

# Morphological alteration in response to endogeic habitat and ant association in two new planthopper species from New Caledonia (Hemiptera: Auchenorrhyncha: Fulgoromorpha: Delphacidae)

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## Abstract

Two new endogeic species of the delphacid genus *Notuchus* are described from New Caledonia, *Notuchus kaori* sp. nov. and *Notuchus ninguae* sp. nov. Both species are soil-dwelling and display the highest degree of troglomorphy observed in any subterranean Fulgoromorpha species. *Notuchus kaori* appears to be associated with ants of the genus *Paratrechina* (Formicidae: Formicinae). Information on their ecology and distribution is provided, and morphological characters which may be indicative of adaptation to the subterranean environment and/or the degree of integration into the host society are discussed.

**Keywords:** *Adaptive shift, morphological regression, subterranean environment, troglomorphies, trophobiosis*

## Introduction

Auchenorrhyncha, as phytophagous insects, constitute a significant faunal element in many terrestrial ecosystems in temperate, subtropical, and tropical climates, especially grasslands and forests where they feed by sucking sap from various epigeic parts of living plants. It thus seems unlikely that such species would colonize hypogeic or subterranean habitats such as the interstitium of soil or caves, where conditions appear less favourable: low availability of food and permanent darkness pose serious impediments to feeding and reproduction. Nevertheless, several lineages within the Auchenorrhyncha have invaded subterranean habitats. All these lineages belong to the Fulgoromorpha; no Cicadomorpha species which complete their life cycle underground have been reported, although nymphs of some taxa live in underground environments, e.g. cicadas (Fabre 1897) and certain spittlebug species (Cercopidae) (e.g. Holzinger et al. 2003). Hitherto, more than 50 Fulgoromorpha species

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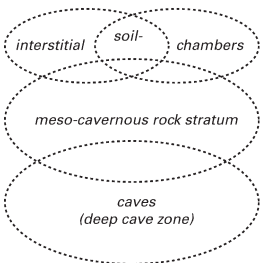
(representatives from Cixiidae, Meenoplidae, Kinnaridae, and Delphacidae) have been described from limestone caves, lava tubes, the mesocavernous rock stratum beneath the soil (or MSS, *milieu souterrain superficielle*: Juberthie and Delay 1981) in many parts of the world, e.g. Australia, New Zealand, New Caledonia, Hawaii, the Galapagos Islands, Argentina, Mexico, Jamaica, the Azores, the Canary Islands, the Cape Verde Islands, Madagascar, and Réunion (Hoch 2002; Hoch et al. 2003). The only truly endogeic Fulgoromorpha species is *Hypochthonella caeca* China and Fennah, 1952 from Zimbabwe, representing its own family, the Hypochthonellidae. Adults and nymphs of *Hypochthonella caeca* apparently live in the soil interstitium where they feed on roots of maize, tobacco, and groundnut, and are attended by ants (China and Fennah 1952). All these species as compared to their epigeic relatives, display morphological alterations (in varying degrees) in response to their habitat, commonly termed troglomorphies. For terminology of interdependence between physical environmental parameters and organismic adaptations, see Table I.

The taxonomic distribution of subterranean Fulgoromorpha species is shown in Figure 1. Colonization of subterranean habitats by Fulgoromorpha species is scattered throughout the taxa, but is comparatively common in those with nymphs living close to or within the soil, the Cixiidae and the Meenoplidae.

Recent field studies by the Queensland Museum revealed the existence of two previously unknown delphacid species of the genus *Notuchus* Fennah (Ugyopinae) which were discovered beneath the soil surface and are apparently endogeic (obligatory soil dwellers). One of the species was collected in association with ants of the genus *Paratrechina* Motschulsky (Formicidae: Formicinae).

Here, we describe the two endogeic *Notuchus* species and discuss characters of their external morphology in relation to adaptation to the habitat and/or to ant association.

Table I. Terminology of interdependence between physical parameters of the habitat and organismic adaptations.

Habitat	Abiotic factors	Life cycle	Morphology
epigeic (surface) habitats <i>(including leaf litter)</i>	unstable physical parameters <i>(ambient climatic influence high)</i>	entirely epigeic / epigean	no troglomorphies
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hypogeic (subterranean) habitats  	↓ temperature, relative humidity, etc.	troglophilic  <i>(facultative soil &amp; cave-dwellers, may live &amp; reproduce underground as well as in surface domain)</i>	troglomorphies of varying degrees  e.g. - reduction of eyes, body pigmentation & wings
		endogeic / endogean  <i>(obligatory soil dwellers)</i>	- decreasing cuticle sclerotization
		troglobitic  <i>(obligatory cavernicoles, restricted to cave environment)</i>	- specialized sensory organs - elongate appendages
	stable / constant physical parameters <i>(ambient climatic influence low)</i>		

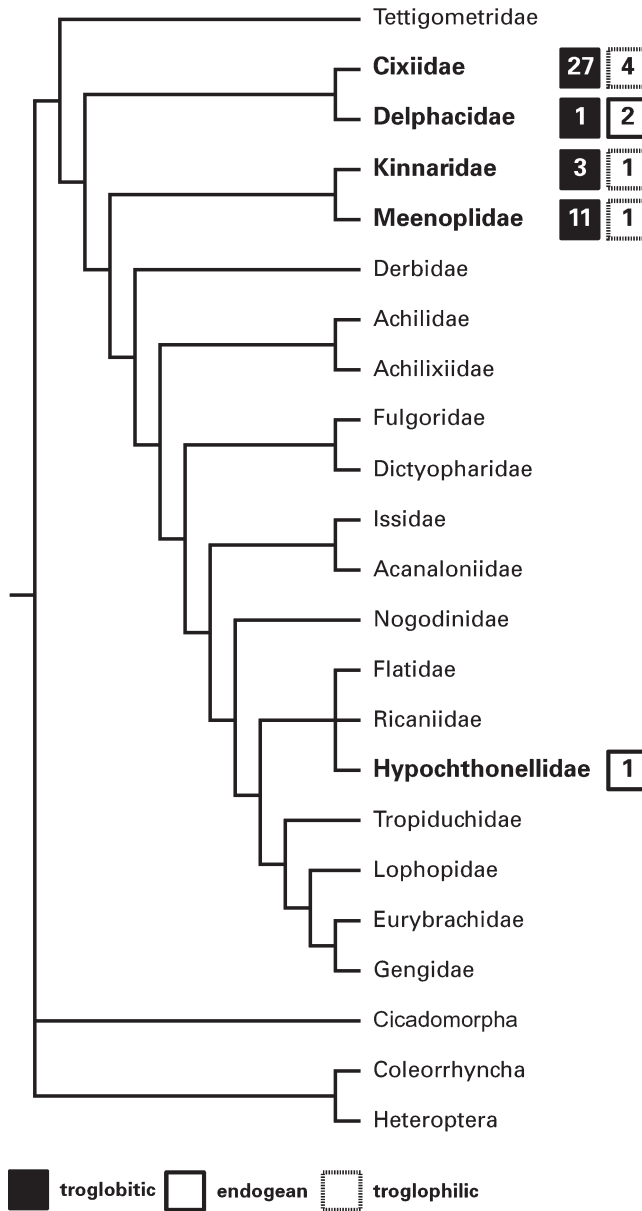


Figure 1. Taxonomic distribution of hypogeic (troglitic, endogean, and trogliphilic) Fulgoromorpha species. Morphology-based consensus cladogram combined after Asche (1987), Bourgoin (1997), and Emeljanov (1990).

