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## Chrysomelid males with enlarged mandibles: three new species and a review of occurrence in the family (Coleoptera: Chrysomelidae)

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### Abstract

Three new species of Chrysomelidae with extraordinary extensions of the male mandibles are described: *Scaphodius drehu* **sp. nov.** and *S. ferox* **sp. nov.** (Cryptocephalinae), from New Caledonia, and *Chaloenus gajah* **sp. nov.** (Galerucinae), from Borneo. Designation of the type species of *Chaloenus* Westwood, 1861, is clarified. Synonymy of *Scaphodius* Chapuis, 1874, with *Nyctra* Baly, 1877, is supported. Four species of *Ditropidus* Erichson, 1842, described from New Caledonia, but hitherto regarded as *nomina nuda*, are shown to be available and are placed in *Scaphodius*: *S. aeneus* (Fauvel, 1907), **comb. nov.**, *S. nitidus* (Fauvel, 1907) **comb. nov.**, *S. striolatus* (Fauvel, 1907) **comb. nov.**, *S. sulcatus* (Fauvel, 1907) **comb. nov.** *Ditropidus opacicollis* Fauvel, 1907, is also transferred to *Scaphodius*, as *S. opacicollis* (Fauvel) **comb. nov.** The genus *Ditropidus* does not occur on New Caledonia.

Male mandible enlargement in the Chrysomelidae is reviewed: it is common in Cryptocephalinae, but otherwise restricted to a few species of Chrysomelinae, Eumolpinae and Galerucinae. Possible reasons for its distribution in the Chrysomelidae are discussed.

**Key words:** leaf beetle, Cryptocephalinae, Galerucinae, taxonomy, sexual dimorphism, mandible, agonistic behaviour, Borneo, New Caledonia

### Introduction

For several years the senior author (CAMR) has been ‘sitting on’ specimens of unusual species of leaf beetle discovered in museum collections. Originally it was intended to include these species within generic revisions, but it seems unlikely that these objectives will be realised, as discussed below. Therefore, we describe the species here and summarise the distribution of similar features in Chrysomelidae.

One species was discovered as a unique specimen in the Zoological Museum, Bogor (ZMB), while CAMR was employed to sort the Coleoptera collection in 1999. It belongs to the south-east Asian genus *Chaloenus*, unusual for the sexual dimorphism displayed by some species and the non-alticine appearance of these flea-beetles. The senior author had collected several new species of *Chaloenus* in Borneo 1996–1997, and was considering a generic revision. Since then many new species have been described, especially from Borneo, and two generic revisions published (Medvedev 2002, 2004, 2007; Takizawa 2012). The ZMB specimen, with its unique mandibular horns, remains unknown to both these authors and is described below.

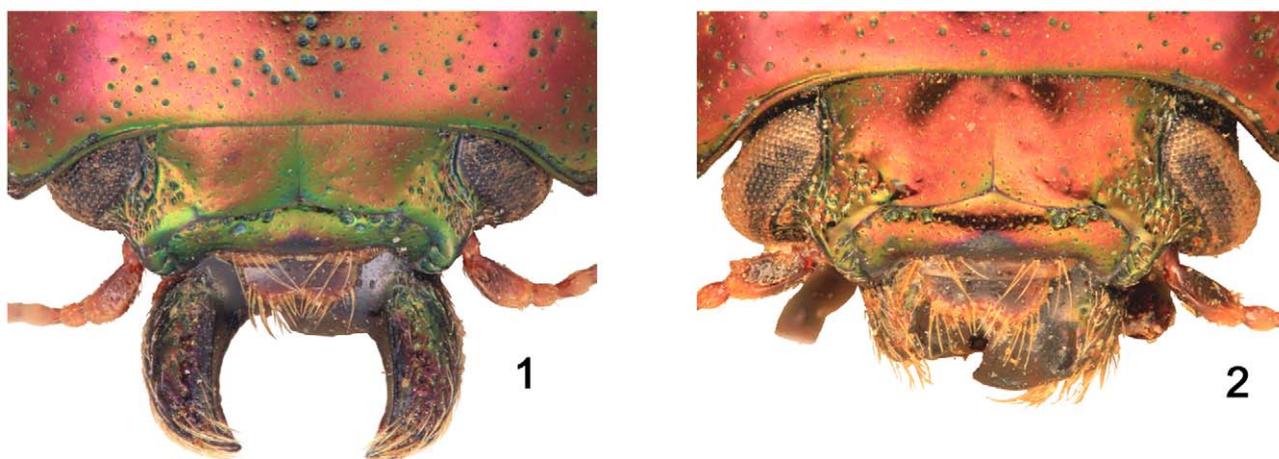
Another species was discovered amongst material of *Scaphodius* loaned from the Bishop Museum, Hawai’i, for CAAMR’s doctorate on Cryptocephalinae (awarded more than 20 years ago). This species is remarkable for the asymmetric mandibular horn in the single male specimen. The senior author’s original intention was to revise *Scaphodius*, endemic to New Caledonia, but what at first appeared to be a relatively small genus has become greatly expanded by availability of additional material from other sources. We are aware of at least 50 species in *Scaphodius*, requiring a major study for which time is lacking. A few of these species have been described recently (Schöller 2009). *Scaphodius* shows extreme sexual dimorphism in some species, perhaps more than any other taxon in the Cryptocephalinae. The new species is described below together with another unusual species, recently collected.

Mandibular sexual dimorphism is frequent in Chrysomelidae, but has not been reviewed. It is particularly associated with clytrine Cryptocephalinae (Monrós 1953; Agrain, Roig-Junent & Dominguez 2007; Agrain & Roig-Junent 2011), but occurs more widely, for example in Chrysomelinae (Figs 1–2). The distribution of mandibular sexual dimorphism in Chrysomelidae is reviewed below and its function discussed.

## Methods

Genitalia were dissected from abdomens washed in water after being soaked in cold 10% KOH overnight. After examination they were stored in glycerol in a microvial, pinned with the rest of the specimen. Morphological terminology is based on Lawrence, Beutel, Leschen & Slipinski (2010).

Abbreviations: BPBM (Bernice P. Bishop Museum, Hawai'i); c. (circa); MHNP (Natural History Museum, Paris); WUP (Wroclaw University, Poland); QMB (Queensland Museum, Brisbane); ZMB (Zoological Museum, Bogor).



FIGURES 1–2. *Callidemum cornutum* Baly. 1, male head, dorsal; 2, female head, dorsal.

## Taxonomy

### Subfamily Galerucinae

#### *Chaloenus* Westwood 1861: 216

Type species: *Chaloenus latifrons* Westwood, by subsequent designation (Wilcox 1973)

**Diagnostic description** (based on Takizawa, 2012, and examination of 12 species). Small to medium sized alticine, length 3–8mm; head deflected at antennal insertions, especially in males, with genae and clypeus elongated; genae long, 0.5–2.0x eye length; male frontoclypeus without pits, setose foveae, tubercles or spines; postantennal calli well-defined, adjacent, convex, triangular to rectangular; antennal insertions close, separated by less than socket diameter; first antennomere greatly elongated, much longer than eye, second short, third elongated; labrum with truncate or convex apical margin; apical maxillary palpomere conical, shorter and narrower than pre-apical; pronotum strongly transverse, width 1.5–2x length, broadest at anterior half (usually at anterior angles); pronotum with or without discal depressions (not sharply defined); anterior pronotal border usually absent; procoxae strongly protruding, adjacent; prosternal process narrow but present between coxae; procoxal cavities closed by insertion of hypomera into apex of prosternal process; elytra non-striate to striate, rarely partially costate; elytra glabrous or with scattered erect setae; epipleuron broad at base (0.15–2x elytral width), gradually narrowed, upper and lower margins fusing well before elytral apex; mesoventrite process almost triangular, with truncate

apex; metaventricle without posterior lobes between hind coxae; metafemur 1.5–2x width mesofemur, with internal folded extensor endosclerite for jumping; tibiae rarely sharply ridged externally, without apical spurs; length of first metatarsomere slightly shorter to slightly longer than 2+3; third tarsomere deeply bilobed; tarsal claws appendiculate with basal lobe large and acute; ventrites not laterally ridged; male last ventrite trilobate, with two slots defining median apical lobe; female last ventrite simple; penis elongate-cylindrical with expanded basal foramen, apex symmetrical.

**Notes.** The original paper erecting *Chaloenus* was published in issue ‘IV’ of the *Journal of Entomology*, dated December, 1861 (Westwood 1861). The statement that Medvedev “erroneously dated it as 1861” (Konstantinov & Prathapan 2008: 391) is therefore incorrect. Furthermore, the genus was originally credited with two species, both new, one described by Westwood and one by Baly. A type species was not clearly designated and the genus was not monotypic, therefore the statement by Wilcox (1973: 656), that *C. latifrons* Westwood is the type species by monotypy, was erroneous. Ironically, Wilcox’s statement constitutes a type species designation in itself (International Code of Zoological Nomenclature 1999, Art. 69.1.1), which is *C. latifrons* Westwood, by subsequent designation of Wilcox. This was overlooked by Konstantinov & Prathapan (2008), who unnecessarily made the same designation.

