

## A revision of the genus *Amblycara* (Hemiptera: Heteroptera: Pentatomidae)

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**Abstract.** The Oriental and Austro-Pacific stink bug genus *Amblycara* Bergroth, 1891 (Hemiptera: Heteroptera: Pentatomidae: Pentatominae: Pentatomini) is redescribed and revised. Two species are recognized: the type species, *A. gladiatoria* (Stål, 1876), is redescribed and recorded for the first time from India, Laos, Cambodia, Malaysia, Indonesian and Papuan parts of New Guinea, New Caledonia, and Fiji; *A. innocens* sp. nov. is described as new based on specimens from Taiwan and the Philippines (Palawan). A lectotype is designated for *A. gladiatoria*. The taxonomic placement, systematic relationships, and zoogeography of the genus and its included species are discussed.

**Key words.** Heteroptera, Pentatomidae, taxonomy, nomenclature, new species, new records, Oriental Region, Australasian Region, Oceanic Region

### Introduction

The genus *Amblycara* Bergroth, 1891 (Hemiptera: Heteroptera: Pentatomidae: Pentatominae: Pentatomini) has remained monotypic so far; the single included species, *A. gladiatoria* (Stål, 1876) was recorded from several scattered localities in the Oriental Region and Australia (RIDER 2006). The genus and its included species are redescribed and an additional new species is described in the present paper.

### Material and methods

External structures were examined using a stereoscopic microscope (Opton 475052-9901). Drawings were made with the aid of a camera lucida. Male genitalia were dissected after careful heating in hypertonic KOH solution, stained with Chlorazole Black E if necessary, and examined using stereoscopic microscopes (Olympus SZX12, Zeiss Discovery V8).

Measurements were taken using a micrometer eyepiece. Digital photographs were taken with a Nikon D90 camera equipped with an AF-S Micro Nikkor 60mm f/2.8G ED lens.

Morphological terminology mostly follows TSAI et al. (2011). The two species of this genus are similar in their colour, integument, vestiture, and morphology of the exoskeleton, but they differ strikingly in their external male and female genitalia. Therefore in order to avoid repetitions a detailed description of the genus is provided, but the species descriptions are short and focus on the diagnostic characters of the two species.

Localities verified by us based on voucher specimens are marked with exclamatory point '!'. Besides the specimens directly examined by us, Joseph E. Eger, Henrik Enghoff, Zdeněk Jindra and David A. Rider were kind enough to verify additional specimens deposited in collections not accessed by us, using the manuscript and illustrations of the present paper. These records are included as verified records in the distribution lists and map (Fig. 42), but they are referred to as personal communications of the above colleagues when listing the locality information.

#### Abbreviations for depositories:

BMNH	Natural History Museum, London, United Kingdom;
DARC	David A. Rider Collection, Department of Entomology, North Dakota State University, Fargo, North Dakota, USA;
HNHM	Hungarian Natural History Museum, Budapest, Hungary;
IANC	Laboratoire d'Entomologie Appliquée, Institut Agronomique Néo-Calédonien, La Foa, New Caledonia;
ISNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium;
JEEC	Joseph E. Eger Collection, Tampa, USA;
MMBC	Moravian Museum, Brno, Czech Republic;
NHMW	Naturhistorisches Museum, Vienna, Austria;
NMNS	National Museum of Natural Science, Taichung, Taiwan;
NMPC	National Museum, Prague, Czech Republic;
SEHU	Laboratory of Systematic Entomology, Hokkaido University, Sapporo, Japan;
TFRI	Insect Collection, Taiwan Forestry Research Institute, Taipei, Taiwan;
ZJPC	Zdeněk Jindra Collection, Prague, Czech Republic;
ZMUC	Zoological Museum, University of Copenhagen, Copenhagen, Denmark.

## Taxonomic part

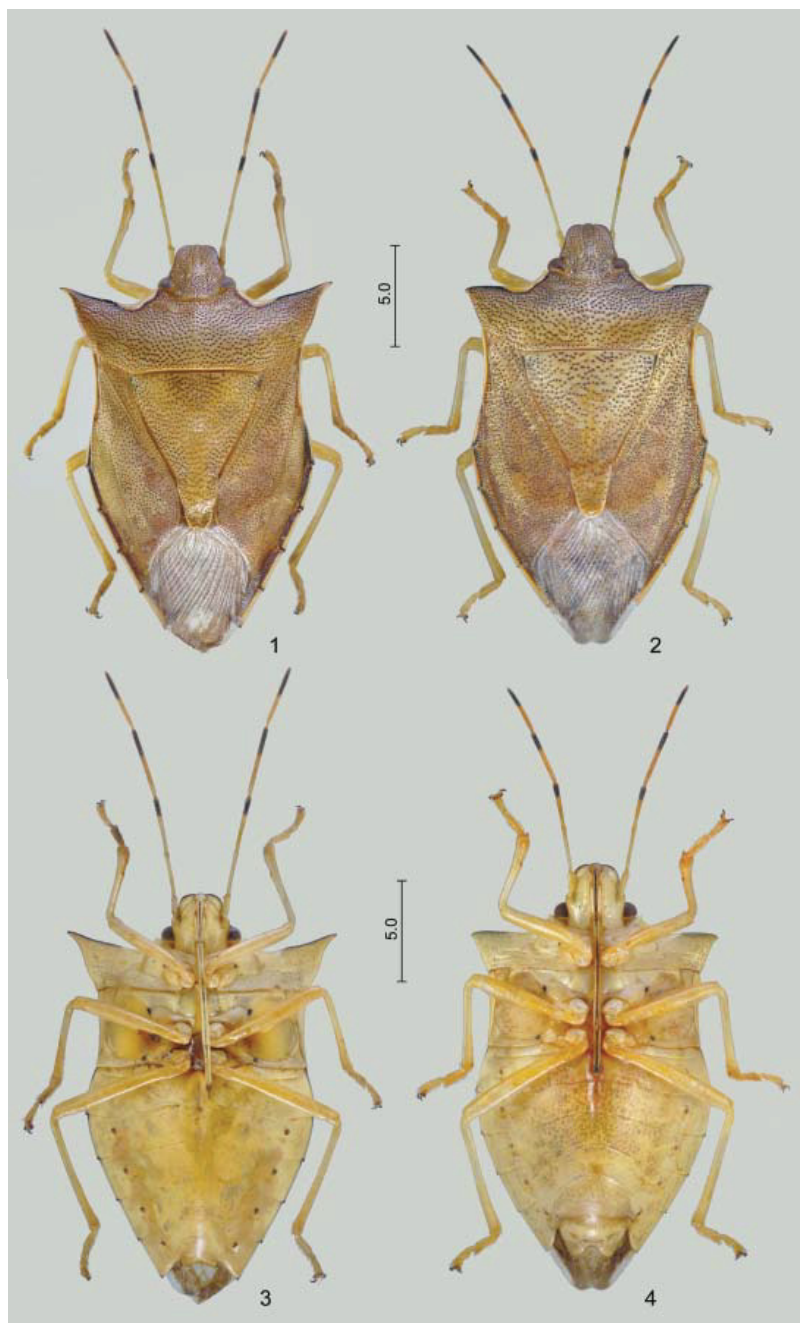
### Genus *Amblycara* Bergroth, 1891

*Abeona* Stål, 1876: 67, 102. Type species by monotypy: *Abeona gladiatoria* Stål, 1876. Junior homonym of *Abeona* Girard, 1855 (Pisces).

*Amblycara* Bergroth, 1891: 214. New name for *Abeona* Stål, 1876.

**References.** ATKINSON (1888): 146 (*Abeona*, redescription, fauna of India); LETHIERRY & SEVERIN (1893): 179 (catalogue); DISTANT (1902): 211 (in key), 217 (redescription, fauna of British India); KIRKALDY (1909): 140 (catalogue); DISTANT (1918): 139 (listed); TAKARA (1957): 31 (listed); GROSS (1975): 51 (diagnostic characters, taxonomic placement); CASSIS & GROSS (2002): 524 (catalogue, Australia); RIDER (2006): 326 (catalogue, Palaearctic); TAKAI & ISHIKAWA (2012): 488 (redescription).

**Diagnosis.** Large (17–21 mm), light brownish pentatomids which can be recognized by the following combination of characters: conspicuous, broad, stramineous callosity present along anterior portion of lateral margin of pronotum; humeral angle produced, far surpassing margin of corium, apically sharply pointed; mesosternum with distinct but relatively low carina along



Figs 1–4. Males of *Amblycara* in dorsal (1–2) and ventral view (3–4). 1, 3 – *A. gladiatoria* (Stål, 1876); 2, 4 – *A. innocens* sp. nov. (holotype).



Figs 5–7. Lectotype of *Amblycara gladiatoria* (Stål, 1876). 5 – dorsal view; 6 – ventral view; 7 – labels. Scales in mm. © NHMW.

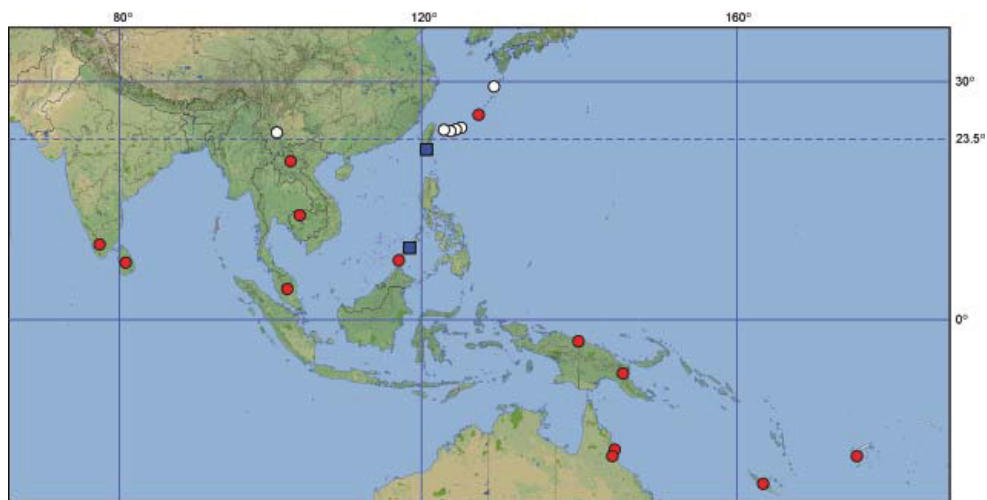


Fig. 8. Distribution of *Amblycara gladiatoria* (Stål, 1876) (circles) and *A. innocens* sp. nov. (squares). Filled symbols represent records based on specimens examined by us or verified literature records, open symbols represent unverified literature data.

midline; abdominal sternite II without process or projection; abdominal venter with a short longitudinal furrow occupying sternites III, IV and base of V.

