

New taxonomic and ecological data for *Paraprisopus apterus*, the smallest stick insect from French Guiana (Phasmatodea, Pseudophasmatidae, Paraprisopodini)

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Abstract. – The egg and the adult female of *Paraprisopus apterus* Conle, Hennemann, Bellanger, Lelong, Jourdan & Valero, 2020, from French Guiana, are described here for the first time. Ant-mimicking morphology and behaviour of post-hatch *Paraprisopus* nymphs are reported and discussed.

Résumé. – **Nouvelles données taxonomiques et écologiques pour *Paraprisopus apterus*, le plus petit phasme de Guyane (Phasmatodea, Pseudophasmatidae, Paraprisopodini).** L’œuf et la femelle adulte de *Paraprisopus apterus* Conle, Hennemann, Bellanger, Lelong, Jourdan & Valero, 2020, de Guyane française, sont ici décrits pour la première fois. La morphologie et le comportement de mimétisme imitant une fourmi des *Paraprisopus* juvéniles aux premiers stades sont décrits et discutés.

Keywords. – Taxonomy, ant-mimicking morphology, behaviour.

The genus *Paraprisopus* focused recent interest following the affiliation of closely related species and the description of new species. *Paraprisopus* was originally described by REDTENBACHER (1906: 156) for a new species, *P. foliculatus* Redtenbacher, 1906, from Ecuador, and then for a second species *P. merismus* (Westwood, 1859) from Venezuela, although the later was first assigned to *Dinelytron* Gray, 1835, by its author. Two more species were then successively added in the genus, first *P. antillarum* Caudell, 1914, from West Indies (CAUDELL, 1914: 491); then *P. spicatus* Hebard, 1924, from Ecuador (HEBARD, 1924: 141). More recently, CONLE *et al.* (2011: 249) described three species from Colombia, initially classified within *Melophasma* Redtenbacher, 1906. Two further species from French Guiana were described: *P. apterus* and *P. multicolorus* (CONLE *et al.*, 2020: 33). In the same publication, *Melophasma* was synonymized with *Paraprisopus*, and the closely related *Dinelytron agrion* (Westwood, 1859) was lumped with genus *Paraprisopus*. As a result of these taxonomic updates, *Paraprisopus* grew up to 10 species. Based on this taxonomic rearrangement, the authors argued displacing the genus and consequently its tribe (Paraprisopodini) from subfamily Prisopodinae to Pseudophasmatinae (CONLE *et al.*, 2020: 33).

The placement of Paraprisopodini within Pseudophasmatinae is based both on egg morphology and laying behavior of *Paraprisopus* species more closely matching those of Pseudophasmatinae (egg dropping) than that of Prisopodini (eggs glued). A second important feature is the elongated and convex subgenital plate of females. While thus currently included within Pseudophasmatinae, Paraprisopodini differ from the other members of the subfamily by short mesonotum and short head, much shorter and more robust antennae, shorter and generally lobed legs and most importantly, the lack of typical gland and defensive spray that characterize the remaining of the subfamily (CONLE *et al.*, 2020). As a consequence, this placement may be considered a temporary arrangement reflecting best current hypothesis regarding general morphology.

In November 2019, several sampling campaigns and Phasmatodea inventories in French Guiana for INPN (Inventaire National du Patrimoine Naturel) were managed by T. Jourdan. Three nights of prospectations near Camp Caïman in the Kaw Mountains resulted in the capture of additional *Paraprisopus* specimens. Among them was an adult female of *Paraprisopus apterus* Conle, Hennemann, Bellanger, Lelong, Jourdan & Valero, 2020, a species until then only described from one male (holotype) and one juvenile female (paratype). This specimen was kept in breeding in order to obtain eggs. Its further culture in Europe allowed confirming species assigned via the males growing from the eggs, which were compared to the holotype and were completely matching. It also provided another adult female used in the present work, thus allowing for a complete description of the species. Breeding cultures allowed the observation of ant-mimicking morphology in juveniles and behavior from post-hatch nymphs suggesting close ecological ties with ants, which is reported in more detail in this manuscript.