Konstantinov & Prathapan (2008) synonymised *Priostomus* Jacoby, 1884, with *Chaloenus*. The genus *Chaloenus* has recently been revised (Takizawa 2012) with these two concepts, *Chaloenus* and *Priostomus*, retained as subgenera, separated primarily by antennal proportions.

*Chaloenus* is one of many genera of the leaf beetle subfamily Galerucinae with greatest diversity on the Sunda Shelf of south-east Asia. There are 42 described species (Takizawa 2012), 36 of which are recorded from Borneo. The new species described below is also Bornean and belongs to the nominate subgenus.

### ***Chaloenus gajah* sp. nov.**

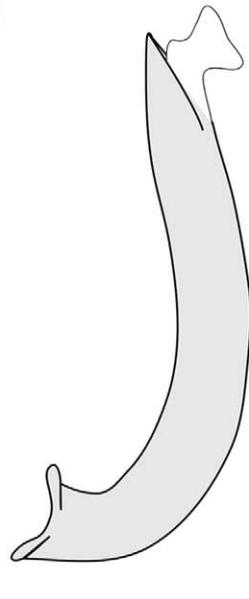
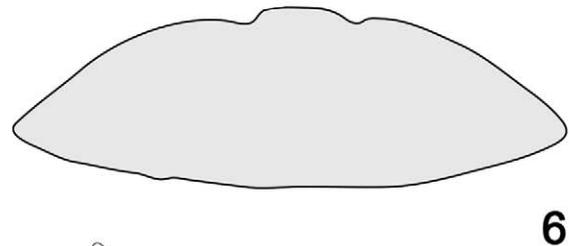
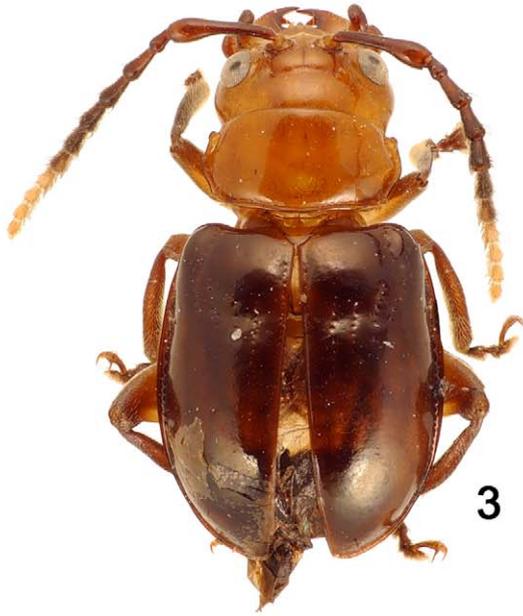
(Figs 1–6)

**Material examined.** Holotype: m/ [INDONESIA] East Borneo, Balikpapan, Wain River [c.1°06’S 116°49’E], 50m, xi.1950, A. M. R. Wegner/ (ZMB).

**Description** [slightly teneral male; female unknown]. Length 6.5mm. Colour: entirely yellowish-brown to orange-brown, except antennomeres 8–11 white, mandibular teeth, lateral edges of buccal cavity, antennomeres 1–7, elytra (but not edges of basal half), tibiae, tarsomeres 1–3 dark brown to almost black (elytra and antennomeres 4–7 darkest). Abdominal ventrites densely and finely setose.

Head (Figs 1–3): impunctate or almost so, vertex shining, not microsculptured, frontoclypeus dull with fine microreticulation; head glabrous, except trichobothrium between postantennal callus and eye, short recumbent setae between antennae and buccal cavity and on upper surface of mandibles; frontoclypeus slightly ridged between antennae, otherwise almost flat with truncate apical margin; antennal cavities large, separated from each other and from eyes by about 0.75x socket diameter; postantennal calli elevated, well-defined, transverse, adjacent for entire length; eyes small, situated dorsally on head not laterally, oval, separated by c. 3x eye length; gena long, equal to eye length; antennae c. 0.75x body length, reaching apical third of elytra if reflexed, all segments elongate but decreasingly so from 3–10, and 8–11 moniliform in shape, antennomere 1 greatly elongated (length 2x eye length) and expanded at apex; relative lengths of antennomeres 1–11, as ratios of the shortest (10): 5, 1.25, 2, 1.9, 1.75, 1.5, 1.35, 1.25, 1.15, 1, 1.35; labrum large, semicircular, with 2 pairs of large setae; mandibles symmetrical, upper surface setose, elongated, laterally swollen at base, with vertical blunt tipped horn in middle of base and three apical teeth (visible ventrally); apical maxillary palpomere elongate-conical, about half length of penultimate.

Thorax: pronotum and hypomera shining, unmicrosculptured, minutely and sparsely punctured, glabrous except trichobothrium in each angle; pronotum transverse, broadest anterior to middle, width c. 2x length, all angles slightly produced; pronotal disc convex but with pair of small circular depressions at sides; anterior edge truncate, not margined, sides strongly margined, sinuate, hind edge strongly margined, shallowly convex; prosternum glabrous, prosternal process reduced to a thin ridge between coxae, triangularly expanded at apex;



**FIGURES 3–8.** *Chaloenus gajah* sp. nov., male holotype. 3, habitus; 4, head, antero-lateral; 5, head, dorsal; 6, apical ventrite; 7, penis lateral, ventral; 8, tegmen dorsal.

procoxal cavities closed, by elongate hypopleural lobes reaching apex of prosternal process; scutellum triangular; elytra shining but outer half finely microreticulate, glabrous except 5–6 setae at apices; each transversely depressed a third from base, from suture to slightly more than half width, with groove from this to base at inner margin of humerus; elytra impunctate except: finely punctured sutural striole, 4 short striae of large punctures in transverse depression, the fourth reaching elytral base; epipleura with upper margin elevated, broad at base, narrowing to a single elytral edge before apex; mesoventrite glabrous, other ventral mesothoracic sclerites finely and densely setose; mesoventrite process elongate triangular (but appearing slightly shrivelled); ventral metathoracic sclerites finely and densely setose (metaventrite shrivelled); procoxae globular, strongly projecting; femora glabrous or almost so on basal half, remainder of leg densely and finely setose; pro- and mesofemora almost parallel-sided, metafemora elongate-ovate, width c. 1.5x mesofemur; pro- and mesotibiae externally weakly ridged in basal half, metatibiae expanded at middle and sharply ridged for basal 2/3; length hind tarsus c. 0.5x hind tibia; first metatarsomere slightly shorter than 2+3, fifth as long as first; claws appendiculate, small right-angled basal lobe.

Abdomen (Figs 5–8): ventrites weakly sclerotised, without lateral keels; male: apex of last ventrite weakly medially lobed, shallowly excavate either side of lobe; penis basal foramen circular, thick lipped, shaft cylindrical, sharply reflexed at base then straight, to semi-circular apex; endophallic sclerite thin with poorly defined base; tegmen thin, elongated, Y-shaped.

**Notes. Etymology:** from the Malay for elephant (*gajah*), a noun in apposition, referring to the two tusk-like mandibular tubercles.

*Chaloenus gajah* is the only species of *Chaloenus* with male mandibular horns and therefore easily distinguishable from all other males (Medvedev 2004; Takizawa 2012). In other *Chaloenus* species the female has a simple unmodified head and narrower prothorax; this is likely to be true of *C. gajah*.

Apart from its unique mandibles, *Chaloenus gajah* is separated from similar *Chaloenus* species, as keyed and described by Takizawa (2012), as follows: *C. brunneus* Bryant, 1943, is small (4.8mm), yellowish with black margins to the elytra, and with flat apex to penis in profile; *C. lanjakensis* Takizawa, 2012 (female unknown), has black elytra, abdomen and legs, and broadly explanate lateral elytral margins; *C. yukikoeae* Takizawa, 2012, has more elongate antennae and penis expanded at apex and flattened in lateral view.

The type locality is probably the Wain River Forest Reserve, just north of the city of Balikpapan. This isolated 10,000 hectare reserve of lowland forest (maximum elevation 110m) has been seriously degraded in the last 15 years, with approximately 30% lost to fire, logging and cultivation (Craven 2002; Cleary & Priadjati 2005; Google Earth, images accessed July 2010).

Some of the larger species of *Chaloenus* with sexually dimorphic males are known to aggregate at flowers of Araceae subfamily Aroideae (Kumano-Nomura & Yamaoka 2009; C. Darling *pers. com.* 2010; Takizawa 2012), and it is possible that *C. gajah* shows this behaviour. Aroideae are particularly diverse in Borneo (Mayo, Bogner & Boyce 1997).

*Chaloenus gajah* appears to be the first record of this genus from Indonesian Borneo (Kalimantan) (Takizawa 2012), however the senior author has collected an additional 8 species from there.