**Redescription.** *Body* large (total length about 17–21 mm), broadly oval, dorsoventrally somewhat flattened (Figs 1–4). *Colour, integument and vestiture.* Dorsum rather uniformly yellowish brown to light brown, with dense, dark punctation; anterior portion of lateral margin of pronotum and basal fourth of anterior (= external) margin of fore wing with a conspicuous, broad, stramineous callosity; lower surface of fore wings, abdominal mediotergites and inner margins of outer laterotergites red; venter of body stramineous, unpunctured. Integument glabrous except for short hairs on appendages, labium, and terminalia; integument rather smooth.

*Head and cephalic appendages.* *Head* rather elongate, 1.0–1.05 times as broad as its median length, 1.6–1.7 times as broad as interocular distance, dorsally flat, slightly narrowing anteriad, lateral margin weakly emarginate anteriad of eye, broadly rounded apically, clypeus slightly surpassing mandibular plates apically; antenniferous tubercle slightly surpassing lateral margin of head in dorsal view; buccula low, obtusely angulate subapically. *Antenna* simple, five-segmented, first segment not reaching apex of head, segment IIb 1.1–1.2 times as long as segment IIa. *Labium* reaching abdominal sternite III, apex of first segment not reaching base of head.

*Thorax and thoracic appendages.* *Prothorax.* Anterior margin of pronotum deeply concave, distinct impressed anterior collar not developed; anterolateral angle of pronotum surpassing lateral margin of eye, produced into a small, laterally or anterolaterally directed denticle; lateral margin of pronotum deeply concave, smooth, posterior portion directed subhorizontally, humeral angle more or less produced, directed anterolaterad or laterad, far surpassing costal margin of corium, sharply pointed apically; posterior margin nearly straight along base of scutellum. Prosternum flattened, bordered by a pair of low, obtuse, longitudinal carinae. *Pterothorax.* Scutellum of medium size, about 1.2 times longer than its width across base, frenal portion occupying approximately basal two thirds, gradually narrowing, rounded laterally, postfrenal portion occupying approximately apical third, narrowly tongue-shaped. Mesosternum with a distinct, relatively low, continuous median carina continued on metasternum as a somewhat broader elevation. Metathoracic scent gland ostiole associated with an elongate, rather straight peritreme gradually narrowed distally, approaching lateral margin of metapleurite; evaporatorium occupies most of metapleuron except for metepimeron and broadly extends onto mesopleuron approaching its anterior margin. *Fore wing.* Basal fourths of costal margins of the two wings nearly parallel in resting position, then conspicuously diverging, and strongly converging in their apical halves; apical margin strongly S-shaped; apex of membrane rather narrowly V-shaped, distinctly surpassing apex of abdomen in rest. *Legs* simple; femora unarmed; dorsal surface of tibiae, particularly those of mid and hind legs, with more or less distinct furrow; tarsal segment I about as long as or somewhat shorter than combined length of segments II+III, segment II very short.

*Pregenital abdomen.* Venter with a rather broad and deep, obtuse median longitudinal furrow (Fig. 34: mfu) occupying sternites III, IV and base of V; posterolateral angles of segments III–VII slightly but distinctly produced into a minute, black, sharp denticle. Tergite VIII of female broadly and shallowly emarginate posteriorly.



**Distribution and diversity.** The genus has remained monotypic so far, with the type species broadly distributed in the Oriental, Australasian and Oceanian Regions. A new species is described in the present paper from Taiwan and Palawan.

***Amblycara gladiatoria* (Stål, 1876)**

(Figs 1, 3, 5–6, 9–13, 17–20, 25–28, 33–34, 37–38, 41–42)

*Abeona gladiatoria* Stål, 1876: 102. SYNTYPE(S): ♀: “India orientalis” [= East Indies]; NHMW.

*Amblycara gladiatoris*: LIN & ZHANG (1985): 7; HUA (2000): 171. Incorrect subsequent spelling.

**References.** ATKINSON (1888): 146 (English translation of original description, distribution); LETHIERRY & SEVERIN (1893): 179 (catalogue, distribution); DISTANT (1902): 217 (redescription, habitus, figures, distribution); DISTANT (1908a): 420 (record); DISTANT (1908b): 127 (record); KIRKALDY (1909): 140 (catalogue, distribution), 381 (record); DISTANT (1918): 139 (listed, distribution); ESAKI (1937): 89 (redescription, record); TAKARA (1957): 31 (record, distribution); BLACK (1968): 562 (record); LIN & ZHANG (1985): 7, 10 (*gladiatoris*, record); MIYAMOTO & YASUNAGA (1989): 184 (listed, distribution); CASSIS & GROSS (2002): 524 (catalogue, distribution, biology); ISHIKAWA (1999): 24 (distribution, record, photo); HUA (2000): 171 (*gladiatoris*, listed, distribution); HAYASHI (2002): 147 (distribution); RIDER et al. (2002): 136 (listed, distribution); RIDER (2006): 326 (catalogue, distribution); TAKAI & ISHIKAWA (2012): 488 (redescription, distribution, records, photos of adult, egg batch, 4th and 5th instar larvae).

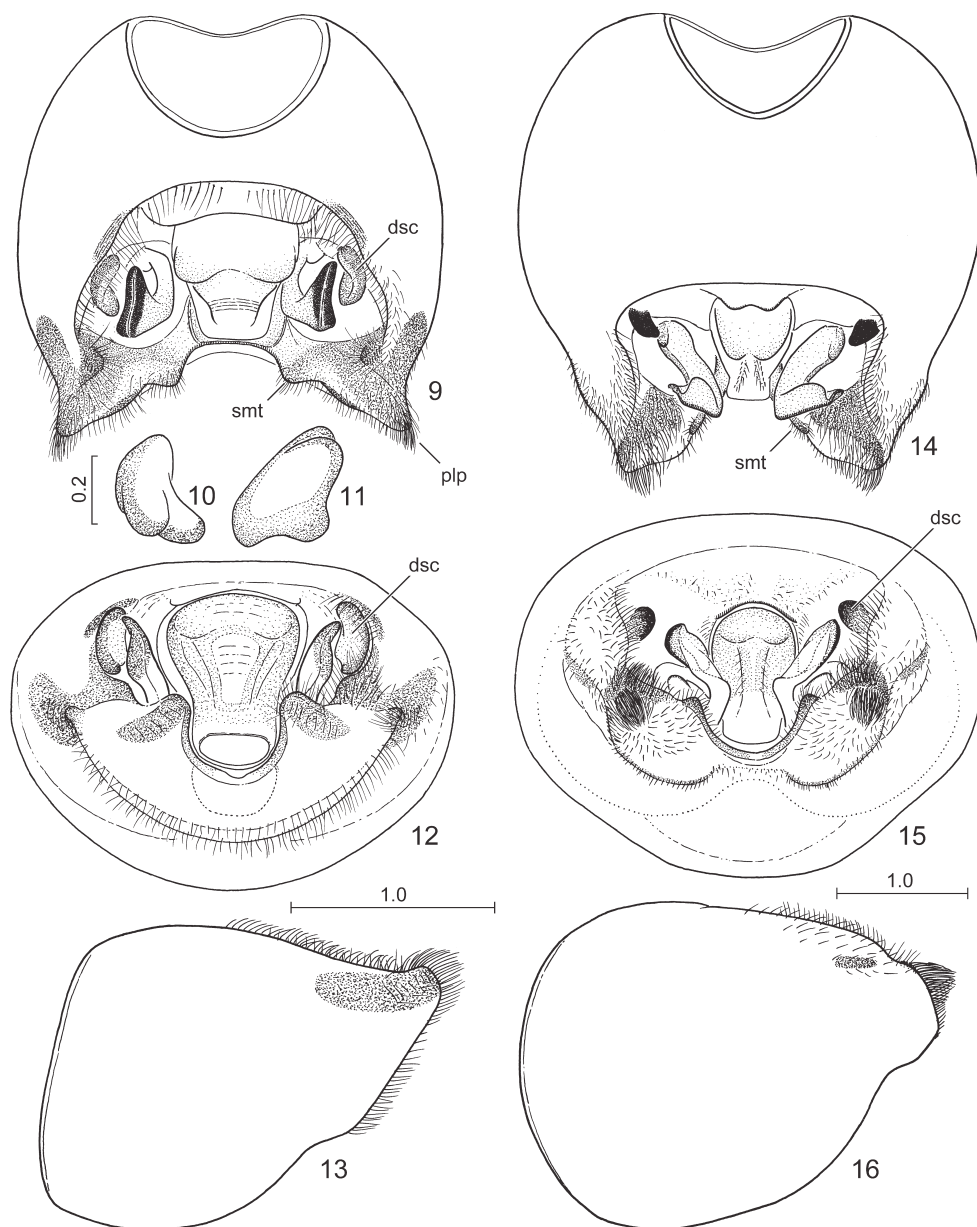
**Type material examined.** LECTOTYPE (present designation): ♀, “Ostindien [handwritten] \ coll. Signoret [printed]”, “gladiator [handwritten] \ det. Stal [printed]”; left antenna, right antennal segments IIa–IV, labial segments II–IV, right fore leg, tibia and tarsus of left mid leg lacking; deposited in NHMW (Figs 5–7).

**Additional specimens examined.** JAPAN: Okinawa Is., date unknown, leg. Sakaguchi (1 ♀, SEHU). – SRI LANKA: “Ceylon”, Kandy, coll. H. Rolle (1 ♂ [Figs 1, 3, 9–13, 17–20, 25–27], det. G. Horváth, HNHM); “Ceylon”, leg. [E.E.] Green, coll. W.L. Distant 1911-383 (1 ♂, BMNH). – INDIA: KERALA: Kardamon Hills, 50 km NW of Pathanamthitta, near Pambaiyar river, 77°05'E 9°25'N, 6–9.v.1994, leg. Z. Kejval (2 ♂♂ 1 ♀, ZJPC) – LAOS: Louang Phrabang Prov., Muang Ngoy, 20°43'N 102°41'E, 500 m, 22.iv.1999, leg. V. Kubáň (1 ♂, det. P. Kment 2007, MMBC); Attapeu Prov., Bolavens Plateau, bridge ca. 4 km E Tad Katamtok, 15°07.8'N 106°40.1'E, 260 m, 11–12.v.2010, at light, leg. J. Hájek (1 ♂, det. P. Kment, NMPC). – CAMBODIA: Siem Reap, Angkor Thom, 26.v.2003, light trap, leg. J. Constant, K. Smets & P. Grootaert (1 ♀, ISNB). – MALAYSIA: Malay Penin[sula], Kuala Lumpur, ex coll. Agri. Dept., ex F[ederated] M[alay] S[tates] Museum, B.M. 1955-354 (1 ♂, BMNH). – PHILIPPINES: BALABAC: Dalawan Bay, 5.x.1961 (1 ♀, det. G.M. Black, ZMUC, H. Enghoff pers. comm.). – INDONESIA: “Dutch New Guinea”, Humboldt Bay Dist., Bewani Mts., ix.1937, W. Stüber, B.M. 1938-177 (1 ♀, BMNH). – PAPUA NEW GUINEA: NE Wau, 1750 m, 5.ii.1966, leg. J. & M. Sedlacek (1 ♂, DARC, D.A. Rider pers. comm.). – AUSTRALIA: QUEENSLAND: Mt. Garnet, 15–19.i.1989, leg. S. Lamond (1 ♀, JEEC, J.E. Eger pers. comm.); Queensland, unspecified locality, leg. F.P. Dodd, 1904-284 (1 ♀, BMNH). – NEW CALEDONIA: Farino, 31.iii.[20]01, leg. I. Salesne (1 ♂, IANC, D.A. Rider pers. comm.). – FIJI: Viti Levu, SW-Suva, 22.x.1985, leg. G.F. Bornemissza (1 ♀ [Figs 28, 33–34, 37–38], HNHM); Viti Levu, Nandarivatu, 16–20.xii.1968, leg. H.S. & G.S. Robinson, B.M. 1969-516 (1 ♀, BMNH).