MATERIAL AND METHODS

Measurements are given in millimetres with a precision of ± 0.1 mm for the insects, and ± 0.01 mm for the eggs and were made with a calliper. Adults and eggs were examined under Novex AP-8 and Wild Heerbrugg MB binoculars. Pictures of specimens were taken with Nikon D5200 with a AF Micro Nikkor 40 mm lens, 1:2.8G, for the adult. Pictures of the eggs were taken with a Nikon D800 with a AF Micro-Nikkor 60 mm lens with 68 mm extension tubes and SB-R200 flashes. Focus stacking is performed with an automated rail StackShot from Cognisys and Zerene Stacker softwares.

The specimen was collected at night using a LED flashlight and was kept alive in a mosquito net cage to observe behavior and obtain eggs. It was then killed with ethyl acetate, eviscerated and cleaned out from thoracic and abdominal content, which was replaced by a mix of boric acid and talc (50/50) and cigar-shaped cotton, and dried for transport. Back to France, the collected eggs were kept in a small plastic box on wet peat at a temperature of 20°C. Freshly hatched nymphs were kept in a small cage with one side of mosquito net, with a mix of plants until finding a substitute foodplant. They were moved in a larger cage once a substitute plant was found and juveniles were growing, until adulthood, at a temperature ranging from 18 to 25°C. Preserving and collecting methods are detailed in JOURDAN *et al.* (2014). The dates written on the specimen's labels are the date when specimens were killed and naturalised. Colours are mostly described from live specimen and can vary a lot after specimens are dried.

The classification used here follows the recent proposal from SIMON *et al.* (2019). The terminology of the egg capsule follows the seminal work of CLARK-SELLICK (1997).

Abbreviations used. – HT, Holotype; PT, Paratype; MNHN, Muséum national d'Histoire naturelle, Paris, France; SEAG, Société Entomologique Antilles-Guyane; ZSMC, Zoologische Staatssammlung, München, Germany; coll. INRAE, collection of INRAE, Centre de Ressources Biologiques, Petit-Bourg, Guadeloupe; coll. ASPER, collection of the members of ASPER (PL: housed in Philippe Lelong collection, Sainte-Foy-d'Aigrefeuille, France; TJ: housed in INRAE collection, Petit-Bourg, Guadeloupe; YB: housed in Yannick Bellanger collection, Trédias, France); coll. OC, collection of Oskar Conle, Duisburg, Germany.

RESULTS

Phasmatodea, Neophasmatodea

Occidophasmata, Pseudophasmatidae, Pseudophasmatinae, Paraprisopodini

Genus *Paraprisopus* Redtenbacher, 1906

Paraprisopus Redtenbacher, 1906: 156. Type-species: *Paraprisopus foliculatus* Redtenbacher, 1906: 156, by subsequent designation (ZOMPRO, 2001). CAUPELL, 1914: 491. MOXEY, 1972: 38. BRADLEY & GALIL, 1977: 202. BRAGG, 2001: 590, 640. ZOMPRO, 2000: 96. ZOMPRO, 2002: 6. ZOMPRO, 2004: 62, 317. OTTE & BROCK, 2005: 253. BÜSCHER & GORB, 2017: 3.

Syn. *Melophasma* Redtenbacher, 1906: 157. Type-species: *Melophasma vermiculare* Redtenbacher, 1906, by monotypy. MOXEY, 1972: 38. BRADLEY & GALIL, 1977: 202. LANGLOIS & LELONG, 1998: 454. BRAGG, 2001: 637. LELONG *et al.*, 2003: 65. ZOMPRO, 2004: 314. OTTE & BROCK, 2005: 199. CONLE *et al.*, 2011: 19. GOLDBERG *et al.*, 2015 : 3. BÜSCHER & GORB, 2017 : 3. HELEODORO & RAFAEL, 2020 : 37. CONLE *et al.*, 2020: 33 (syn.).