## Subfamily Cryptocephalinae

### *Scaphodius* Chapuis 1874: 179

Type species: *Scaphodius comptus* Chapuis 1874, by monotypy.

**Diagnostic description** (based on examination of c. 50 species). Small to medium sized cryptocephalines, length 1–6mm. Head: eyes small, convex, without a distinct internal canthus; male usually with elongated or laterally enlarged mandibles; clypeal area not sharply delimited, or if so, transversely triangular with obtuse upper angle and widely splayed raised margins for holding antennae in repose; antennae not serrate, longer than head width, antennomeres 7–11 elongate and expanded, each with dense basiconic sensilla in apical circular pit. Thorax: front angles pronotum not abruptly constricted as a collar; pronotum with triangular posterior lobe, usually medially notched for retention of scutellum; hind margin pronotum with row of teeth, usually hidden by base of elytra; hind angles of pronotum posteriorly produced; prosternal process broad, sides parallel and usually ridged; scutellum

abruptly raised from mesoscutum, fusiform or oval, and anteriorly stepped; mesoscutum on either side of scutellum with narrow strip of microchaetae; elytra striate; elytral suture not serrate; elytral epipleuron entirely visible in lateral view, expanded at humerus, with sinuate lower margin; tibiae without spurs; claws appendiculate. Abdomen: ventrites III, IV and V fused; penis with distinct apical setae; vaginal palpi flat, semi-ovate; spermatheca falciform; dorsal transverse sclerites of kotpresse extending beyond sides of rectum.

**Notes.** The genus *Scaphodius* is endemic to New Caledonia and was recently redescribed by Schöller (2009), with several new species. We have revised the description here, based on a larger sample of species. Schöller also included *Nyetra* Baly 1877 as a junior synonym of *Scaphodius*, with which we concur. *Nyetra* was described for a large species, with dorsal pubescence and extreme sexual dimorphism, in contrast to the type species of *Scaphodius*, small, dorsally glabrous and with slight sexual dimorphism, but there are intermediates in size and structure between these extremes, as noted by Schöller.

Schöller listed 12 species in *Scaphodius* but this figure excludes species wrongly placed in the Australo-Papuan genus *Ditropidus* Erichson, 1842 (Schöller 2009). Schöller treated the five species of *Ditropidus* described by Fauvel (1907) as either belonging to that genus (*D. opacicollis* only) or *nomina nuda*, because they lacked detailed descriptions. However, these latter names were partially described by Fauvel (1907) as part of a key written to differentiate the species, which therefore makes them available (ICZN 1999, Art 12.1), although the species are unidentifiable from the key. Fauvel seems to have placed his species in *Ditropidus* based on size and colour, neither of which is valid, and faulty biogeography, influenced by Chapuis (1875a, b). Chapuis had listed *D. punctulum* Chapuis, 1875a, from Sydney, Adelaide and Fiji, and *D. tibialis* Chapuis, 1875a, from Sydney, Clarence River, Brisbane and Fiji. Chapuis also described *Cryptocephalus fraterculus* Chapuis, 1875b, from Fiji. All three of these species are Australian, absent from Fiji (Bryant & Gressitt 1957; types examined by CAMR) and the specimens from Fiji examined by Chapuis must have been wrongly labelled. Note that *D. punctulatus* of Bryant & Gressitt (1957) is a misidentification. Fauvel was therefore misled in believing that *Ditropidus* occurred in “Polynesia” (Fauvel 1907: 152).

We have examined the male holotype of *D. opacicollis*. This is a small but otherwise typical species of *Scaphodius*, with ovate eyes, laterally expanded mandibles, strongly divergent facial antennal grooves and strigose pronotum (= *S. opacicollis* (Fauvel), **comb. nov.**). We have not seen any *Ditropidus* species in abundant material of Cryptocephalinae from New Caledonia. Fauvel’s generic diagnoses are clearly incorrect. We therefore feel justified in placing all of the other Fauvel names in *Scaphodius*: *S. aeneus* (Fauvel, 1907), **comb. nov.**, *S. nitidus* (Fauvel, 1907) **comb. nov.**, *S. striolatus* (Fauvel, 1907) **comb. nov.**, *S. sulcatus* (Fauvel, 1907) **comb. nov.**

The only species of *Scaphodius* supposedly from outside New Caledonia, *S. compactus* Sharp, 1881, was described from New Zealand. This is an Australian species of *Ditropidus*, either mislabelled from New Zealand or adventive but no longer extant in that country (Leschen & Reid 2004; Schöller 2009).

The net result of these changes is that *Scaphodius* is endemic to New Caledonia and *Ditropidus* is confined to Australia and New Guinea.

Two new species in the material available to us show particularly bizarre sexual dimorphism and are described below. This brings the total number of valid *Scaphodius* species to 19.

### *Scaphodius drehu* sp. nov.

(Figs 7–18)

**Material examined.** Holotype: ♂/Loyalty Is, Ouvea, Fayaoué, 0–50m, xii.1968/ N. L. H. Krauss collector Bishop Museum/ *Nyetra* sp., G. A. Samuelson det. 1971/ (BPBM); paratype: ♀, same data as holotype except i.1969 (BPBM).

**Description.** Length: 5mm (male = female), greatest width 3mm (male), 3.5mm (female). Colour: reddish-brown, except (i) antennomeres 8–11, female mandibles, disc of pronotum and elytral humeri, distal half female tibiae, darker brown; (ii) antennomeres 1–5, labiomaxillary complex, frontoclypeus of female, legs paler brown; (iii) labrum, posterior angles pronotum (dorsal and ventral), prosternal and mesoventrite processes, anterior margin metaventrite, mesanepisternum, mesepimeron, deep yellow to orange. Dorsal pubescence: head, pronotum [except disc—rubbed off?] and elytral striae with dense recumbent silvery setae.

Head: roughly circular, broadest at genae below eyes (male) or at eyes (female); male frontoclypeus diamond

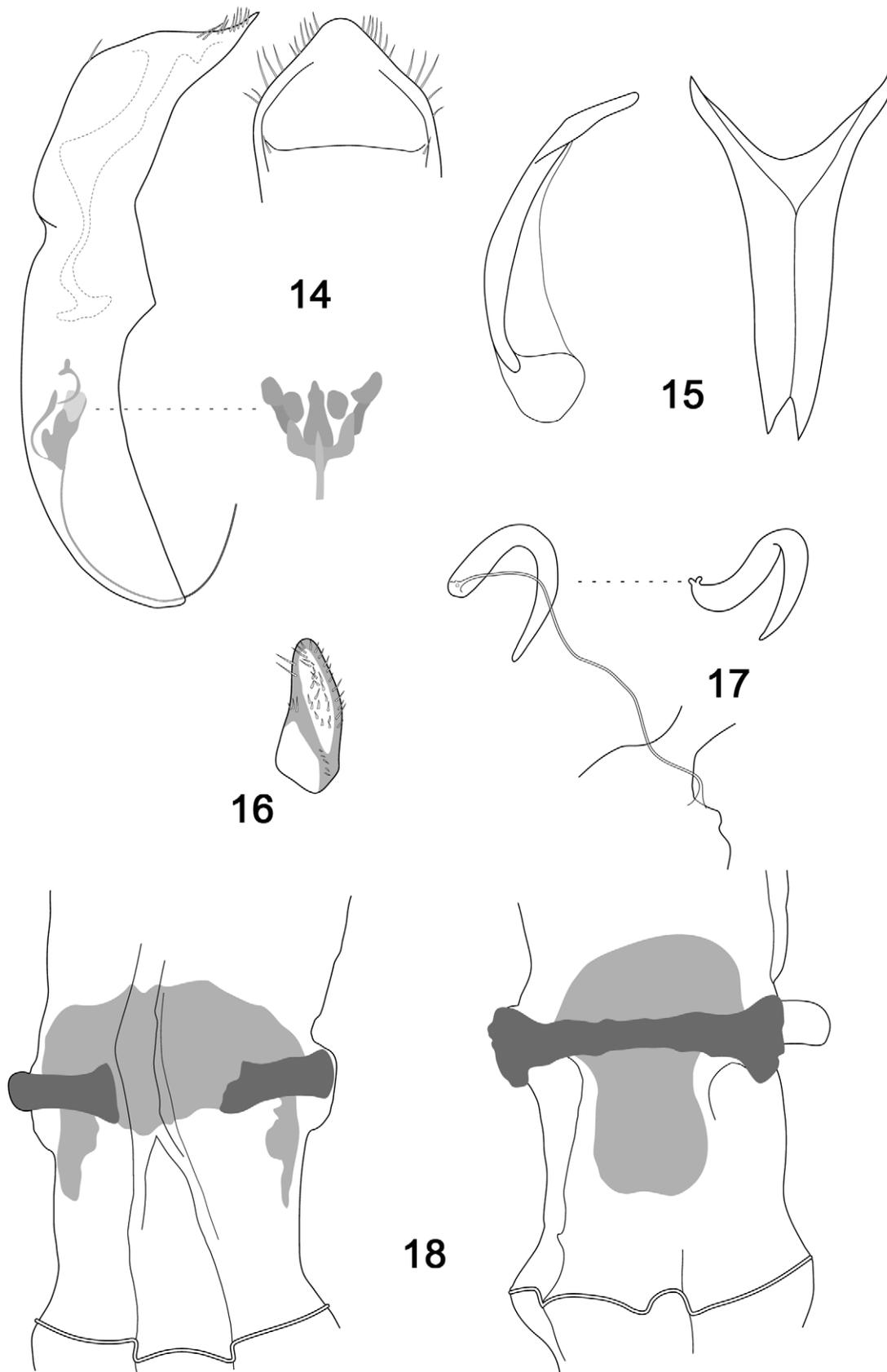
shaped, convex, except reflexed anterior edge which is produced apically and bilobed; female frontoclypeus not anteriorly produced, apical margin flat, shallowly triangularly excavate; sides frontoclypeus bounded by oblique antennal grooves from antennal sockets to lateral margins buccal cavity; head densely and finely punctured (punctures separated by their diameters, about eye facet sized) and clothed in silvery recumbent setae, except antennal grooves, antennal tubercles and shallowly depressed centre of vertex impunctate and glabrous; eyes oval (female larger than male), inner margin feebly concave; interocular space 2.5x (male) or 2x (female) length of eye; gena long, minimum length 0.4–0.45x eye length; antennae much longer than width of head (male) or slightly longer than width of head (female), all segments elongate, 1–5 sparsely setose and thin, almost parallel-sided, 6–10 densely setose and triangular with apical sensory patch, 11 elongate oval (10 & 11 absent in male); antennomere 1 longest, greatly elongated, length 0.8x eye length (male) or 0.35x (female); labrum transverse with convex apex, apically swollen in male, flat in female; mandible apices normal in both sexes, with two interlocking teeth; male with massive horn arising from base of left mandible, curving across face and upwards in front of right eye; apical maxillary palpomere flattened-cylindrical in male, elongate conical in female (apex narrowly truncate).