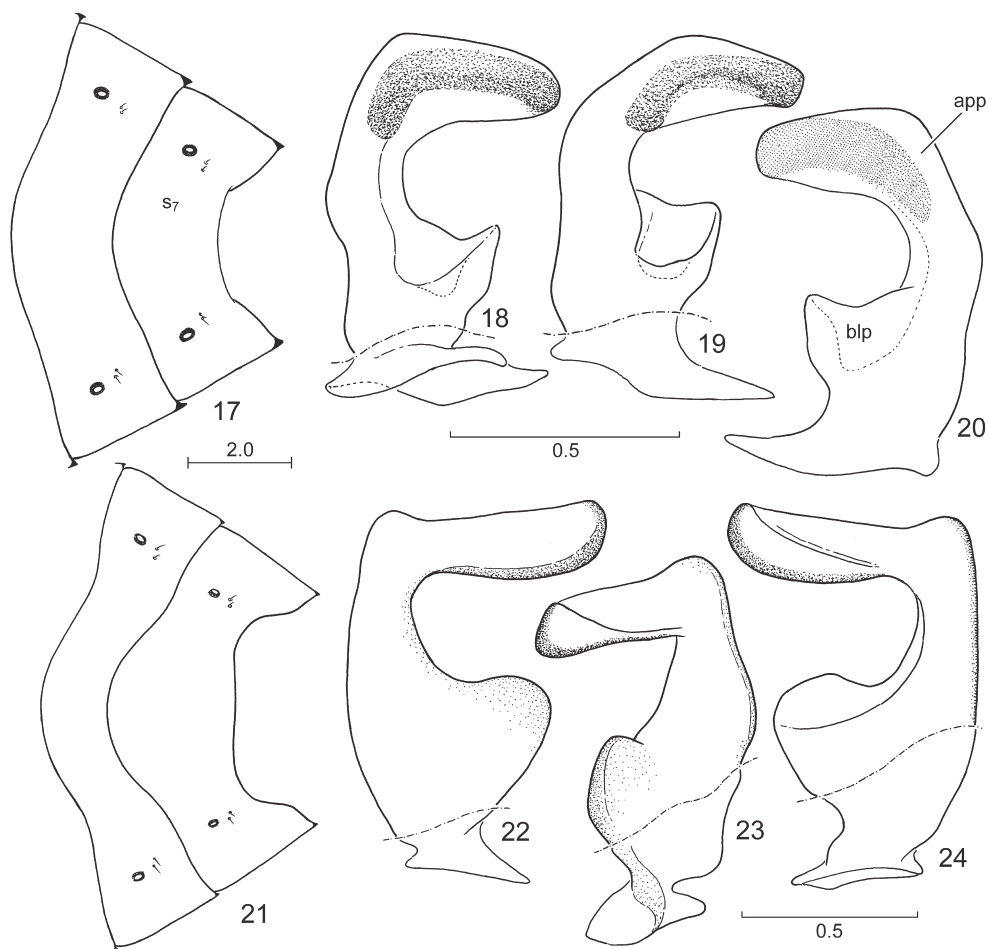
**Diagnosis.** Distinguished from the only known congener, *A. innocens* sp. nov., by the humeral angle being produced into a long, anterolaterally directed process (Figs 1, 3) and by the genitalia of both sexes. A detailed comparison of the diagnostic characters of the two species is provided in Table 1.

**Redescription.** Macropterous male and female.

**Colour, integument and vestiture.** Dorsum yellowish brown to light brown, with dense, dark punctation; head (lateral margin of mandibular plates and apical margin of clypeus) narrowly black; antenna stramineous, apical fourths of segments IIb and III and apical third of segment IV black; anterior portion of lateral margin of pronotum with a conspicuous, broad, stramineous callosity bordered by an irregular series of densely arranged, confluent,



Figs 9–16. *Amblycara gladiatoria* (Stål, 1876) (9–13) and *A. innocens* sp. nov. (14–16), genital capsules. 9 and 14 – dorsal view; 10–11 – dorsal sclerite, two different views; 12 and 15 – posterodorsal view; 13 and 16 – lateral view. Scales in mm. Lettering: dsc = dorsal sclerite; smt = submedian tumescence; plp = posterolateral projection.



Figs 17–24. *Amblycara gladiatoria* (Stål, 1876) (17–20) and *A. innocens* sp. nov. (21–24), pregenital abdomen and paramere of male. 17 and 21 – abdominal sternites VI and VII, ventral view; 18–20 and 22–24 – right paramere, different views. Scales in mm. Lettering: app = apical process; blp = basal process (sensory lobe); s<sub>7</sub> = sternite VII.

brown punctures, posterior portion of lateral margin narrowly margined with black and usually also with more or less strong metallic lustre; lateral margin of scutellum with a pair of small, elongate, longitudinally directed black spots subbasally; basal fourth of anterior (= external) margin of fore wing thickened, callose, stramineous; puncturation of exocorium denser and finer than that of endocorium; membrane colourless, with a brown patch apically; legs stramineous, impunctate; connexivum brown to black, puncturation partly confluent, each segment with lateral margin broadly stramineous, impunctate, denticle of posterolateral angle black; venter stramineous, preocular portion of head with a short, narrow longitudinal



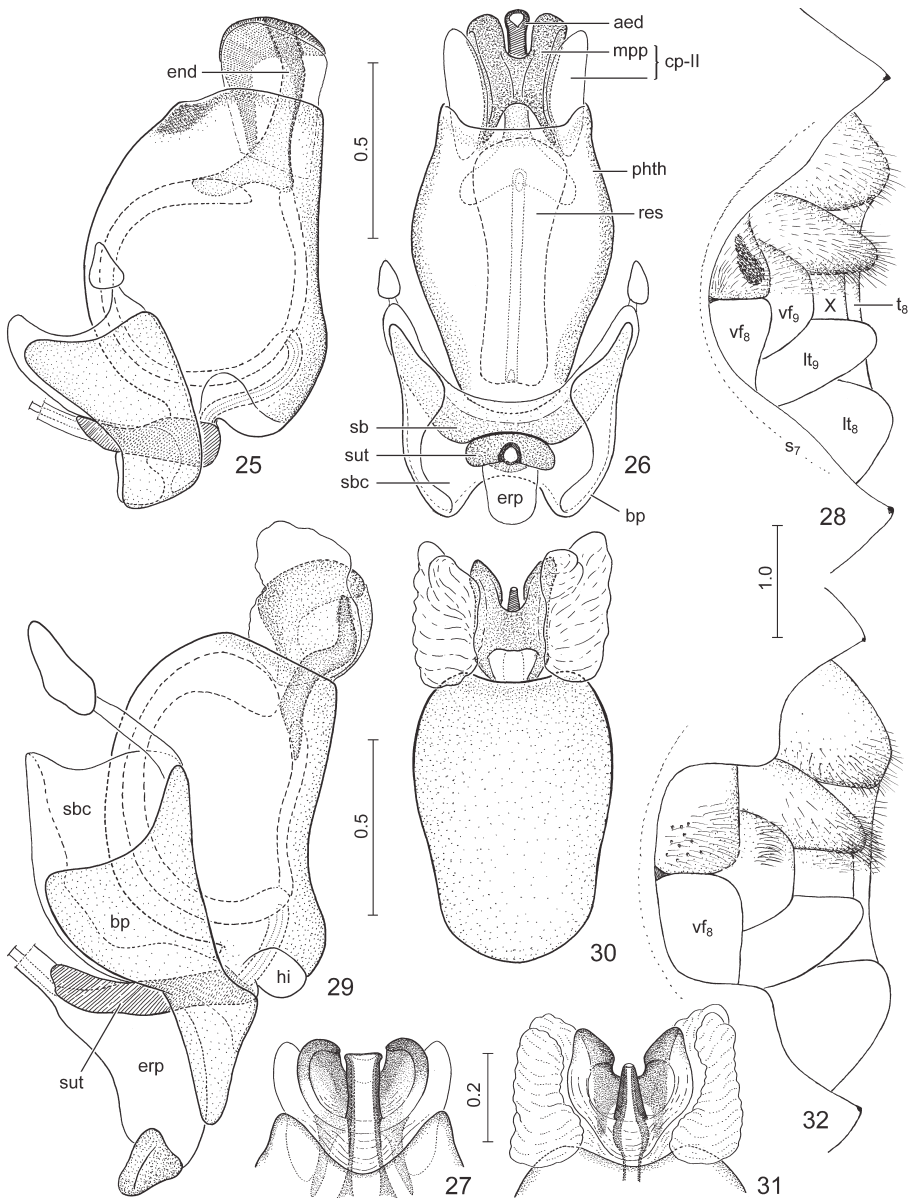
vitta dorsad of antenniferous tubercle, a small black spot at dorsal extremity of supracoxal clefts; abdominal spiracles III–VII narrowly surrounded by brown or black. Body glabrous; short, fine, semierect or erect, inconspicuous hairs present on antenna, labium, legs, and terminalia; integument rather smooth, except of inconspicuous rugosity on dorsum of head; venter mostly impunctate, smooth.

*Structure* mainly as in generic description. *Pronotum* 3.6–3.7 times as broad across humeri as its median length, humeral angle produced into a long process directed slightly anterolaterad.

