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Small giants from Madagascan caves: autapomorphic giantism in the new cave-dwelling planthopper Tsingya clarkei gen. nov., sp. nov. (Hemiptera: Fulgoroidea: Meenoplidae)

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Small giants from Madagascan caves: autapomorphic giantism in the new cave-dwelling planthopper *Tsingya clarkei* gen. nov., sp. nov. (Hemiptera: Fulgoroidea: Meenoplidae)

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A new giant cave-dwelling species of planthopper of the family Meenoplidae (Fulgoromorpha) is described from the Tsingy de Bemaraha National Park in western Madagascar, with information on its distribution and ecology. As the new species could not be placed in any of the previously described genera, a new genus is established. This is the first record of a cavernicolous meenoplid from the Afrotropical Region, and the second cave-dwelling Fulgoromorphan species from Madagascar. It is also the second example of island gigantism in the Fulgoromorpha from Madagascar.

Une nouvelle espèce géante de Meenoplidae (Hémiptera: Fulgoromorpha) provenant d'une grotte du Parc National Tsingy de Bemaraha est décrite de Madagascar. Des informations sur son écologie et sa distribution sont apportés, ainsi que sur sa position taxonomique. C'est la première mention d'une Meenoplide cavernicole de la région Afrotropicale, et la seconde espèce cavernicole de Fulgoromorpha de Madagascar. C'est également le second exemple de gigantisme insulaire chez les Hémiptères Fulgoromorphes de Madagascar.

Introduction

Madagascar is well known for its extraordinary richness in endemic plant and vertebrate species, and has been recognized as one of the planet's biodiversity hotspots (Myers et al. 2000; Ganzhorn et al. 2001; Goodman & Benstead 2003). Together with the Philippines and Sundaland, Madagascar is among the "hottest hotspots" when five of the key factors relating to the biodiversity and conservation of species are considered, i.e. numbers of endemic species and endemic species: area ratios for both plants and vertebrates, as well as habitat loss (Myers et al. 2000, p. 856). Information on the invertebrates in Madagascar is much less elaborate, but evidence is emerging that this same pattern of high biodiversity is paralleled by its fauna, including the insects (Paulian & Viette 2003; Vuataz et al. 2013).

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While the surface biota in Madagascar has continued to become better known in the last decades, little is known about subterranean environments. There are several extensive limestone plateau karst areas in the west of the island, which are of Jurassic and Upper Cretaceous/Eocene age, respectively (Juberthie & Decu 2001; see Figure 1) primarily derived from ancient coral reefs. While other tropical karst areas are known to harbour a rich and diverse cave arthropod fauna (e.g. Australia: Queensland: see Hoch 2002), the subterranean fauna of Madagascar is still largely unexplored and very few studies have been undertaken. Hitherto a single obligate cavernicolous planthopper species has been described: *Typhlobrixia namorokensis* Synave, 1953 (Hemiptera: Fulgoromorpha: Cixiidae) from caves in the Tsingy de Namoroka Strict Nature Reserve, a limestone karst region, situated approximately 200 km north-northeast from the National Park boundary of the Tsingy de Bemaraha karst in northwest Madagascar.

Here we describe a new cave-dwelling planthopper species of the fulgoromorphan family Meenoplidae which was discovered during the production of a wildlife documentary film featuring the flora and fauna in the unique pinnacle karst of the Tsingy de Bemaraha, National Park (Gabriel 2003). The specimens of the new species were collected from Anjohy Manitsy, a limestone cave in the southern "petit (little) tsingy" region of the Bemaraha Park, and this is the first record of a cave-dwelling meenoplid from the Afrotropical Region. The new species could not be accommodated in any of the existing genera of the Meenoplidae; so a new genus is erected.

The Meenoplidae are one of the smaller Fulgoromorpha families representing small-sized species, usually less than 5 mm body length. According to the FLOW database (Bourgoin 2013), there are currently 158 species in 22 genera, occurring in the Old World, Australia and the Western Pacific (Tsaur et al. 1986; Bourgoin 1997). Outside Madagascar, cavernicolous Meenoplidae are known from the Canary Islands (Remane & Hoch 1988; Hoch & Asche 1993; Hoch et al. 2012), the Cape Verde Islands (Hoch et al. 1999), Western Samoa (Hoch & Asche 1988), Australia (Fennah 1973; Hoch 1990, 1993), and New Caledonia (Hoch 1996). As in another fulgoroid family, the Cixiidae containing many cavernicolous species, meenoplid nymphs live close to, or inside the soil, from where it might be a small step for an evolutionary switch to a permanent life underground (Hoch & Asche 1993).

