Discovery of a living fossil: a new xylastodorine species from New Caledonia (Heteroptera: Thaumastocoridae) and first record of the subfamily from the eastern Hemisphere

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A new species belonging to the genus *Proxylastodoris* Heiss & Popov, 2002, *P. kuscheli* spec. nov., of the subfamily Xylastodorinae Barber, 1920 (Heteroptera: Thaumastocoridae) is described from New Caledonia. It is the first recent record outside the western Hemisphere of the Xyalstodorinae and is the largest known member of the family Thaumastocoridae. The new species was collected on inflorescences of the native New Caledonian palm species *Burretiokentia vieillardii* (Brongn. & Gris) Pichi-Serm. The habitat, collecting methods, host plant and biology of the new species are described. The biogeography of the Thaumastocoridae and Xylastodorinae is discussed and suggestions for further research are proposed. This discovery is characterised as the discovery of a living fossil as the new species is assigned to the genus *Proxylastodoris*, previously a monotypic genus described from Baltic amber.

Introduction

An unknown male specimen from New Caledonia, collected by the coleopterist Dr G. Kuschel on Mt Rembai in 1978, proved to be a new species of the subfamily Xylastodorinae Barber, 1920, of the family Thaumastocoridae (Insecta: Heteroptera). The discovery of this species is remarkable for several reasons: xylastodorines were previously known from the Neotropical region only and *Proxylastodoris* was known only from Baltic amber before it was known as an extant taxon. When we rediscovered it as an extant taxon, it was found still living just on one remote island on the other side of the world from Europe. So it not only has 'temporal disjunction' but also 'spatial disjunction' and 'restricted area, narrow endemicity', hence our designation of this new species as a living fossil, akin to taxa such as the Wollemi pine, *Wollemia nobilis* Jones, Hill & Allen, 1995 (Gilmore & Hill, 1997; Woodford, 2000).

A search for more material was undertaken by one of us [GBM] in 2004/5 and 2005 expeditions to New Caledonia. Under the assumption that this species lives on palms, like its described Neotropical xylastodorine relatives, searches were made amongst young leaves and the inflorescences of palms. At three collecting sites this xylastodorine species, including its nymphal stages, was found on the inflorescences of the endemic New Caledonian palm species, *Burretiokentia vieillardii* (Brongn. & Gris) Pichi-Serm.

To ascertain the systematic position of the new xylastodorine species, we compared it with known recent and fossil species. Based on comparative morphology, the new species is placed in the same genus as the Baltic amber [Eocene 40-50 my bp] fossil species *Proxylastodoris gerdae* (Bechly & Wittmann, 2000), and here described as *Proxylastodoris kuscheli* spec. nov. Bechly & Wittmann (2000) originally described *Xylastodoris gerdae* for two female specimens while Heiss & Popov (2002) recorded another two male specimens from Baltic amber and regarded this species as sufficiently distinct that it required erection of a new genus, *Proxylastodoris* Heiss & Popov, 2002. Xylastodorinae are also known from Dominican amber: *Paleodoris lattini* Poinar and Santiago-Blay, 1997 [Oligocene, 35 million years bp]. More recently, Nel, Waller & Ploëg (2004) described a new genus and new species (*Protodoris minusculus)* from the lowermost Eocene amber [55 my bp] of the Paris Basin, assigning it to the Thaumastocoridae. Cassis & Schuh (2009) regarded their argumentation to be flawed and that there was insufficient evidence to assign this taxon to any land bug family-group.

The Thaumastocoridae is a highly specialized (Slater & Drake, 1958) and putatively a relictual group of phytophagous cimicomorphan bugs (Schuh & Štys, 1991, Schuh et al., 2009; for alternative view see Cobben, 1978: 357), comprised of three subfamilies: the Eastern Hemisphere Thaumastocorinae Kirkaldy, 1907 (four genera and 13 species) and Thaicorinae Kormilev, 1969 (one species from Thailand and Java) and the Xylastodorinae Barber, 1920 (two genera and six species) from the Western Hemisphere.

The description of this taxon is of great importance from a biogeographic perspective, because it not only provides a major trans-oceanic range extension (> 14000 km) for a higher taxon (i.e., Xylastodorinae), it also provides a novel case study for addressing current polemics of New Caledonian biogeography. At present, views are polarized as to the age and origins of the New Caledonian biota, with arguments in two camps: 1) relictual and Gondwanan vicariant theory (Sharma & Giribet, 2009; Edgecombe & Giribet, 2009) and 2) recent and southwest Pacific dispersalist theory (Grandcolas et al., 2008).

The host plants records of the Thaumastocoridae were most recently compiled by Cassis et al. (1999), confirming the phylogenetic decoupling of food plant preferences at the subfamily level (see also Drake & Slater, 1957). Most members of the Thaumastocorinae feed on dicot angiosperm families, with only one of these being a monocot. In contrast, the Xylastodorinae are all palm feeders, and the fact that this is true for our new New Caledonian xylastodorine species supports a relictual Gondwanan origin.

In this paper we describe the largest known extant thaumastocorid species with a maximum length of 5 mm. Its documentation provides further insight into the evolution, host plant associations and distribution of the Thaumastocoridae.

Material and methods

Material.— The specimens examined in this study are deposited in the following collections:
NZAC (earlier DSIR) = New Zealand Arthropod Collection, Auckland, New Zealand
MNHN   = Musée National d'Histoire Naturelle, Paris, France
RMNH   = Netherlands Centre for Biodiversity Naturalis, Leiden, The Netherlands

QM   = Queensland Museum, Brisbane, Australia
UNSW   = University of New South Wales, Sydney, Australia

Methods.— All measurements are given in mm and represent maximum lengths. For orientation, the appendages are viewed from the 'inner surface' of other authors in the anterior position, such that the 'inner surface' of a tibia is referred to herein as the ventral surface of the tibia. In the captions of the figures, 'b' is used as an abbreviation of the scale bar.

Genitalia were prepared by macerating in 10% KOH, rinsing in distilled water, and dissecting in glycerol, under a Leica MZ16 stereomicroscope. Line drawings of the genitalia were made using a Leica DMB compound microscope and camera lucida, resp. Zeiss SR stereo- and Wild M20 compound microscopes both with camera lucida.

Scanning electron micrographs were taken at the Australian as well as at the Leiden Museum Scanning Electron Microscopy laboratory. In the Australian Museum material

Fig. 1. *Proxylastodoris kuscheli* spec. nov., male holotype from Mt. Rembai, habitus, length 4.6 mm.

Fig. 2. *Proxylastodoris kuscheli* spec. nov., male paratype from Mandjélia, habitus; length 4.7 mm.

was air-dried, coated with gold and examined using a Hitachi electron miscroscope, whereas in Leiden the material was coated with palladium and examined with a JEOL electron miscroscope.

Systematic part

Thaumastocoridae Kirkaldy, 1907

The Thaumastocoridae are divided into the following three subfamilies:

1. Thaumastocorinae Kirkaldy, 1907, are diagnosed by the pretarsus having setiform parempodia and lacking pseudopulvilli, the left paramere present and the right paramere absent. They are found exclusively in the Eastern Hemisphere (India and Australia). Aside from a single species from southern India (*Wechina chinai* Drake & Slater, 1957), the remaining twelve species are endemic to Australia (including Tasmania): *Baclozygum* Bergroth, 1909 [4 species], *Onymocoris* Drake & Slater, 1957 [4] and *Thaumastocoris* Kirkaldy, 1907 [4] (Cassis & Gross, 1995, Cassis et al., 1999). They are found on a broad range of dicot angiosperms (Cassis et al., 1999).

2. Thaicorinae Kormilev, 1969, are closely allied to the Xylastodorinae with the pretarsus possessing pseudopulvilli and setiform parempodia (Heiss & Popov, 2002, fig. 7- Pv, Pe). They are differentiated by the elongate body and the pronotum and head with exaggerated projections. The subfamily is monogeneric and monotypic, with *Thaicoris* Kormilev, 1969 represented by a single species, described from Thailand (holotype), and also known from Java (Kormilev, 1969; Heiss & Popov, 2002).

3. Xylastodorinae Barber, 1920, are diagnosed by the presence of pseudopulvilli, and are without exaggerated projections of the head and pronotum. They comprise the monotypic genus *Xylastodoris* Barber, 1920 (Cuba, Florida) and the Neotropical genus *Discocoris* Kormilev, 1955 with five extant and one fossil species, from Argentina, Colombia and Venezuela. All xylastodorines are palm-feeders. It also includes *Proxylastodoris* Heiss & Popov, 2002, from Baltic amber, and now New Caledonia, and *Paleodoris* Poinar & Santiago-Blay, 1997, from Dominican amber.