***Paraprisopus apterus* Conle, Hennemann, Bellanger, Lelong, Jourdan & Valero, 2020**

Paraprisopus apterus Conle *et al.*, 2020: 38.

Type material. – HOLOTYPE: ♂, “Französisch Guyana: Commune de Régina, Crique Orfion, Orapu RN 2 pk 65, 4°29’46,29”N - 52°20’43,30”W, SEAG, Malaise-trap, leg. Stéphane Brulé 24.09.2016; Ex coll. Conle; OC-0403-2” [ZSMC].

PARATYPE: ♀ (nymph), “Französisch Guyana: Commune de Régina, Crique Orfion, Orapu RN 2 pk 65, 4°29’46,29”N - 52°20’43,30”W, SEAG, Malaise-trap, leg. Stéphane Brulé 01.10.2016” [coll. OC, No. 0403-1].

Material studied. – 1 ♀, GUY19-004, Camp Caïman, Montagnes de Kaw, Roura, 4°34’10”N 52°13’11”W, 21.X.2019, rec. & det. TJ BOLD GFPHASM19-052 [coll. INRAE]; 1 ♀, GUY19-034, élevage F1 Yannick Bellanger from ♀ GUY19-004, II.2021; 2 ♂, GUY19-035 and -036, *idem*, II.2021 and 11.X.2020 [coll. ASPER-YB]; 1 ♂, GUY19-038, *idem*, 18.X.2020 [coll. ASPER-PL]; 1 egg from GUY19-004 [coll. ASPER-TJ]; 1 egg from GUY19-004 [coll. ASPER-PL]; 10 eggs from GUY19-034 [coll. ASPER-YB].

Diagnosis. – Females of this species are easily distinguished from all other species in the genus by the much smaller size, a very large head with raised vertex and a raised verrucous bulb on the terga V-VI.

Description of the female. – Fig. 1-8, 12, 14; table I. Small for the genus (45.6 mm), apterous.

Colour. General coloration dark brown with pale beige margins of thoracic segments and orangish margins of terga. Ventral part entirely beige-orangish. Eyes yellow to orange marbled in black. Mouthparts beige orangish. Antennae ringed, alternating brown and orangish colours. Posterior margin of pronotum white-creamish with a median dull black spot. Posterior surface of mesofemora almost entirely dark brown, bright and smooth; dorso-basal part of metafemora creamish.

Head. Slightly wider and 1.5× longer than pronotum; whole surface covered by tubercles and with two broad and symmetric auriform lobes. Eyes large and globose. Antennae compounded of distinct articles; more than 1.5× longer than anterior legs, apical half distinctly ringed; scapus, pedicellus and first flagellomeres slightly hairy; scapus flattened dorsally and about 2× longer than pedicellus; pedicellus almost cylindrical.

Thorax. Entirely granulose. Pronotum subquadrate, slightly wider than long; median sulcus distinct; lateral edges irregular and with a deep indentation anteriorly. Mesonotum 1.4× longer than wide, about 2× longer than pronotum and 2.8× longer than metanotum; narrowing toward the anterior. Metanotum short, 2× wider than long. Mesopleurae extended by a thin, undulate and hairy fringe. Prosternum almost

Table I. – Measurements of the females of *Paraprisopus apterus* (in mm).

	♀, GUY19-004	♀, GUY19-034
Body	45.6	45.7
Antennae	20.7	19.0
Head	4.3	4.2
Pronotum	2.7	3.3
Mesonotum	5.9	6.5
Metanotum	2.4	2.3
Median segment	2.8	3.0
Profemora	5.4	5.6
Mesofemora	4.0	4.7
Metafemora	6.8	7.8
Protibiae	3.4	4.0
Mesotibiae	4.5	4.4
Metatibiae	7.6	8.1

smooth except few granules laterally. Mesosternum smooth and slightly bright. Metasternum bearing few granules laterally in front of coxae ; anterior first third creamish and remaining posterior dark brown, with a distinct limit between both parts; sometimes with a pair of lateral dull black spots.