Material and methods

Specimens were collected directly from tree roots growing on the earthy substrate near the wall of the cave, in the transition zone, and were preserved in 70% ethanol. They are deposited in the Muséum national d'Histoire naturelle, Paris, France (MNHN).

External body parts were examined without treatment or manipulation, and drawings of the pertaining structures (head, tegmina) were made from specimens in ethanol. For examination of male and female genital morphology, the genital capsule (male) and the abdomen (female) were removed from specimens and macerated in 10% KOH (24 h) at room temperature, washed in water, transferred to glycerine jelly for drawings, and to glycerine for storage. Staining of delicate tissues was carried out according to Bourgoin (1993a). For permanent storage, genitalia were transferred to polyethylene vials and associated with the vial containing the pertaining specimen. Examinations and drawings were generated using a Leitz stereo-microscope and a Leica MZ12 both with a camera lucida setting. Terminology of tegmina venation follows Bourgoin (1997).
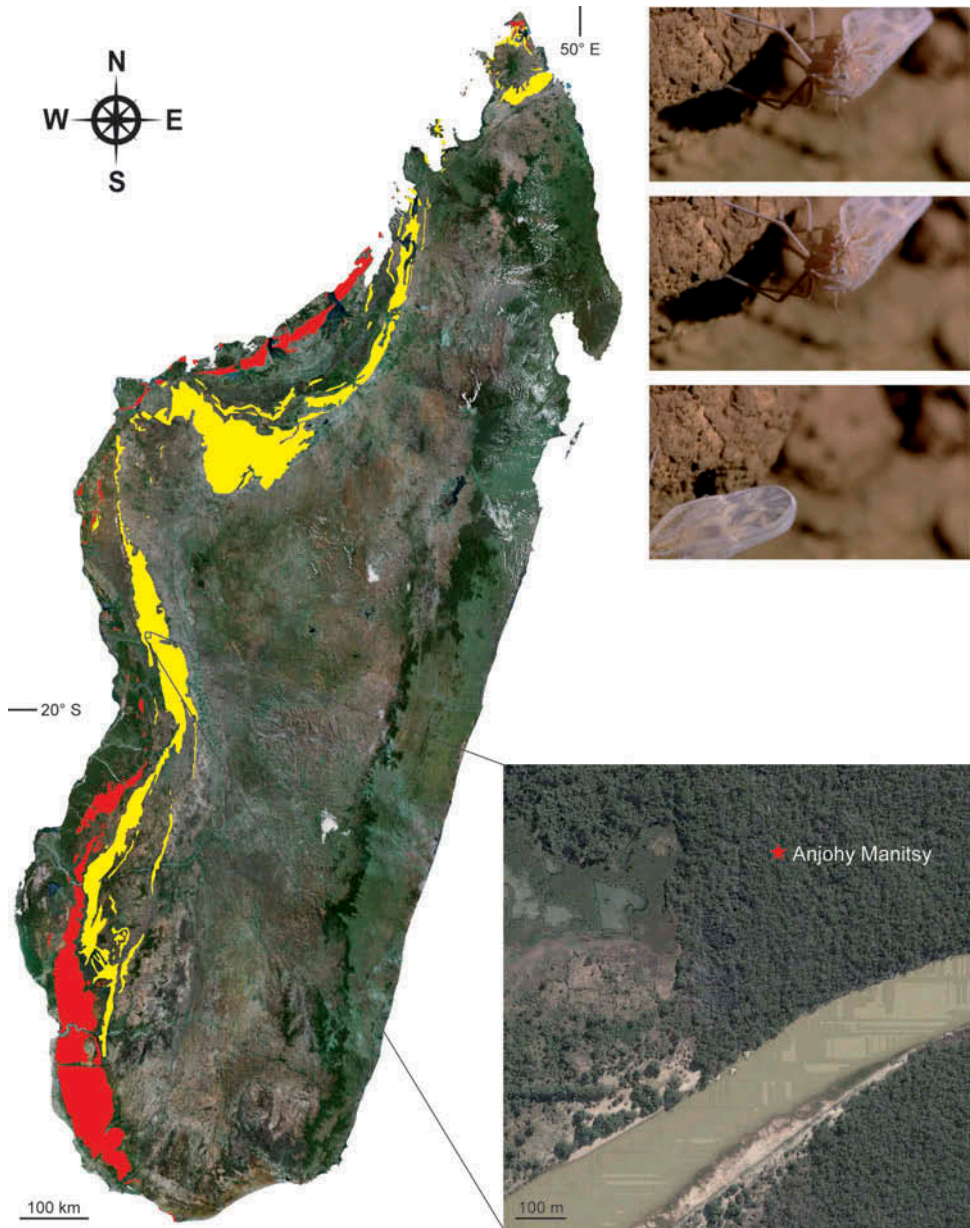
Figure 1. Map of Madagascar (composed and modified from satellite photos provided by Google Earth™), the simplified geology shows the limestone areas (red = Tertiary limestones + marls and chalks; yellow = Mesozoic limestones + marls (incl. "tsingy"), modified after Du Puy and Moat 1996: Figure 1), area enlarged (bottom right): southernmost Petit Tsingy ("Little Tsingy") section of the Tsingy de Bemaraha National Park east of Bekopaka, just north of the Manambolo River. Upper right corner: *Tsingya clarkei* sp. nov. (still images from the wildlife documentary "Voyage to the center of the stone": Gabriel 2003), see also supplementary movie.