## Material and methods

All specimens were preserved in 70% ethanol. Genitalia were macerated in 10% KOH (24h) at room temperature, washed in water, transferred to glycerine for storage, and to glycerine-jelly for drawings. Drawings were made using a Leitz stereomicroscope with camera lucida. For scanning electron microscopy, specimens were dehydrated in increasing ethanol concentrations, and mounted on aluminium specimen stubs with adhesive pads.

Specimens were coated with gold–palladium and studied with a LEO 1450VP scanning electron microscope (software: 32 V02.03) at 10 kV.

Specimens are deposited at the Musée National d'Histoire Naturelle, Paris (MNHN) and Queensland Museum, Brisbane (QM).

## Taxonomy

**UGYOPINAE** Emeljanov, 1995

**UGYOPINI** Fennah, 1979

***Notuchus*** Fennah, 1969

*Notuchus* Fennah 1969, p 32. Type species: *Notuchus risioides* Fennah 1969, p 32 (New Caledonia), by original designation.

The genus *Notuchus* was previously known from three species from northern Queensland, Australia (*N. kurandae* Donaldson, 1979, *N. oresebios* Donaldson, 1988, and *N. rotundifacies* Donaldson, 1979), two species from Lord Howe Island (*N. monticola* Fennah, 1972 and *N. howensis* Donaldson, 1987), and two species from New Caledonia (*N. risioides* Fennah, 1969 and *N. larvalis* Fennah, 1980). All *Notuchus* species (except *N. larvalis* and the two new species described below) are epigeic but display morphological characters, such as depressed body shape and brachyptery (Donaldson 1979, 1987, 1988; Fennah 1969) that are indicative of an adaptation to a cryptic way of life, in habitats such as leaf litter. Most specimens have been collected by berlese extraction of leaf litter samples from rainforest vegetation. The species accommodated in *Notuchus* may or may not form a monophyletic group; no characters shared by *Notuchus* species have yet been recognized as probable synapomorphies. A cladistic analysis of *Notuchus* and related ugyopine delphacids, especially of the *Ugyops annulipes* Stål-group, would be necessary to infer the evolutionary history of the taxa concerned but is beyond the scope of the present work.

***Notuchus kaori*** Hoch and Asche sp. nov.

(Figures 2–29)

### Description

Small, highly troglomorphic delphacids with compound eyes absent and tegmina vestigial. Head and thorax weakly pigmented, almost white, abdomen brown. Body with a distinct constriction at the base of the abdomen (Figure 2).

*Body length.* Male 3.0 mm ( $n=2$ ). Female 2.7 mm ( $n=1$ ).

*Colour.* Head and legs pale yellow. Anterior margin and lateral portions of pronotum pale yellow, posterior margin white. Mesonotum white except for a median longitudinal yellow stripe. Vestigial tegmina white, anterior margin proximally yellow. First two abdominal tergites white, with a yellow median portion. Remaining abdominal tergites brownish, thus abdomen contrasting sharply with light anterior part of body (Figure 2). This colour pattern, in combination with the petiole-like constriction between thorax and abdomen, results in a certain similarity with the habitus of the associated *Paratrechina* ants. Abdominal sternites 3–6 conspicuously coloured: laterally, posteriorly,

and medially on each side with a brown margin, enclosing a white discoidal anterior area (Figure 3).

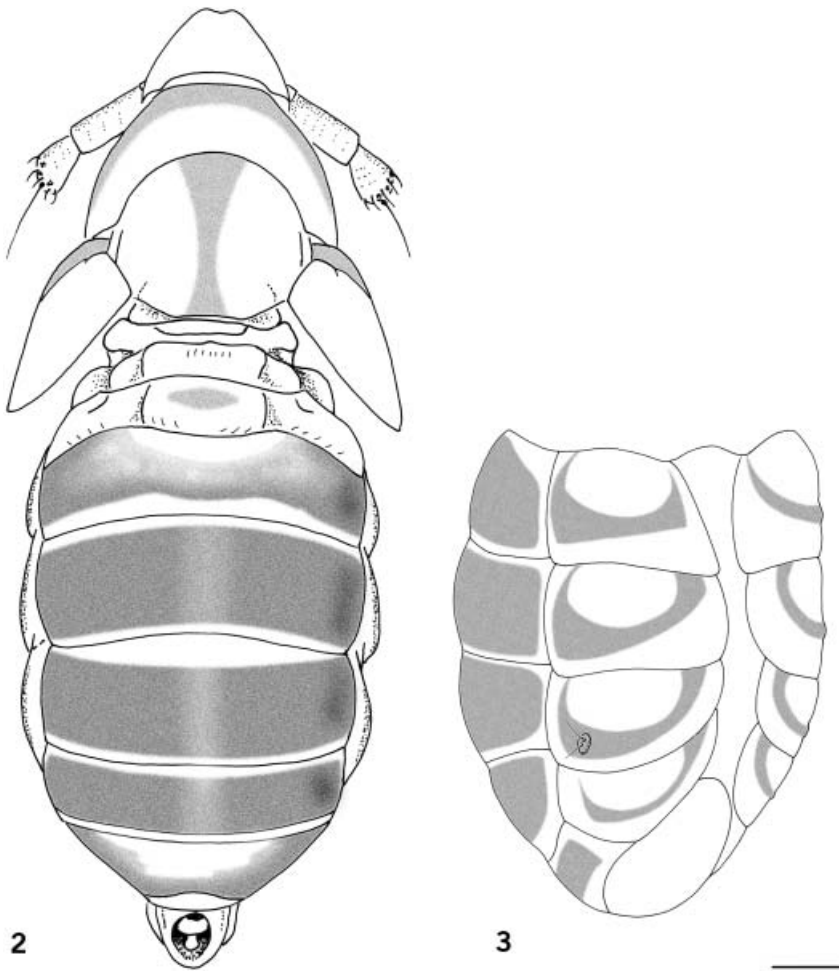
*Head.* Vertex (Figures 4, 7) without distinct carinae, at posterior margin ca 1.6 times as wide as medially long; lateral margins more or less parallel, anterior margin broadly rounded; area of vertex convex, not distinctly separated from genae and frons. Compound eyes and lateral ocelli absent (Figures 7, 8). Frons ca 0.9 times as high as maximally wide, and 0.7 times as high as post- and anteclypeus together; frons widest below antennae. Frons and clypeus smooth, slightly convex, without median carinae. Frontoclypeal suture nearly straight, only slightly vaulted anteriorly. Rostrum very long, surpassing metatrochanters, in repose nearly reaching anterior margin of genital segment in male, and reaching posteriorly to mid-length of ovipositor in female. First antennal segment cylindrical, ca 2.3 times as long as its diameter; 2nd antennal segment club-like, proximally narrow, distally expanding, apically truncate, with conspicuous hair sensilla around distal margin, sensory fields concentrated around apical margin, proximally fringed by a single row of strongly developed setae curved medially (Figures 8–10).

*Thorax.* Pronotum (Figures 2, 4, 6) short, at mid-length half as long as vertex, with lateral portions extending posteriorly. Mesonotum (Figure 4) short, ca half as long as maximum width, strongly vaulted dorsally, smooth, without longitudinal carinae, posterior margin truncate. Tegulae absent. Tegmina (Figures 4, 5) vestigial, narrowly lanceolate, surface smooth, veins reduced, but movable at base. Tegmina not tectiform as is common even in brachypterous delphacid species, but directed posteriolaterally, exposing junction of thorax and abdomen. Metanotum short, not bearing any wings or remnants thereof.