Subfamily Xylastodorinae Barber, 1920

Xylastodorinae Barber, 1920: 100; Drake & Slater, 1957: 368 (monograph); Slater & Drake, 1958: 321.

Genus *Proxylastodoris* Heiss & Popov, 2002

Type species: *Xylastodoris gerdae* Bechly & Wittmann, 2000, by original designation.

Diagnosis.— *Proxylastodoris* is recognised by the following characters: body broadly ovate, densely and deeply punctate; head wider than long; clypeus longer than jugae; antenna long and slender, two basal segments thicker than distal segments, last narrowly spindle-shaped; labium elongate, four-segmented, surpassing thoracic sterna, first segment exposed, margins of head anteriad to antennophores barely tapering; ocelli widely separated, behind posterior margins of eyes; disc of pronotum without a distinct transverse depression; lateral margins of pronotum and costal margins of coria expanded, margins of the latter reaching tip of membrane; clavi distally broadened;

claval suture as long as scutellum; pretarsus with large pseudopulvilli, parempodia setiform, thin, placed close together; abdomen in both sexes broad.

Remarks.— Heiss & Popov (2002) named a new genus, *Proxylastodoris*, for the amber fossil species *Xylastodoris gerdae* Bechly & Wittmann. Examination of the images and description given in Bechly & Wittmann (2002) indicate a striking similarity between our new species from New Caledonia and the fossil species. On the basis of the generic diagnosis of Heiss & Popov (2002) we have placed the former species within *Proxylastodoris*, and in so doing, no modification of its definition is required.

Proxylastodoris is differentiated from the Western Hemisphere genus *Xylastodoris* by its larger size, oval form and much longer rostrum; from *Discocoris* by the narrower pronotum with straight anterior margin and from both by the characteristic deep punctation of the upper side of the body; fore wings with apically broadened clavi, claval commissure as long as the scutellum and the possession of a (short) medial fracture; abdomen with only one dorsal scent gland. Tibial fossulae spongiosae could not be determined in *P. gerdae* (see discussion).

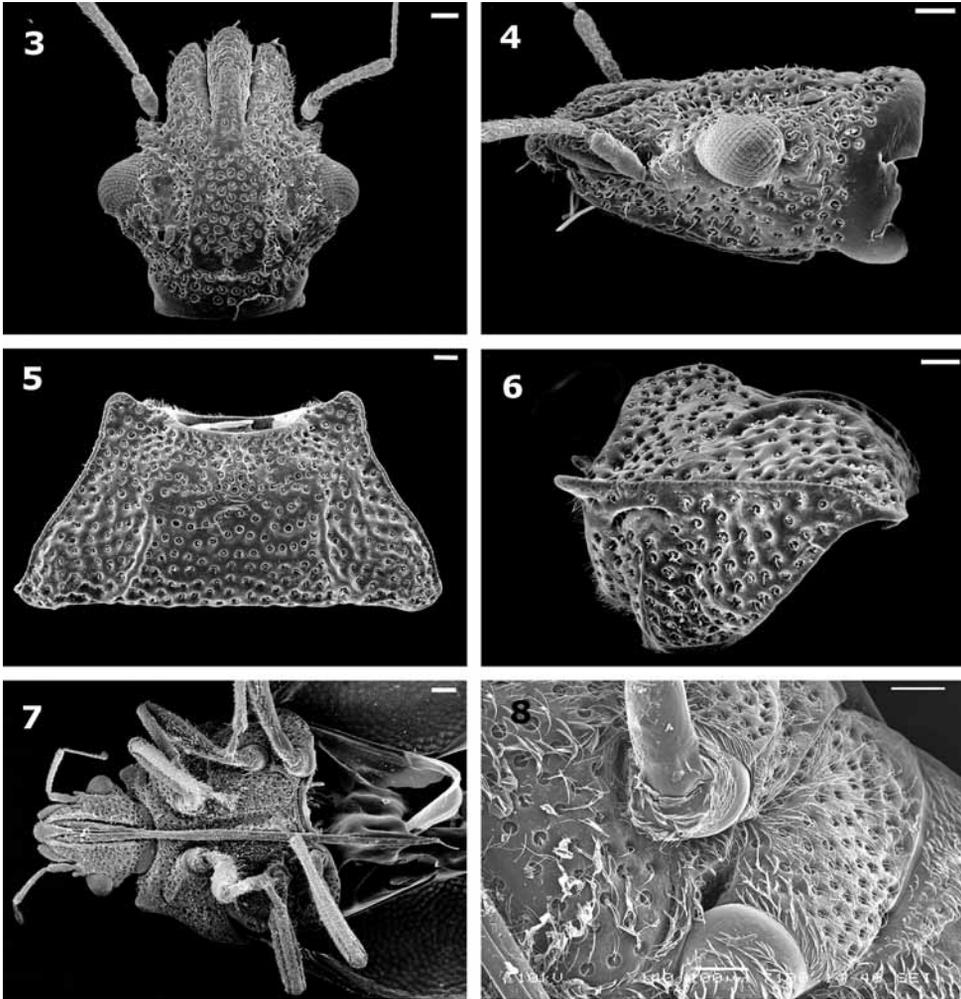*Proxylastodoris kuscheli* spec. nov.
(figs 1-16, 20-24, 26-42)

Material.— Holotype (fig. 1): ♂ 'New Caledonia, Mt Rembai, 700 m, 18.x.1978, G. Kuschel'. Deposited in the New Zealand Arthropod Collection, formerly, Entomology Division, D.S.I.R., Auckland, New Zealand (NZAC). Paratypes: 2♂♂, 1♀ (QM), 1♂ (RMNH, fig. 2) 'New Caledonia, Mandjélia, 1 km SW, rainfor., 750 m, on palm inflor., pyrethrin spray, 5.i.2005, G. Monteith, # 11903, 20°24'S-164°32'E'; 2♂♂, 1♀ (QM), 1♀ (RMNH) 'New Caledonia, Pic d'Amoa, N. Slope, 480 m, on palm inflor., pyrethrin spray, 16.xii.2004, G. Monteith, # 11911, 20°58'S-165°17'E'; 3♂♂, 1♀ (QM), 'New Caledonia, Aoupinié sawmill, 500 m, on palm inflor., pyrethrin spray, 17.xii.2004, G. Monteith, # 11915, 21°09'S-165°19'E'.

Diagnosis.— *Proxylastodoris kuscheli* spec. nov. differs from *P. gerdae* by the following characters: larger (4.3-5.0 mm) and broader body; eyes smaller; antenniferous tubercles well developed; labium longer, reaching abdominal sternite IV; anterior angles of pronotum produced; venation of forewings obscure; male genital capsule shorter.

Description.— Male (fig. 1: holotype). Length 4.6 mm, ovoid-shaped, dorsoventrally flattened; head and pronotum declivous; dorsum uniformly heavily and deeply punctate, with setiferous punctures; ventral surface setose, except pro- and metapleura; labium very long, attaining at least the fourth abdominal sternite.

Head (figs 3-4).— Head almost as long as broad, inclusive of eyes (17:18), declivous, strongly broadened from occiput towards eyes; eyes of moderate size, half spherical, black but posteriorly often red, width of an eye in dorsal aspect 1/6th of width of head inclusive of eyes (0.98 mm); synthlipsis 0.65 mm; vertex medial to eyes with a shallow longitudinal smooth concavity, posteriorly ending against red ocelli; ocelli large, situated just behind posterior margins of eyes, equidistant from eyes and pronotum, synthlipsis of ocelli 0.55 of that of eyes, 0.36 mm; frons and vertex strongly convex; genae well developed, a little tumescent, tapering to occiput, broad ventrad to eyes, smooth with about 20 large punctures, anteriorly tapering towards apex of head, with finer and denser punctation; jugum shorter than clypeus, basal parts parallel, anteriorly rounded; clypeus broader and somewhat longer than jugum, rounded apically, roundly keeled

basally, boundary between clypeus and jugae marked by sharp longitudinal furrow at both sides; postclypeus raised; antenniferous tubercles anterior of eyes, low, with weakly developed raised edge, somewhat downward directed; rim of each laterodorsally extended into small blunt tooth, visible from above; antennae slender, moderately long, 1.7 times longer than length of head, the apical two segments much narrower than the basal two segments, first segment short and thick, three times longer than wide, basally tapered, apex rounded, in middle somewhat constricted, not surpassing tylus; second segment a little slimmer than first, somewhat club shaped, slightly curved in basal half, third longest, straight, and very thin, two times the length of first, last segment thinly spindle to club-shaped, pale yellow subhyaline, apical ¾ darkened to blackish; antennal

Figs 3-8. *Proxylastodoris kuscheli* spec. nov., adult male. 3, head dorsal aspect, b [= scale bar] = 100 μm; 4, head lateral aspect, b = 100 μm; 5, pronotum dorsal aspect, b = 100 μm; 6, pronotum lateral and left aspect, b = 100 μm; 7, thorax and head ventral aspect, b = 200 μm; 8, part of thorax ventral aspect, left side, showing opening scent gland, b = 100 μm.

ratio: 14:25:28:20 (roughly 3:5:6:4); bucculae long, parallel, narrow, somewhat converging and extended almost to posterior margin of head, enclosing at both sides the first rostral segment; rostrum (fig. 7) very long, four segmented, reaching fifth abdominal sternite, first segment fully exposed, almost as long as underside of head, sides with a fringe of fine setae; lengths ratio of the segments: 27:28:36:41; labrum triangular, sharply pointed at apex, 1.5 × longer than wide at base; dorsal aspect of head densely punctate, setation moderate.

