae. This may correspond to the fact that mossy microhabitats are often highly saturated by water especially in areas of high rainfall in much of western New Zealand, and the function of trichobothria and formation of an air bubble is still required during times of microhabitat flooding. In *Afrotormus*, trichobothria are completely absent from all body parts. Fusion of the mesoventrite with mesanepisterna and the corresponding loss of the anapleural sutures is typical for a number of terrestrial taxa (all higher Sphaeridiinae, *Petasopsis* Hansen, 1995 in the Borborophorini and *Micramphiops* Short, 2009 in the Chaetarthriini). Clear anapleural sutures are present in *Tormus* and *Afrotormus metallescens*, whereas they are obliterated in *A. minutus*. Based on the two character systems, *Afrotormus* is more terrestrialized' than *Tormus*.

Larvae of *Tormus* are terrestrial, inhabiting the same habitats as adults. When compared with known larvae of *Paracymus* (which are aquatic to semiaquatic: ARCHANGELSKY 1997, 1999a), the most apparent difference is the dense pubescence present in the mouthparts of *Tormus* (inner face of antennae and maxillae and dorsal and lateral faces of labium) and the absence of the ligula (which is present in all known larvae of *Paracymus*). The presence of such pubescence is unique for *Tormus* within the Hydrophilidae. The pubescence on the maxillary stipes seems to be derived from spine-like cuticular projections, which are covering its inner face in all known larvae of Laccobiini (ARCHANGELSKY 2004, see also above). The densest and longest pubescence is found between labial palps, on the place of the reduced ligula, which somewhat resembles the situation in the sphaeridiine tribe Megasternini in which a large densely pubescent hypopharyngeal lobe' is present on the place of the reduced ligula (a similar lobe but likely of different origin is also present in *Sphaeridium* Fabricius, 1775 and some *Dactylosternum* Wollaston, 1854 in which the ligula is present; ARCHANGELSKY 1997). ARCHANGELSKY (1999b) supposes that the dense pubescence of the hypopharyngeal lobe may help with absorption of the preorally digested prey (i.e. preorally digested small invertebrates) and/or to filter the small

particles which may be mixed with the food. The function of the dense pubescence of the *Tormus* mouthparts may be analogous. Of the other larval adaptations for terrestrial life listed by Archangelsky (1999b), only a slight reduction of legs is present in *Tormus*: legs are rather short, not or only slightly seen in dorsal view, but still have the complete number of five segments. Another unusual character of *Tormus* larva is the morphology of the abdominal segment 9 (i.e. the posterior portion of the spiracular atrium), which bears two apparent lobes (Fig. 14G). This contrasts to the simple unilobate abdominal segment 9 known in larvae of all groups of the Hydrophilidae (Archangelsky 1997; Minoshima & Hayashi 2011a,b, 2012) with the only exception of those of the tribe Omicrini (*Omicrus* Sharp, 1879: Hansen & Richardson 1998; *Peratogonus* Sharp, 1884: Hayashi 1986). *Tormus* is not closely related to the Omicrini and the observed similarity is undoubtedly due to convergence. Both *Tormus* and Omicrini larvae are terrestrial, but it is unclear at the moment whether the unusual abdominal morphology may have something to do with their similar lifestyle.

Biogeography of *Tormus* in New Zealand. Both species of *Tormus* are wingless, and therefore, the genus may be a model taxon to examine biogeographic patterns in New Zealand. *Tormus posticalis* is restricted to Fiordland while *T. helmsi* is located mostly west and north of the Alpine fault (see Heads 1998), a distribution also matching other taxa, for example, the majority of wingless species of the genus *Priasilpha* Broun, 1893 (the *P. angulata* clade in the South Island, Leschen & Michaux 2005) and roughly corresponding to the Buller/Takaka terranes, New Zealands oldest rocks dating from the Cambrian to Devonian (Wandres & Bradshaw 2005, Liebherr et. al. 2011). It would be tempting to consider *Tormus* an ancient lineage, with links to southern Gondwana (e.g. see supplemental information in Bunce et al. 2009) but to determine age would require a global phylogeny of hydrophilid genera and *Paracymus*, its likely sister group.

While isolation by distance does not fully explain population structure as in some other New Zealand beetle taxa (e.g. see Leschen et al. 2008), the presence of environmental or geographic barriers may have contributed to the formation of some or all of the major five clades of the two species. *Tormus posticalis* is restricted to Fiordland and is edge-limited by the Arawhata River Valley that drains into southern Westland from northern Fiordland. As indicated in our haplotype trees, there is a south to north spread of taxa that indicate *Tormus* may have originated in the southern portion of the South Island (a potential refugium, see Marske et al. 2012) and spread northward, eventually forming a monophyletic haplogroup in the North Island. The '*T. helmsi* s. str.' haplogroup is restricted to the westward portion of the Northwest Nelson and south into the Paparoa Range, and may be indicative of another glacial refugium, but more intensive genetic sampling is required to reconstruct phylogenetic history and patterns of fragmentation that have occurred within the Pleistocene (e.g. Marske et al. 2011, 2012).

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