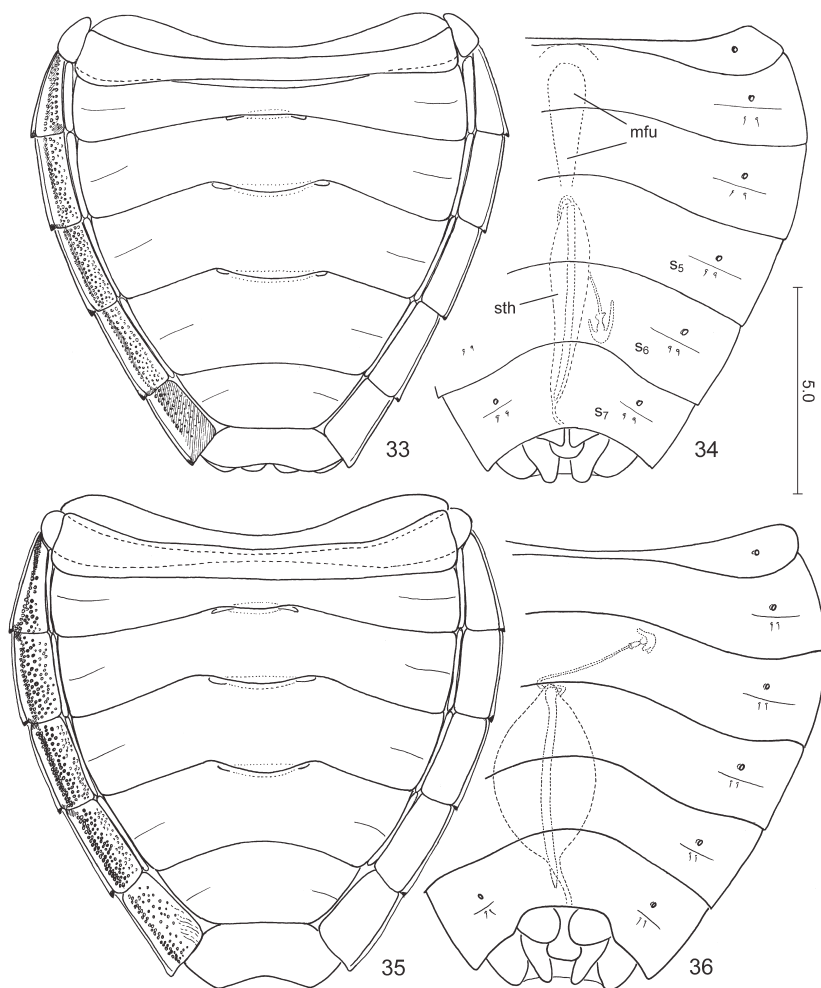
*Pregenital abdomen.* Connexivum narrower than in *A. innocens* sp. nov. (width of each laterotergites of segments III–VII smaller) (Fig. 33) and more broadly covered by the fore wing. *Male:* Posterior margin of sternite VII relatively narrowly emarginate medially (Fig. 17). *Female:* Posterior margin of sternite VII broadly concave along its whole width (Fig. 28).

*External male genitalia.* Genital capsule (Figs 9, 12–13) relatively small in relation to pregenital abdomen, convex, posterior margin broadly concave, with a pair of distinct posterolateral projections (Fig. 9: plp) directed posterolaterad, infolding of ventral rim provided with a pair of strongly protruding submedian tumescences (Fig. 9: smt); dorsal sclerite (Figs 9, 12: dsc; Figs 10–11) relatively large, kidney-shaped. Paramere (Figs 18–20) with subtriangular basal process (sensory lobe) (Fig. 20: blp), apical process (Fig. 20: app) obliquely angled apicad of basal lobe and again around its middle, apical portion slightly narrowed towards apex, provided with an elongate patch of pigmented, scaled texture, obtuse apically. Phallus (Figs 25–27): basal plates (Fig. 26: bp) broadly laminate, subquadrate and relatively short in lateral view; phallosome (Fig. 26: phth) barrel-shaped, broadest around middle, base and apex constricted; second conjunctival process (Fig. 26: cp-II) with lateral part forming a fully membranous lobe, inner part heavily sclerotized and those of the contralateral processes fused along midline (“median penial plates”, Fig. 26: mpp); endophallic duct (Fig. 25: end) nearly straight, abruptly bent subapically, apical portion directed posterodorsad, ensheathed within aedeagus (Fig. 26: aed; Fig. 27); phallosome (opening of the aedeagus) relatively broad (Fig. 27).

*External female genitalia.* Laterotergites VIII (Fig. 28: lt<sub>8</sub>) broadly rounded, exposed portion conspicuously smaller than that of *A. innocens* sp. nov.; visible portion of valvifers VIII (Fig. 28: vf<sub>8</sub>) subtriangular, posterior margins oblique, laterotergites IX (Fig. 28: lt<sub>9</sub>) surpassing posterior margin of tergite VIII (Fig. 28: t<sub>8</sub>). Gynatrium (Fig. 37: gy; Fig. 39) simple, saccular; spermathecal opening associated with a small annular sclerite which has a pair of oblique projections surrounding spermathecal opening laterally, and a larger, arch-shaped sclerite surrounding the previous sclerite; ring sclerites could not be traced in the single examined female. Spermatheca: proximal duct (Fig. 37: pd) short, somewhat shorter than gynatrium, narrow; dilation long (Fig. 37: dil), apex of dilation reaching middle of sternite V within abdomen (Fig. 34); basal cross-striate portion restricted to about basal 1/5 of total length of distal invagination (“sclerotized rod”), distinctly broadened distally (Fig. 38); distal invagination (Fig. 37: div) subparallel in most of its length, weakly and gradually broadened subbasally, then relatively strongly narrowed to its base; distal duct (Fig. 37: dd) much thinner than proximal duct, longer than half of length of distal invagination; intermediate part of spermatheca rather narrow, broadened distally, proximal flange much smaller than distal flange,



Figs 25–32. *Amblycara gladiatoria* (Stål, 1876) (25–28) and *A. innocens* sp. nov. (29–32), phallus and female terminalia. 25 and 29 – phallus, lateral view; 26 – same, dorsal view; 30 – same, articular apparatus omitted; 27 and 31 – apex of phallus, posteroventral view; 28 and 32 – terminalia of female, most exposed (posteroventral) view. Scales in mm. Lettering: aed = aedeagus; bp = basal plates; cp-II = second conjunctival process; end = endophallic duct; erp = erection fluid pump; hi = hinge; lt<sub>8</sub>–lt<sub>9</sub> = laterotergites VIII and IX; mpp = median penial plate; phth = phallosome; res = endophallic reservoir; s<sub>7</sub> = sternite VII; sb = support bridge; sbc = support bridge complex; sut = support tube; t<sub>8</sub> = tergite VIII; vf<sub>8</sub>–vf<sub>9</sub> = valvifers VIII and IX; X = segment X.

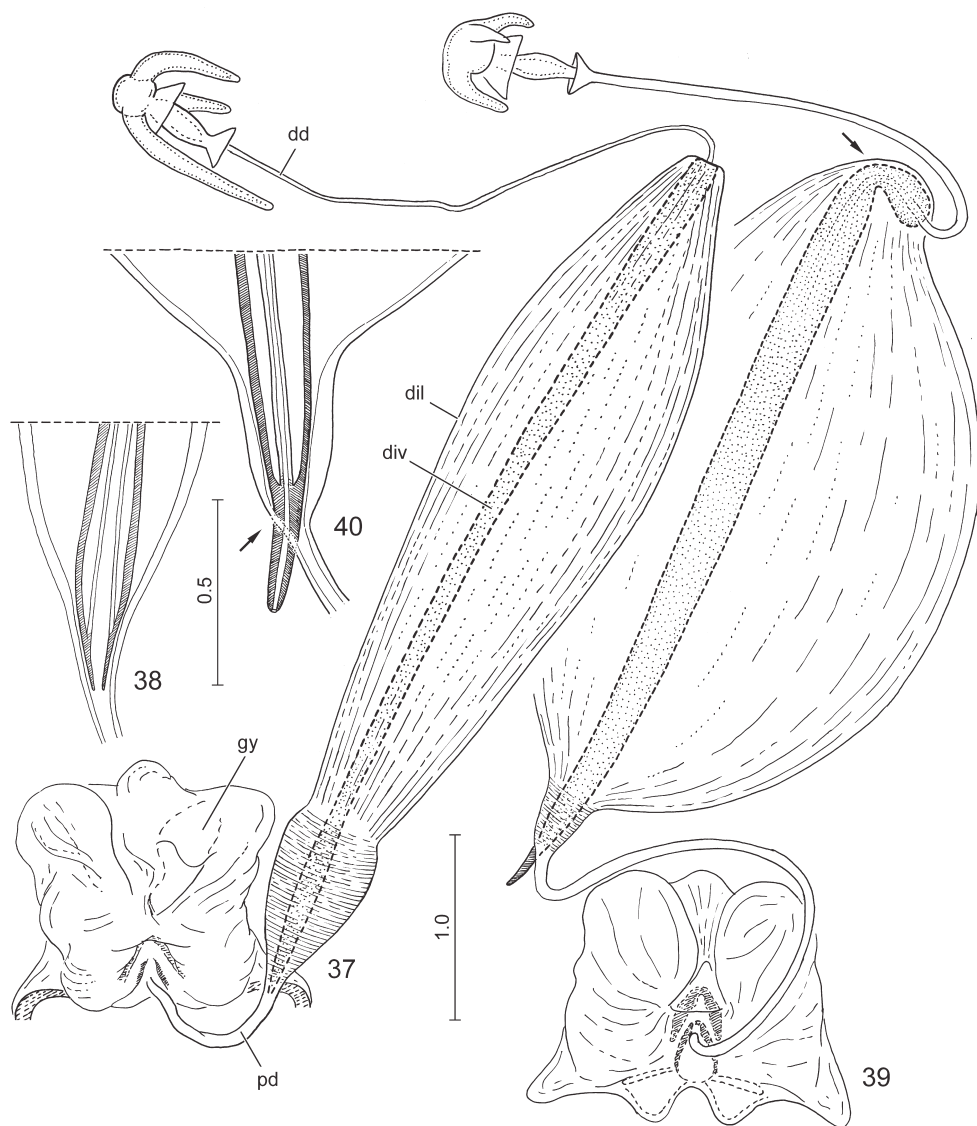


Figs 33–36. *Amblycara gladiatoria* (Stål, 1876) (33–34) and *A. innocens* sp. nov. (35–36), abdomen of female. 33 and 35 – dorsal view; 34 and 36 – ventral view. Scales in mm. Lettering: mfu = median furrow; sth = spermatheca;  $s_5$ – $s_7$  = sternites V–VII.