Thorax: pronotum: strongly transverse, width male 1.7x length, width female 1.8x length, anteriorly strongly laterally arched, front angles almost hidden by curvature; strongly and closely punctured on disc (puncture diameters c. 2x head punctures, generally separated by one puncture diameter, some coalescent), but basal half midline smooth and impunctate (slightly raised in male), becoming finer and slightly sparser at sides; pronotum with dense recumbent silvery setae except disc [irregularly setose, possibly worn off] and trichobothrium at each angle; anterior and lateral edges finely margined, posterior edge presumed to have row of small teeth as in other *Scaphodius* species (not seen in entirety); anterior angles rounded, posterior angles posteriorly produced, 90° in perpendicular view; pronotal basal lobe triangular with slightly bilobed apex, basal margin hidden by raised anterior edge of elytra; hypomeron glabrous, impunctate, except densely setose posterior lobe; prosternum closely setose and punctate, anterior margin reflexed; prosternal process transverse, ventral surface flat, laterally bounded by parallel ridges, apex evenly arcuate; scutellum smooth, glabrous and impunctate, minute, length equal width 3rd elytral interval, elliptical; elytra almost quadrate but apices rounded with c. 45° sutural angle; basal margin elytra smooth, slightly overlapping basal margin pronotum; elytra striate, with striae and 10 striae (10th adjacent to epipleuron) but each 'stria' consisting of confused fine punctures, with recumbent setae (similar to head), in a straight groove with convex glabrous impunctate interstriae (except base of 9th interval); striae 4 and 5 anastomised before apex, striae 3 and 6, and 7 and 8, at apex; humeri prominent, swelling divided by base of 9th stria; epipleura sparsely and minutely setose, ventrally produced at humeri, broad at base (= width third elytral interval), abruptly narrowed at postcoxae, then narrowing to a single edge before elytral apex; mesoventrite process similar to prosternal process, but shorter, with convex anterior and laterally projecting apical angles; mesanepisternum and mesepimeron glabrous, impunctate, but densely microsculptured; fully winged; metaventrite densely punctured and pubescent at sides, glabrous and transversely strigose (more so in male) at middle; metepisternum densely setose; femora elongate-ovate, similar sized; tibiae gradually expanded to rounded apices, pro- and mesotibiae finely grooved on basal half outer edge; hind tarsi 0.75x length hind tibiae, length metatarsomere 1 < 2+3; male first pro- and mesotarsomeres expanded, width 3/5 length, female first tarsomeres not expanded, width 2/5 length; claws appendiculate, lobe large, right-angled.

Abdomen: paired patches of wing-folding spicules on each tergite except pygidium, patches increasing in size from II-VII; pygidium entirely punctured and pubescent with dense recumbent setae, without median ridge; ventrites without lateral ridges, densely punctured and recumbent-setose; ventrite V with truncate apex in both sexes, male with median sparsely setose shallow depression, female ventrite V with deep hemispherical transversely strigose depression and median excavation of apical margins of ventrites III and IV. Male genitalia: spiculum Y-shaped; penis in lateral view with apical half constricted at base, bent towards acute apex; penis dorsally parallel-sided to right-angled apex with blunt tip, pair of setae at base of ostium and c. 11 pairs of setae on apical margin; tegmen broadly Y-shaped, with deep internal keel; endophallic sclerite roughly trident-shaped in dorsal view with oval apical lobes. Female genitalia: vaginal palp elongate-triangular, with darkly sclerotised anterior margin; spermatheca falcate, twisted at base, with uncoiled duct; rectum with well-developed kotpresse: dorsum with rectangular sclerites, simply rounded at their laterally projecting apices, and ovate patch of microspicules; venter with narrow parallel-sided transverse bar, projecting apices greatly expanded; sides with posteriorly directed sclerotised strip.



**FIGURES 9–13.** *Scaphodius drehu* sp. nov. 9, male, habitus; 10, male head, anterior; 11, male head, lateral; 12, female, habitus; 13, female head, anterior.



**FIGURES 14–18.** *Scaphodius drehu* sp. nov. 14, penis lateral, dorsal, endophallic sclerite; 15, tegmen lateral, dorsal; 16, vaginal palp; 17, spermatheca and duct; 18, rectal kotpresse, dorsal (left), ventral (right) (lighter shading = internal spicule patches).

**Notes. Etymology:** named for the major endemic language of the island of Ouvea, Drehu (Anonymous 2010), a noun in apposition.

Sensory organs on the head are sexually dimorphic in size, as compared against body length, measured from anterior margin of pronotum to apex of elytra: greatest diameter of eye 14.5% (male) or 13.5% (female) body length; antennal length approximately 66% (male) or 50% (female).

Amongst described species of *Scaphodius*, *S. drehu* is nearest to *S. amieus* Schöller, 2009, which differs by colour, mandibular structure, frontoclypeal margin and penis shape. The female of *Scaphodius drehu* is most similar to an undescribed species with only females available, from the nearby island of Livou (Loyalty Islands; in BPBM), but *S. drehu* differs by denser punctures on pronotum, more elongate hind angles of pronotum and broader lines of setae on elytra.

### *Scaphodius ferox* sp. nov.

(Figs 19–28)

**Material examined.** Holotype: ♂/ Mandjelia (summit), 20:23:09S 164:31:09E, 750–780m, beating montane rainforest, 12.i.2007, M. Wanat & R. Dobosz (MHNP); paratypes (4): ♀/ Mandjelia (subsummit), 20:23:09S 164:32:00E, 700–750m, night beating, 11.i.2007, M. Wanat (WUP); ♀/ Mandjelia, summit, 20:24S 164:32E, 780m, beating rainforest, 13.xii.2004, G. Monteith (QMB); ♀/ Mandjelia, lower creek, 20:24S 164:31E, 550m, malaise, 29.xi.2003–31.i.2004, G. Monteith (QMB); ♀, same data, except ‘580m, beating rainforest, 12–13.xii.2004’ (MNHP).

