

NUMBER 128, 16 pages

21 May 2019

BISHOP MUSEUM OCCASIONAL PAPERS

A NEW SPECIES OF
ENDOCLITA C. & R. FELDER, 1874
(LEPIDOPTERA: HEPIALIDAE)
FROM THE PHILIPPINES, WITH
BIOGEOGRAPHIC COMMENTS

JOHN R. GREHAN &
CARLOS G.C. MIELKE



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Cover photo: *Endoclita headsii* Grehan & Mielke, sp. n. from the Philippines.

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ISSN 0893-1348 (print)
ISSN 2376-3191 (online)
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A new species of Endoclita C. & R. Felder, 1874 (Lepidoptera: Hepialidae) from the Philippines, with biogeographic comments. John R. Grehan & Carlos G.C. Mielke. *Bishop Museum Occasional Papers* 128: 1–16 (2019)

Isid:zoobank.org:pub:5BE2B563-BECF-4115-AA73-18636318FC8F

A new species of *Endoclita* C. & R. Felder, 1874 (Lepidoptera: Hepialidae) from the Philippines, with biogeographic comments

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Abstract. Hepialidae in the Philippines was previously known for only a single species, *Endoclita williamsi* Tindale, 1958, known from a single female specimen from Luzon Island. Here we describe a second species for the Philippines, *E. headsii*, **sp. n.**, based on a single male specimen from Busuanga Island. Both species share a lack of discal forewing shading and costal lobe found in various other *Endoclita* spp., but the phylogenetic significance of these features has not been determined. The bifurcated corpus bursae of the female genitalia of *E. williamsi* is also of uncertain phylogenetic significance, and further detailed study of other species may clarify its character status. The anogenital rim of the pseudotegumen in the male genitalia of *E. headsii*, **sp. n.**, has a prominent dentate edge not reported for other *Endoclita* spp. The respective tectonic correlations of the two species suggests that they have been brought into close geographic proximity as a result of tectonic movements about 15 million years ago.

Keywords: description, distribution, Laos, Malaysia, systematic characters, taxonomy, tectonics

INTRODUCTION

The genus *Endoclita* C. & R. Felder, 1874 is one of the largest and most widespread of the Hepialidae in southern and eastern Asia. It is also one of the most challenging for the accurate recognition of species as there are many species with close or overlapping ranges that cannot be confidently distinguished by general appearance such as color and wing pattern. Detailed descriptions of genitalic characteristics are essential for distinguishing such species but while the taxonomic revisions by Tindale (1941, 1942, 1958) described and illustrated almost every species of *Endoclita* known at the time, almost all the genitalic descriptions were limited to externally visible features that are often generalized and insufficient for conclusive identification. Recent studies indicate that there remains a considerable number of species still to be described (Grehan & Mielke 2016, Buchsbaum *et al.* 2018, Buchsbaum & Grehan 2019).

A further problem for the recognition and identification of *Endoclita* spp. is that some species are described from a unique male or female. This hinders comparison of

specimens from different location that are of a different gender. This situation applies to *E. williamsi* Tindale, 1958, described for a unique female specimen from Luzon Island in the Philippines (Tindale 1958). A new record from Busuanga Island is represented by a single male specimen. The allopatric occurrence of the two specimens allows for the possibility that the Busuanga specimen represents a different species even though a direct genitalic comparison between them is not possible at this time.

MATERIALS AND METHODS

The abdomen was removed and macerated in a cold solution of 5% KOH. The abdominal integument was opened by a right lateral cut from the tergo-sternal bar to the genitalia which was removed and stained in Chlorazol black. The labrum was exposed for examination and imaging by brushing scales from the surface. Terminology for genitalia and wings follows that of Mielke & Casagrande (2013), and tergo-sternal connection labeling follows Grehan & Mielke (2017). Outline diagrams of the wings were made by tracing over photographs using InkScape Scalable Vector Graphics (SVG) 1.1 (Second Edition), version <http://www.w3.org/TR/2011/REC-SVG11-20110816/>. Images of abdomens and genitalia were captured using a Macroscopic Solutions Macropod Pro and Canon EOS 6D DSLR camera body using the Macro Photo MP-E 65mm f/2.8 1–5× manual focus lens for EOS. Images were stacked as needed using Zerene Stacker[®] software, version 1.04 (Zerene Systems, LLC, Richmond, Washington, USA). Figures were manipulated with Adobe Photoshop[®] CC 2018. Abbreviations: FW = forewing; HW = hindwing; BPBM = Bernice P. Bishop Museum, Honolulu, Hawai'i, USA.

TAXONOMY

Endoclita C. & R. Felder

Endoclita in C. & R. Felder, 1874: 316. Type species: *Endoclita similis* C. & R. Felder, 1874, by original designation.

Endoclita headsii Grehan & C. Mielke, sp. n.

(Figs. 1a, 1b, 3, 4a, 4b, 5, 6a, 6b, 6c, 8a, 8b, 8c)

Description. Male (Figs. 1a, 1b). Wingspan: ~84 mm; FW length: 43 mm, width: 14 mm, ratio 3.1: 1; HW length: 35 mm, width: 19 mm, ratio 1.8: 1.

Head. Scales piliform, pale yellowish brown, inter ocular-antennal scales absent. Eyes large, exceeding 1/3 of head width in dorsal view and with dorsal edge subequal to vertex (Fig. 3a). Antenna filiform with 24 flagellomeres, annuli covered with scattered sensilla trichodea, scape barrel-shaped, covered with piliform scales; pedicel ovoid, wider than flagellomeres. Prelabium subrectangular, angled to median distally, labial palp two segmented, palpomeres covered with pale yellowish brown to pale greyish brown scales, distal palpomere subcylindrical, slightly narrower than basal palpomere (Fig. 3b).

Thorax. Scales piliform, short, concolorous with head.