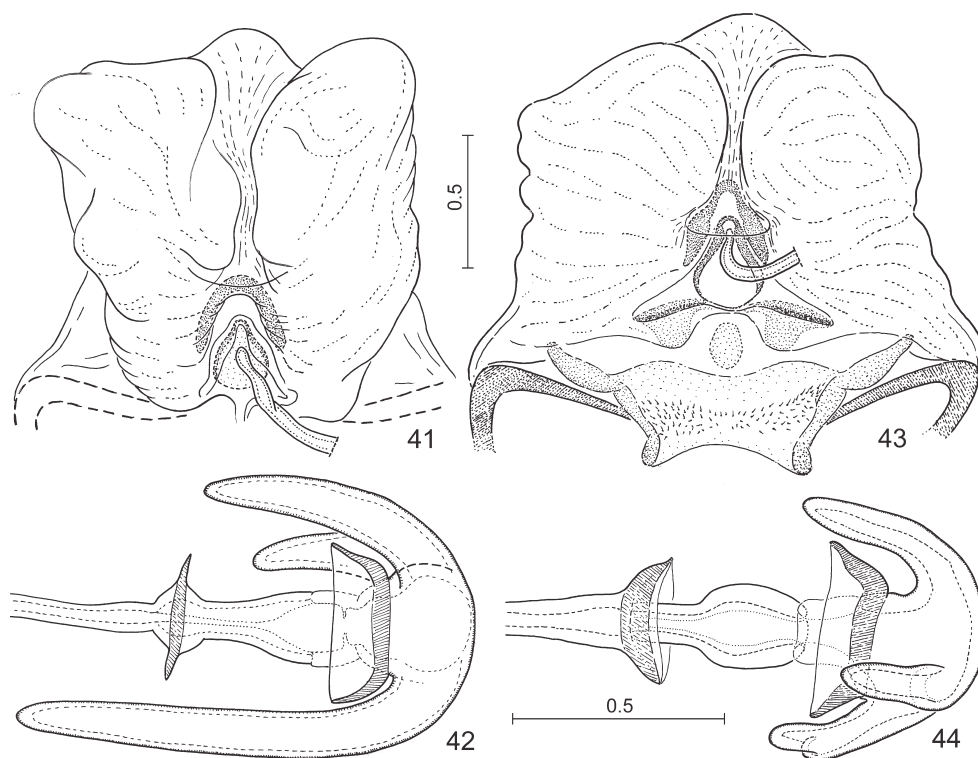
apical receptacle subglobular, with three long projections directed proximad, all of them far surpassing proximal flange, one of them even far surpassing distal flange (Fig. 42).

**Measurements** ( $n = 3 \text{ ♂♂}$   $2 \text{ ♀♀}$ ) (in mm). Body length 17.0–21.6, length of head 3.50–3.80, width across eyes 3.65–3.99, interocular distance 2.04–2.45, lengths of antennal segments I : IIa : IIb : III : IV as 0.98–1.10 : 2.05–2.40 : 2.47–2.96 : 3.25–3.80 : 3.00–3.35, median length of pronotum 3.45–3.68, width across apices of humeral processes 12.5–13.9, median length of scutellum 7.10–8.07, greatest width 5.90–6.64, greatest width of abdomen 10.4–11.9.

**Immatures.** Photographs of an egg batch and 4th and 5th instar larvae were presented by KOHNO & TAKAI (2003) and TAKAI & ISHIKAWA (2012).



Figs 37–40. *Amblycara gladiatoria* (Stål, 1876) (37–38) and *A. innocens* sp. nov. (39–40), female ectodermal genital tracts. 37 and 39 – gynatrium and spermatheca; 38 and 40 – basal portion of dilation of spermatheca with distal invagination (“sclerotized rod”), longitudinal optical section. Scales in mm. Lettering: dd = distal duct of spermatheca; dil = spermathecal dilation; div = distal invagination of spermathecal duct; gy = gynatrium; pd = proximal duct of spermatheca. Arrow shows possible artefactual distortion of apical portion (Fig. 39) and basal portion (Fig. 40) of distal invagination of spermathecal duct.



Figs 41–44. *Amblycara gladiatoria* (Stål, 1876) (41–42) and *A. innocens* sp. nov. (43–44), female ectodermal genital tracts. 41 and 43 – gynatrium; 42 and 44 – intermediate part and apical receptacle of spermatheca. Scales in mm.

**Habitat and bionomics.** All available observations were made in the Ryukyu Archipelago of Japan (Ishigaki and Miyako Islands). Larvae of *A. gladiatoria* were recorded to feed on fruits of the evergreen tree *Drypetes matsumurae* (Koidz.) Kaneh. (Putranjivaceae, formerly Euphorbiaceae) in July, and adults on fruits of *Antidesma pentandrum* Merr. (Phyllanthaceae, formerly Euphorbiaceae) in early October (KOHNO & HAYASHI 2003, TAKAI & ISHIKAWA 2012). Both host plants are native in the Ryukyu Archipelago and commonly occur in coral-reef habitats.

Of the above mentioned two host plants, *D. matsumurae* is a species endemic to the Ryukyu Archipelago. The species was not included in the monograph of Euphorbiaceae (sensu lato) of Taiwan by HSIEH et al. (1993). It was listed, however, from southern Taiwan by LI (1994) without any further information; this record is apparently erroneous and probably pertains to *D. littoralis* Merr. which is rather common in the Hengchun Peninsula. *Antidesma pentandrum* is restricted to the Ryukyus, the northern Philippines, and southern and eastern parts of Taiwan (LI 1963, HSIEH et al. 1993, LI 1994). Since both of the two reported host plants are narrowly distributed, *A. gladiatoria* obviously feeds on different, so far unknown host plants

in other parts of its area of distribution. Both *Drypetes* and *Antidesma* are species-rich genera widely distributed in the Oriental Region (LI 1994), also represented by several species in New Guinea, northern Australia (AIRY SHAW 1980), New Caledonia (McPHERSON & SCHMID 1991) and Fiji (SMITH 1981); at least part of the included species, perhaps also members of other related genera or families of Malpighiales could potentially be consumed by *A. gladiatoria*. Most species of *Drypetes* and *Antidesma* are commonly found in damp understorey, in riverine forests, swamps, frequently on seashores; coastal forests are perhaps the preferred habitat of *A. gladiatoria*.

The only paper providing data on the bionomics of *A. gladiatoria* is that of KOHNO & HAYASHI (2003) based on observations in uplifted coral-reef forests of Ishigaki Island in early June of 2002. During this period aggregations of several larvae of 3rd–5th instars were observed to feed on fruits of the host plant at about 3–4 m above the ground. Not a single individual was found after July, according to the authors adults presumably left the plant soon after emergence and migrated to *A. pentandrum*. Two observed egg batches contained 81 and 58 eggs, respectively.

**Note.** The original description of *A. gladiatoria* does not state the number of specimens available to the author, and it cannot be excluded that the description was based on more than one specimen. The specimen illustrated in Figs 5–6 was apparently figured by DISTANT (1902: 217, fig. 137), although with a modified position of legs and antennae. This author referred to the specimen as “a typical one”, making it clear by the use of an indefinite article that he considered that the original description was possibly based on more than one specimen. Because of this the above expression cannot be considered the equivalent of the term lectotype, and therefore Distant’s act cannot be considered a valid fixation of lectotype under the International Code of Zoological Nomenclature (ICZN 1999, Articles 74.5 and 74.6). As a consequence, the identity of the species is fixed in the present paper by designating (presumably) the same specimen (Figs 5–7) as lectotype.

**Distribution.** **SRI LANKA:** Kandy! **INDIA:** **KERALA:** Kardamon Hills! (new record). **CHINA:** **YUNNAN:** Jingdong (LIN & ZHANG 1985). **JAPAN:** **TOKARA ISLANDS:** Akuseki Is. (HAYASHI 2002, KOHNO & HAYASHI 2003, TAKAI & ISHIKAWA 2012); **RYÜKYÜ ISLANDS:** Okinawa Is.!, **SAKISHIMA ISLANDS:** Miyako Is., **YAEYAMA ISLANDS:** Ishigaki Is., Iriomote Is., Yonaguni Is. (ESAKI 1937, TAKARA 1957, MIYAMOTO & YASUNAGA 1989, ISHIKAWA 1999, HAYASHI 2002; KOHNO & HAYASHI 2003, TAKAI & ISHIKAWA 2012). **LAOS:** **ATTAPEU PROV.:** Muang Ngoy! (new record). **CAMBODIA:** Siem Reap, Angkor Thom! (new record). **MALAYSIA:** **MALAY PENINSULA!** (new record). **PHILIPPINES:** **BALABAC IS.:** Dalawan Bay! (BLACK 1968). **INDONESIA:** **PAPUA:** Bewani Mts.! (new record). **PAPUA NEW GUINEA:** Wau! (new record). **AUSTRALIA:** **QUEENSLAND!:** Mt. Garnet!, Kuranda (CASSIS & GROSS 2002). **NEW CALEDONIA:** Farino! (new record). **FIJI:** **VITI LEVU!** (new record).

The species has a broad distribution area from Sri Lanka apparently all over South and Southeast Asia and the Malay Archipelago to northern Australia and Fiji (Fig. 8). However, it is rarely captured and only a few sporadic records exist, except for the Ryukyu Archipelago of Japan where it was recorded from several islands. We present the first record from Laos, Cambodia, Malaysia, New Guinea (both Indonesian and Papuan parts), New Caledonia and Fiji (partly based on personal communication of D. A. Rider). The record from Balabac Is. (BLACK



1968) was verified by H. Enghoff by comparing the voucher specimen to the illustrations of the present paper. The source of the record from Queensland: Kuranda (CASSIS & GROSS 2002) is unknown, but a specimen from an unspecified locality in Queensland deposited in BMNH was seen; its collector, F. P. Dodd collected extensively around Kuranda, therefore the specimen potentially comes from the same region. Another female from the nearby Mt. Garnet was communicated by J. E. Eger. Papers listing the species from India or “E. India” apparently refer to the original description, however, the type locality, “India orientalis” (= “East Indies”) pertains to a much broader area comprising practically the whole Oriental Region. Based on personal communication of Z. Jindra we present the first confirmed record from India.