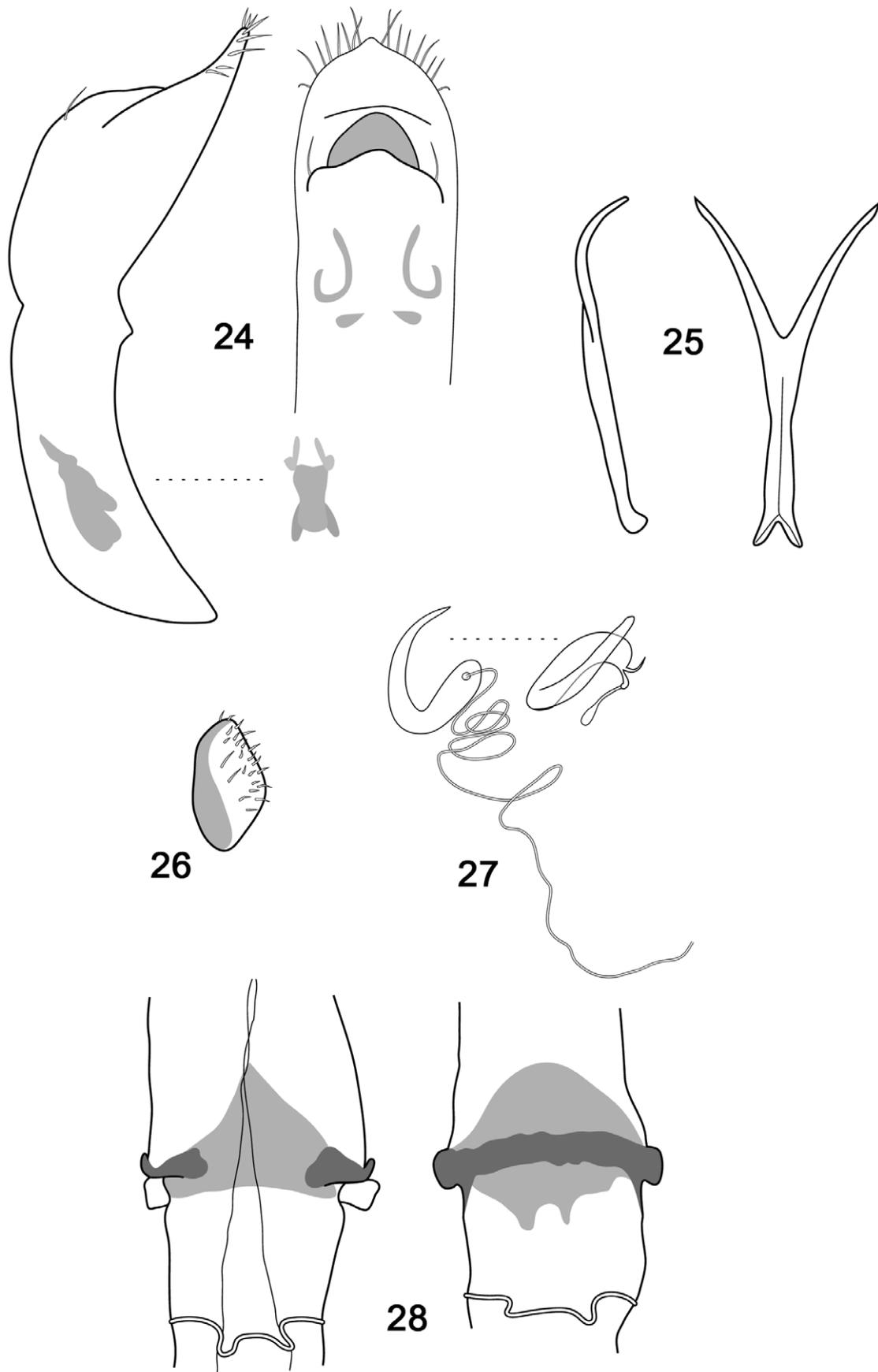
**Description.** Length: 2.5mm (male = female), greatest width 1.3mm (male), 1.5mm (female). Colour: black, except (i) labrum, labiomaxillary complex, pale yellow; (ii) antennomeres 1 up to 6, apices trochanters, middle of thoracic venter, sometimes brown [probably slightly teneral examples]. Dorsal pubescence: almost entirely glabrous.

Head: male anterior half with sides produced and middle deeply cleft, head almost circular in female, broadest at genae below eyes in both sexes; vertex with minute (much smaller than eye facet) and sparse punctures with minute recumbent setae; frontoclypeus similar but strongly microreticulate and genae coarsely microreticulate; male frontoclypeus deeply bilobed, median cleft almost reaching antennal sockets, but lateral triangular lobes projecting beyond genae; female frontoclypeus flat, semi-ovate, apical margin narrowly concave; sides frontoclypeus bounded by oblique antennal grooves from sockets to lateral margins buccal cavity (male), or flat with almost vertical sutures which may be raised as fine ridges [teneral examples]; eye oval, inner margin feebly concave; interocular space 1.4x (male) or 1.2x (female) length of eye; gena long, minimum length 0.6x (male) or 0.8x (female) eye length; antennae 1.5x (male) or 1.3x (female) width head, all segments elongate, 1–6 sparsely setose and thin, almost parallel-sided; male antennomere 7 triangular with scattered setae, 8–10 triangular and densely setose, 11 elongate-oval and setose, female similar but 7–10 elongate-oval in shape; antennomeres 7–11 with apical sensory patch; antennomere 1 longest, greatly elongated in male (1.1x eye length) less so in female (0.7x eye length); male labrum massive, flat, elongate rectangular, apex almost truncate, female labrum small, slightly swollen, transverse; male mandibles greatly elongated, apices with 3 interlocking teeth and middle with elongate semi-circular horn curving inwards; female mandibles normal, extending just beyond labrum with 2 visible interlocking teeth; labio-maxillary complex elongated in male, normal in female, apical maxillary palpomere elongate-cylindrical in both sexes, much longer than pre-apical.

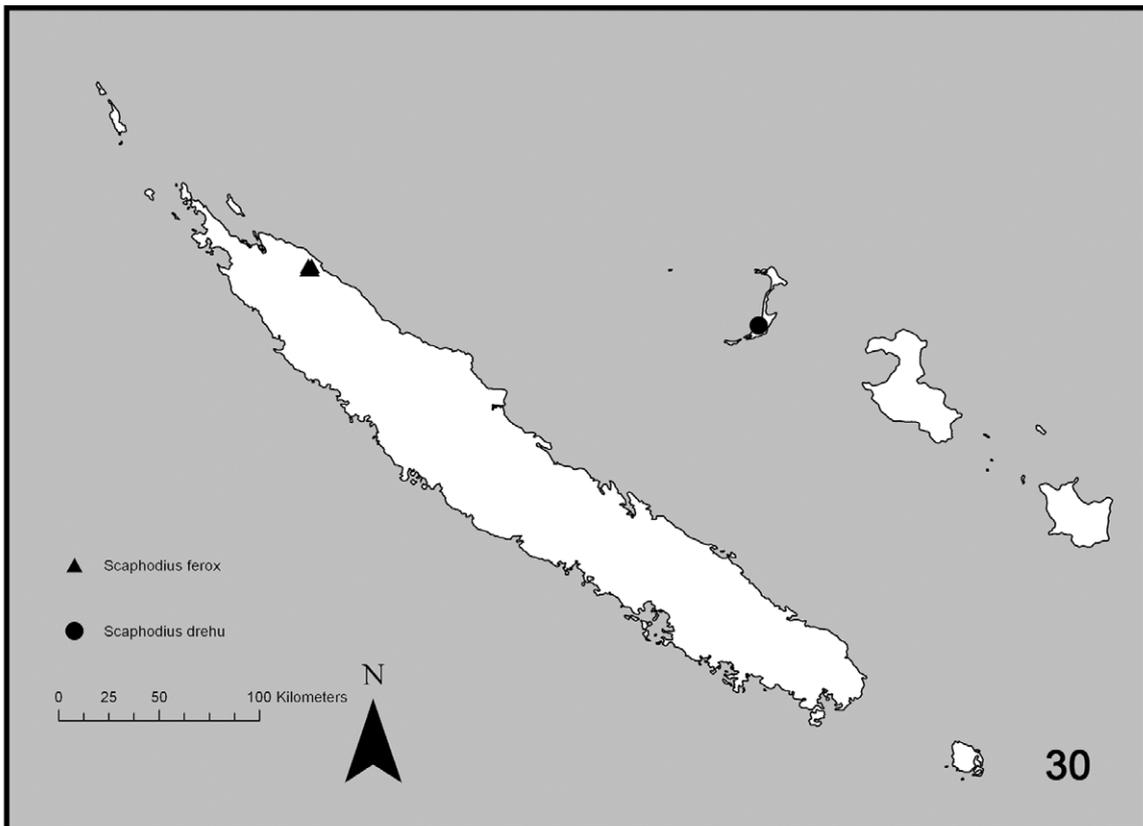
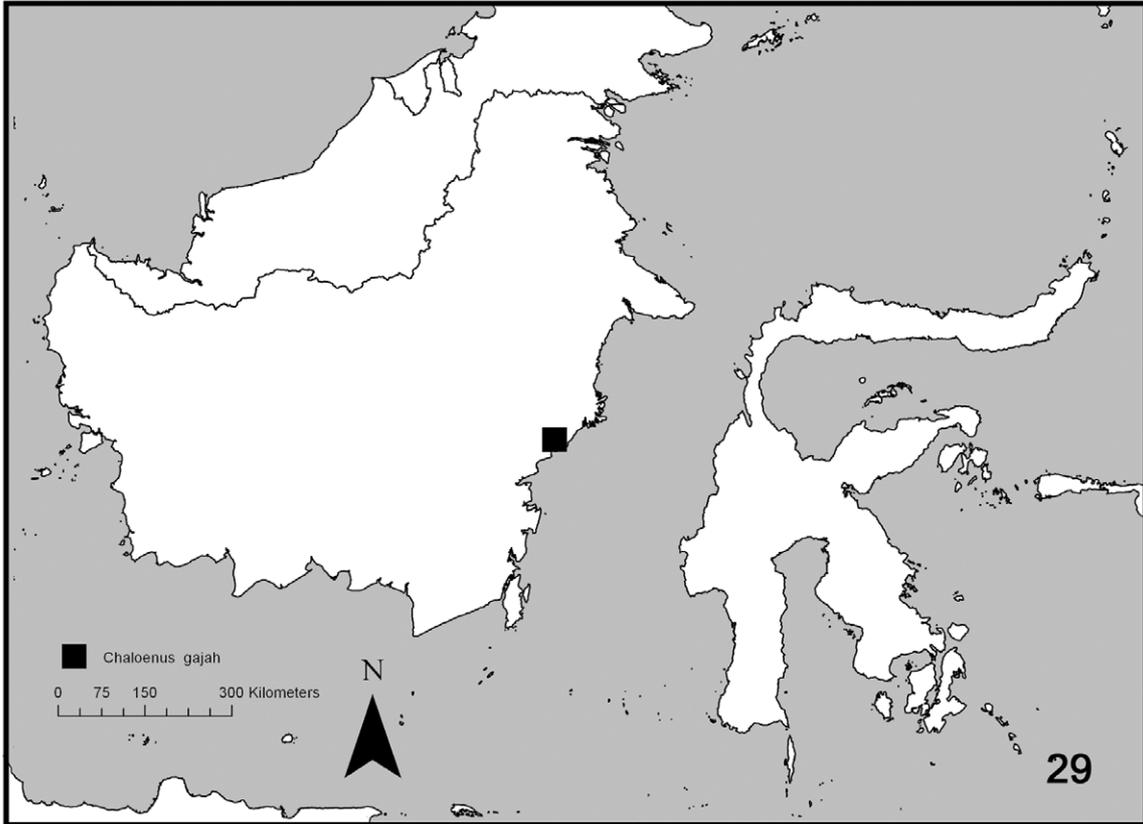
Thorax: pronotum: strongly transverse, width 1.6x length (both sexes), anteriorly strongly laterally arched, front angles hidden by curvature; impunctate and glabrous except trichobothrium at each angle; anterior and lateral edges finely margined; anterior angles rounded, posterior angles posteriorly produced, 75° in perpendicular view; pronotal basal lobe shallowly triangular with bilobed apex, posterior margin finely and evenly toothed; hypomeron glabrous, impunctate; prosternum with large close punctures and erect setae, anterior margin reflexed; prosternal process strongly transverse, ventral surface flat, laterally bounded by parallel ridges, apex feebly concave to truncate; scutellum smooth, glabrous and impunctate, minute, length shorter than width 3rd elytral interval, elliptical; elytra tapered from humeri to rounded apices with c. 45° sutural angle; basal margin elytra smooth, slightly overlapping basal margin pronotum; elytra glabrous, striate, with striae and 10 striae (10th adjacent to