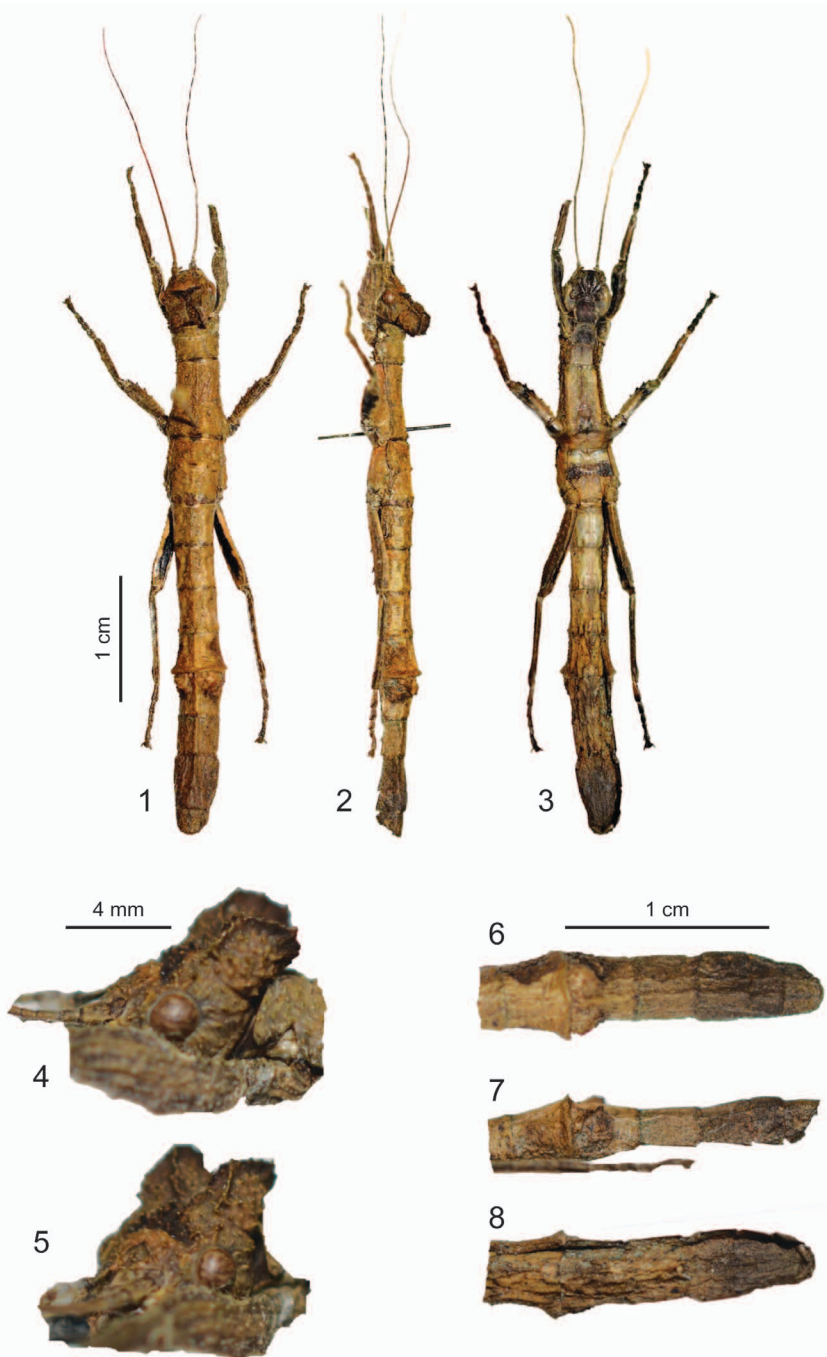


Fig. 1-8. – *Paraprisopus apterus* Conle *et al.*, ♀ GUY19-004. – 1-3, Habitus: 1, dorsal view; 2, lateral view; 3, ventral view. – 4-5, Close-up on the head. – 6-8, Abdominal extremity: 6, dorsal view; 7, lateral view; 8, ventral view.