*Legs.* Hind tibia laterally unarmed, distally with one stronger triangular tooth and one or two minute teeth. Posttibial spur (Figures 11, 12) minute, movable. Metabasitarsus distally with four minute teeth in a row, 2nd metatarsus distally with two minute lateral teeth. Basitarsus slightly longer than 2nd and 3rd tarsal segments together. Pretarsus (Figure 13) inconspicuous, arolium and claws well developed.

*Abdomen.* Tergites of first two abdominal segments narrow, abdominal tergites of segments 3–6 ca 1.5–2 times as wide, thus creating the impression of a “petiole”. Fifth abdominal sternite laterally on each side bearing two distinctly visible sensory pits.

*Male genitalia* (Figures 14–23). Genital segment in lateral aspect nearly triangular, four times as long ventrally as dorsally; in caudal aspect slightly higher than wide; ventral margin bilobate, caudally semicircularly incised between the lobes; caudal margins smoothly rounding into diaphragm; diaphragm filling the lower third of the caudal area; opening for parameres widely ovate. Anal segment hood-shaped, in dorsal aspect nearly round, caudal margin medially with a deep, bluntly V-shaped incision. Parameres simple, slender, slightly dilated in basal half, shallowly S-shaped, distally bluntly rounded, subtruncate. Aedeagus: periandrium of shaft sclerotized in basal two-thirds, membraneous distally. Shaft without spinose processes. Flagellum in repose exposed dorsally to left side, long, circularly curved. Ejaculatory duct well sclerotized, produced into an ampulla-shaped structure near apex; phallosome terminal (Figure 22, arrow). Flagellum without spinose processes, but with a taeniform sclerite in membrane exposed towards shaft. Tip of taeniform sclerite laterally produced to the right into a lobate membranous process (Figure 23, arrow).



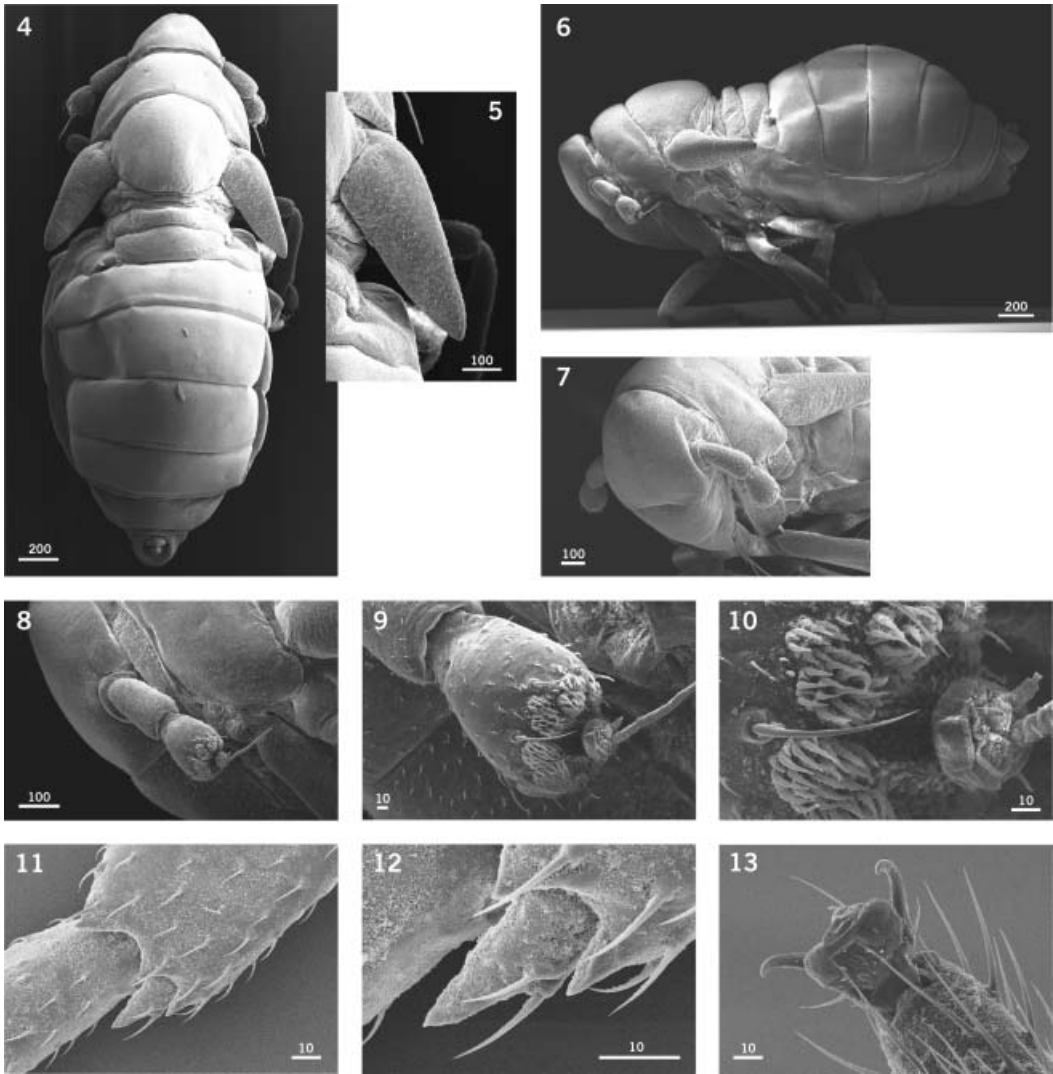
Figures 2, 3. *Notuchus kaori* sp. nov., adult male. (2) Habitus with colour pattern, dorsal aspect, paratype male. (3) Colour pattern of abdomen, ventrolateral aspect (genital capsule removed), holotype male. Scale bar: 0.2 mm.

*Female genitalia.* Anal tube short. Ovipositor complete, as in other *Notuchus* and Ugyopine species, ensiform, posteriorly not surpassing caudal margin of anal tube.

*Larval morphology* (Figures 24–29). Fifth instar nymph eyeless, body unpigmented, white. Carination of head and thorax distinctly pronounced. Lateral portions of frons with two irregular rows of sensory pits. Proportions of antennae and distribution of sensory fields and setae as in adults. Surface of abdomen smooth.

#### *Distribution*

Endemic to New Caledonia. Currently known from a single collection from Pic du Grand Kaori, a botanical reserve located in the extreme south of the main island, just south of the Plaine des Lacs.