Thorax.— Pronotum (figs 5-6): trapezoidal, much wider than long, ratio 9:5; anterior margin slightly concave in middle 3/5, posterior margin faintly convex, corners a little inflated; lateral margins shallowly sinuous, borders narrowly explanate, anteriorly widened into flat, anteriorly expanded laminate corners; boundary between anterior and posterior parts indistinct; punctation of fore part fine and dense, of posterior part, especially medially, coarse and more remote, laterally more or less swollen and ivory coloured, forming an oblique row; anterior part with a medial protuberance and a pair of shallow calli; with a small, deep pit posteriad to medial protuberance.

Scutellum triangular, wider than long, ratio 8:5; surface densely punctate; apex a little enlarged, flattened and rounded; basal margin high, sharply separated from partly exposed black mesoscutum; lateral angles black, ending in a transverse delicate ridge.

Underside of thorax (fig. 7): anteriorly with a rather broad collar (0.12), medially confluent with small square prosternum; mesosternum much broader, longitudinally shallowly grooved to accommodate rostrum; rostral furrow increasingly shallower posteriorly to flat fused meso- and metasternum and anterior abdominal sternites; pro- and metapleura setose with more or less decumbent silvery setae, ca. 0.05 mm; MTG orifices (fig. 8) greatly reduced, anterior to hind coxae, as a very small opening, laterally narrowed to a small peritreme extending onto the metepisternum.

Wings.— Forewing (figs 9-11) broad, at rest obovate, covering similarly shaped abdomen in males, in females last tergite extending beyond wing tips; clavi broadened apically, claval suture well developed, claval commissure as long as scutellum; costal margins evenly rounded, coria broad, extending to apex of wing; costal edge narrowly expanded, anteriorly broader, semitransparent and upturned, lighter in colour; hypocostal ridge proximally broadened, covering lateral edges of mesopleura, abruptly narrowed at base of abdomen; forewings uniformly densely punctate, on clavus and towards claval vein punctures larger, more scattered and foveate (fig. 10); punctures setiform, each seta arising from anterior wall, generally directed dorsoposteriorly, short of or surpassing opposite rim of puncture; in smaller punctures, seta born on outside of rim (fig. 11); venation obscure; medial fracture short, $2/7^{th}$ of forewing length; membrane smooth, without veins, hyaline with more or less blackish patches, with black basal round patch, behind a white opaque transverse (wings at rest) band, posterolaterally uncoloured surface shallowly and very finely wrinkled transversely. Hindwing (fig. 12): fully developed.

Legs.— Homomorphous, slender, uniformly setose; femora sturdy, slightly club shaped, distally with more elongate setae, especially ventrally; metafemora longest (4:3), lightly bent, dorsal surface with setae bearing minute tubercles, ventral surface with three small, blackish pustules subapically (fig. 20); tibiae cylindrical, slender; foretibia a little broader apically; tibial apices bear dorsal and ventral ctenidia of six flattened spicules (figs 14, 22), except on foretibiae where dorsal ctenidia have 15-16
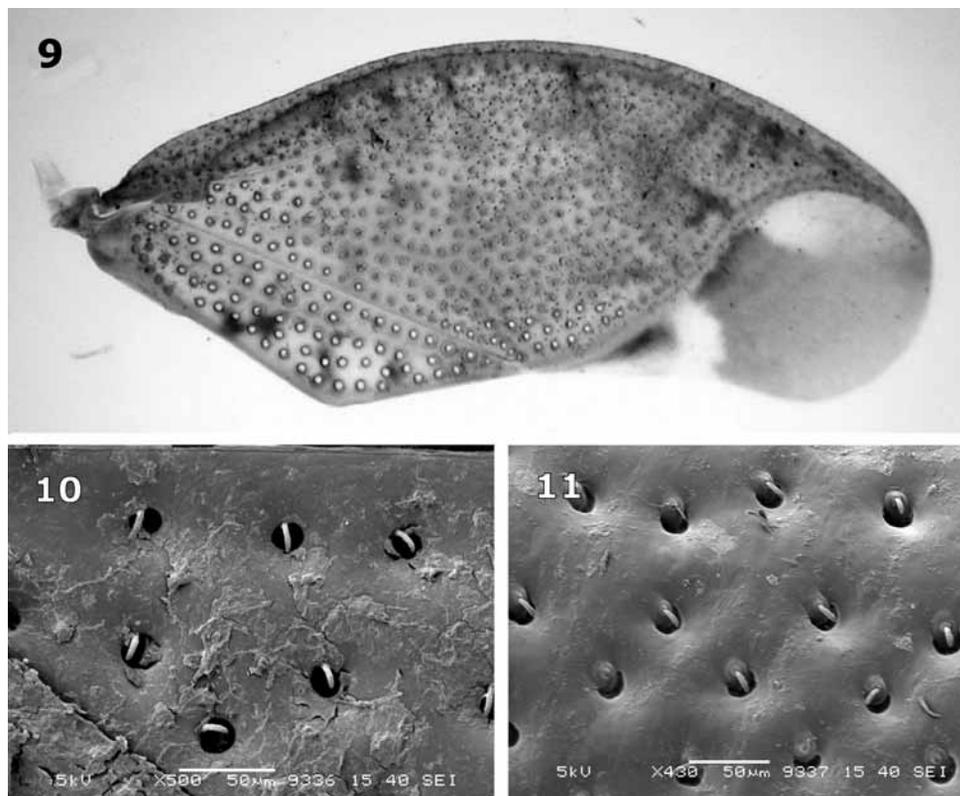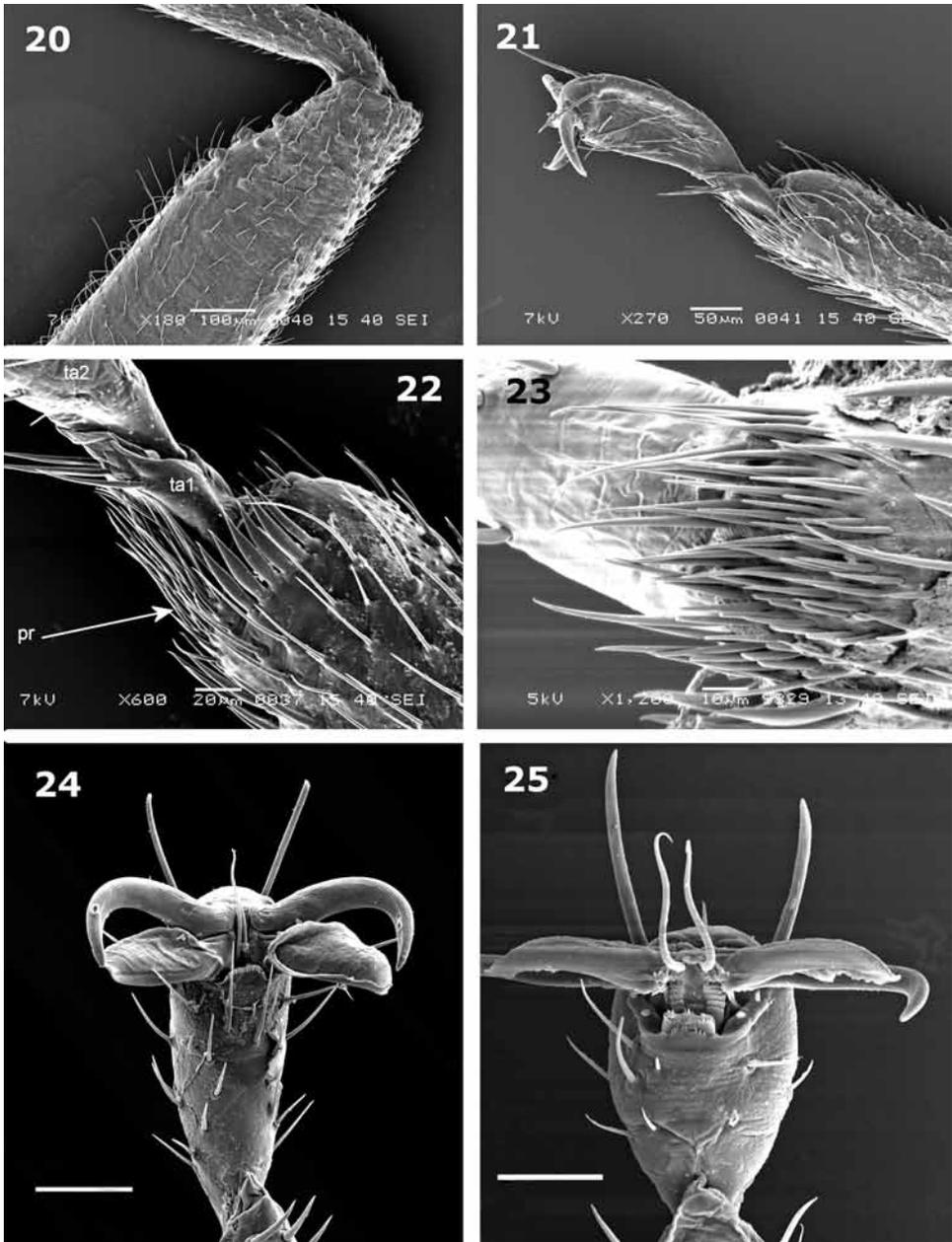
Figs 9-11. *Proxylastodoris kuscheli* spec. nov. 9, Right fore wing, showing punctation and the colour pattern of the membrane, length = 3.25 mm; 10, 11, details of the fore wing, 10, the bigger punctures on the clypeus, 11, the small punctures of central part. b = 50 μm.