**FIGURES 19–23.** *Scaphodius ferox* sp. nov. 19, male, habitus; 20, male head, anterior; 21, male head, lateral; 22, female, habitus; 23, female head, anterior.



**FIGURES 24–28.** *Scaphodius ferox* sp. nov. 24, penis lateral, dorsal, endophallic sclerite; 25, tegmen lateral, dorsal; 26, vaginal palp; 27, spermatheca and duct; 28, rectal kotpresse dorsal (left), ventral (right) (lighter shading = internal spicule patches).



**FIGURES 29–30.** 29, map of Borneo, showing distribution of *Chaloenus gajah* **sp. nov.**; 30, map of New Caledonia, showing distributions of *Scaphodius drehu* **sp. nov.** (●) and *S. ferox* **sp. nov.** (▲).

epipleuron), each stria consisting of single line of large punctures, increasing in size from stria 1 to 9, interstriae impunctate, flat, except slightly convex intervals 7–9; striae 4, 5, 7 and 8 abbreviated before apex, striae 3 and 6 anastomised at apex; humeri prominent, swelling divided by base of 9th stria; epipleura glabrous and impunctate, ventrally produced at humeri, broad at base (= width third elytral interval), abruptly narrowed at postcoxae, then narrowing to a single edge before elytral apex; mesoventrite process similar to prosternal process; mesanepisternum and mesepimeron glabrous, impunctate, but densely microsculptured; fully winged; metaventrite with median groove, distinctly but sparsely punctured and pubescent throughout; metepisternum with scattered setae; femora elongate-ovate, similar sized; tibiae gradually expanded in basal 2/3, then contracted to apex, outer margins basally ridged; hind tarsi 0.75x length hind tibiae, length metatarsomere 1 < 2+3; male first pro- and mesotarsomeres feebly expanded, female first tarsomeres not expanded; claws appendiculate, lobe large, right-angled.

Abdomen: paired patches of wing-folding spicules on each tergite including pygidium, increasing in size from II–VII; pygidium entirely punctured with recumbent setae, but basal bi-arcuate patch of wingfolding spicules present, without median ridge; ventrites without lateral ridges, distinctly punctured and recumbent-setose; ventrite V with truncate apex in both sexes, male with median shallow depression, female ventrite V with moderately deep bowl-shaped transversely strigose depression and median excavation of apical margin of ventrite IV. Male genitalia: spiculum Y-shaped; penis in lateral view with swollen apical half, constricted at base, acute apex; penis dorsally parallel-sided to rounded apex with small mucronate tip, pair of setae at base of ostium and c. 9 pairs of setae on apical margin; tegmen narrowly Y-shaped, without deep internal keel; endophallic sclerite roughly rectangular in dorsal view with thin apical lobes. Female genitalia: vaginal palp ovate, with transparent anterior margin; spermatheca falcate, twisted at base, with long loosely coiled duct; rectum with well-developed kotpresse: dorsum with triangular sclerites, narrowly hooked at projecting apices, and triangular patch of microspicules; venter with narrow parallel-sided transverse bar, projecting apices not greatly expanded; sides with posteriorly directed sclerotised strip.

**Notes. Etymology:** named for the fierce (Latin: *ferox*) appearance of the male.

Sensory organs on the head are sexually dimorphic in size, as compared against body length, measured from anterior margin of pronotum to apex of elytra: greatest diameter of eye 16% (male) or 14–15% (female) body length; antennal length 76% (male) or 45–46% (female).

This is one of many species of *Scaphodius* with greatly modified mandibles and extended clypeal or genal lobes (Schöller 2009; *pers. obs.* CAMR). Six of the 41 species with males available to us have a spine on the inner edge of the male mandible. However, *S. ferox* is the only species we are aware of with a smooth glabrous dorsum and an elongate dorsally directed tooth at the base of each mandible. There are several shining black undescribed species, but with relatively unmodified male mandibles and at least slightly punctate or strigose pronotum. The black head with contrasting yellow mouthparts also seems to be diagnostic for *S. ferox*.

## Review of occurrence of enlarged male mandibles (EMM) in Chrysomelidae

General morphological literature on each subfamily of Chrysomelidae has been surveyed to determine the presence and frequency of modification of male mandibles (Table 1). It is likely that several species have been overlooked, either because males are inadequately described or we have not thoroughly searched the literature. With that proviso in mind, there are clear trends in the different subfamilies, discussed in more detail below.

### Bruchinae

Bruchinae are barrel-shaped with enlarged hind legs, but with small flattened and deflexed heads. Sexual dimorphism in bruchines is primarily found in the antennae, used in mate location, but this distinction is not universal. The remaining head appendages including mandibles do not appear to diverge between sexes and EMM are absent. Surprisingly, the large hind legs, often supplemented with spines, are not used in any special way by males in copulatory behaviour, and are therefore monomorphic within species. Rapid mate location (using modified male antennae) is probably the key mating strategy (Borowiec 1987; Nilsson & Johnson 1993; Savalli & Fox 1999; Johnson, Southgate & Delobel 2004; Arnqvist & Tuda 2009).