Taxonomy

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Family **MEENOPLIDAE** Fieber, 1872

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The Meenoplidae are currently divided into 2 subfamilies: Kermesiinae Kirkaldy, 1906 (= Nisiinae Muir, 1930) and Meenoplinae Fieber, 1872. The new species from Madagascar does not fully correspond to any of the alternatives given in the key based on wing characters provided by Tsaur et al. (1986). The fusion of the claval veins near middle would support its placement into the Meenoplinae, the presence of two rows of sensory pits accompanying the first claval vein, however, renders it a member of the Kermesiinae. The Sc + R and M fork is situated neither "near the base" (as in Kermesiinae) nor "near the apex" (as usually in Meenoplinae) but at about midlength of Sc + R.

The new *Tsingya* species described below should be placed within Meenoplinae on the basis of the A2 vein being covered with sensory pits that are arranged irregularly. Indeed, the rows of sensory pits on each side of A1 are more or less developed, often more developed on the costal side and only developed in one row in *Muirisinia* (see Bourgoin 1997, fig. 52). The variability of this character contrasts with (1) a late separation of Sc + R and M; (2) the non-apical fusion of anal veins; and (3) the presence of many sensory pits on A2 that agree with diagnostical meenopline characters.

Bourgoin (1993b), however, argued that if Meenoplinae form probably a monophyletic group, monophyly of Kermesiinae remains questionable. Obviously the generic concepts in the Meenoplidae still need to be tested more thoroughly and subdivision of the Meenoplidae must therefore be regarded preliminary.

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Subfamily **MEENOPLINAE** Fieber, 1872
Tsingya Hoch and Bourgoin gen. nov.

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Type species: *Tsingya clarkei* Hoch and Wessel sp. nov. Type locality: Madagascar.

Description

Habitus. Large meenoplid (c.1 cm), with small compound eyes, well-developed tegmina and wings, and long forelegs. Body pigmentation pale and whitish, except light red compound eyes.