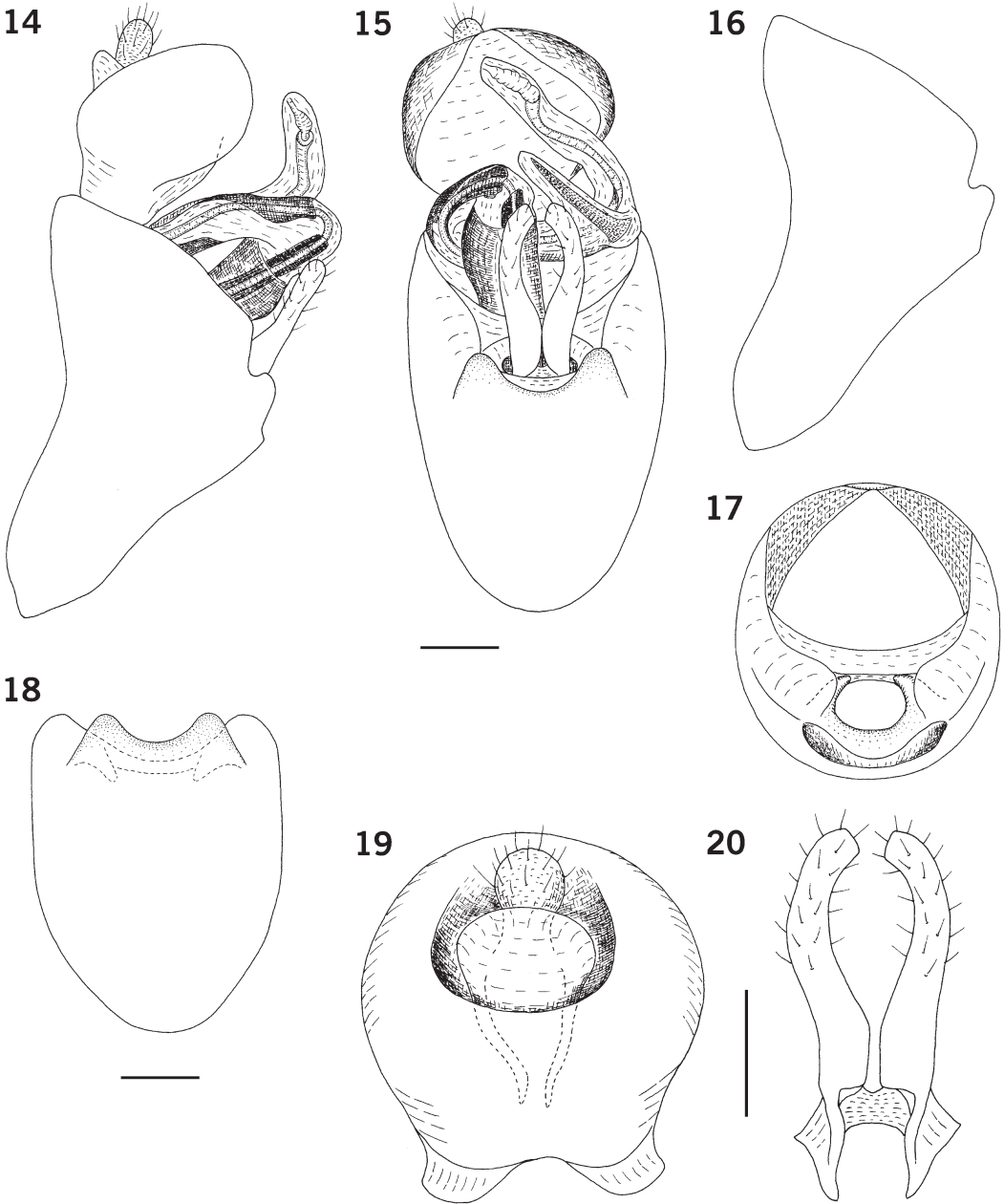
Figures 4–13. *Notuchus kaori* sp. nov., adult male (paratype). (4) Habitus, dorsal aspect. (5) Detail: right tegmen, dorsal aspect. (6) Habitus, left lateral aspect. (7) Head, anterolateral aspect. (8) Left antenna. (9) Same, pedicel with sensory plaques and macrosetae. (10) Same as in Figure 9, detail. (11) Post-tibial spur. (12) Same as in Figure 11, detail. (13) Pretarsus (arolium and claws), ventral aspect. Scale bars in  $\mu\text{m}$ .

### Ecology

Collected in rainforest beneath a large, embedded rock together with ants of a species of *Paratrechina* (Formicidae: Formicinae).

### Diagnosis

*Notuchus kaori* sp. nov. adults can be easily distinguished from the epigeic *Notuchus* species by the light body colour and other troglomorphic characters, such as the loss of compound eyes and ocelli, and reduction of tegmina and wings.

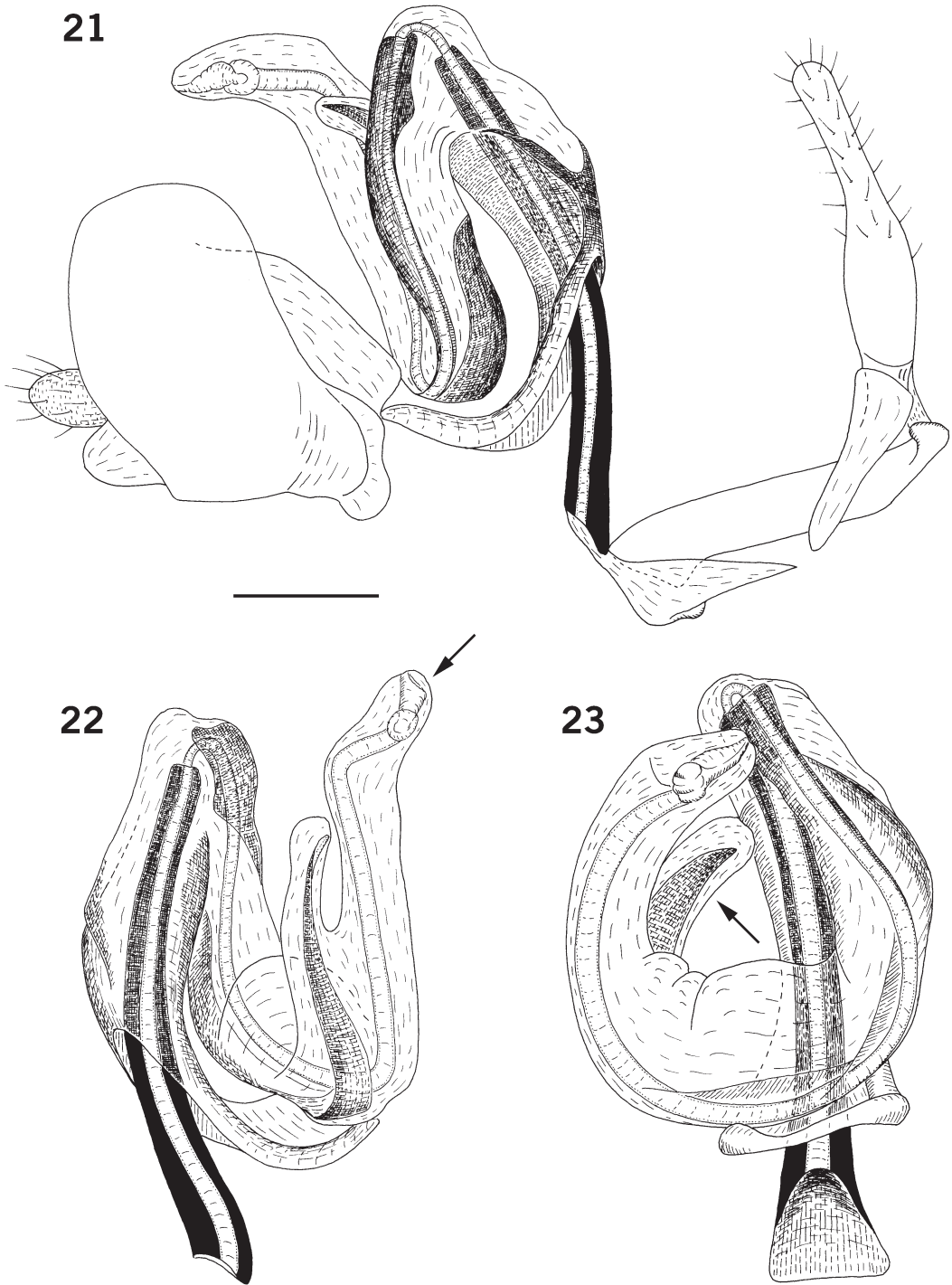


Figures 14–20. *Notuchus kaori* sp. nov., male genitalia (holotype). (14, 15) Genital capsule, left lateral and ventrocaudal aspects, respectively. (16–18) Genital segment, left lateral, caudal, and ventral aspects, respectively. (19) Anal segment, dorsal aspect. (20) Parameres, ventrocaudal aspect. Scale bars: 0.1 mm.