Abdomen. Median segment distinct, 1.3× longer than metanotum. Abdominal segments III-VI of same length and the longest; II and VII slightly shorter and about of same length; VIII slightly shorter than the latter; IX and X the shortest and of same length. Terga II-X granulate, with a medio-longitudinal carina; V trapezoidal, widened and higher posteriorly forming a raised verrucous bulb with VI; epiproct slightly exceeding the anal segment. Sterna II-III almost smooth, sterna IV-VII granulate and covered with irregular ridges. Preopercular organ visible, with a small orangish and rounded hump. Subgenital plate short and lanceolate, granulate, with a longitudinal ridge on its whole length, and not reaching the anal segment apex; genital valve exceeding the subgenital plate apex. Cerci conical, almost straight and short, sometimes slightly exceeding the abdominal apex.

Legs small and granulate. Profemora longer than protibiae and basally compressed; anterior half of antero-dorsal carina lobate and postero-dorsal carina elevated with about five rounded small lobes, with an outer lobe at apical margin. Protibiae as long as corresponding tarsi and claws combined. Mesofemora roughly of same length than mesotibiae, covered with small tubercles; antero-ventral carina with three small spines. Medio-dorsal carina of mesotibiae slightly raised and undulated. Metafemora shorter than metatibiae; antero-ventral carina with 3-4 small rounded spines. Metatibiae slightly widened apically, 1.4× longer than corresponding tarsi and claws combined. All carinae of femora and tibiae more or less hairy.