Legs. Pale yellowish brown; epiphysis absent, lateral tibial scales long, project laterally in flat plane; dorsal scales of tarsi long, ventral tarsal scales short; arolium absent. Hind tibia with yellowish orange androconia (Fig. 4a), each forming an elongate scale with swollen base tapering distally to thin thread (Fig. 4b).

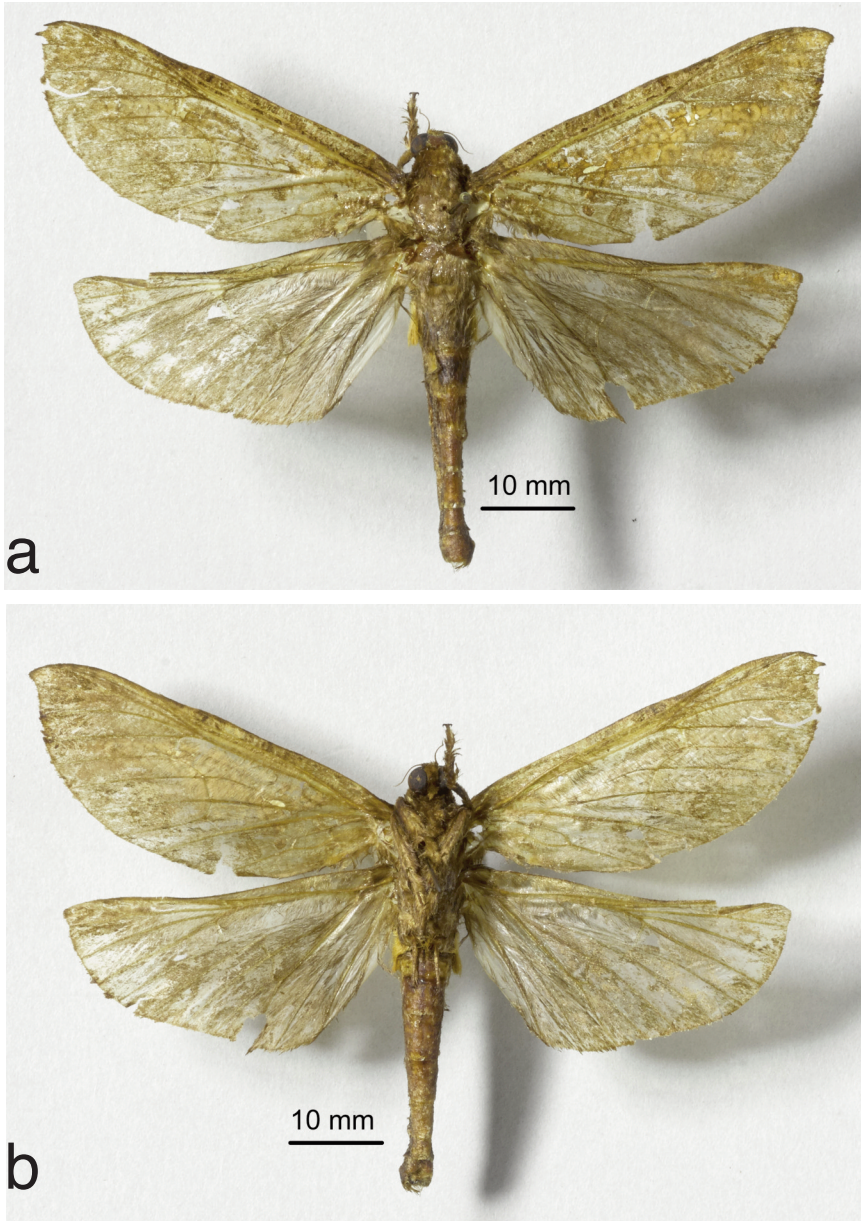


Fig. 1. *Endoclita headsi*, sp. n., HT male; (a) dorsal, (b) ventral (photos by Neal Evenhuis).