spicules (fig. 13), with first and last spicules longest; all tibiae apically with a small dome-shaped, blunt fossula spongiosa on ventral surface, heavily set with long thin tenent hairs, forming a small tuft (figs 13-14, 22-23); tarsi two segmented; first tarsomere very small, bearing ventrally three large setae (figs 14, 21); second tarsomere (fig. 24) large, club shaped; claws widely separated; parempodia moderately long, thin, parallel, placed close together on apex of unguitractor; adjacent to parempodia, behind bases claws, with large fan-like pseudopulvilli; pretarsus terminating ventrally in broad lingual process, apex with two rows of fine denticles.

Abdomen (figs 34, 37).— Broad, rounded, shield shaped, about as long as broad; dorsally red to brownish red, matt, anterior margins of tergites narrowly glossy, T7 and T8 densely punctate medially; T8 and pygophore not visible from above with wings at rest; laterotergites not visible; T1 laterally shortened, not reaching lateral margins of abdomen (fig. 34); dorsal abdominal scent glands present on T3-5, red gland reservoir internally observable medially on T3 (fig. 35), divergently broader anteriorly; dorsal scent gland outlet not visible; T8 asymmetrical, posterior margin almost straight, slanting, left lateral margin longer than right; sternites 2-7 visible, spiracles all ventral, anterior margin of S2
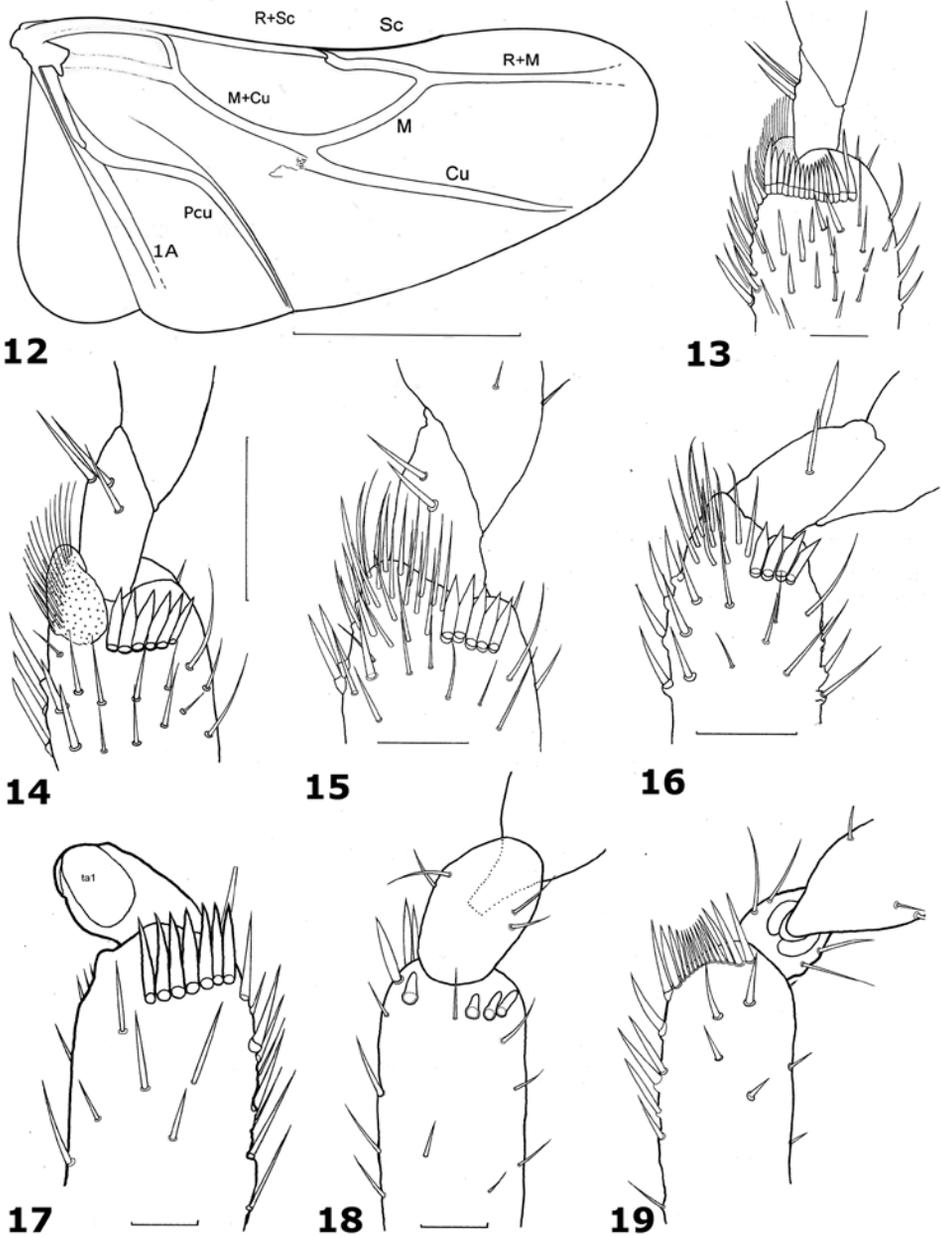
Figs 12-16. *Proxylastodoris kuscheli* spec. nov. 12, right hind wing, b = 1 mm; 13, male, right fore leg, showing end of tibia with cleaning comb, b = 50 μm; 14, male, hind leg, end of tibia showing comb with six flattened spicules and a blunt papilla (schematically), b = 100 μm; 15, nymph V, end of tibia, b = 50 μm; 16, nymph IV, end of tibia, b = 50 μm. Fig. 17. *Discocoris vianai* Kormilev. Middle tibia, dorsal side, b = 20 μm. Figs 18-19. *Xylastodoris luteolus* Barber. 18, hind tibia, ventral side; 19, fore tibia, dorsal side, b = 20 μm.