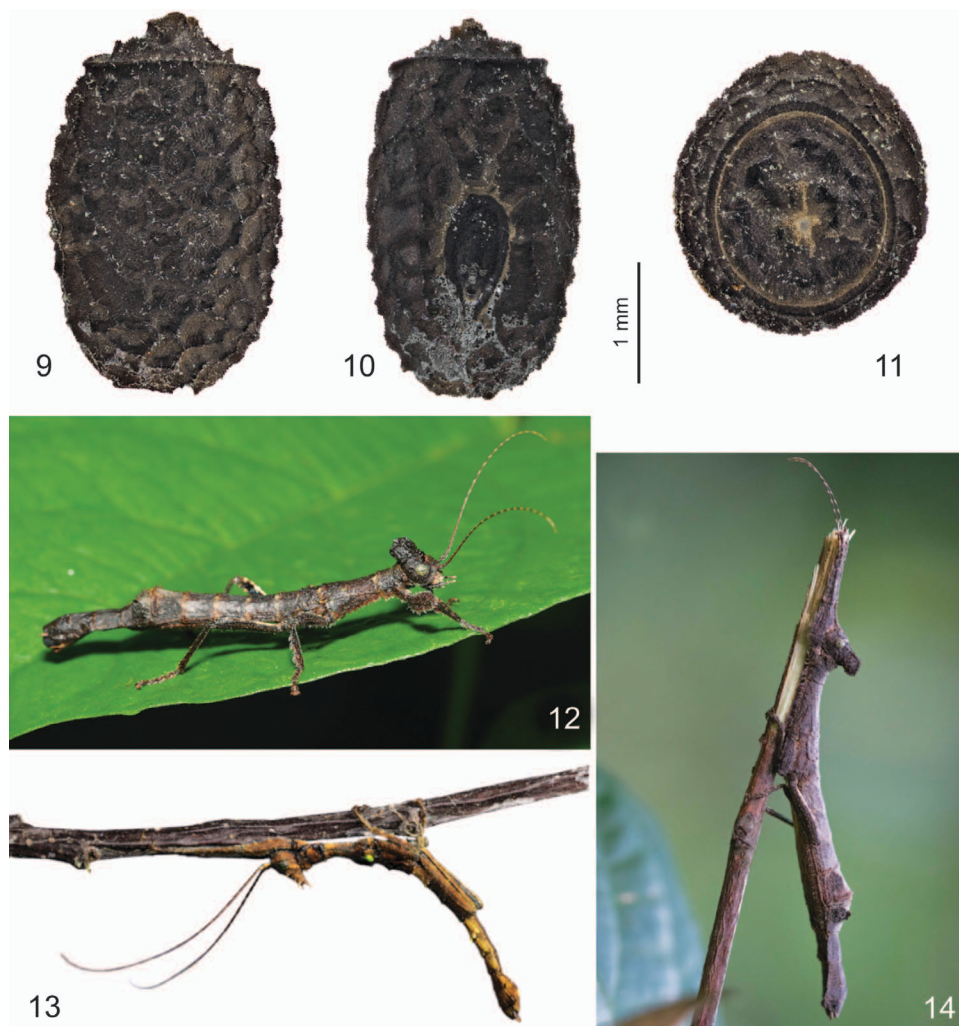


Fig. 9-14. – *Paraprisopus apterus* Conle *et al.*, egg and adult *in vivo*. – 9-11, Egg: 9, dorsal view; 10, lateral view; 11, apical view of operculum. – 12-14, Adults *in vivo*: 12, female (photo Marine Perrier); 13, male; 14, female (photo Vincent Guillemot).

Table II. – Measurements of the egg of *Paraprisopus apterus* (in mm).

	Capsule total length (incl. operculum)	Capsule length	Capsule height	Capsule width	Operculum large diameter	Micropylar plate length
1 egg from GUY19-004 (coll. TJ) / wild specimen	3.05	2.73	1.85	1.76	1.52	1.17
5 eggs from GUY19-034 (coll. YB), (means) / breeding sample	3.31	2.86	2.22	1.94	1.64	1.23

Description of the egg. – Fig. 9-11; table II. Capsule barrel-shaped, dark brown; surface entirely covered with a sinuous net of thin and raised ridges; 1.5× longer than wide and slightly higher than wide.

Micropylar plate leaf-shaped, 2× longer than wide and covering slightly less than half the length of the capsule; surface slightly rugose; micropylar cup distinct and raised; posterior part tapering gradually until median line; median line distinct.

Operculum almost circular, dark brown, with a dome formed by the same net of raised ridges than capsule, gradually raised in the centre.

Description of post-hatch nymph morphology. – Fig. 15-16. Very small (less than 1 cm). Body black with legs brown reddish. Eyes dark of the same colour as the head. Junction pro- and mesonotum white, as are junctions of meso- and metanotum and junctions of median segment and tergum II.

Head large and rounded, larger and longer than pronotum. Head and pronotum combined slightly longer than mesonotum.

Behaviour. – Fig. 13, 15-17. Post-hatch juveniles of *Paraprisopus apterus* move constantly and very quickly even during daytime, a rather rare behaviour in stick insects. Their abdomen is ventrally folded, forming a small ball-shaped abdomen (see arrow in fig. 15-16). The head looks very large, because it is closely associated to the pronotum, and it is always leaning toward the ground during movement. Both behaviour and morphology seem to mimic ant's pace and race. Males were observed keeping that behaviour well into adulthood (fig. 17) when they move. When they rest, both males (fig. 13) and females (fig. 12, 14) stay on branches, mimicking a stem like regular Phasmatodea do.

Ecology. – The sampled female was found on a lianescent plant which was not identified, at a height of about 2.5 meters. Breeding was successful in Europe using mostly *Eucalyptus sp.* (Myrtaceae) and small amount of *Hypericum × hidcoteense* “hidcote” (Hypericaceae) as substitute food plants. Incubation of eggs was about 160 days at a temperature of 18-20°C. In the same conditions, males reached maturity in 95 days and females in 110 days. Female began laying about 13 days after the imaginal moult.