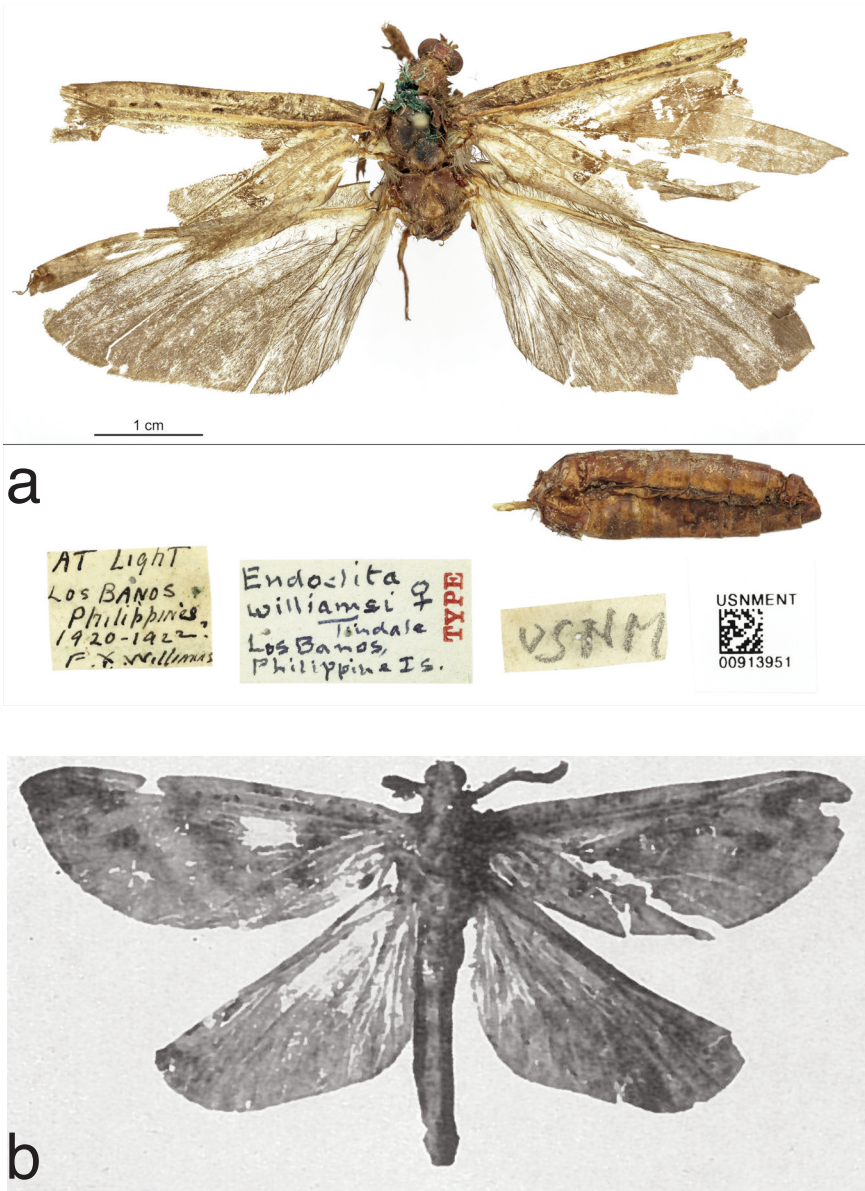


Fig. 2. *Endoclista williamsi* HT female; (a) dorsal with labels, (b) dorsal from Tindale (1958) (photo 2a by Karolyn Darrow).

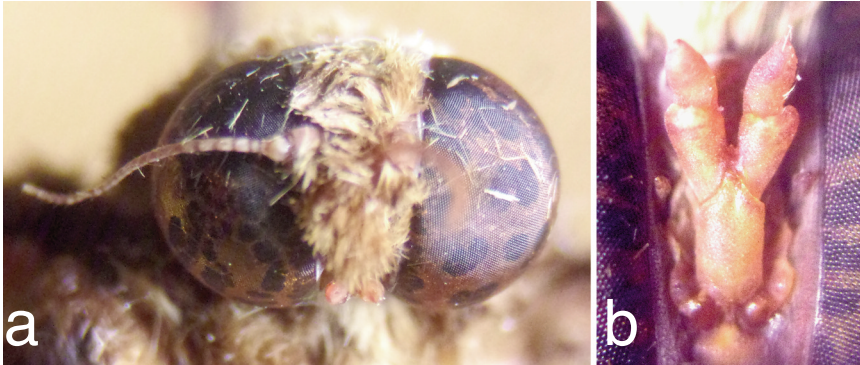


Fig. 3. *Endoclita headsi*, sp. n. HT male; (a) head and eyes, anterior view, (b) mouthparts, ventral view (photos by John Grehan).

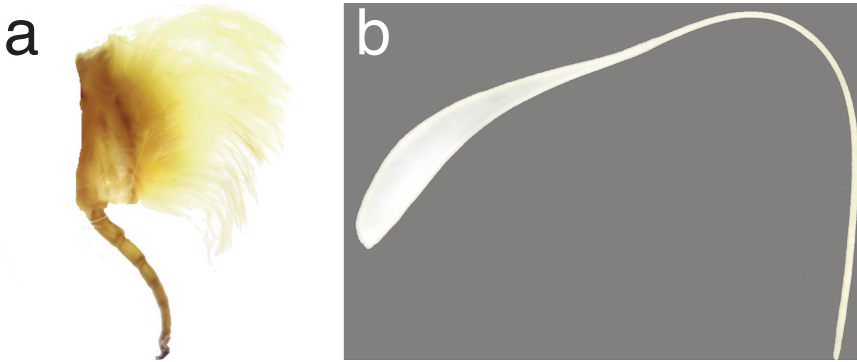


Fig. 4. *Endoclita headsi*, sp. n. HT male; metatibial androconia; (a) metatibia with androconial brush, (b) single androconial scale (photos by John Grehan)

Wings. (Figs. 1, 5). FW with nearly straight costal margin, very slight costal lobe, apex slightly falcate, termen continuous with inner margin without distinct tornus. Venation hepialine (*sensu* Dumbleton 1966). FW with Sc₁ present, CuP merging with A about halfway to inner margin; HW without Sc₁, R and Sc closer to each other than FW, but distinctly separated. FW extensively rubbed, dorsal ground color pale yellowish brown, especially centrally, and pale grayish brown, with scattered darker grayish brown markings. White fish-shaped discal stigma in the basal axil of M₂ + M₃, three white spots at r-m-M₁ junction. Ventral FW surface greyish brown, dorsal ornamentation between costa and Sc₁; Sc₁ lined with posteriorly directed piliform scales, shorter piliform scales over most of wing surface, merging with short lamellar scales towards outer margin. Dorsal and ventral HW greyish brown, covered with piliform scales basally and lamellar scales distally.