Figs 20-24. *Proxylastodoris kuscheli* spec. nov. 20, male hind leg showing small tubercles ventrally near end of femur, b = 100 μm; 21, apex of male right middle leg, showing tarsus; 22, male, right middle leg, apex of tibia, anterior aspect, showing a comb with six flattened spicules and a blunt papilla (p), heavily set with long thin setae, forming a small tuft, ta1 and ta2 = first and second tarsal segment, b = 20 μm; 23, the tuft of setae ['tenent hairs'] enlarged, 10μm; 24, apex of the pretarsus showing accessory parempodia laterally connected to the unguitractor, b = 50 μm. Fig. 25. *Xylastodoris luteolus* Barber, apex of praetarsus, b = 20 μm.
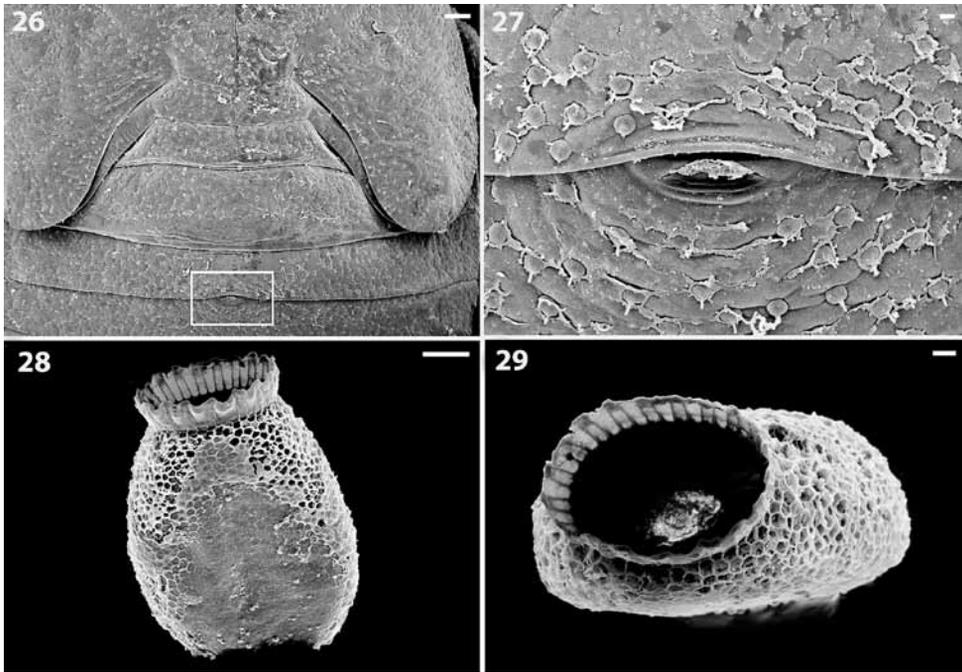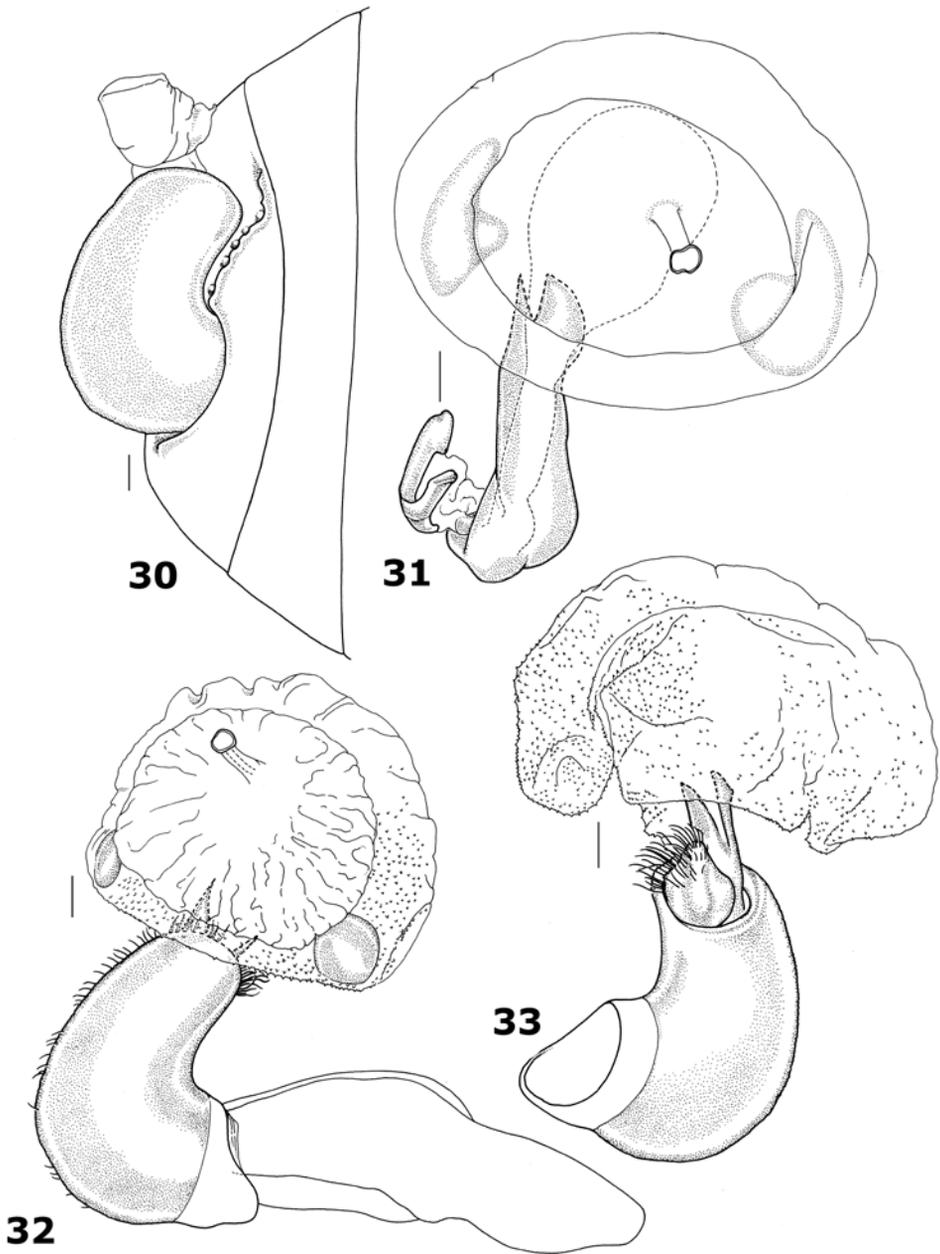
Figs 26-29. *Proxylastodoris kuscheli* spec. nov., egg and larva. 26, nymph V, thorax and abdomen dorsal aspect, showing scent gland outlet, b = 100 μm; 27, id., abdominal scent gland outlet at higher magnification, b = 10 μm; 28, egg lateral aspect, b = 100 μm; 29, egg dorsal aspect, b = 30 μm.

deeply excavated at posterior coxae, medially produced anteriad between coxae, as in female (fig. 36); S8 (fig. 37) asymmetrical, laterally fused with T8, forming ring-like eighth urite, right lateral margin shorter than left.Pygophore situated on posterior margin of the arcuate S8; this on the right side posteriorly transversely sulcate, depressed, basin-like, receiving apex of pygophore at rest (figs 30, 37), anterior boundary of sulcation arcuate, sharply marginate; basin-like depression with closely set, minute, medially oriented, sharp teeth; pygophore tumid, tube-shaped, extended and curved to right side, set with short, erect silvery setae (± 0.045 mm), more so towards apex and small decumbent setae posteriorly.

Aedeagus (figs 31-33): The somewhat cylindrical sclerotized phallotheca of the aedeagus distally forked by a deep indentation, contains the endosoma which, expanded, forms a big membranous bag with the secondary gonopore apically on a tube-like structure which may represent the vesica; there are no parameres; proctiger protrusile, set with a loose bunch of setae and its end swollen.

Female.— Salient features as in male, including micropustules on underside of femora.