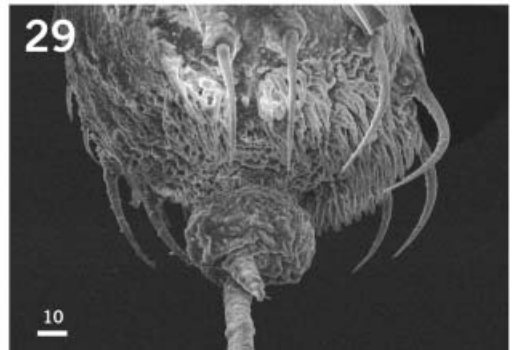
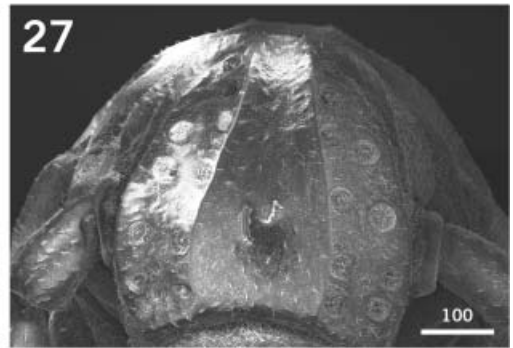
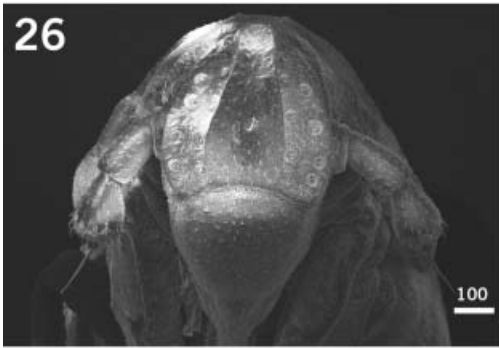
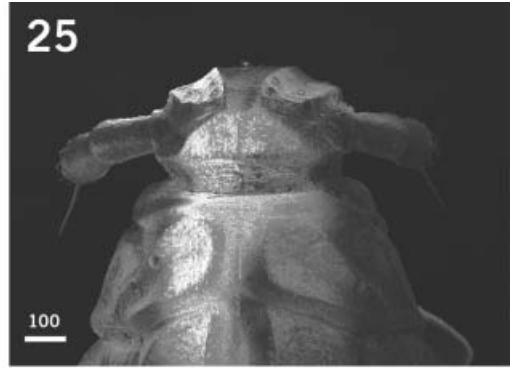
*Material examined*

Holotype: male. New Caledonia, Pic du Grand Kaori; site 2; 250 m, 22°17'S, 166°53'E, 22–24 November 2004, rainforest (11772), QM Party (MNHN). Paratypes: two males, one female, same data as holotype (QM).





Figures 21–23. *Notuchus kaori* sp. nov., male genitalia (holotype). (21) Anal segment, aedeagus, paramere in situ, left lateral aspect. (22, 23) Aedeagus, right lateral and dorsal aspects, respectively. Scale bar: 0.1 mm.



Figures 24–29. *Notuchus kaori* sp. nov., nymph (5th instar). (24) Habitus, dorsal aspect. (25) Head and prothorax, dorsal aspect. (26) Head, anterior aspect. (27) Frons, anterior aspect. (28) Head and thorax, anterolateral aspect. (29) Distal margin of pedicel. Scale bars in  $\mu\text{m}$ .

*Additional material.* Two nymphs (5th instar, females), QM.

***Notuchus ninguae*** Hoch and Asche sp. nov.  
(Figures 30–40)

*Description*

Small, highly troglomorphic delphacids with compound eyes absent and tegmina vestigial. Body pigmentation strongly reduced.

*Colour.* Head and legs pale yellow. Thorax including vestigial tegmina uniformly white. First two abdominal tergites white, 3rd abdominal tergite laterally on each side with yellow portions, the remaining abdominal tergites yellow throughout. Abdominal sternites with similar colour pattern as in *N. kaori* sp. nov. Male and female genitalia well sclerotized, stramineous.

*Head.* Head as in *N. kaori* sp. nov. except rostrum shorter, in repose not reaching anterior margin of genital segment in male, and reaching proximal third of ovipositor in female.

*Thorax.* Thorax as in *N. kaori* sp. nov. except pro- and mesonotum slightly more strongly vaulted dorsally. Tegmina vestigial as in *N. kaori* sp. nov., however slightly shorter and distally more rounded, wings absent.

*Legs.* Metatibia laterally unarmed, distally with one minute tooth. Posttibial spur vestigial, as in *N. kaori* sp. nov. Metabasitarsus and 2nd tarsal segments with distal teeth largely reduced. Basitarsus slightly longer than 2nd and 3rd tarsal segments together.

*Abdomen.* Abdomen as in *N. kaori* sp. nov. with a distinct constriction between thorax and abdomen due to narrow mesonotum and narrow first and second abdominal segments; abdomen wide in both sexes. Fifth abdominal sternite with two sensory pits laterally on each side, however, not as readily visible as in *N. kaori* sp. nov.

*Male genitalia* (Figures 30–40). Genital segment in shape and proportions similar to *N. kaori* sp. nov. Genital segment in caudal aspect slightly higher than wide, ventrocaudal margin medially shallowly incised, medially notched (Figure 34), not bilobate as in *N. kaori* sp. nov. Caudal margins of genital segment smoothly rounding into diaphragm; diaphragm filling lower third of caudal area; opening for parameres widely ovate. Anal segment similar to that of *N. kaori* sp. nov. Parameres shaped as in *N. kaori* sp. nov., slightly more stout, apically rounded. Aedeagus similar in shape to that of *N. kaori* sp. nov. Flagellum with filiform sclerite (versus taeniform in *N. kaori* sp. nov.) integrated into membrane, exposed towards shaft (Figure 39, arrow); ejaculatory duct distally ending with a wide opening, phallosome subapical (Figure 40, arrow).

*Female genitalia.* Female genitalia as in *N. kaori* sp. nov.