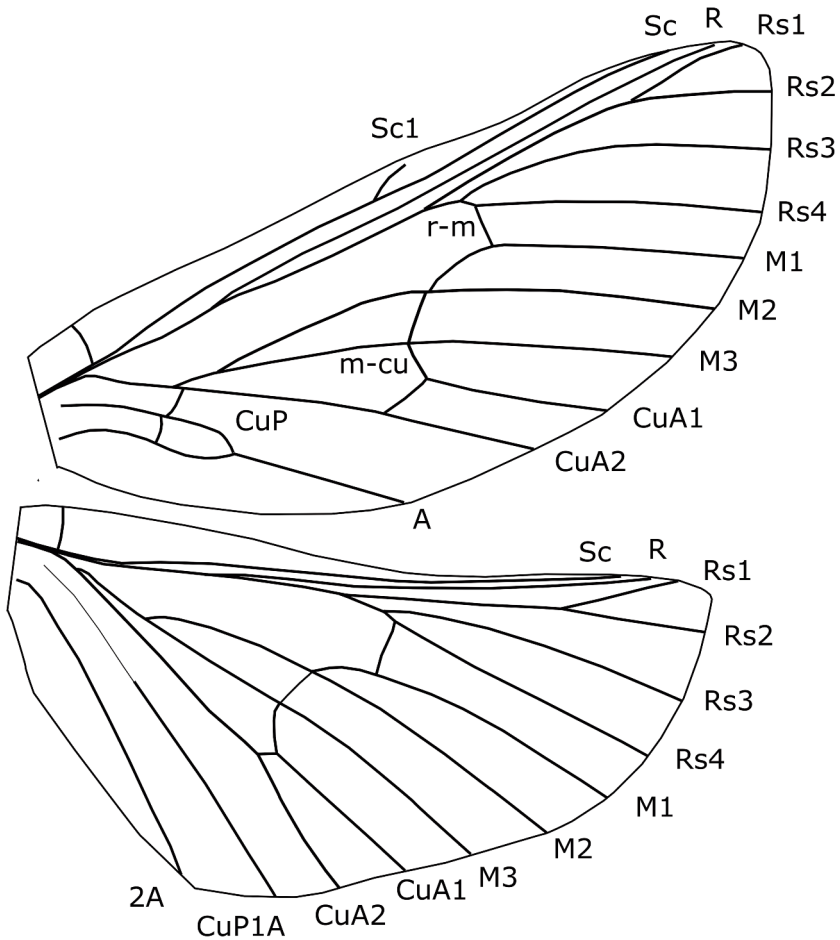


Fig. 5. *Endoclita headsi*, sp. n. HT male; wing venation.

Pregenital abdomen. Concolorous with thorax, other than the darker brown to black plural region (precise color of abdomen difficult to determine due to condition of specimen). Abdominal segments lightly sclerotized except for moderately sclerotized sternum VIII (Fig. 6a). Tergosternal connection with short lateral and dorsal brace, merging as a slightly obtuse curved angle; tergosternal bar forming an elongate triangle from central region down to apex adjacent to sternum II, anterior margin meeting ventral margin of lateral brace at right angle; posterior margin of central region anterior to deep sinus laterally edged with sclerotized zone from posterior margin to antero-lateral ridge of tergum II, tergal knob absent (Fig. 6b). Tergum II with robust and strongly sclerotized lateral ridge extending posteriorly from ventral corner of lateral tuberculate plate to transverse sclerotized zone near posterior margin; anterior ridge not fused medially; pleura II with pleural

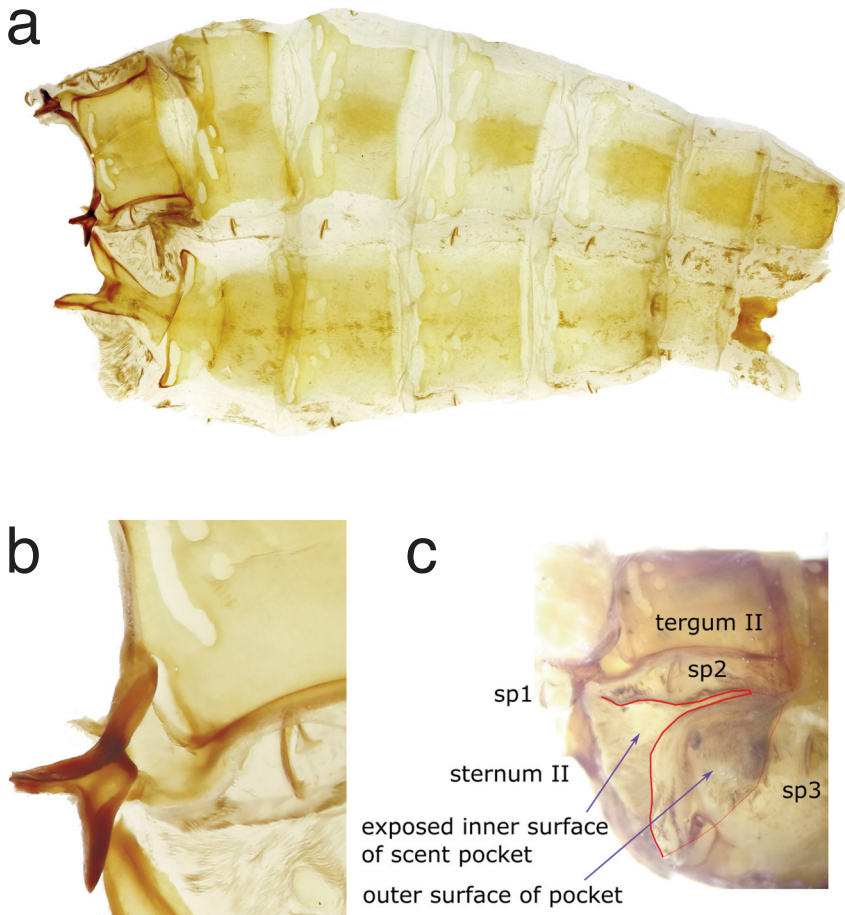


Fig. 6. *Endoclita headsii*, sp. n. HT male abdomen; (a) whole abdomen, (b) tergosternal connection, (c) scent pocket (photos by Kyhl Austin).

fold (Fig. 6c) that encloses part of the metatibial androconia (JRG, pers. observ.); sternum II centrally narrow, lateral arms long, about 1/3 of segment length, angled laterally, central anterior margin straight to base of lateral arms; tergum VIII subsquare, slightly longer than wide; sternum VIII subsquare, slightly wider than long, margins irregularly curved, posterior margin with deep central notch with setose and rounded lateral corners.