Abdomen.— Abdomen broad, as in male but posteriorly a little narrower and longer (figs 35-36); six visible sternites (2-7); spiracles all ventral; lateral margins of S7 widely emarginate subposteriorly; S8 eighth sternite divided, laterally connected to T8, in part ventrally covered by S7, lateral parts just visible (fig. 36), with seventh spiracles present;

Figs 30-33. *Proxylastodoris kuscheli* spec. nov., male genitalia. 30, ventral view of sternites 7 and 8 with pygophore in lateral view and in rest position; 31, dorsal view of aedeagus (pygophore removed) showing basal plates on which the sclerotized phallotheca and the expanded membranus endosoma; visible through the endosome the ending ductus seminis; 32, ventral view of pygophore with expanded phallotheca showing on top the secundary gonopore; 33, dorsal view of pygophore showing the proctiger and the forked top of the phallotheca with the expanded endosoma, (no parameres); b = 100 μm.

abdomen posteriorly roundly truncate, closed by rounded wall of T9; dorsal aspect: eight tergites visible (fig. 35); apparent T8 comprises fused T8 and T9, with T9 forming end of abdomen, as rounded posterior wall; anterolateral angles of T9 and posterolateral angles of T9 not fused, as movable flap-like structure (figs 35, 38, 39), connective integument between two tergites thin and flexible.
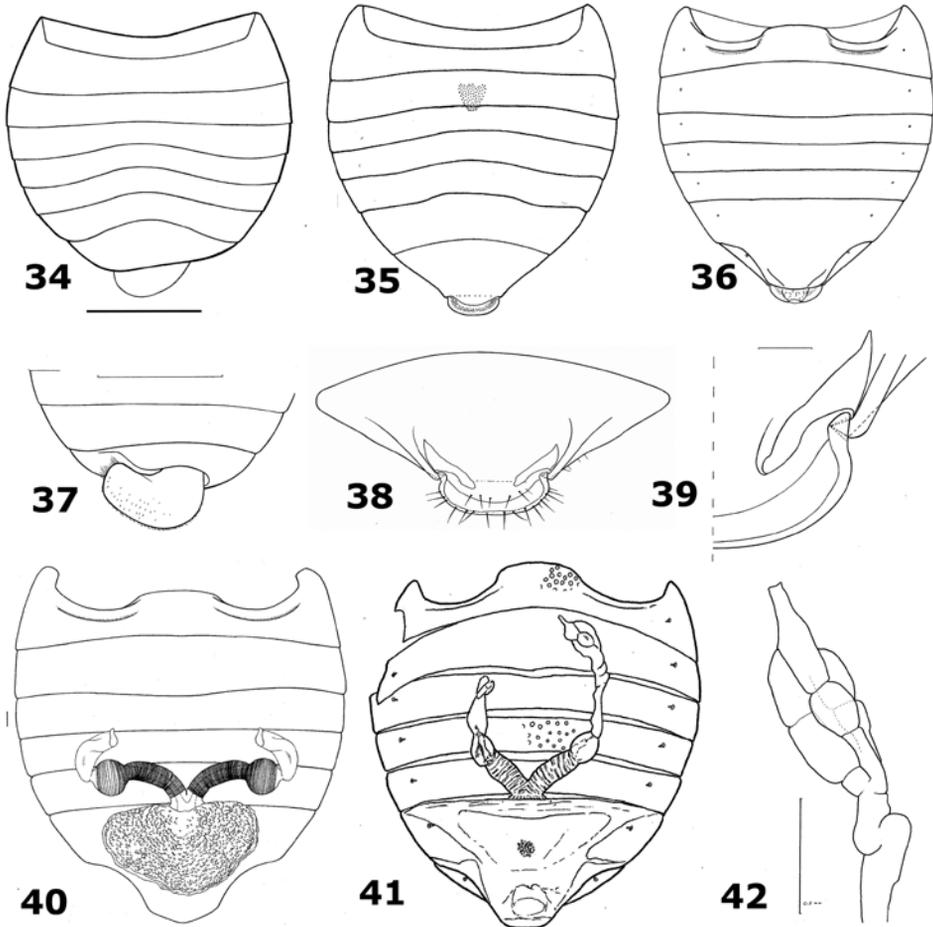
Figs 34-42. *Proxylastodoris kuscheli* spec. nov. 34, 35, male and female abdomen in dorsal aspect, respectively; 36, female abdomen, ventral aspect, at both sides the lateral parts of the eighth sternite just visible; 37, end of male abdomen in ventral view showing asymmetry of the first segments and the pygophore; 38, ventral view of female last tergites: triangular eighth tergite with attached flap-like ninth tergite that seems to be hinged on the lateral struts of the eighth tergites' lateral margins; 39, left hinge, ventral aspect, enlarged (see description), b = 100 μm; 40-42, female internal genitalia, dorsal aspect showing genital chamber with common and lateral oviducts and ball-shaped swellings 'reservoirs', of lateral oviducts in different stages. 40, ball-shaped swellings full-grown, ovarioles lost; 41, right oviduct unimpaired, ovariole visible (left one may be lost); 42, oviduct enlarged showing three ovarioles, b = 500 μm. Bars for abdomen = 1 mm.

Genitalia (figs 40-41): internal female reproductive tract comprised of broad, round genital chamber (bursa copulatrix), with short common oviduct, with paired lateral oviducts large, with enlarged ball-shaped reservoirs, with internal ducts; lateral oviducts, distal to reservoirs, running anteriorly, each terminating in an ovary bearing three ovarioles (figs 41, 42).

Egg (figs 28-29).— Barrel-shaped, somewhat narrowed cephalically, more or less oval in cross section; width 0.465 (without rim), height 0.5 mm; chorion finely hexagonal, collar with about forty contiguous micropylar processes, forming an undulate rim; operculum not observed.

Measurements.— Male: mean body length 4.54 (n = 9), range 4.26-4.8, mean body width 2.46, range 2.28-2.76. Female: mean body length 4.59 (n = 4), range 4.26-5.04; mean body width 2.51, range 2.28-2.76. Holotype: body length 4.6; maximal abdominal width 2.4; elytra length 2.85; elytra width 2.44; head length 0.92; head width across eyes 0.98; head width between eyes, 0.66; eye width 0.165; width between ocelli, 0.36; ocelli diameter 0.07; antenna: total length 1.38; I 0.20, II 0.40, III 0.46, IV 0.32; rostrum: total length 3.22; I 0.66; II 0.61; III 0.96; IV 1.0; pronotal length 0.98; maximal pronotal width 1.89; anterior pronotal width 1.26; scutellum length 0.55; scutellum width 0.87.

Fig. 43. Flowering specimen of the palm *Burretiokentia vieillardii* (Brongn. & Gris) Pichi-Sermolli (arrow) near the sawmill at Aoupinié, New Caledonia on 17 December 2004 following spraying with aerosol pyrethrin. Photograph shows the blue nylon sheets spread on ground to collect falling specimens. Contents of sheets are shaken into the red fabric funnel to collect the sample.

Host plant.— This species was collected on the palm species *Burretiokentia vieillardii* from three localities on New Caledonia (Mandjélia, Pic d'Amoa and Aoupinié). The specimens were collected by pyrethrin-knockdown, using household aerosol cans, sprayed from ground level up into the lower canopy of palms with inflorescences and/or infructesences (figs 43, 44). Specimens were then gathered from nylon sheets spread on the ground to collect insects that dropped down. This sometimes produced considerable numbers of the bugs, with 26 individuals taken from the tree shown in fig. 43. The original specimen of *Proxylastodoris kuscheli* was collected at 700 m on Mount Rembai by G.A. Kuschel in October 1978. This locality was visited twice, in December 2004 and January 2005, with the express purpose of recollecting the species. Though dense stands of flowering *Burretiokentia vieillardii* were located at around 700-800 m, and conditions were ideal for pyrethrin spraying, no bugs were collected. All recorded localities for the thaumastocorid are shown in fig. 45. All are in well-developed rainforest at altitudes from 450 m up to a maximum of 750 m at Aoupinié and Mandjélia. All sites are in the main part of the Central Cordillera, except for Pic d'Amoa which is the lowest site and on a wet, eastern side range of the central chain. There are no collections from the southern third of the main island and the southernmost locality (Mt Rembai) has not yielded recollections in recent times. The centre of distribution of this interesting species is in the island's north.

Fig. 44. Detail of flowering and fruiting inflorescences of the palm *Burretiokentia vieillardii* (Brongn. & Gris) Pichi-Serm. at Pic d'Amoa, New Caledonia on 16 December 2004. Six males, 2 females and 18 nymphs of *Proxylastodoris kuscheli* spec. nov. were obtained on that day by spraying this palm.
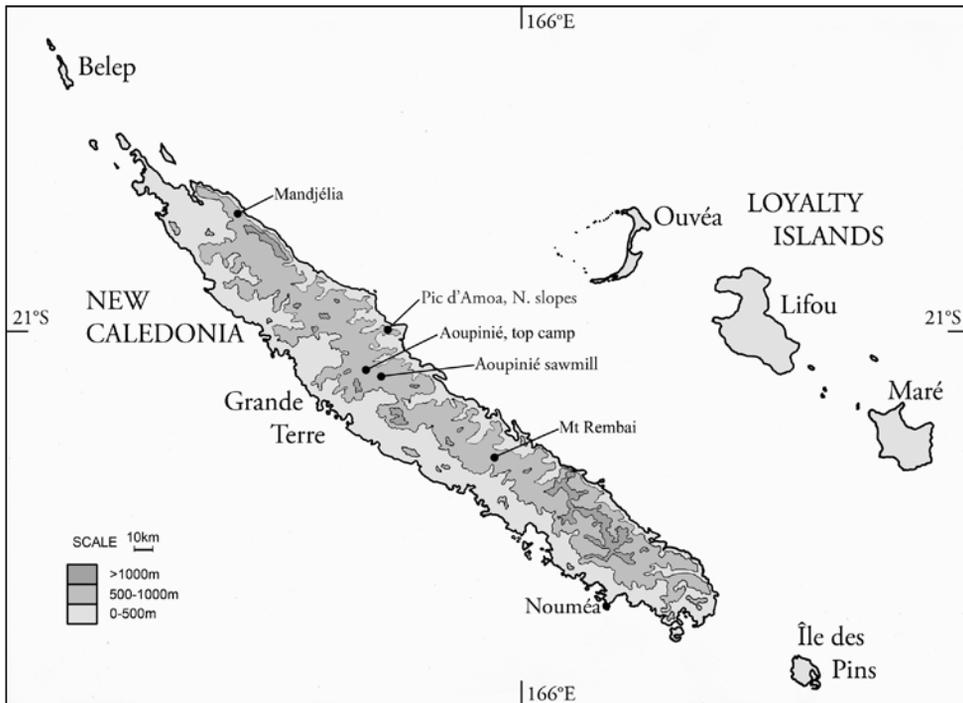
Fig. 45. Map of New Caledonia showing all collection sites for *Proxylastodoris kuscheli* spec. nov.