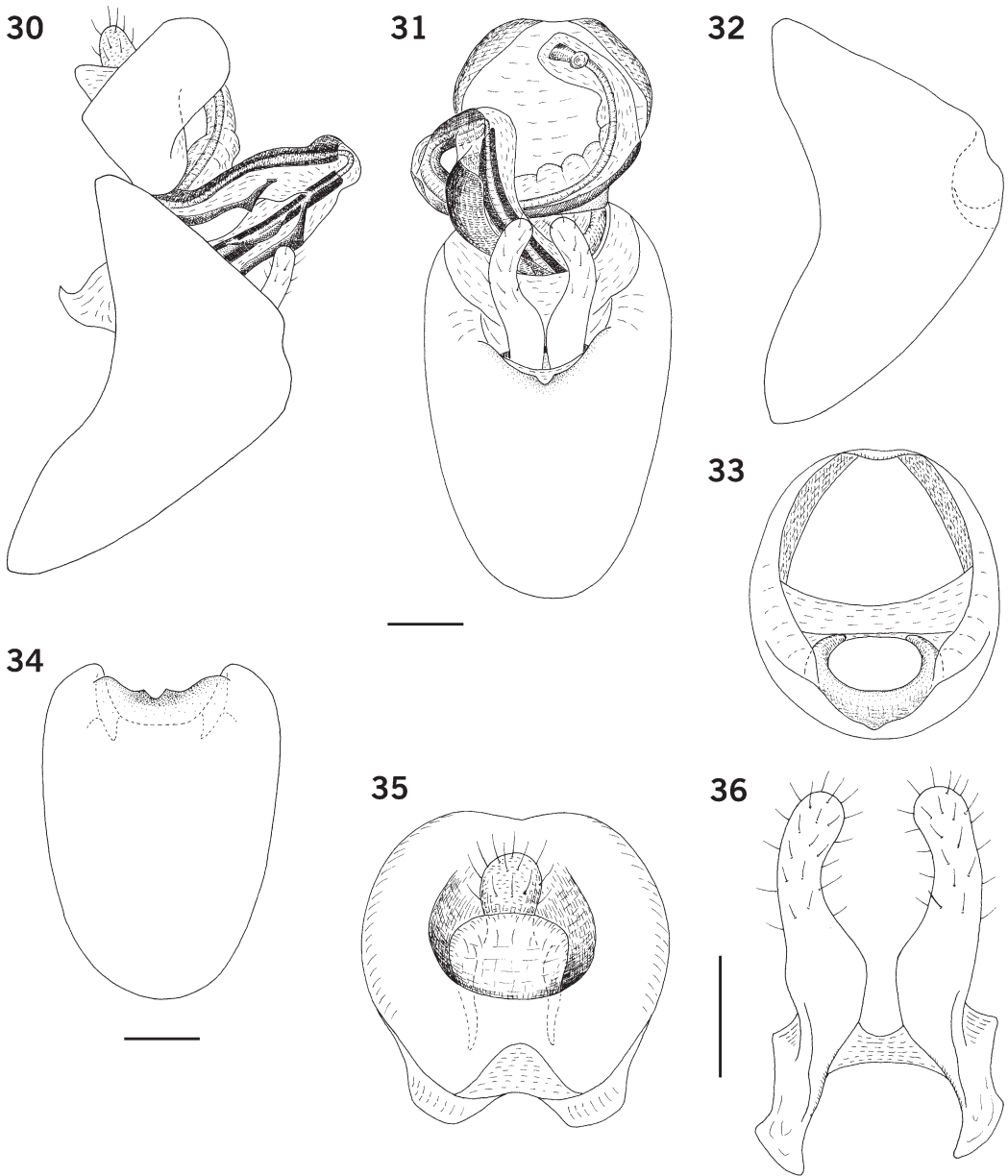
*Larval morphology.* Unknown.

*Distribution*

Endemic to New Caledonia. Known from a single collection from Pic Ningua, a botanical reserve located about midway between Bouloupari and Thio, approximately 65 km north-west of Noumea.

*Ecology*

Collected in rainforest in a 15–20 mm diameter chamber in the soil. The chamber was exposed when a small log was turned over. Ants were not actively searched for when the collection was made.



Figures 30–36. *Notuchus ninguae* sp. nov., male genitalia (holotype). (30, 31) Genital capsule, left lateral and ventrocaudal aspects, respectively. (32–34) Genital segment, left lateral, caudal, and ventral aspects, respectively. (35) Anal segment, dorsal aspect. (36) Parameres, ventrocaudal aspect. Scale bars: 0.1 mm.

*Diagnosis*

Habitus very similar to *N. kaori* sp. nov. but differing in details of colour (head and thorax without remnants of pigmentation as in *N. kaori* sp. nov.), of external morphology (e.g. length of rostrum: slightly shorter than in *N. kaori* sp. nov.; shape of vestigial tegmina: more rounded than in *N. kaori* sp. nov.) and especially in the male genital structures (ventrocaudal margin of genital segment: medially shallowly incised, notched versus bilobate in *N. kaori* sp. nov.; parameres: apically rounded, more stout than in *N. kaori* sp. nov.; aedeagus: sclerite of flagellum membrane filiform versus taeniform in *N. kaori* sp. nov.).

Troglophorities even more strongly expressed than in *N. kaori* sp. nov.

*Material examined*

Holotype: male. New Caledonia, Ningua Res. Camp, 1100 m, 21°45'S, 166°09'E, 12–13 November 2001 [8641], hand collected, C. Burwell, G. Monteith (MNHN). Paratypes: two males, two females, same data as holotype (QM).

**Discussion***Ecology and distribution*

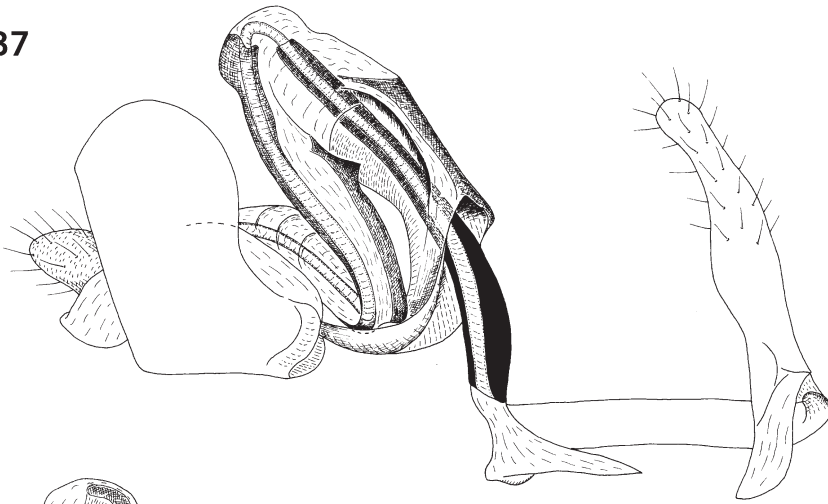
The two new *Notuchus* species are morphologically highly modified as compared to epigeic *Notuchus* species, in fact displaying the highest degree of troglomorphy observed in any subterranean Fulgoromorpha species.

*Notuchus kaori* and *Notuchus ninguae* were found in soil chambers, in one case beneath a large, deeply embedded rock and in the other case under a small log. The specimens of *N. kaori* were collected together with ants of an undescribed species of *Paratrechina*. Both *Notuchus* species display morphological alterations which indicate a permanently endogeic lifestyle: complete absence of compound eyes and ocelli, strong reduction of body pigmentation (particularly of head and thorax), vestigial tegmina and loss of wings. The ants are pale-coloured and have, relative to epigeic *Paratrechina* species, very small compound eyes, and are likely to be endogeic as well. The species of *Paratrechina* that is associated with endogeic *Notuchus* is widely distributed within New Caledonia (unpublished data).

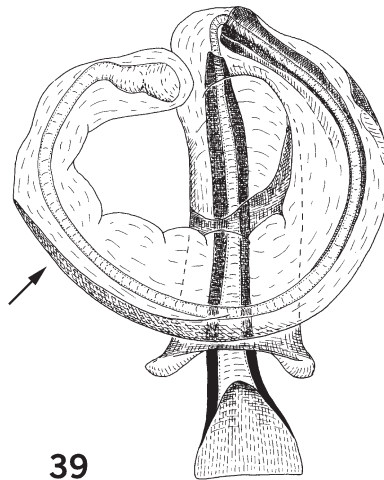
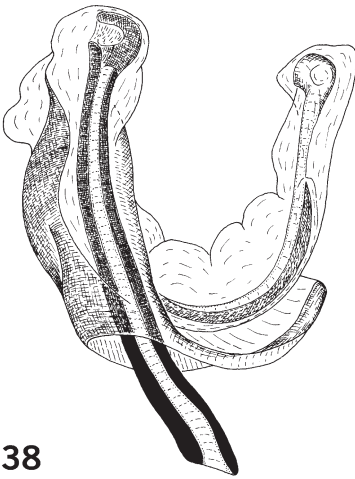
Although no direct interactions between the *Paratrechina* ants and the endogeic *Notuchus* species were observed, some characters of the external morphology of the two new *Notuchus* species are suggestive of a possible trophobiotic relationship.