**TABLE 1.** Distribution of modified male mandibles in subfamilies of Chrysomelidae. See text for source references.

Taxon	#species (approximate)	#spp with enlarged male mandibles	%spp with enlarged male mandibles	% of total EMM occurrence
Bruchinae	1700	0	0	0
Cassidinae	7000	0	0	0
Chrysomelinae	3000	1	<0.1	<1
Criocerinae	1400	0	0	0
Cryptocephalinae	3900	165 (approx.)	4.2	88.7
Clytrini	600	100 (approx.)	17	53.8
Cryptocephalini	3000	60 (approx.)	2	32.2
Fulcidacini	300	5	1.7	2.7
Donaciinae	150	0	0	0
Eumolpinae	5000	15 (approx.)	<1	8.1
Galerucinae	12000	3	<0.1	1.6
Lamprosomatinae	120	2	1.7	1.1
Sagrinae	50	0	0	0
Spilopyrinae	35	0	0	0

### Cassidinae

Cassidinae are generally flattened, circularly so in cassidoid species, elongately so in most hispid species, some of which are also dorsally spined (Chaboo 2007). The usually deeply inserted head has a small deflexed mouth with compacted appendages, similar to the curculionoid mouth, therefore mandibles are unlikely to be significant in sexual behaviour. No species are recorded with EMM. Intraspecific male antagonism occurs in the cassidoid *Acromis* Chevrolat, 1837, with elongated corners of the elytra used to flip over rivals (Windsor 1987), and in the hispid *Xenarescus* Weise, 1905, with an elongated head used for levering off rival males (Beaman 1980, cited in Chaboo 2007). Male head elongation occurs in several hispid genera (Gressitt 1963; Chaboo 2007) and use of it for dislodging rival males may be a common phenomenon in these taxa. Some species have a greatly elongated male flagellum, which, combined with prolonged copulation (1–3 hours), may indicate female mate choice during the copulatory process (Rodriguez, Windsor & Eberhard 2004).

### Chrysomelinae

Chrysomelinae are generally ventrally flattened and dorsally convex, with ovate body shape. The head is broad and relatively prognathous. *Callidemum cornutum* (Baly, 1875) was described as unique in the subfamily for its male mandibular horns (Figures 1–2). No additional species have been found with EMM (Daccordi 1996; Reid 2006). Nothing is known about the biology of *C. cornutum*, which is confined to Central Queensland, but it is in the same species group (formerly a genus) as *C. hypochalceum* (Germar, 1848), which feeds on *Dodonaea* (Sapindaceae) (Matthews & Reid 2002; Reid 2006) and a sapindaceous host seems likely.

Sternal horns, anterior projections formed from the meso and/or metaventrite, are fairly frequent in Chrysomelinae but not sexually dimorphic. In a study of *Doryphora* Illiger, 1807, Eberard (1981) noted that the horns are used by both sexes in intraspecific fights, probably to defend limited hostplant resources and prevent cannibalism by adults of immatures.

In a study of *Chrysolina aurichalcea* (Mannerheim, 1825), a species without any obvious secondary sexual dimorphism, head-on combat was successful for larger males (Shimizu & Fujiyama 1986). This observation suggests that size and physical strength are important traits for male selection.

### Criocerinae

Criocerinae are relatively elongate, depressed to cylindrical, with large head, narrow prothorax and often broad elytra. Many species have enlarged hind legs in both sexes. There is little external sexual dimorphism in Criocerinae and the two sexes are usually difficult to separate externally (Monrós 1960). EMM are unknown. Mate

guarding is present in some species, with males clasping females (Düngelhoef & Schmitt 2006), but pre- and post-copulatory attention of male to female is absent in other species (Matsumura & Akimoto 2009). The extremely elongated flagellum in some species may indicate female sexual selection during a prolonged copulation (*loc. cit.*).

### **Cryptocephalinae**

EMM are common in this subfamily, which is best discussed under its constituent tribes. We estimate 165 of 3900 species have EMM.

#### **Cryptocephalinae—Clytrini**

Many species of this tribe show strong sexual dimorphism in the mouthparts, and this character has been used to define genera (Jacoby 1908; Monrós 1953). However, genera with this trait do not form a single clade (Schöller & Witte 2007) and recent systematic studies of Clytrini suggest that mandible sexual dimorphism, like many other secondary sexual characters, has multiple origins within the tribe (Agrain *et al.* 2007; Agrain & Roig-Junent 2011). The most interesting genus is *Megalostomis* Chevrolat, 1837, with a species group (formerly a genus) characterised by strongly tusked male mandibles, remarkably similar to *Scaphodius ferox* described above (Agrain *et al.* 2007; Agrain & Roig-Junent 2011). Nothing is known of the biology of this species group, but males in the clytrine genera *Labidostomis* Germar, 1817, and *Coptocephala* Chevrolat, 1837, both with EMM, are known to dislodge copulating or mate guarding males with their mandibles (Medvedev & Pavlov 1987).

#### **Cryptocephalinae—Cryptocephalini**

This is the most speciose tribe of the subfamily, with several genera of more than 100 species. Sexual dimorphism is common, particularly in modifications of the legs and antennae. The tribe is divided into several subtribes. The genera of the dominant subtribes Cryptocephalina and Monachulina comprise barrel-shaped species, with the head usually deeply inserted in the pronotum (Reid 1990) and the head of the male distant from the female during copulation (Reid 1999). In most species males are much smaller than females. Nevertheless the mouths of some males are greatly widened to enclose enlarged mandibles. This occurs in at least 10 out of c. 250 species of *Ditropidus* Erichson, 1842, (*sensu lato*, as in Matthews & Reid 2002), for example *D. concolor* (Saunders, 1847) (Lea 1920). In the related genus *Scaphodius* most species have EMM (Schöller 2009), although only slightly so in *S. oxycedrus* Fauvel, 1907. Thirty-eight of 41 species with males available to us show EMM; the three exceptions are 1.5mm or less in length. The genus-group *Cryptocephalus* rarely shows such dimorphism: we are aware of only 3 (all undescribed) of c. 250 species in Australia (Reid 1990). The genera of subtribe Pachybrachina include species with more loosely organised bodies and more prominent heads, but EMM are rare, occurring in 3 of c. 125 species of *Acolastus* Gerstaecker, 1855, known (Schöller 2010). Many species of this group have enlarged male forelegs, for example in *Mylassa* Stål, 1857, (Monrós 1949). In the few remaining genera, most of which comprise small individuals, EMM are known in *Achenops* Suffrian, 1857 (3 of 7 described species; Schöller 2006) and *Leasia* Jacoby, 1907 (one species of at least 10 in collections; Monrós 1951a; Matthews & Reid 2002).

#### **Cryptocephalinae—Fulcidacini**

Most of the species of this small tribe are similar to Lamprosomatinae (see below) in being small, cryptic and using thanatosis as an escape mechanism. They have ventral grooves for retraction of appendages and a small head which is protected by the surrounding prothorax. As in that subfamily, there is little room for expansion of mouthparts. However, a single genus, *Pseudochlamys* Lacordaire 1848, with 5 species, is defined by the males having expanded mandibles (Monrós 1951b, Chamorro-Lacayo & Konstantinov 2009). Sexual behaviour in this tribe is unknown except that the male of one of the largest species, *Fulcidax monstrosa* (Fabricius, 1798), copulates with its body at right-angles to the female, with their heads far apart (Flinte & Valverde de Macedo 2004).

#### **Donaciinae**

Donaciines, like related criocerines, are loosely organised, elongate and delicate beetles, but always with enlarged hind femora, those of males larger. The heads are remarkably uniform in structure and EMM are absent (Askevold 1990). Males use mate guarding by straddling their female partners (Bienkowski 1999). Male combat has rarely been observed; in one species head-on confrontation is avoided and combatants push against each other tail to tail, using their enlarged hind femora (Konstantinov 2004).

## Eumolpinae

Eumolpinae are diverse in body form, from convex and compact to depressed and elongate. Several American genera show EMM, this character being used in their definition: monotypic *Glyptosceloides* Askevold & Flowers 1994 (q.v.), *Eurysarcus* Lefevre, 1885, with at least four species (Lefevre 1885; Askevold & Flowers 1994) and *Metaparia* Crotch, 1873, with nine species (Flowers 1996; Riley, Clark, Flowers & Gilbert 2002; Perkins, Naskrecki & Farrell 2005). One of 125 species of the American genus *Metachroma* Chevrolat, 1837, has enlarged mandibles (Blake 1970); this species was described from only the male but is likely to be sexually dimorphic. In the above examples, male mandibles are slightly enlarged compared with the female. EMM are not used for generic diagnosis in non-American faunas (for example: Lea 1915; Gressitt & Kimoto 1961; Selman 1965; Gressitt 1969; Kimoto & Gressitt 1982) and we are unaware of any other examples, although they may occur.

## Galerucinae

Galerucinae are morphologically diverse. Typically they are treated as two groups, Alticini *s. str.*, which are able to hop from an extensor sclerite in the hind femora, and Galerucini *s. str.*, which lack this organ. These groups are clearly polyphyletic artificial assemblages (Ge *et al.* 2012), but in the absence of a replacement classification it is convenient to retain them for discussion here. In general they show different body form: alticines more compactly ovate and convex; galerucines more loosely elongate and depressed.