Etymology.— This species is named in honour of Dr Guillermo (Willy) Kuschel who collected the first specimen, the holotype designated herein. This patronym is in recognition of his exemplary fieldwork and taxonomic research on the weevils of the Southern Hemisphere, including those of New Caledonia.

Discussion

Morphology

Wing venation.— The hind wing venation in *Proxylastodoris kuscheli* (fig. 12) is as expected, and resembles greatly that of *Discocoris vianai* Kormilev (Kormilev, 1955, fig. 8), and also that of the anthocorid species *Lyctocoris campestris* (Fabricius) (Davis, 1961: fig. 25), where the A1 (= Pcu in Davis) is strongly s-curved towards its base. Further-more, it is striking that at the base of the wing, the individual bases of the veins R, M and Cu are distinguishable. Kormilev's interpretation of the venation (Kormilev, 1955, figs 8-9) were wrongly criticized by Drake and Slater (1957), with the latter contending that Kormilev's AI represents the vannal fold.

Leg morphology.— The tibial ctenidia of the Thaumasocoridae have not been pre-viously discussed, although the figure given by Schuh & Slater (1995) of the foretibial ctenidium in *Baclozygum depressum* comprises 15 setae. According to Lis & Schaefer (2005) these tibial combs are present in all infraorders of terrestrial Heteroptera, and the

presence of tibial combs on all legs should be regarded as plesiomorphic. We found tibial ctenidia on all legs on both sides in *Proxylastodoris kuscheli* spec. nov. (figs 13-16), *Discocoris vianai* Kormilev (fig. 17) and *Xylastodoris luteolus* Barber (figs 18, 19).

Tibiae of members of the subfamily Thaumastocorinae possess apically a flattened lobate structure, previously referred to as the tibial appendix (Schuh & Štys, 1991, Cassis et al., 1999), which extends from the apex of all tibiae. This structure has been previously considered absent in the Xylastodorinae (Drake & Slater, 1957; Cassis et al., 1999). We can confirm that this is true in *Xylastodoris luteolus* Barber, for specimens we examined from Florida and Cuba. However, in our new species from New Caledonia, a setose apical tibial papilla (fig. 14) is found on all legs. If we compare these with the tibial appendix of *Baclozygum depressum*, (also fig. 52.3-C in Schuh & Slater, 1995), their homology is apparent by similarity in position and morphology, although they are less prominent in the new species, especially in development in nymphs V and IV (figs 15-16). Drake & Slater (1957: 356/b) and later, Weirauch (2007: 155, 156f), compared the tibial appendix of the Thaumastocorinae with the fossula spongiosa of the Reduviidae, which they posited as being a homologous structure, also mentioning the nabid genus *Carthasis* as having a similar structure. Weirauch (2007) new theory on setose attachment structures in the Cimicomorpha, defined, in part, the fossula spongiosa as bearing tenent setae, which appears the case in *Proxylastodoris kuscheli*, although they are unmodified and simply pointed (fig. 23). On this basis, we conclude that *P. kuscheli* possess fossula spongiosa, which is strongly supported by them comprising tenent setae (= lacking epidermal sockets). These structures are found on all legs, with about the same development, just as in the Thaumastocorinae, further supporting their homology. This differs in comparison to the fossula spongiosa in Reduviidae, where it is often vestigial in the mid leg, and nearly always absent in the hind leg, except for some Triatominae (Weirauch, 2007: table 1).

Schuh (1976) first proposed the term pseudopulvilli for fleshy pretarsal structures, which originate from the unguitractor plate, laterad to the parempodia, but have the appearance of pulvilli. Cobben (1978) referred to them as the accessory parempodia. They differ from pulvilli of land bugs, which arise from the ventral surface of the claws. Schuh (1976) documented that the pseudopulvilli occurred in the mirid tribe Dicyphini. The pseudopulvilli of the Xylastodorinae (figs 24-25) are nearly identical to those found in the Dicyphini, although clearly they have evolved independently. Recently, Cassis & Schuh (2009) have discussed extensively pretarsal structure in the order Hemiptera, differentiating between pseudopulvilli, parempodia and pulvilli. Within the Geocorisae, pseudopulvilli are only found in the above taxa of the Cimicomorpha, and not within the Pentatomomorpha. Parempodia are universally found in the Geocorisae, and are nearly always setiform, although in some subfamilies of the Miridae (Orthotylinae, Phylinae: Pilophorini, Mirinae), the parempodia can also be lamellate, and be mistaken as pulvilli. The pulvilli are found in many taxa of the Geocorisae but are less ubiquitous.

Another remarkable feature of the pretarsus is the peculiar structure bounding the opening, posteriad of the bases of the pseudopulvilli and unguitractor plate, which has a broad linguiform sclerite ventrally (fig. 24). This whole structure strongly gives the impression that this opening could be neatly closed, perhaps by adduction of the unguitractor plate. We found the same structure, although even more distinct, in *Xylastodoris luteolus* Barber (fig. 25).

The combination of the fossula spongiosa and elaborate pretarsus of the thaumastocorids, including our new xylastodorine species, point towards structures that have surface adhering function. It is hard to imagine any other true bug that has the capacity to remain attached to a surface more than thaumastocorids. When collected, they require considerable force to detach them from natural and synthetic substrata. Weirauch (2007) has reinforced the hypothesis that fossula spongiosa has importance in locomotion, and in adults acts as an adhesive mechanism.

Dorsal abdominal scent glands.— In the adult one abdominal scent gland visible but no outlet opening detectable. In the nymph V there is one round gland and a slit-like unpaired opening on the anterior margin of the fourth tergite (figs 28-29). This seems unique for *Proxylastodoris* as up till now, nymphs of xylastodorine as well as thaumastocorine species were found to possess two dorsal glands (Drake & Slater, 1957: 358a), in *Xylastodoris luteolus* even with double openings (Schaefer, 1969: 252).

Sperm storage structures.— Sperm storage structures in the Heteroptera are extremely diverse, and the site of fertilisation exhibits great variability (Schuh & Štys, 1991, Schuh & Slater, 1995, Schuh et al. 2009). In the Cimicomorpha, there are macro-evolutionary differences, where homological inferences are difficult to draw; for example, the enlarged seminal depository found in Miridae appears to have evolved independently to the pseudospermathecae found in Reduviidae and Tingidae (*e.g.*, Cassis and Symonds, 2008). Thaumastocorids exhibit no structures that are comparable to either of these two systems. The ball-shaped reservoirs found at the base of the lateral oviducts (figs 40-41) are unlike any structure we have found in the female reproductive tract of other Cimicomorpha. Although Kumar (1964: 48) already noted for *Thaumastocoris australicus* Kirkaldy: 'the lateral oviducts frequently swell at their base; no trace of any special sperm storing device detectable'. In the cases of the seminal depository of Miridae and the pseudospermathecae of Reduviidae and Tingidae, their connection to the remainder of the female tract is at or adjacent to the common oviduct, implicating it as the site of fertilisation. In the Australian thaumastocorid *Thaumastocoris peregrinus* Carpintero & Dellapé (Noack, pers. comm.) it has been observed that two fertilised eggs per day are oviposited. One of us [GC] has found that the same ball-shaped reservoirs exist in this thaumastocorid species, and more broadly it has been observed that females exhibit repeated matings, highly likely combined with polyandry. The universality of the ball-shaped reservoirs in the Thaumastocoridae has yet to be determined, and any putative sperm storage function requires further examination.