Genitalia (Fig. 8). Tegumen subrectangular, narrowing medially with submedial concavity at junction with posterior lateral apex of saccus, not fused with pseudotegumen. Saccus broadly U-shaped; apodemal suture close to anterior margin, forming prominent anterior Y-shaped anterior lateral ridges (alr); lateral arms narrowing to point at junction with the tegumen. Postero-dorsal margin of pseudotegumen with narrow and weakly

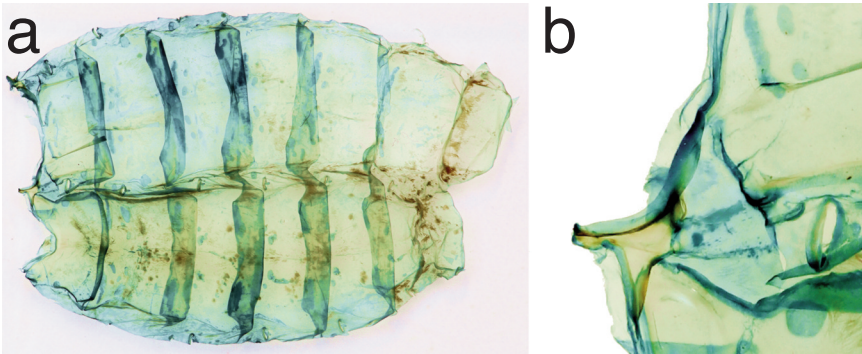


Fig. 7. *Endoclita williamsi* HT female abdomen; (a) whole abdomen, (b) tergosternal connection (photos by Kyhl Austin).

sclerotized rim (Fig. 8b – tlo) that does not fuse across the dorsal median, lined with scales and interpreted here as possibly homologous with the tergal lobes present in many other Hepialidae. Rim of pseudotegumen bordering anogenital field strongly sclerotized ventrally, extending medially as an anteriorly curved posterior-ventral arm and ventrally to apex as an antero-ventral arm with slightly bifurcated apex, dorsal branch meeting posterior margin of fultura superior; anterior margin of posterior-ventral arm and entire margin of antero-ventral arms strongly toothed; dorsal margin of pseudotegumen not fused across median. Valve short relative to size of pseudotegumen, lobate, glabrous, apex rounded, sacculus broad. Fultura superior weakly sclerotized, rectangular; fultura inferior rectangular, lateral and posterior margins concave, posterior corners forming narrow lobes, anterior margin strongly convex either side of median. Phallus entirely membranous, short, bulbous, cornutus absent (as in almost all species of Hepialidae).

Distribution (Fig. 11). Philippines, known only from the type locality (Busuanga Island).

Material examined. Holotype ♂ (BPBM 17844) (with the following labels separated by forward slashes): / PHILIPPINES: Busuanga Is, 4 km N San Nicolas, 21.v.1962 / M. Thompson, Collector, Bishop [Museum] / *Endoclita headsii* ♂, Grehan & C. Mielke des. 2018/. Dissection JRG M287 (BPBM). Figs. 1a, 1b. Holotype deposited in BPBM.

Etymology. Named for Michael Heads, in recognition of his extensive and pioneering biogeographic analysis and synthesis of South East Asia and other regions of the world.

***Endoclita williamsi* (Tindale, 1958: 191)**

(Figs. 2a, 2b, 7a, 7b, 9a, 9b, 10a, 10b)

This species is known from the female type only. The wings are considerably damaged (Fig. 2a), but enough detail is present in the photo by Tindale (1958) (Fig. 2b) and the present specimen to conform to general aspects of the original description. Tindale (1958) recorded a FW length of 44 mm and wingspan 93 mm, and described the following features: “eyes large, body pale ‘fawn’, hind legs small and lacking specialized scales (male androconia); FW with a straight costa and slightly falcate tip, dull brown with unobtrusive paler transverse bands, indistinct black spots along costa, three small silvery-white spots around junction of r-m and

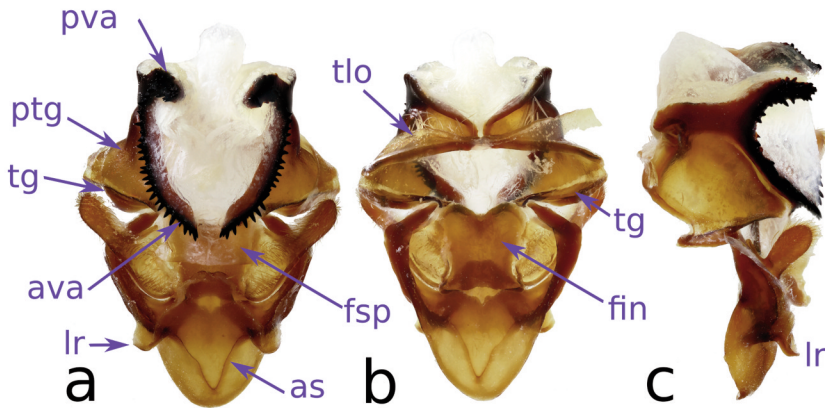


Fig. 8. *Endoclita headsi*, sp. n. HT male genitalia; (a) ventral, (b) dorsal, (c) lateral. Abbreviations: ava - antero-ventral arm, as - apodemal suture, fin - fultura inferior fsp - fultura superior (membranous and folded over fultura inferior in this view), lr - lateral ridge, ptg - pseudotegumen, pva - postero-ventral arm, tg - tegumen, tlo - tergal lobe (or equivalent) (photos by Kyhl Austin).

M₁, a white spot at junction of M₂-M₃, and traces of small ochreous spots outlined in dark brown across apical third of wing; HW with both Pcu (CuP) and IV (A) veins present, smoky brown except narrowly at wing tip, opalescent blue sheen under variable light”.

Pregenital abdomen (Fig. 7): segments lightly sclerotized; tergum II rectangular, lateral ridge well developed; tergosternal connection (Fig. 7b) with lateral and dorsal brace short, tergosternal bar narrowing ventrally, fused to central region, tergal lobe absent; sternum II (Fig. 7a) rectangular with short, subtriangular anterior lateral branches and anterior margin with U-shaped medial notch; tergum VIII rectangular; sternum VIII rectangular, V-shaped, antero-posteriorly short, half length of sternum VII, anterior margin centrally concave, V-shaped, posterior margin centrally convex (Fig. 7a).