DISCUSSION

The sampled wild female *Paraprisopus apterus* is the first specimen found from this species after five expeditions in French Guiana devoted exclusively to stick insect fauna. Moreover, it was found at a place known to be heavily sampled by both professional and hobbyist entomologists, namely Montagne de Kaw. In addition, the two other known wild specimens from this species were caught by SEAG with Malaise traps in a nearby area. *Paraprisopus apterus* may be rarely observed because traditional methods do a poor job of sampling this species. Its apterous condition rules out light and interception traps, and other methods seem to be weakly efficient for catching at best. Only three specimens were observed *in natura* up to now and we know very little about populations and the species ecology in the wild. Close ties with ants suspected from post-hatch nymph behaviour might suggest an important part of life cycle is occurring near soil and undergrowth.

While ants foraging on eggs is already reported from Neotropical stick insect species (*Calynda bicuspis* Stål, 1875) (WINDSOR *et al.*, 1996), and also recently described for the first time in Asia (YAMADA *et al.*, 2021), *Paraprisopus apterus* is the first documented case of post-hatch ant-mimicking behaviour actually reported from the Neotropics. This behaviour is known from stick insect

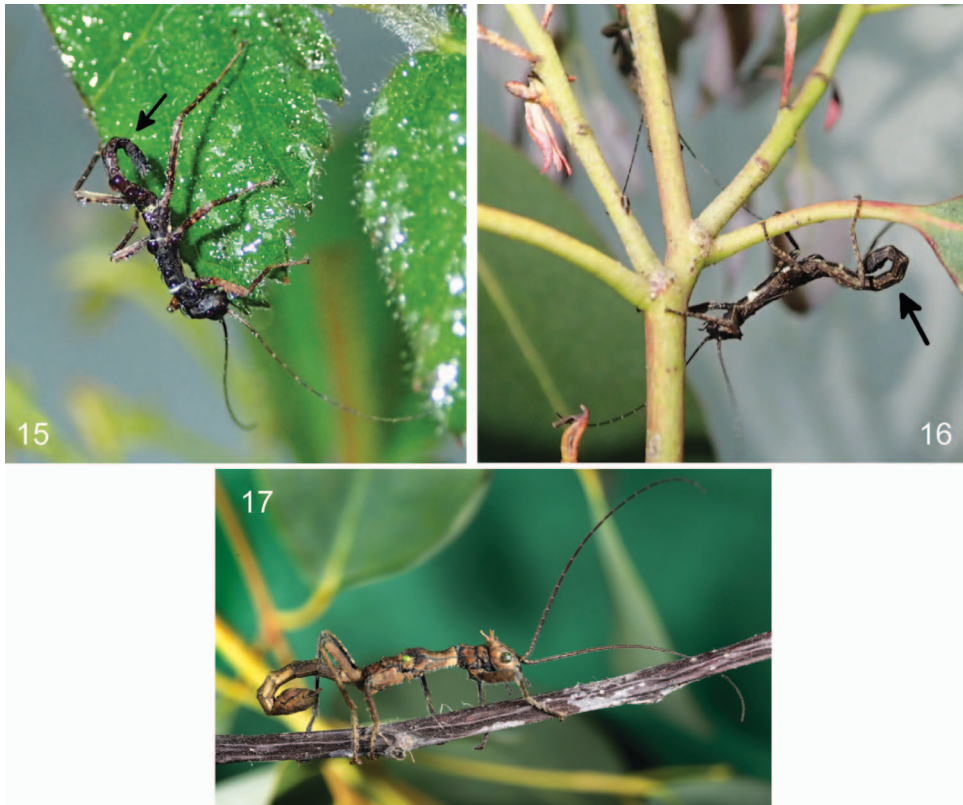


Fig. 15-17. – *Paraprisopus apterus* Conle *et al*, ant-mimicking behaviour. – 15-16, Post-hatch nymph. – 17, Adult male.

breeders with the species *Extatosoma tiaratum* (Macleay, 1826) (Australia), which is an ant-mimic at first instar stage, and the species is located from North Queensland (BROCK, 2001). *Paraprisopus agrion* nymph seems to have a similar behaviour though slightly less pronounced (pers. obs. in culture). It is particularly interesting that males continue displaying ant-mimicking behaviour well into adulthood, despite the loss of ant-like features consequently to substantial morphology change.

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