***Amblycara innocens* sp. nov.**

(Figs 2, 4, 14–16, 21–24, 29–32, 35–36, 39–40, 43–44)

**Type locality.** Taiwan: Pingtung County, Nanrenshan.

**Type material.** HOLOTYPE: ♂, “TAIWAN: Pingtung Co. \ Nanrenshan ([‘Nanrenshan’, in Chinese script]) \ by light. 2010. VIII. 14. \ leg. ‘Chui-Sheng Chiu, Yen-Chiu Lan’ [in Chinese script]” [yellow square, printed], “22°05′03.3″N, 120°50′08.3″E \ #347” [yellow square, printed]; mounted on card, segments IV of both antennae glued on the card, genitalia preserved in microvial with glycerine, pinned with the specimen; deposited in NMNS (Figs 2, 4). PARATYPES: 3 ♀♀; **TAIWAN:** “TAIWAN: Pingdong Co. \ Lanren River ([‘Lanren River’, in Chinese script]) \ 2010. XII. 19 by Hand” [yellow square, printed], “leg. [‘Yen-Chiu Lan, Chui-Sheng Chiu’, in Chinese script] \ 22°3′0.6″N, 120°51′18.5″E \ #399” [yellow square, printed]; mounted on card, abdomen detached and mounted on card, genitalia dissected (1 ♀, NMNS); “TAIWAN: Pingdong Co. \ Sheding ([‘Sheding Shika Deer Restoration Site’, in Chinese script]) \ 2010. VIII. 18 by light” [yellow square, printed], “leg. [‘Chui-Sheng Chiu, Yen-Chiu Lan’, in Chinese script] \ 21°57′52.8″N, 120°49′37.8″E \ #355” [yellow square, printed]; pinned (1 ♀, TFR1). **PHILIPPINES:** “PHILIPPINES \ Aborlan, Palawan \ VII-22-23-1985 \ Coll. D.J. Boethel” [printed]; pinned (1 ♀, DARC).

**Diagnosis.** Differs from the only known congener, *A. gladiatoria* in the short, laterally directed humeral processes (Figs 2, 4) and in the genitalia of both sexes. A detailed comparison of the diagnostic characters of the two species is provided in Table 1.

**Description.** Macropterous male and female.

*Colour and integument* as in *A. gladiatoria*.

*Structure* mainly as in generic description. *Pronotum* 3.6–3.7 times as broad across humeri as its median length, humeral angle produced into a short process directed laterad.

*Pregenital abdomen.* Connexivum broader than in *A. gladiatoria* (diameter of each laterotergites of segments III–VII larger) (Fig. 35) and more narrowly covered by the fore wing therefore more exposed. *Male:* Posterior margin of sternite VII broadly, subquadrately emarginate medially (Fig. 21). *Female:* Posterior margin of sternite VII with a deep, subquadrate median excision surrounding valvifers VIII (Fig. 32).

*External male genitalia.* Genital capsule (Figs 14–16) conspicuously large in relation to pregenital abdomen, convex, posterior margin broadly concave, with a pair of relatively small posterolateral projections, with a pair of submedian tumescences (Fig. 14: smt) hardly protruding from surface of infolding of ventral rim; dorsal sclerite (Fig. 15: dsc) small, tubercle-like. Paramere (Figs 22–24) with broad, rather rounded basal process (sensory lobe), apical process straight basally, nearly perpendicularly angled around middle, apical portion straight, slightly broadened towards apex, obtuse apically. Phallus (Figs 29–31): basal plates

**Table 1.** Diagnostic characters of species of *Amblycara*.

<i>A. gladiatoria</i> (Stål, 1876)	<i>A. innocens</i> sp. nov.
1. Humeral processes strongly produced, anterolaterally directed (Fig. 1).	Humeral processes short, laterally directed (Fig. 3).
2. Connexivum narrower (diameter of each laterotergite of segments III–VII smaller) (Figs 1, 33).	Connexivum broader (diameter of each laterotergite of segments III–VII larger) (Figs 3, 35).
3. Abdominal sternite VII of male relatively narrowly emarginate medially (Fig. 17).	Abdominal sternite VII of male broadly, subquadrate emarginate medially (Fig. 21).
4. Posterior margin of sternite VII of female broadly concave along its whole width, medially broadly rounded (Figs 28–34).	Posterior margin of sternite VII with a deep, subquadrate median excision surrounding valvifers VIII (Figs 32–36).
5. Genital capsule as in Figs 9, 12–13: with a pair of strong posterolateral projections (Fig. 9: plp) directed posterolaterad and a pair of marked submedian tumescences (Fig. 9: smt).	Genital capsule as in Figs 14–16: with a pair of posterolateral projections directed posteriad and a pair of small, weakly protruding submedian tumescences (Fig. 14: smt).
6. Dorsal sclerite (Figs 9, 12: dsc, Figs 10–11) large, kidney-shaped.	Dorsal sclerite (Fig. 15: dsc) small, tubercle-like.
7. Paramere as in Figs 18–20.	Paramere as in Figs 22–24.
8. Phallus as in Figs 25–27, endophallic duct (Fig. 25: end) nearly straight with apical portion directed dorsad, phallotreme broad.	Phallus as in Figs 29–31, endophallic duct S-shaped, tapering towards apex, phallotreme narrow.
9. Exposed portion of laterotergites VIII of female (Fig. 28: lt <sub>8</sub> ) relatively smaller.	Exposed portion of laterotergites VIII of female relatively larger (Fig. 32).
10. Visible portions of valvifers VIII of female (Fig. 28: vf <sub>8</sub> ) subtriangular, posterior margins oblique.	Visible portions of valvifers VIII of female (Fig. 32: vf <sub>8</sub> ) situated within excision of sternite VII, subquadrate, posterior margins nearly parallel.
11. Spermatheca with distal duct (Fig. 37: dd) much longer and thinner than proximal duct (Fig. 37: pd), diameter of distal invagination (“sclerotized rod”) (Fig. 37: div) smaller, basal cross-striate portion of dilation restricted to about 1/5 of total length of distal invagination.	Spermatheca with proximal and distal ducts subequal in length and diameter, diameter of distal invagination (“sclerotized rod”) larger, basal cross-striate portion of dilation restricted to about 1/14 of total length of distal invagination (Fig. 39).

(Fig. 29: bp) broadly laminate, strongly produced posteriad; erection fluid pump (Fig. 29: erp) much larger than that of *A. gladiatoria*; phallosome barrel-shaped, broadest in its apical half, apex rounded; second conjunctival process with lateral part forming a fully membranous lobe which is larger than that of *A. gladiatoria*, inner parts of the contralateral processes forming “median penial plates” as in Figs 30–31. Endophallic duct S-shaped, apical portion ensheathed within aedeagus gradually tapering towards apex; phallotreme (opening of the aedeagus) narrow (Fig. 31).

*External female genitalia* (Figs 32, 39–40, 43–44). Laterotergites VIII broadly rounded, exposed portion conspicuously larger than that of *A. gladiatoria*; visible portions of valvifers VIII situated within excision of sternite VII, subquadrate, posterior margins nearly parallel, laterotergites VII approaching but not reaching posterior margin of tergite VIII. Gynatrium

(Fig. 43) simple, saccular; spermathecal opening associated with a small conoid sclerite and a larger, bell-shaped sclerite surrounding it; ring sclerites could not be traced in the single examined female. Spermatheca: proximal duct longer than gynatrium, narrow; dilation long, apex of dilation reaching at least base of sternite V within abdomen (Fig. 36); basal cross-striate portion restricted to about basal 1/14 of total length of distal invagination (“sclerotized rod”); distal invagination subparallel in most of its length, gradually narrowed to its base, apically strongly curved which is probably an artefact due to strong inflation of dilation (Fig. 39: arrow); diameter and length of distal duct subequal to those of proximal duct; intermediate part of spermatheca rather abruptly broadened around its middle, proximal flange much smaller than distal flange, apical receptacle subglobular, with three relatively short projections directed proximad, only slightly surpassing distal flange, one of them bifurcate in the single examined female (Fig. 44).

**Measurements** (holotype ♂ + 2 ♀♀ paratypes) (in mm). Body length 20.1–21.8, length of head 2.40–2.90, width across eyes 3.90–4.10, interocular distance 1.45–1.60, lengths of antennal segments I : IIa : IIb : III : IV as 0.85–0.90 : 2.05–2.15 : 2.00–2.30 : 3.00–3.10 : 2.85–3.05, median length of pronotum 3.15–3.25, width across apices of humeral processes 11.62–12.06, median length of scutellum 7.75–8.64, greatest width 6.25–6.70, greatest width of abdomen 11.0–11.9.

**Etymology.** The specific epithet is the Latin adjective *innocens* (*m, f, n*) meaning ‘harmless’, referring to the short humeral process of the new species in contrast with the strongly produced humeri of *A. gladiatoria*.

**Habitat and bionomics.** Specimens were collected in monsoon rain forest (in Nanrenshan Ecological Protection Area) and uplifted coral-reef forest (in Sheding Nature Park). No observations were made on its host plant or bionomics.

**Distribution.** **TAIWAN:** PINGTUNG COUNTY: Nanrenshan!, Nanren River!, Sheding!. **PHILIPPINES:** PALAWAN: Aborlan!

The examined specimens were collected in the southernmost part of Hengchun Peninsula, southern Taiwan, and in Palawan.

## Discussion

**Phylogenetic relationship with other related genera.** Both *Amblycara* and *Bathycoelia* Amyot & Serville, 1843 are apparently related to other medium- and large-bodied genera of Pentatomini usually having variously produced humeri, namely *Priassus* Stål, 1868, *Lelia* Walker, 1867, and the generic complex of *Pentatoma* Olivier, 1789 and its close relatives (*Acrocorisellus* Puton, 1886; *Bifurcipientatoma* Fan & Liu, 2012; *Ramivena* Fan & Liu, 2010). These genera form a group well recognizable by the following external and male genital characters (based on information published by GROSS (1978), ZHENG & LING (1983), LING & ZHENG (1987), ZHENG & LIU (1987), FAN & LIU (2009, 2010a,b, 2012), and our own dissections of selected representatives of the genera in concern):

- (1) humeral angle at least slightly (*Bathycoelia*), more commonly strongly produced, surpassing costal margin of corium;

- (2) ventral rim of genital capsule deeply sinuated, sharply folded anteriorly forming a broad infolding extending to the cuplike sclerite, therefore posterior portion of genital capsule deeply excavated;
- (3) second conjunctival processes with median sclerotized ("median penial plates") and lateral membranous portions;
- (4) endophallic duct straight behind endophallic reservoir, positioned between the second conjunctival processes, its apical portion is enclosed by the median penial plates;
- (5) aedeagus relatively short, neighbored by the median penial plates, its apex hardly surpasses apex of median penial plates.

GROSS (1978) recognized morphological similarity between genitalia of *Bathycoelia* and those of *Plautia* Stål, 1865 (Antestiini), *Glaucias* Kirkaldy, 1908 and *Alciphron* Stål, 1876 (Pentatomini). However, *Plautia* markedly differs from *Bathycoelia* in the completely different paramere, and the median penial plates usually broadly fused with their counterparts and frequently even with the thin aedeagus (cf. LIU & ZHENG 1994, 1995). *Glaucias* differs from *Bathycoelia* in the long and exposed aedeagus which is not surrounded by the large, frequently greatly membranous medial lobes of the second conjunctival processes (cf. GROSS 1976); sensu stricto median penial plates homologous with those found in other Pentatomini are apparently lost in this genus. *Alciphron* was not available for us to study, but based on the sketchy figures of GROSS (1976: 450, Figs 202A, B) its genitalia do not look particularly similar to those of *Bathycoelia*.