Female genitalia (Figs. 9, 10): External genitalia (Figs. 9a, b) with dorso-ventrally tall dorsal plate (tergum IX) forming a narrow arch fused across dorsal median, anal papillae not projected as distinct lobes; subanal plates tall, sub-rectangular, curving laterally at base; lamella antevaginalis with lateral and medial lobes, the latter large, rectangular with rounded corners dorsally, externally membranous, internal surface with sclerotized plate either side of median; lateral lobes dorsoventrally shallow, extending posteriorly as a triangular point projecting medially either side of the central lobe (left lateral lobe visible in oblique profile, Fig. 9b). Ductus and corpus bursae sub-equal in length (Fig. 10a); ductus bursae narrowing, lateral caecum joining corpus bursae at junction of ductus bursae, caecum cylindrical, slightly narrower than corpus bursae. Spermatheca elongate, about half length of ductus bursae (Fig. 10b).

Distribution. Northern Philippines, Luzon Island.

Material examined. Holotype ♀ (with the following labels separated by forward slashes): / AT LIGHT, Los Baños, Philippines, 1920–1922, F.X. Williams / TYPE *Endoclita williamsi* ♀ Tindale, Los Baños, Philippine Is. / USNENT 0091351. Holotype in the United States National Museum.

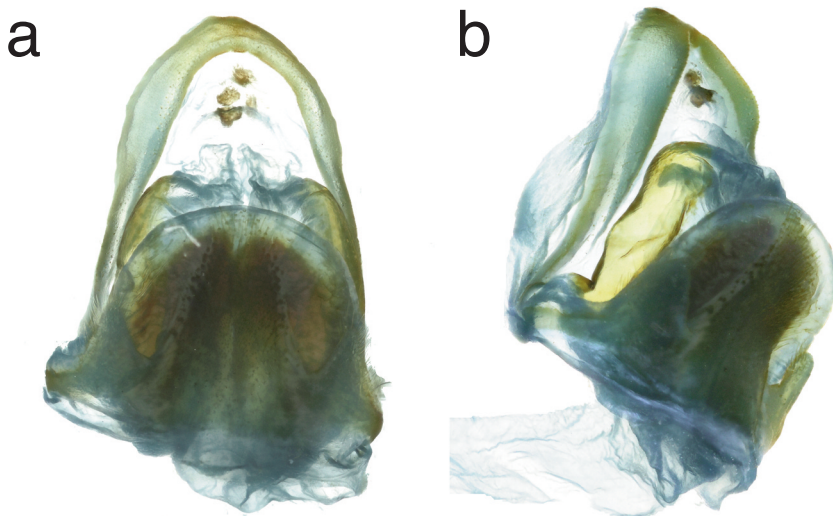


Fig. 9. *Endoclita williamsi* HT female external genitalia; (a) posterior view, (b) lateral oblique view (photos by Kyhl Austin).

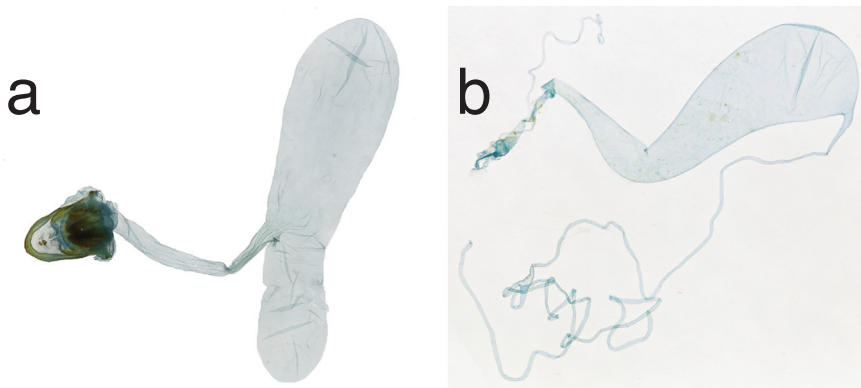


Fig. 10. *Endoclita williamsi* HT internal female genitalia; (a) bursa copulatrix, (b) spermatheca and spermathecal ducts (photos by Kyhl Austin).

Etymology: Named for Mr. Francis X. Williams, for his many observations on Hepialidae provided to Tindale (Tindale 1958).

Systematic remarks

Two aspects of wing morphology are potentially informative about species relationships within *Endoclita*. The first of these is the presence of a costal lobe corresponding to the position of Sc1 that is distinct in some species but less so in others (Buchsbbaum & Grehan 2019). This lobe represents a uniquely derived feature within the Hepialidae (as it is absent in the

other hepialoid families and Mnesarchaeoidea) and therefore represents a potentially informative phylogenetic character state. However, the demarcation between a lobe being present or absent due to variation in size limits the current utility of this feature. The Philippine species both lack a recognizable costal lobe which may exclude them from those species with a lobe, but does not identify their particular affinities with respect to other species lacking a lobe (since the shared absence of a lobe is a primitive feature). The second feature involves two wing markings on the FW: a triangular dark shaded area mainly across the discal cells and a trapezoidal pale area long the anterior margin of the shaded patch. These patterns represent a derived condition within the Hepialidae, but without other corroborating characters the shared presence of these features must be regarded as provisional (Buchsbaum & Grehan 2019). Again, both Philippine species lack these features of the FW.

The shape of the HW in the Philippine species is almost trapezoidal, where the outer margin is angled centrally so that there are two distinct submargins, here referred to anterior (apex to about M_1) and posterior M_1 to 2A sections (Fig. 5). The trapezoidal shape of the HW is a derived condition within the Hepialidae as non hepialid families have a broadly triangular HW as do most Hepialidae. The condition may be unique within *Endoclita* and is shared by many species, including those with or without a costal lobe. Because of variability in the angle and relative length of wing margins this feature cannot be used at this time as definitive evidence of close relationship between the Philippine and other species.