Such a trophobiotic relationship is conceivable, as *Notuchus*, like all Auchenorrhyncha and Sternorrhyncha, are sap-feeders and as such produce honey-dew which may be attractive to and utilized by the ants. Within the Hemiptera, including some epigeic Fulgoromorpha, ant-mutualism is so widely distributed that it had once been hypothesized to be a ground-plan attribute (Schaefer 1987). Bourgoïn (1997) rejected this hypothesis and rationalized that ant-mutualism arose independently several times in groups that primarily live in above-ground habitats (Bourgoïn 1997, p 109). Nevertheless, ant-mutualism is common in Auchenorrhyncha taxa which live in or close to the ground (Bourgoïn 1997, p 112). It should be noted though, that trophobiosis involving ants and delphacids is quite uncommon and has only been reported in a few cases (Dejean et al. 1996; Delabie 2001).

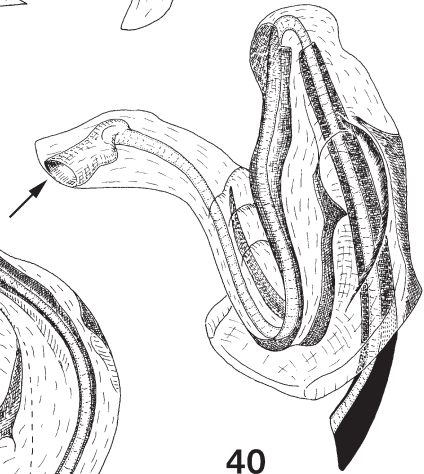
37



38



40



39

Figures 37–40. *Notuchus ninguae* sp. nov., male genitalia (holotype). (37) Anal segment, aedeagus, paramere in situ, left lateral aspect. (38–40) Aedeagus, right lateral, dorsal, and left lateral aspects, respectively. Scale bar: 0.1 mm.

Close associations or even mutualistic relationships of Fulgoromorpha and ants require a minimum of adaptation in the trophobiont including morphological and behavioural traits (Wilson 1971) which are common in myrmecophiles. The degree of modification is correlated with the degree of integration of the trophobionts into the host society. Typical modifications include lighter body colouration, morphological regression, and protective structures (Wilson 1971). Some of these are also found in the endogeic *Notuchus* species, although it is difficult to clearly distinguish adaptations to the endogeic habitat from those of a potential trophobiosis without experimental evidence.

In both *Notuchus* species the pigmentation of head and thorax is strongly reduced, in *N. ninguae* to an even higher degree than in *N. kaori*, which maintains remnants of slightly darker pigmentation on the head, the anterior margin of the pronotum and the middle portion of the mesonotum. However, in both species the abdominal tergites are distinctly darker and the abdominal sternites display a characteristic pigmentation pattern, so that the body appears divided into a light anterior and a dark posterior part.

In the endogeic *Notuchus* species the compound eyes, ocelli, and wings are absent and the tegmina are reduced to tiny non-functional vestiges. The species are blind and flightless. Correlated with this regression is a reduction of head and thorax carination and a reduced sclerotization of the cuticle resulting in a smooth body surface. Another striking modification in the endogeic *Notuchus* species is the strong reduction of the post-tibial spur, which is vestigial in *N. kaori* and *N. ninguae* adults while it is well developed in adults of epigeic species.

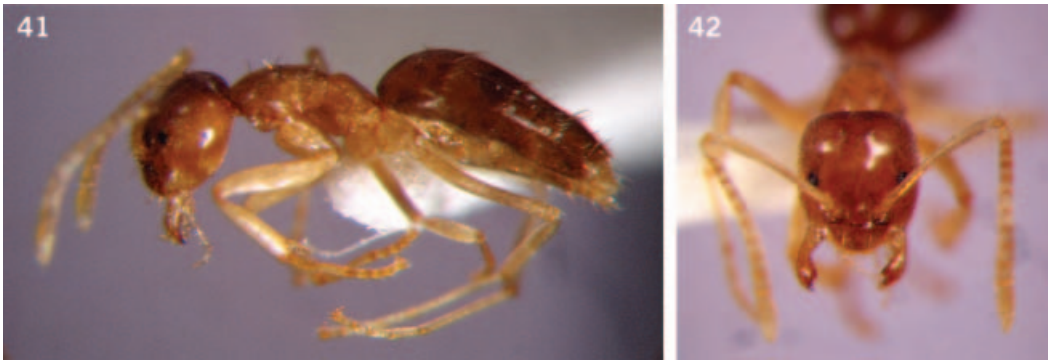
In contrast to epigeic *Notuchus*, in *N. kaori* and *N. ninguae*, the antennal sensory plaques are concentrated around the distal margin of the pedicel (versus distributed in rows all over the pedicel), and are surrounded by an irregular row of macrochaetae. This arrangement is also found in *Notuchus* nymphs (of epigeic species) and thus considered here as persistence of a larval character.

Most of these reduction characters are also found in other hypogeic Fulgoromorpha, e.g. in cavernicolous Cixiidae and Meenoplidae (Hoch 1994) which have not been observed to be ant-attended, and are thus likely to be adaptations to the subterranean habitat. A smooth body surface may facilitate movements in dense soil substrate, and reduced cuticle sclerotization may be a response to high relative humidity levels in soil chambers. The endogeic *Notuchus* species expose a minimum of tangible points of attack through their smooth body surface, the vestigial post-tibial spur, and the arrangement of sensilla and macrochaetae on the pedicel of the antenna. Whether or not this is a strategy in defence of predator attacks can only be demonstrated by a behavioural study.

At first glance, *Notuchus kaori* (Figure 2) and *N. ninguae* specimens resemble *Paratrechina* workers (Figures 41, 42) and display a set of characters that create the impression of an ant-like body. These consist of the narrow tergites of the first two abdominal segments forming a “petiole”, a bloated (“physogastric”) abdomen in both sexes that, in dorsal aspect, is wider than the thorax, a smooth body surface, and comparatively dark coloured abdominal tergites and sternites. The similarity of the delphacids and the ants is enhanced by the transversely banded abdomen (the darkly coloured portions of the tergites are of almost the same length as those in the *Paratrechina* and alternate with nearly white intersegmental membranes) and similar body length. This set of characters might provide optical (colour) and tactile (physogastric abdomen, petiole) recognition clues to mislead the ants into recognizing the delphacids as conspecifics. However, Wilson (1971, p 406–407) questioned the validity of morphological mimicry in ant symbionts, particularly in endogeic species. It cannot be excluded that the resemblance between endogeic *Notuchus* and *Paratrechina* is just coincidental.

Alternatively, the petiole-like structure in *Notuchus* may be an adaptation to facilitate their transport by the ants, a phenomenon well-known from other Hemiptera–ant associations, e.g. aphids and coccids (see information in Wilson 1971, p 423).