Head. (Figure 2).Vertex short, c.7× wider than medially long, posterior margin convex, separated from frons by a distinct carina concave towards frons. Frons subrectangular, with lateral carinae strongly ridged, with a dense row of sensory pits along outer margin. Frons and postclypeus medially smooth, anteclypeus with a distinct median carina. Frontoclypeal suture nearly straight, slightly arched towards frons. Rostrum elongate, in repose well surpassing hind-coxae. Compound eyes present, comparatively small, lateral ocelli present, median frontal ocellus vestigial. Antennae with scape cylindrical, pedicel subcylindrical, c.2× as long as scape, with distinct rows of sensory plaque organs.
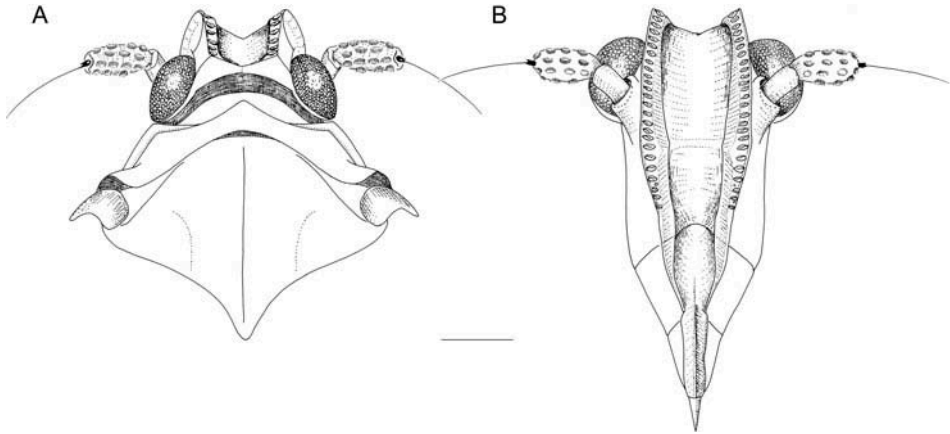
Figure 2. (A) Head and thorax, dorsal aspect; (B) head, ventral aspect. Scale bar 0.5 mm.

Thorax. (Figures 2 and 3). Pronotum short, 1.54 × wider than maximum width of head (including eyes), lateral carinae sinuate, running parallel to posterior margin of head, median carina obsolete; posterior margin of pronotum sinuate, distinctly concave. Mesonotum tricarinate, carinae obsolete, c.1.48× wider than long. Tegmina well developed; c.2.7× longer than maximal width; anterior and posterior margin nearly parallel, distal margin rounded; distal part not notably expanded; fork of Sc + R and M at about the midlength of Sc + R, Sc + R in proximal three-quarters with two rows of sensory pits; fusion of claval veins near middle, claval veins proximally of fusion each with two rows of sensory pits; second claval vein only slightly curved, nearly parallel with posterior margin of tegmen. Wings well developed; venation not notably reduced. Legs overall long and narrow, fore femora distinctly longer than middle femora, middle femora slightly longer than hind femora. Hind tibiae laterally unarmed, distally with a row of eight equally small teeth, arranged in two groups (medially three, laterally five; group of five slightly more proximally than group of three); metabasitarsus and second metatarsal segment each with seven small teeth distally, arranged in a slightly arched row. Metabasitarsus about one-third longer than second and third metatarsal joints together.
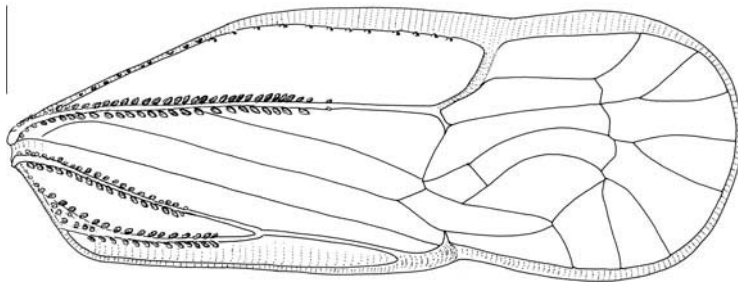

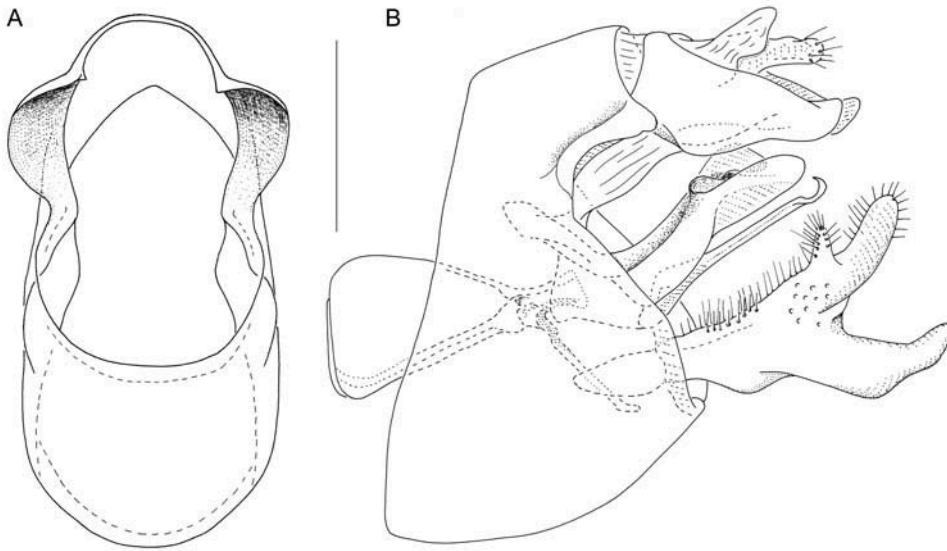Figure 3. Right tegmen, maximal aspect. Scale bar 1 mm.