Genitalia are most often a defining morphological characteristic for species of Hepialidae (cf. Nielsen & Robinson 1983, Nielsen & Kristensen 1989, Dugdale 1994, Simonsen 2018), and genitalic structures often show differences among genera and also between species within genera. The principal challenge for assessing relationships within *Endoclita* is the lack of published descriptions of the complete genitalia. Comparisons made here refer to those species for which adequate genitalic descriptions are available. One of the most prominent features in the male genitalia of *E. headsii*, sp. n. is the dentate rim of the pseudotegumen along the postero-ventral and antero-ventral arms. The antero-ventral arm may be homologous to the more lobate shaped medial posterior projection in the genitalia of *E. meifenga* Buchsbaum & Grehan, 2019 (Buchsbaum & Grehan 2019, fig. 9a) from Taiwan where the pseudotegumen rim has a jagged edge, but lacks the definite tooth-like spines of *E. headsii*, sp. n. The male genitalia of *E. kosemponis* (Strand, 1916) of Taiwan has both a medial posterior projection (= postero-ventral arm?) and a lobate postero-ventral projection, but lacks the dentate margins (Buchsbaum & Grehan 2019, fig. 9b). In the genitalia of *E. sinensis* (Walker, 1856) from Taiwan, both arms are present as shorter lobes that lack dentate margins (Buchsbaum & Grehan 2019, fig. 9c.). The male genitalia of *E. inouei* Ueda, 1987 of Taiwan differs from all the previous species in lacking pseudoteguminal arms or projections and by fusion of the ventral pseudotegumen across the median (Ueda 1987, fig. 6). The Japanese *E. excrescens* (Butler, 1877) also has two pseudoteguminal arms where the postero-dorsal arm forms an expanded triangular lobe and the postero-ventral arm narrows to the tip where it fuses across the midline. The rim of the postero-dorsal arm is dorsally lined with minute dentate projections (Grehan & Mielke 2017, fig. 13). The male genitalia of the northern Vietnam *Endoclita coomani* Viette, 1961 also has a pseudotegumen rim with a medial lobe (= postero-ventral?) and an ascending spine that is fused across the median, but without a dentate margin, and a further branching structure involving a T-shaped formation is present dorsally. A further two new species from northern Laos also possess a similar structure. These species also share a V-shaped sternum VIII that is fused to the sacculus and a basal lobe on the valva and in these features show no evidence of a close affinity



Fig. 11. Species records and tectonics; red line – trench at boundary of continental plate, blue line – trench at boundary of Philippine plate. Points in direction of subduction. Locality of *Endoclita headsii* sp. n. – Busuanga Island, *Endoclita williamsi* – Luzon Island.

with the Philippine species. Another northern Laos species, *E. salvazi* Tindale, 1958, has a costal FW lobe and the pseudotegumen rim lacks the medial projection found in *E. headsii*, sp. n. (Grehan *et al.* 2019).

The external female genitalia of *E. williamsi* is distinctive for the large rounded sub-square lobular dorsal margin of the posterior surface of the antrum to which the narrow, vertically tall sclerotized central lobe of the lamella antevaginalis is appended externally while the lateral lobes of the lamella antevaginalis comprise smaller triangular lobes to

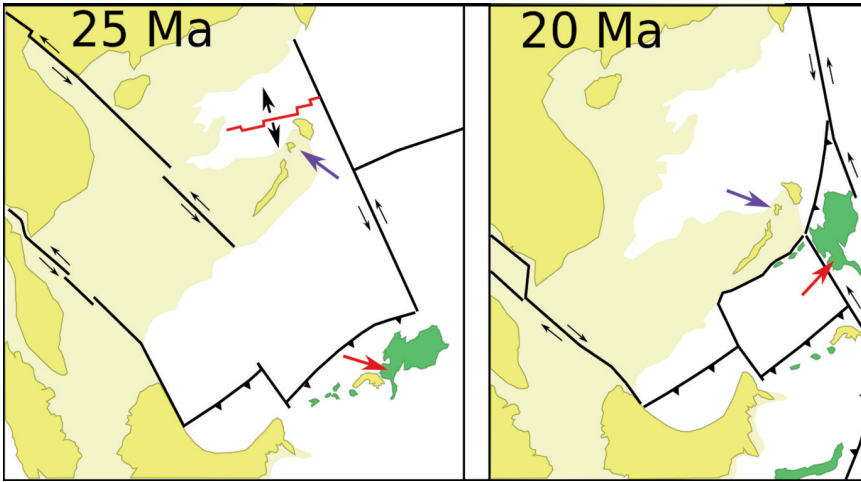


Fig. 12. Paleo-tectonic reconstruction of paleo positions of the Palawan block in relation to Luzon Island. **Left**, position of Palawan block about 25 Ma as it is split apart from by the newly forming South China Sea. **Right**, Palawan block coming into proximity with Luzon about 20 Ma. Blue arrow = *Endoclita headsii*, sp. n. locality of Busuanga Island; red arrow = *E. williamsii* location on Luzon Island. Figure modified from Hall (2002).

either side (best seen in oblique lateral view in Fig. 9b). The central rounded formation does not occur in the Taiwanese *Endoclita atayala* Buchsbaum & Hsu, 2018, *E. kosempo-nis*, or *E. sinensis* (Buchsbaum *et al.* 2018, Grehan & Buchsbaum 2019). There are two principal arrangements of the bursa copulatrix in Hepialidae, either it is linear with the corpus and ductus bursae in line or the corpus bursae is bifurcated at the junction with the ductus bursae as seen in *E. williamsii*. Usually there is a larger section that is referred to here as the corpus while the smaller section is referred to here as the caecum. The linear form appears to represent the primitive condition as it is the only form recorded in other Hepialoidea. Both forms occur within *Endoclita* and also in *Aenetus* Herrich-Schäffer, 1855 and *Abantiades* Herrich-Schäffer, 1855 (Simonsen 2018) so the phylogenetic significance of this feature within *Endoclita* is equivocal. However, characterization of further *Endoclita* species may clarify whether particular details of bursa copulatrix morphology may be phylogenetically informative.