Classification

Our documentation of the Xylastodorinae from the paleotropics results in no significant changes to the higher classification of the Thaumastocoridae. Their morphology is commensurate with the Western Hemisphere xylastodorines. However, there is cause for reconsideration of the recognition of *Thaicoris* at subfamilial ranking, as they too possess pseudopulvilli. Their exaggaerated head and pronotal processes are more likely to be generic differences, rather than having suprageneric importance. However, this requires further examination of the latter taxon, and particularly the morphology of their genitalia. On the basis of the shared possession of pseudopulvilli alone, a sister-taxon relationship between the Thaicorinae and Xylastodorinae can be supposed, however cladistic analysis of the total evidence is required.

Host plant associations and biology

Xylastodorines are known commonly as palm bugs, because of the obligate association of *Xylastodoris* and *Discocoris* with palms in the Western Hemisphere (Cassis et al., 1999; Couturier et al., 2002). Our new species from New Caledonia, *Proxylastodoris kuscheli* spec. nov., supports the palm association theory for xylastodorines, as it was collected on inflorescences of the palm, *Burretiokentia vieillardii* (Brongn. & Gris) Pichi-Serm. (figs 43-44). The Western Hemisphere species, *Xylastodoris luteolus*, is only known to feed on the compressed young leaves of the royal palm, *Roystonea regia* (Kunth) O.F.Cook, 1900 (Moznette, 1921; Baranowski, 1958). In this case it seems obvious that the male asymmetrical genitalia are an adaptation to this way of living and may demonstrate the direct origin of this asymmetry in Thaumastocoridae.

As the New Caledonian xylastodorine species was only collected on palms that were either in flower or fruit, we assume that it feed at least on the palm reproductive organs. But, as the inflorescences and infructescences and certainly the young leaf buds are above inspection height no direct observation of them feeding was possible. However, in May 2005, a single female was beaten directly from a low inflorescence at Aoupinié, which suggests that the palm inflorescence is the feeding and/or breeding site for this species. The Aoupinié inflorescence was early in development, with flowers and small developing fruit.

Burretiokentia vieillardii is one of the commonest and most widespread palms in New Caledonia and occurs throughout the Grande Terre, but only in rainforest habitat (Hodel & Pintaud, 1998). It often forms gregarious stands and may be the dominant palm over large areas, frequently projecting a little above the forest canopy. Many other species of palms were sampled by one of us [GBM and colleagues] but no xylastodorines were found. Four additional species of *Burretiokentia* are known (Pintaud & Hodel, 1998) but these are more localized and were not recognized in the field. *Burretiokentia vieillardii* is unusual among New Caledonian palms in bearing inflorescences year round (Pintaud & Hodel, 1998) and this may be a factor in the apparent close relationship between it and the xylastodorine.

What the foodplant of *Proxylastodoris kuscheli* spec. nov. reveals about its geographic relationships is problematic. The New Caledonian palm flora is famously diverse and endemic, and has undergone much classificatory flux in recent years. Within the Grand Terre, which is 450 km long and 50 km wide, there are currently 37 species recognised (Hodel & Pintaud, 1998; Pintaud & Baker, 2008), all of them occurring nowhere else. Their diversity is greatest in rainforests at low to medium altitude and proportional to rainfall (Pintaud et al., 2001). At the generic level, the palm flora has traditionally been regarded as comprising 15 or 16 genera (Moore & Uhl, 1984; Uhl & Dransfield, 1987; Pintaud & Hodel, 1998; Dransfield et al., 2005) but these have recently been reduced by synonymy to 10 by Pintaud & Baker (2008). Eight of those 10 genera, including *Burretiokentia,* are restricted to the Grand Terre. *Cyphophoenix* has a species on the nearby Loyalty Islands while *Cyphosperma* has species in Fiji and Vanuatu.

At the suprageneric level, two of the major cosmopolitan palm groups recognised by Moore (1973) are represented in New Caledonia. *Pritchardiopsis* is the only member of the radial-leaved 'coryphoid' palms while all the other genera, including *Burretiokentia*, belong to the pinnate-leaved 'arecoid' group. Under the older classification

Moore & Uhl (1984) distinguished two 'alliances' of genera within the New Caledonian arecoid palms. The first, a group of four genera, belonged to the '*Archontophoenix* alliance' and has relatives in Queensland, Lord Howe Island and New Zealand. The remaining genera, including *Burretiokentia*, belonged to the more widespread '*Clinostigma* alliance' with representatives in Madagascar, southern India, the Ryukus, Malesia, New Guinea, Solomons, Fiji and Lord Howe. The more recent re-classification proposed by Dransfield et al. (2005) and followed by Pintaud & Baker (2008) places *Burretiokentia* in a monophyletic clade (subtribe Basseliniinae) with 5 other genera. Three occur on Grand Terre (*Basselinia, Cyphophoenix* and *Cyphosperma*), one is restricted to Lord Howe Island (*Lepidorrhachis*) and the last (*Physokentia*) has species in the Bismarcks, Solomons, Vanuatu and Fiji. The whole clade is thus restricted to the SW Pacific. While Moore & Uhl's (1973) interpretation inferred some links between *Burretiokentia* and the 'gondwanan' lands of Madagascar and southern India, the new system does not, and neither suggests links to South America where the other extant xylastodorines occur.

Biogeography

Considerable controversy now exists concerning the origins and relationships of the New Caledonian biota, with two primary competing theories. These were best summarised by Sharma & Giribet (2009) and Edgecombe & Giribet (2009), who characterised the theories as: 1) dispersalist: Pliocene derivation, post-Paleocene submersion; and, 2) vicariant: ancient Gondwanan origins. The latter theory is supported by the propensity of ancient lineages of low vagility, such as the most plesiomorphic flowering plant *Amborella* (Soltis et al., 2000), the harvestman family Troglosironidae (Sharma & Giribet, 2009), the Gondwanan moss bugs (Burckhardt, 2009) and the beetle family Passalidae (Boucher, 1991). The dispersalist theory is rooted strongly on geological reconstructions for the southwest Pacific, *e.g.*, Schellart et al., 2006. At present, we have no knowledge of the phylogenetic relationships of the Thaumastocoridae, other than the putative monophyly of the three constituent subfamilies. Nonetheless, the remarkable transoceanic disjunction of the Xylastodorinae, as documented in this work, establishes a pantropical distribution for the subfamily, beyond the previous Western Hemisphere restrictedness of the subfamily. On Recent taxa alone, 'jump' dispersal across the Pacific Basin cannot be ruled out, especially when considering the dispersability of the now pestiferous plantation thaumastocorid, *Thaumastocoris peregrinus* (Carpintero et al., 2006). However, the fact that the only representative of *Proxylastodoris*, aside from our new New Caledonian species, is from Baltic amber (Eocene, 40-50 mya), suggests that *Proxylastodoris* was ubiquitous within the Cenozoic. However, the biogeographic significance of this species in New Caledonian is enhanced greatly by the fact that the palm association theory is upheld on both sides of the Pacific Basin. The invocation of two major 'jump' dispersals from the Neotropics, or from any other area, for both insect and plant, and maintenance of their association at a higher taxonomic level is highly unlikely. However, as stated above, *Proxylastodoris kuscheli* is found on the palm species, *Burretiokentia vieillardii*, whose relationships are with palms in the Eastern Hemisphere and not the Neotropics. This suggests that there may be a largely undiscovered fauna of Eastern Hemisphere xylastodorines, and we need to explore other palms in the Eastern Hemisphere for additional species of *Proxylastodoris*. In addition, it may be instructive to ex-

plore palms within the geographic range of *Thaicoris*, a taxon for which no host plant information is known. Alternatively, xylastodorines may have been more widespread, but have been subject to significant extinction, and the discovery of *Proxylastodoris kuscheli* from New Caledonia represents an ancient and relictual distribution.

Fossils and 'living fossils'

Cassis & Schuh (2009) recently critiqued the use of fossil taxa in classification, and their misuse in heteropteran classification. They argued that in general they have no special significance beyond recent taxa in establishing phylogenetic relationships. In the case of *Proxylastodoris kuscheli*, however, its significance lies in it being the first recent representation of the genus, a taxon previously known only from Baltic amber; hence it establishes a minimum age for the genus of 40 million years. This temporal disjunction, affords its designation as a living fossil, and brings into question what the past diversity and distribution of thaumastocorids has been.

Acknowledgements

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