Strongly expressed sexual dimorphism is common in this subfamily, especially among the Galerucini *s. str.* The abundant secondary sexual modifications of head, thorax, abdomen and appendages have been reviewed by Mohamedsaid & Furth (2011), who found some modification in 24% of species in this large subfamily. Remarkably, none of the 1298 species examined showed EMM. Enlarged mandibles are described for *Buphonida*, but in both sexes (Maulik 1936). In *Diabrotica* Chevrolat, 1836, which lacks secondary sexual modifications, cryptic female choice occurs during copulation and there is little or no courtship (Tallamy, Powell & McClafferty 2002).

Among Alticini *s. str.* EMM are also rare. Several *Chaloenus* species have males with grossly enlarged heads, but apart from *C. gajah*, described above, the mandibles are not especially enlarged or modified (Takizawa 2012). Sexual behaviour of *Chaloenus* has not been studied. The laterally enlarged heads of *Chaloenus* species, almost stalk eyed, may function like those of similar male insects, for example in Diopsidae and Platystomatidae. In these flies, males oppose each other territorially or at leks (Wilkinson & Didson 1997). Many males and females of a species of *Chaloenus* have been found in a single spathe of an aroid (C. Darling, *pers. com.* 2012).

One of two species of the alticine *Normaltica* Konstantinov, 2002, has a male with enlarged mandibles and elongated mouthparts similar to those found in *Chaloenus* and *Scaphodius*. At least one of 42 species of *Euphitrea* Baly, 1875, has EMM (laterally and anteriorly projecting), which are slightly asymmetric (Zhang & Yang 2006).

## Lamprosomatinae

Sexual behaviour has not been described. EMM appear to be almost absent from Lamprosomatinae, only two out of c. 120 species showing this trait (Monrós 1956). One is amongst the largest species known in the subfamily (*Lamprosoma incredibilis* Monrós, 1956, 9mm long). There is otherwise very little sexual dimorphism in this subfamily (Monrós 1956; Chamorro & Konstantinov 2011). The reason is probably functional; these are cryptic small beetles using thanatosis as an escape mechanism in which the appendages are folded into ventral grooves and the head retracted into the pronotum. There is therefore no room for extravagant morphological embellishments.

## Sagrinae

Sagrines have similar body form to related criocerines and donaciines, but include much larger species (Monrós 1960). Hind femora are at least slightly enlarged in all species, like bruchines and donaciines, and much more so in males of some species. Species of *Megamerus* Macleay, 1827, have enlarged mandibles, but this is an interspecific feature not sexual (Monrós 1960). Sexual behaviour has not been recorded but given the physical and phylogenetic similarity of Sagrinae to Criocerinae and Donaciinae (Reid 1995, 2000), is likely to be similar to these two subfamilies.

## Spilopyrinae

Sexual behaviour has not been described. Sexual dimorphism is minimal in this subfamily, even in the more robust genera such as *Cheiloxena* Baly, 1860, (Reid 1992) and *Spilopyra* Baly, 1860 (Reid & Beatson 2010b). Males have slightly larger sensory organs (eyes, antennae, maxillary palpi), as is normal in Chrysomelidae, and sometimes larger forelegs (Reid 1992, Reid and Beatson 2010a, 2010b, 2011), but are otherwise not known with strongly modified body structures. Species are rarely collected and rarity may reduce the need for male combat.

## Summary

The distribution of EMM is not random, but predominates in clusters of genera or species in a few subfamilies, strongly suggesting that there is a phylogenetic signal in the pattern.

The family Chrysomelidae includes 11–12 subfamilies, depending on the treatment of tribe Synetini. Molecular and morphological evidence suggests that this is sister to the Eumolpinae (Reid 1995, 2000; Gomez-Zurita, Hunt & Vogler 2007), therefore we treat Synetini as a tribe of that subfamily (Table 1). The chrysomelid subfamilies may be considered as three independent clades, as suggested by both morphological and molecular analyses (Reid 2000; Gomez-Zurita *et al.* 2007).

In the sagrine clade (Bruchinae, Criocerinae, Donaciinae, Sagrinae) there are no known EMM. In this group mating may be rapid (Bruchinae, Criocerinae), or more prolonged with pre-coital male to male combat involving use of hind legs (Donaciinae), or more prolonged with cryptic female choice (Criocerinae).

In the chrysomeline clade (Chrysomelinae, Galerucinae and perhaps also Cassidinae), which dominates the diversity of Chrysomelidae, EMM are rare. Strong secondary sexual dimorphism is only common in Galerucinae and in almost all examples involves development of sensory structures for mate location and clasping organs, rather than weaponry (Mohamedsaid & Furth 2011). *Chaloenus* is an exception, for which no behavioural information is available, but in which head-to-head male agonistic behaviour is likely. Cryptic female choice occurs and appears likely to dominate in the three subfamilies.

In the cryptocephaline clade (Spilopyrinae, Eumolpinae, Lamprosomatinae, Cryptocephalinae) EMM are present in all but one subfamily, Spilopyrinae. The probable phylogeny of this group, (Spilopyrinae + (Eumolpinae + (Lamprosomatinae + Cryptocephalinae))) (Reid 2000), shows increasing compaction of body form. Notably, Lamprosomatinae and Cryptocephalinae have the relatively highest within-subfamily proportions of EMM, 1.7% and 4.2% respectively (Table 1). In Chrysomelidae, EMM are most common in Cryptocephalinae (88.7% of all occurrences). In Cryptocephalinae, EMM are scattered throughout the various tribes and subtribes (Table 1). This pattern suggests that presence of EMM should only be used with caution as a supraspecific diagnostic character within Cryptocephalinae.

## Discussion: the significance of enlarged male mandibles in Chrysomelidae. Why is EMM prevalent in Cryptocephalinae?

As noted above, any analysis is seriously hampered by lack of studies of sexual behaviour in species with modified males. Two theories for development of EMM have been proposed.

### EMM used as clasping organs in copulation

Konstantinov and Korotyaev (2004) suggest that the enlarged mouthparts of *Normaltica obrieni* are clasping organs for copulation rather than for fighting rival males. Dungelhoefer & Schmitt (2010) have shown that mate guarding, involving long periods of clasping the female in a copulatory position, but without insertion of the penis, is common in Chrysomelidae. Associated clasping organs are common in males but involve spurs on the legs, or leg enlargement, projections on thoracic and abdominal ventrites, and enlarged tarsi. The head of chrysomelids is poorly placed for clasping in copulation, especially in convex species like cryptocephalines or *Normaltica* in which the two sexes are like two barrels placed at right-angles to each other. EMM are also found in other families in which sexual behaviour has been studied, in all cases these modifications are for male combats, whether threatened or attempted (Miller & Wheeler 2005; Emlen 2008; Okada *et al.* 2008).

In support of their hypothesis, Kontantinov and Korotyaev (2004) noted that the penis may be reduced in modified males (based on a comparison of two species). They suggested its role as a restraining/clasping device was reduced because the enlarged mouthparts were used for this function. We have pointed out above that the enlarged mandibles are unlikely to be involved in copulation. Furthermore, in chrysomelids with incomplete cucujiform genitalia (all subfamilies except Bruchinae, Donaciinae, Sagrinae and the genus *Timarcha*; Reid 2000), the penis is only inserted at its tip, with the endophallic sac filling out the female genitalic cavity (bursa copulatrix) (Düngelhoef & Schmitt 2010). The length of shaft of the penis may be an indication of copulatory position of the male on the back of the female (affecting proximity of the abdominal apices) rather than degree of penetration. The size of the endophallus is more critical, but this has not been investigated in relation to penis size. We also note that males with EMM in the genus *Megalostomis* do not have relatively smaller genitalia compared with normal males (Agrain & Roig-Junent 2011) and males in the genus *Chaloenus* with enlarged heads do not have relatively smaller genitalia compared with normal males (Takizawa 2012). Konstantinov & Korotyaev's hypothesis is not supported by available evidence.

#### EMM used in male agonistic behaviour

The limited observations of chrysomelid sexual behaviour available support an alternative hypothesis: EMM are used in male to male agonistic behaviour (Emlen 2008). Such male to male combat may be in isolation from the female, or may involve dislodging copulating or mate guarding males. The former, which may involve lekking, distracts the agonistic males from the female, allowing other males to copulate with her. This leads to bimodal distribution of horn size, for example in Scarabaeidae (Emlen 1997) or Nitidulidae (Okada *et al.* 2008). In the Chrysomelidae there seems to be a complete lack of a bimodal distribution of male dimorphism within species. For example, species and genera can be defined by the unvarying male secondary sexual characters, including EMM (Agrain, Roig-Junent & Dominguez 2007; Schöller 2009). The lack of bimodality may be explained by the mandibles serving a different agonistic function, dislodging males on females. This supports the observations of Medvedev & Pavlov (1987) that EMM in Clytrini were used in dislodging copulating males.

EMM may be particularly common in Cryptocephalinae because dislodging a rival is easier if the body shape of the rival easily destabilises. With their barrel-shaped bodies Cryptocephalinae have high centres of gravity and are therefore relatively unstable. The few examples of EMM outside Cryptocephalinae also involve taxa with convex, compact, and therefore relatively unstable, bodies.

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