Conforming with the views of STÅL (1876) and ATKINSON (1888), but contrary to the opinion of GROSS (1978), *Amblycara* and *Bathycoelia* indeed exhibit a number of shared characters. These shared characters contrast with the character states occurring in *Pentatoma*, *Acrocorisellus*, *Bifurcipientatoma*, *Ramivena*, *Lelia* and *Priassus* (mentioned as the "*Pentatoma*-complex" from now on) as follows:

- (1) metathoracic scent gland ostiole associated with a long, rather straight peritreme situated close to anterior margin of metapleurite, gradually narrowed towards apex, apex sharp, approaching lateral margin of metapleurite (*Pentatoma*-complex: peritreme shorter, situated at greater distance from anterior margin of metapleurite, apex never approaching lateral margin of metapleurite, obtusely terminated);
- (2) pregenital abdomen with a distinct furrow along midline at least basally (*Pentatoma*-complex: without furrow);
- (3) abdominal sternite unarmed (*Pentatoma*-complex: armed with an anteriorly projecting process which ranges from small but distinct tumescence to long spine);
- (4) median projection (= part of infolding of dorsal rim surrounding proctiger) enclosing an obtuse angle to the dorsal wall of genital capsule, infolding of ventral rim broadly extended in posterior view (Figs 12, 15), perpendicular to the ventral wall of genital capsule (*Pentatoma*-complex: median projection coplanar with the dorsal wall, infolding of ventral rim less extended, occasionally recurved anteriorly and parallel to the ventral wall of genital capsule);
- (5) dorsal sclerites not associated with the bases of the ipsilateral parameres (*Pentatoma*-complex: dorsal sclerites associated with parameres by a sclerotized extension of the former);

- (6) paramere with a lobe-like (*Amblycara*) or finger-like (*Bathycoelia*) basal process and a large, broad apical process (Fig. 20: app, blp) (*Pentatoma*-complex: paramere variously shaped but not similar to the above pattern except for *Lelia*);
- (7) lateral portion of second conjunctival process (Fig. 26: cp-II) short, membranous, at most with occasional small sclerotized areas (GROSS 1978, FAN & LIU 2009) (*Pentatoma*-complex: of various shape and size, frequently voluminous, more extensively sclerotized, occasionally fused ventrad of free portion of endophallic duct);
- (8) dorsal conjunctival process lacking or at most very short (GROSS 1978) (*Pentatoma*-complex: large dorsal process occurs in *Lelia*, *Bifurcipentatoma*, most of *Pentatoma*, it is sclerotized in *Ramivena*, and subdivided into a pair of dorsolateral lobes in *Priassus*);
- (9) aedeagus protruding relatively far away from apex of conjunctiva (*Pentatoma*-complex: aedeagus usually very short except for some species of *Priassus*).

Of the above characters, particularly the highly derived shape of the metathoracic scent gland peritreme and the ventral abdominal furrow are apparent synapomorphies shared by *Amblycara* and *Bathycoelia*, indicating a close phylogenetic relationship, potentially even sister group relation between the two genera.

**Tribal placement.** STÅL (1876) defined a suprageneric group of Pentatomidae without nomenclaturally available name (“*Bathycoelia* et affina”) containing *Bathycoelia* + *Jurtina* Stål, 1868 (now junior synonym of *Bathycoelia*) + *Abeona* (now preoccupied senior synonym of *Amblycara*) based on the sulcate abdominal venter. In the same sense, a suprageneric taxon (division Bathycoelaria, now tribe Bathycoeliini of Pentatominae) was formally proposed by ATKINSON (1888) for *Jurtina* (= *Bathycoelia*) and *Abeona* (= *Amblycara*). No additional genus was subsequently associated with this tribe.

GROSS (1976, 1978) placed *Bathycoelia* as a member of the “*Pentatoma*-group” of Pentatomidae; this group more or less conforms to the tribe Pentatomini of other authors (cf. CASSIS & GROSS 2002). *Amblycara* was correspondingly placed into Pentatomini (CASSIS & GROSS 2002; RIDER 2006), but Bathycoeliini is still recognized as a tribe containing *Bathycoelia* only by subsequent authors (RIDER 2006).

As it was demonstrated above, *Amblycara* and *Bathycoelia* are potential sister groups. As a consequence, their placement into different tribes is unjustified. The close morphological similarity and therefore presumable phylogenetic relationship between *Amblycara* + *Bathycoelia* and the other related genera mentioned above as “*Pentatoma*-complex” indicates that *Bathycoelia* is not of such an isolated position which would justify a placement in a tribe of its own, or even with *Amblycara*. Although in absence of a comparative study involving all relevant genera our evidences cannot be considered conclusive, they call the attention to a possible synonymy between Pentatomini and Bathycoeliini.

**Zoogeography.** Since the most closely related genera occur in the Oriental Region (with a few representatives extending to the Palearctic), the centre of origin of the genus *Amblycara* is most probably in the mainland of Asia.

The distribution pattern of *A. gladiatoria* (Fig. 8) is uncommon in Heteroptera, and its discussion is rendered difficult by the obviously incomplete data due to the scarcity of available specimens and records. It seems clear that the species is strictly restricted to the zone of

evergreen and semievergreen tropical rain forests in Asia and the Pacific (cf. WALTER 1985); even in northeastern Australia it only has been recorded from the ecoregion of the Queensland tropical rain forests.

It is hypothesized that the species spread from the mainland of Asia over the present Malay Archipelago during the late Pleistocene when Sunda Shelf formed an emergent landmass due to the lowering of the sea level resulting of glaciation (VORIS 2000, SATHIAMURTHY & VORIS 2006). Perhaps it colonized New Guinea and Australia through the greatly narrowed ocean strait between the Sunda and Sahul Shelves during the same period. Since Melanesian islands were never joined by Pleistocene land bridges to larger islands or continents (MAYR & DIAMOND 2001), the species must have arrived in Fiji and New Caledonia by inter-island dispersal, probably through the island chains of the Solomon Islands and New Hebrides. In fact, the great majority of the flora and a considerable number of the arthropod fauna of Fiji is shared with New Guinea and the Western Pacific (EVENHUIS & BICKEL 2005). The dispersal is probably facilitated by prevailing trade winds or tropical storms which generally follow a NW–SE direction in the region (GILLESPIE et al. 2012). The preference of *A. gladiatoria* for coastal forests might also increase its transoceanic dispersibility.

Since its spread happened probably in the relatively recent past, *A. gladiatoria* has remained a morphologically remarkably uniform species all over a vast area of Southeast Asia and the Pacific, even though its range became scattered into subpopulations which are apparently strongly isolated geographically. Possibly the vagility of this large-bodied pentatomid also ensures significant gene transfer within the subpopulations.

The distribution of *Amblycara* species in China, Taiwan, and the Ryukyu Archipelago of Japan is of special interest. In spite of the significant collecting activity and excessive literature on the area, *A. gladiatoria* has never been reported from southern and southeastern China (HUA 2000) where the vegetation is dominated by warm-temperature humid woodlands (WALTER 1985). In contrast, it seems widely distributed and rather frequent all over the Ryukyu Archipelago. This subpopulation is apparently a relict one which perhaps colonized the island chain from the surrounding landmasses through land bridges during the Pleistocene (cf. OTA 1998). In spite of the high frequency of heteropteran species shared with the Ryukyus, *A. gladiatoria* apparently does not occur in Taiwan. However, it must be emphasized that the species is very rare in collections, therefore its occurrence in the southernmost, tropical parts of China and in Taiwan can be anticipated.

A new species of *Amblycara* (described in this paper as *A. innocens* sp. nov.) occurs at least in Palawan and the main island of Taiwan. In Taiwan it seems to be restricted to the Hengchun Peninsula, the only part of the island which is characterized by wet tropical climate. The apparently broadly disjunct area of the new species is surprising. Although no specimens have been seen so far, the species presumably occurs in other islands of the Philippines too, at least in Luzon. Taiwan resulted from the collision of the Luzon volcanic arc (located on Philippine sea plate) either with the Eurasian continental margin (HALL 1998, HUANG et al. 2006) or with the former Ryukyu subduction zone (HSU & SIBUET 1995). The Luzon arc itself emerged during the early to middle Miocene (HSU & SIBUET 1995), opening a new dispersal pathway between Taiwan and Luzon (ESSELSTYN & OLIVEROS 2010, MÜLLER & BEHEREGARAY 2010). The new species perhaps colonized Taiwan and the Philippines either through a northern



route from the current China, or by a southern route through Borneo during periods of lowered sea levels during Pleistocene glacial cycles (VORIS 2000, SATHIAMURTHY & VORIS 2006).

The two known species of *Amblycara* are highly similar externally, suggesting that they diverged into different lineages from a common ancestor in the relatively recent past, probably in connection with the tectonic events reorganizing the boundaries of the Eurasian continental plate and the Philippine sea plate during the last five million years (see HALL 1998) which resulted in appearance of new habitats and facilitated speciation events in this region.

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### References

- AIRY SHAW H. K. 1980: A partial synopsis of the Euphorbiaceae-Platylobeae of Australia (excluding Phyllanthus, Euphorbia and Calycopeplus). *Kew Bulletin* **35**(3): 577–700.
- ATKINSON E. T. 1888: Notes on Indian Rhynchota; Heteroptera, No. 4. *Journal of the Asiatic Society of Bengal* **57**(2): 118–184.
- BERGROTH E. 1891: Contributions à l'étude des pentatomides. *Revue d'Entomologie* **10**: 200–235.
- BLACK G. M. 1968: Pentatomidae (Hemiptera, Heteroptera) collected by the Noona Dan Expedition in the Philippine, Bismarck and Solomon Islands. *Entomologiske Meddelelser* **36**: 560–576.
- CASSIS G. & GROSS G. F. 2002: Hemiptera: Heteroptera (Pentatomomorpha). In: HOUSTON W. W. K. & MAYNARD G. V. (eds.): *Zoological Catalogue of Australia. Vol. 27.3B*. CSIRO Australia, Melbourne, xiv + 737 pp.
- DISTANT W. L. 1902: Rhynchota. - Vol. I. (Heteroptera). In: BLANFORD W. T. (ed): *The fauna of British India, including Ceylon and Burma*. Taylor & Francis, London, xxxviii + 438 pp.
- DISTANT W. L. 1908a: Rhynchota, vol. IV. Homoptera and appendix (Pt.). In: BLANFORD W. T. (ed.): *The fauna of British India, including Ceylon and Burma*. Taylor & Francis, London, xv + 501 pp.
- DISTANT W. L. 1908b: Rhynchota Malayana. Part I. *Records of the Indian Museum* **2**(2): 127–151, plates vii–viii.
- DISTANT W. L. 1918: Rhynchota, vol. VII. Homoptera: Appendix, Heteroptera: Addenda. In: SHIPLEY A. E. & MARSHALL G. A. K. (eds.): *The fauna of British India, including Ceylon and Burma*. Taylor & Francis, London, viii + 210 pp.