Direct genitalic comparison between the two Philippine species is not possible due to their respective types being of different gender. Differences in mouthparts may provide evidence of species differences, but it has not been possible to examine those of *E. williamsii* because the specimen is too fragile for mailing (the abdomen had already detached and was sent separately). The only other potential species difference observed here is the tergo-sternal connection angle which is more acute in *E. headsii*, sp. n. where the anterior margin of the tergo-sternal bar meets the lateral brace. Observations of tergo-sternal morphology in other Hepialidae suggest that the shape is consistent between sexes (JRG, pers. observ.). As in other Hepialidae with metatibial androconia, the shape of sternum II in males has a convex lateral margin and is narrower and longer in males than females. While this difference may be considered minor and possibly represent vari-

ation, differences in the genitalia of other Hepialidae are also sometimes of a similar scale of difference. We acknowledge that some may not agree with our choice to treat the specimens as separate species, but in consideration of the tergosternal difference along with the geographic and geological context (see Biogeographic Remarks below) it is our conclusion that the Busuanga specimen is a distinct species from that from Luzon.

Biogeographic Remarks

The fact that *Endoclita* in the Philippines is documented for only two specimens indicates just how little is known about the genus in this region. As a wood-boring group with larvae that feed on live trees and shrubs (Grehan & Ismavel 2017), *Endoclita* could be expected to occur in forest habitats over much of the Philippines. Records are sparse for much of Southeast Asia, with only three species (represented by three specimens) from Borneo (Tindale 1958) while no species are recorded from Sulawesi, the Moluccas, or east of Bali in the Lesser Sunda Islands (Grehan *et al.* 2018). The paucity of records is probably because the moths have a low level of attraction to light sources. Even in Java and Sumatra, where the genus is represented by several species, specimens are rarely collected despite years of effort (B. de Groof, pers. comm.).

The limited geographic sampling and lack of phylogenetic resolution for species relationships precludes precise biogeographic reconstruction of *Endoclita* in the Philippines or south eastern Asia in general. The two Philippines records are of biogeographic interest as they occur on contrasting tectonic formations where *E. headsii*, sp. n is on the eastern Sundaland-Eurasian block, and *E. williamsi* is within the Philippine mobile zone (Fig. 11). Even during the Pleistocene, the two species were geographically isolated by the 120-m isobath between the greater Palawan and Luzon island assemblages (Brown *et al.* 2013, Heads 2014). The Pleistocene separation between Busuanga and Mindoro islands (that later merged with Luzon during the Pleistocene) was only about 30 km (currently the distance is about 70 km). This distance is sufficient to geographically isolate other hepialid species. For example, in New Zealand the 22-km width of Cook Strait is sufficient to provide a current geographic boundary for *Aenetus virescens* (Doubleday, 1843), *Aoraia lenis* (Dugdale, 1994), *Dumbletonius unimaculatus* (Salmon, 1948), and *Wiseana jocosus* (Meyrick, 1912) (cf. distribution maps in Dugdale 1994). The island of Taiwan was connected to China during the Pleistocene and yet supports 10 endemic species and one endemic genus of Hepialidae with no confirmed species in common (Buchsbbaum *et al.* 2018, Buchsbbaum & Grehan 2019). The current distributions of Hepialidae in general appear to be concordant with past or present ecological as well as topographic continuity as they are not strong fliers other than over short distances (particularly for fertilized females) and in the absence of functional mouth parts they are unable to supplement food reserves. There is also biogeographic evidence for species of Australian and New Zealand Hepialidae retaining distributional stability over at least parts of their range since the Mesozoic (Grehan & Mielke 2018).

The Palawan assemblage is of continental origin made up of Sundaland-Eurasian margin-derived ophiolites, while Luzon is located on a belt of central Early to Late Cretaceous Cordilleran ophiolites that extend along the entire length of the central Philippines and originally formed part of the leading edge of the proto-Philippine Sea plate (Yumul *et al.* 2008, fig. 3c). The present day location of Busuanga Island is geographically close to Luzon Island, with the island of Mindoro between the two. Mindoro Island is also considered to be part of the Palawan block (Concepcion *et al.* 2012) which

was situated adjacent to China (Fig. 12) until Oligocene seafloor spreading brought the northern end of the Palawan block in close proximity with Luzon about 20–15 Ma (Hall 1996, 2002). The region between the two *Endoclita* localities is also a zone of differentiation for other taxa, such as frogs of the genus *Platymantis* Günther, 1858 which are absent from Busuanga and other islands of Palawan (Diesmos *et al.* 2015) while widespread across the rest of the Philippines and east to Fiji (Heads 2014: 382). Busuanga Island is also located at the eastern boundary of a scincid lizard clade that does not occur on Luzon (Heads 2014: 379) and is at the boundary between two allopatric clades of the bird genus *Dicrurus* Vieillot, 1816 (Dicruridae) (Heads 2014: 368).

ACKNOWLEDGEMENTS

We are grateful to Neal Evenhuis (BPBM) for bringing a Philippine *Endoclita* specimen to our attention and assisting with loans and specimen photography, and to Jim Boone (BPBM) for his assistance with facilitating access to BPBM material. We also express our gratitude to Donald Davis (United States National Museum, Washington, DC) and Jason Dombroskie (Cornell University, Ithaca, New York) for kindly facilitating access to type material, to Karolyn Darrow (United States National Museum) for photographing the type of *Endoclita williamsi*, to Kyhl Austin (Cornell University) for photographing abdomens and genitalia and commenting on the ms, to Michael Heads (Dunedin, New Zealand) for comments on the manuscript, and Benny de Groof (Lier, Belgium) for information on *Endoclita* distribution in Indonesia.

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