Endogeic *Notuchus* may constitute the ideal trophobionts as postulated by Wilson (1971, p 422): “...one which feeds on a single species of food plant and whose life cycle is not tightly synchronized so that stages capable of producing honey-dew are available



Figures 41, 42. *Paratrechina* spec. (Formicidae), worker. (41) Habitus, lateral aspect. (42) Head, frontal aspect.

throughout the year<sup>9</sup>. Many (epigeic) delphacid species are known to be monophagous (Wilson et al. 1994) and the same may apply for the endogeic *Notuchus*. In return for their honey-dew, the delphacids may benefit in various ways from their hosts: protection from predators and parasites, and possibly transport to appropriate parts of their host plants, allowing the delphacids to build larger, or at least more stable, populations as well as increase their overall rate of dispersal (Wilson 1971, p 421). Although *Notuchus kaori* and *N. ninguae* are known from only one locality each, they are probably more widely distributed. The lack of information can be attributed to insufficient collecting/inventory coverage of New Caledonia rather than to an extremely high level of local endemism.

The mode of dispersal of the endogeic *Notuchus* species is likely to depend on the nature of the association with the ants. The closer the relationship between host and trophobiont, the more important the role of the host in dispersal of the trophobiont is likely to be. Impressive examples are documented from highly mutualistic ant–mealybug (Hemiptera: Sternorrhyncha: Coccoidea) associations with alate ant queens carrying fertile female mealybugs in their mandibles during their nuptial flight to ensure an adequate trophobiont supply for the new colony (see references in Wilson 1971; La Polla 2004). However, such dispersal mechanisms, termed trophoresy (La Polla et al. 2002), are rare, and unlikely for the two endogeic *Notuchus* species. A more likely mechanism by which the *Notuchus* could disperse with the *Paratrechina* has been suggested for some hypogeic species of *Lasius* ants (Formicinae) that tend subterranean mealybugs. It has been postulated that new *Lasius* colonies are formed by fission of existing colonies and the adoption of queens (Malsch et al. 2001). In this way the association with the mealybugs is maintained by the ants carrying them to the new nest site. Interestingly, workers of an unidentified species of *Paratrechina*, associated with nymphs of an (undescribed) cave-dwelling *Phaconeura* species (Meenoplidae) in a cave on Cape Range (Western Australia), were observed to actively transport the trophobiotic nymphs away from the area when disturbed (Humphreys 1998).

#### *Evolutionary implications*

Among all the known subterranean Fulgoromorpha worldwide, only one obligately cavernicolous species is known within the Delphacidae: *Notuchus larvalis* Fennah from New Caledonia, inhabiting the limestone galleries at Hienghène (Fennah 1980). Epigeic



*Notuchus* species are all short-winged and cryptically coloured, and live in leaf litter or close to the ground (M. Asche, personal observation); the nymphs may be soil-dwellers. From this pre-adaptive plateau, it appears to be only a small evolutionary step to adapt to a life underground (Howarth and Hoch 2004). Adaptive shifts from epigeic to subterranean habitats are facilitated, or even driven by availability of suitable food resources such as roots (Howarth 1986). In addition, living roots are ideal communication channels for transmitting the substrate-borne vibrational signals by which small planthoppers communicate for mate location and recognition (Hoch and Howarth 1993). In Fulgoromorpha, these adaptive shifts may also be facilitated by the development of trophobiotic relationships where ants may provide protection from predators and parasites and means of dispersal.

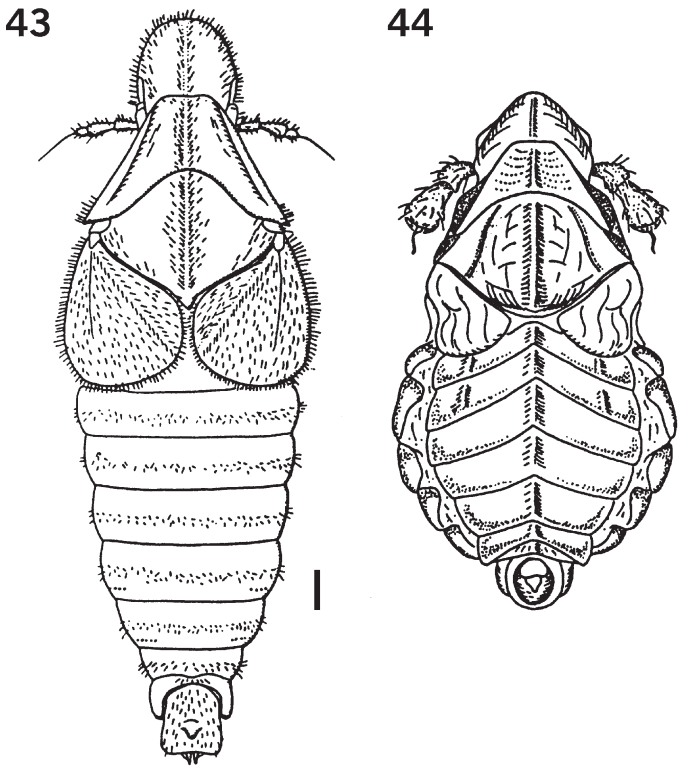
It is clear that within *Notuchus* adaptive shifts from epigeic to subterranean habitats have occurred at least twice on New Caledonia: *Notuchus kaori* and *Notuchus ninguae* as well as *Notuchus larvalis*. Based on morphological information, it is difficult to decide whether *Notuchus kaori* and *N. ninguae* are descendants of the same lineage into the subterranean biome with speciation having occurred subsequent to endogeic adaptation or whether they represent two lineages which independently colonized subterranean habitats.

While it appears obvious that on New Caledonia with its eventful geological history, especially since the Cretaceous period, range fragmentation of an already hypogeic taxon by geodynamic events resulting in the isolation of populations and, eventually, speciation, is the logical explanation for high diversity and local endemism in New Caledonia as has been demonstrated for cockroaches (Murienne et al. 2005), for the endogeic *Notuchus* species, we favour the assumption of parallel evolution. Although the two endogeic *Notuchus* species are seemingly very similar in external morphology, the configuration of the male genitalia (medioventral margin of the genital segment, form and position of the flagellum sclerite of the aedeagus) indicates their origin from separate ancestral (epigeic) species. Each male genital configuration is similarly present in (yet undescribed) epigeic *Notuchus* species (unpublished data), although no sister species among the extant epigeic *Notuchus* species to any of the subterranean *Notuchus* species has yet been identified. The high congruence among the two endogeic *Notuchus* species in external features would be a striking example of parallelism.

It appears remarkable that *Notuchus kaori* and *N. ninguae* display a distinctly different habitus from that of the obligately cavernicolous *Notuchus larvalis*, which is also blind and flightless yet has a far more sculptured body surface (Hoch 1994, p 315), but share the smooth body form with (the unrelated) *Hypochthonella caeca* which is also endogeic and attended by ants (Figures 43, 44). We hypothesize that the habitus differences between *Notuchus larvalis* and the two new species are due to habitat divergence while similarities to *Hypochthonella caeca* may point to similar selection pressure(s) exerted by the mechanical properties of the surrounding medium (soil) and/or the attendance by ants.

Unfortunately, nothing is known about the evolutionary dynamics of *Notuchus*–*Paratrechina* associations. Did *Notuchus* species colonize endogeic habitats first, and subsequently established an association with *Paratrechina*, or was the association with *Paratrechina* perhaps the driving force to adapt to an endogeic habitat?

The *Notuchus*–*Paratrechina* association in New Caledonia offers exciting research perspectives for the study of trophobiotic relationships and the evolution of mutualistic adaptation. Further investigations may also shed new light on our understanding of adaptation to underground environments.



Figures 43, 44. (43) *Hypochthonella caeca* China and Fennah (Hypochthonellidae), endogeic species (from Hoch 1994, used with permission). (44) *Notuchus larvalis* Fennah (Delphacidae), obligately cavernicolous (troglotic) species (from Hoch 1994, used with permission). Scale bars: 0.5 mm.

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