- ESSELSTYN J. A. & OLIVEROS C. H. 2010: Colonization of the Philippines from Taiwan: a multi-locus test of the biogeographic and phylogenetic relationships of isolated populations of shrews. *Journal of Biogeography* **37**: 1504–1514.
- ESAKI T. 1937: Unrecorded or little-known Hemiptera of the Japanese Empire (1). *Mushi* **10**(2): 87–90, 1 plate.
- EVENHUIS N. L. & BICKEL D. J. 2005: The NSF-Fiji Terrestrial Arthropod Survey: Overview. *Bishop Museum Occasional Papers* **82**: 3–25.
- FAN Z. H. & LIU G. Q. 2009: Descriptions of males of *Bathycoclia sinica* Zheng & Liu, 1987 and *Tachengia ascula* China, 1925 (Hemiptera: Pentatomidae). *Entomotaxonomia* **31**: 275–278 (in Chinese, English title).
- FAN Z. H. & LIU G. Q. 2010a: The genus *Lelia* Walker, 1876, with the description of one new species (Hemiptera: Heteroptera: Pentatomidae: Pentatominae). *Zootaxa* **2512**: 56–62.
- FAN Z. H. & LIU G. Q. 2010b: A new genus *Ramivena* (Hemiptera: Pentatomidae), with descriptions of two new species. *Oriental Insects* **44**: 211–223.
- FAN Z. H. & LIU G. Q. 2012: *Bifurcipientatoma*, a new genus of Pentatomini with descriptions of two new species from China (Hemiptera: Heteroptera: Pentatomidae). *Zootaxa* **3274**: 14–28.
- GILLESPIE R. G., BALDWIN B. G., WATERS J. M., FRASER C. I., NIKULA R. & RODERICK G. K. 2012: Long-distance dispersal: a framework for hypothesis testing. *Trends in Ecology and Evolution* **27**(1): 47–56.
- GROSS G. F. 1975: A revision of the Pentatomidae (Hemiptera-Heteroptera) of the *Rhynchocoris* group from Australia and adjacent areas. *Records of the South Australian Museum* **17**(6): 51–167.
- GROSS G. F. 1976: *Plant-feeding and other bugs (Hemiptera) of South Australia. Heteroptera - Part 2*. Handbook of the flora and fauna of South Australia, Handbooks Committee, South Australian Government, Adelaide, pp. 251–501.
- GROSS G. F. 1978: The genus *Bathycoclia* A & S in New Guinea and *Prytanicoris* gen. nov. from the New Guinea area and the New Hebrides (Heteroptera-Pentatomidae-Pentatominae). *Records of the South Australian Museum* **17**(29): 417–428.
- HALL R. 1998: The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. Pp. 99–131. In: HALL R. & HOLLOWAY J. D. (eds.): *Biogeography and geological evolution of SE Asia*. Backhuys, Leiden, 417 pp.
- HAYASHI M. 2002: Heteroptera. Pp. 125–149. In: AZUMA S., YAFUSO M., KINJO M., HAYASHI M., KOHAMA T., SASAKI T., KIMURA M. & WAKAMURA F. (eds.): *Check list of the insects of the Ryukyu Islands. Second edition*. The Biological Society of Okinawa, Nishihara, xxiv + 570 pp (in Japanese).
- HSIEH C. F., CHAW S. M. & WANG J. C. 1993: Euphorbiaceae. Pp. 414–504. In: HUANG T. C. (ed.): *Flora of Taiwan. Second edition. Volume three. Angiosperms, Dicotyledons (Hamamelidaceae – Umbelliferae)*. National Taiwan University, Taipei, x + 1084 pp.
- HSU S. K. & SIBUET J. C. 1995: Is Taiwan the result of arc-continent or arc-arc collision? *Earth and Planetary Science Letters* **136**: 315–324.
- HUA L. Z. 2000: *List of Chinese insects. Vol. I. Zhongshan* (Sun Yat-sen) University Press, Guangzhou, 2 + 7 + 448 pp.
- HUANG C. Y., YUAN P. B. & TSAO S. J. 2006: Temporal and spatial records of active arc-continent collision in Taiwan: A synthesis. *Geological Society of America Bulletin* **118**(3–4): 274–288.
- ICZN 1999: *International Code of Zoological Nomenclature. Fourth edition*. International Trust for Zoological Nomenclature, London, 306 pp.
- ISHIKAWA T. 1999: A new record of *Amblycara gladiatoria* from Yonaguni-jima Island, the Ryukyus, Japan. *Rostria* **48**: 24 (in Japanese).
- KIRKALDY G. W. 1909: *Catalogue of the Hemiptera (Heteroptera) with biological and anatomical references, lists of foodplants and parasites, etc. Vol. I: Cimicidae*. Felix L. Dames, Berlin, xl + 392 pp.
- KOHNO K. & HAYASHI M. 2003: Host plant of *Amblycara gladiatoria* (Heteroptera: Pentatomidae). *Rostria* **51**: 55–59.
- LETHIERRY L. & SEVERIN G. 1893: *Catalogue général des Hémiptères. Tome I. Hétéroptères, Pentatomidae*. F. Hayez, Bruxelles, x + 286 pp.
- LI H. L. 1963: *Woody flora of Taiwan*. Livingston Publishing Co., Narberth, x + 974 pp.
- LIP T. 1994: Angiospermae. Dicotyledonae. Euphorbiaceae. Phyllanthoideae. *Flora Reipublicae Popularis Sinicae* **47**(1): i–viii + 1–207. Science Press, Beijing (in Chinese).

- LIN Y. J. & ZHANG S. M. 1985: New species and new records of Pentatominae from China (Hemiptera: Heteroptera). *Acta Agriculturae Universitatis Jiangxiensis* **1985**(4): 7–10 (in Chinese, English summary).
- LING Z. P. & ZHENG L. Y. 1987: A study on the systematics of Pentatoma Olivier (Heteroptera: Pentatomidae). *Entomotaxonomia* **9**: 39–50 (in Chinese, English summary).
- LIU Q. & ZHENG L. Y. 1994: On the Chinese species of Plautia Stål (Hemiptera: Pentatomidae). *Entomotaxonomia* **16**: 235–248 (in Chinese, English summary).
- LIU Q. & ZHENG L. Y. 1995: Plautia splendens Distant (Hemiptera: Pentatomidae): A new record to China. *Entomotaxonomia* **17**: 231–232 (in Chinese, English title).
- MAYR E. & DIAMOND J. 2001: *The birds of Northern Melanesia. Speciation, ecology, and biogeography*. Oxford University Press, New York, xxiv + 492 pp + 9 plates.
- MCPHERSON G. & SCHMID M. 1991: *Flore de la Nouvelle-Calédonie et dépendances. Vol. 17. Euphorbiaceae – Phyllanthoideae*. Muséum National d'Histoire Naturelle, Paris, 329 pp.
- MIYAMOTO S. & YASUNAGAT. 1989. Heteroptera. Pp. 151–188. In: HIRASHIMA Y. (ed.): *A check list of Japanese insects, vol. 1*. Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka (in Japanese).
- MÜLLER J. C. & BEHEREGARAY L. B. 2010: Palaeo island-affinities revisited – Biogeography and systematics of the Indo-Pacific genus Cethosia Fabricius (Lepidoptera: Nymphalidae). *Molecular Phylogenetics and Evolution* **57**: 314–326.
- OTA H. 1998: Geographic patterns of endemism and speciation in amphibians and reptiles of the Ryukyu Archipelago, Japan, with special reference to their paleogeographical implications. *Researches on Population Ecology* **40**: 189–204.
- RIDER D. A. 2006: Family Pentatomidae Leach, 1815. Pp. 233–402. In: AUKEMA B. & RIEGER Ch. (eds.): *Catalogue of the Heteroptera of the Palaearctic Region. Vol. 5. Pentatomomorpha II*. The Netherlands Entomological Society, Amsterdam, xiii + 550 pp.
- RIDER D. A., ZHENG L. Y. & KERZHNER I. M. 2002: Checklist and nomenclatural notes on the Chinese Pentatomidae (Heteroptera). II. Pentatominae. *Zoosystematica Rossica* **11**: 135–153.
- SATHIAMURTHY E. & VORIS H. K. 2006: Maps of Holocene sea level transgression and submerged lakes on the Sunda Shelf. *Natural History Journal of Chulalongkorn University, Supplement* **2**: 1–44.
- SMITH A. C. 1981. *Flora vitiensis nova. A new flora of Fiji. (Spermatophytes only.) Volume 2. Angiospermae: Dicotyledones, families 44–116*. Pacific Tropical Botanical Garden, Lawai, Kauai, Hawaii, vii + 810 pp.
- STÅL C. 1876: Enumeratio Hemipterorum. Bidrag till en förteckning öfver alla hittills kända Hemiptera, jemte systematiska meddelanden. 5. *Kongliga Svenska Vetenskaps-Akademiens Handlingar (N.F.)* **14**: 1–162.
- TAKARA T. 1957: Provisional list of Hemiptera (Heteroptera) in the Ryukyu Islands. *Science Bulletin of the Agriculture & Home Economics Division, University of the Ryukyus* **4**: 11–90, plates 1–2.
- TAKAI M. & ISHIKAWA T. 2012: Family Pentatomidae Leach, 1815. Stink bugs. Pp. 466–499 + plates 110–122. In: ISHIKAWA T., TAKAI M. & YASUNAGA T. (eds.): *A field guide to Japanese bugs – Terrestrial heteropterans. Vol. 3*. Zenkoku Noson Kyoiku Kyokai Publishing Co., Tokyo, pp. 1–46 + plates 1–128, pp. 177–573 (in Japanese).
- TSAI J. F., RÉDEI D., YEH G. F. & YANG M. M. 2011: *Jewel bugs of Taiwan (Heteroptera: Scutelleridae)*. National Chung Hsing University, Taichung, 309 pp.
- VORIS H. K. 2000: Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* **27**: 1153–1167.
- WALTER H. 1985: *Vegetation of the Earth and ecological systems of the geo-biosphere. Third, revised and enlarged edition*. Springer, Berlin, Heidelberg, XVI + 318 pp.
- ZHENG L. Y. & LING Z. P. 1983: Five new species of Pentatoma Olivier from China (Heteroptera: Pentatomidae). *Entomotaxonomia* **5**: 233–238 (in Chinese, English summary).
- ZHENG L. Y. & LIU G. Q. 1987: New genera, new species of Chinese Pentatomidae and a new Chinese record of Scutelleridae (Heteroptera). *Acta Zootaxonomica Sinica* **12**: 286–296 (in Chinese, English summary).