Figure 4. (A) Male genital segment, caudal aspect; (B) male genitalia, *in situ*, left lateral aspect. Scale bar 0.5 mm.

Male genitalia. (Figures 4–7). Genital segment bilaterally symmetrical, in caudal aspect highly ovate, outline nearly figure-8-shaped; in lateral aspect caudal margin deeply notched in dorsal third; dorsocaudal margin laterodorsally distinctly projected laterally, ear-shaped. Anal segment in dorsal aspect narrow at base, with lateral margins diverging distally; lateral lobes distally well surpassing anal style, converging medially, in lateral aspect distally rounded and slightly bent dorsally.

Parameres bifurcate. Aedeagus differentiated into two processes arising from a common base: dorsal process trilobate, with phallotreme located medially at apex, phallotreme exposed ventrally; ventral process tongue-shaped.

External female genitalia. (Figure 8). Strongly reduced, ventral valvifer laterodorsally rounded; ventral valvulae slender, narrow, tip rounded, directed mediocaudad, laterally and ventrally with several smaller and one prominent, almost claw-like seta ventrally near apex; VIIth sternite in ventral aspect narrow, c.1.3× longer than wide.

The wax-plate areas are of paratopic type (= internal area of wax plate shifted in a median position and joining the body sagittal line) (Bourgoin 1997, p. 202).

Internal female genitalia. (Figure 9). Bursa copulatrix spherical with few rounded sclerotinized ornamentations limited to its posterodorsal part; ductus bursa long and thin, emerging from aliferum (Bourgoin 1997, p. 209), ventral wings and the spermatheca posterior of the aliferum. Spermatheca divided into a long and thin ductus receptaculi, ampulla-like distally (= diverticulum ductus), a long pars intermedialis (= spermathecal pump) and the very thin ramified glandula apicalis. Aliferum long and robust, bearing distally a pair of laterodorsally pointed, foliaceous, ear-like expansions (laterodorsal wings) and a ventral pair of flattened cupula-like expansions (ventral
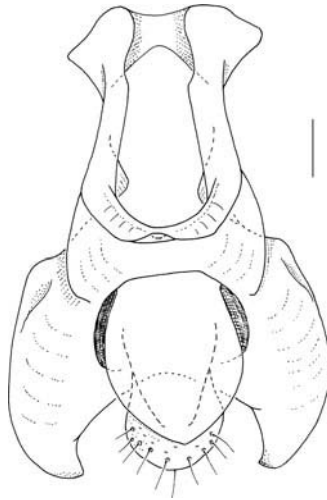
Figure 5. Male genitalia, dissected. Male anal segment, dorsal aspect. Scale bar 0.1 mm.
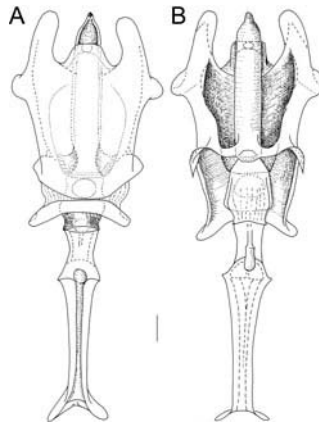
Figure 6. Male genitalia, dissected. Aedeagus (A) dorsal aspect, (B) ventral aspect. Scale bar 0.1 mm.
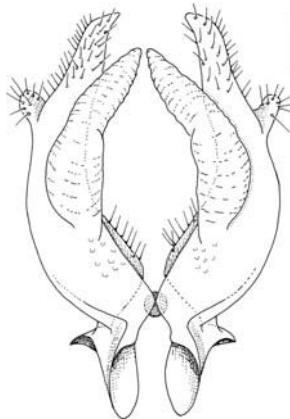
Figure 7. Male genitalia, dissected. Parameres, ventral aspect. Scale bar 0.1 mm.
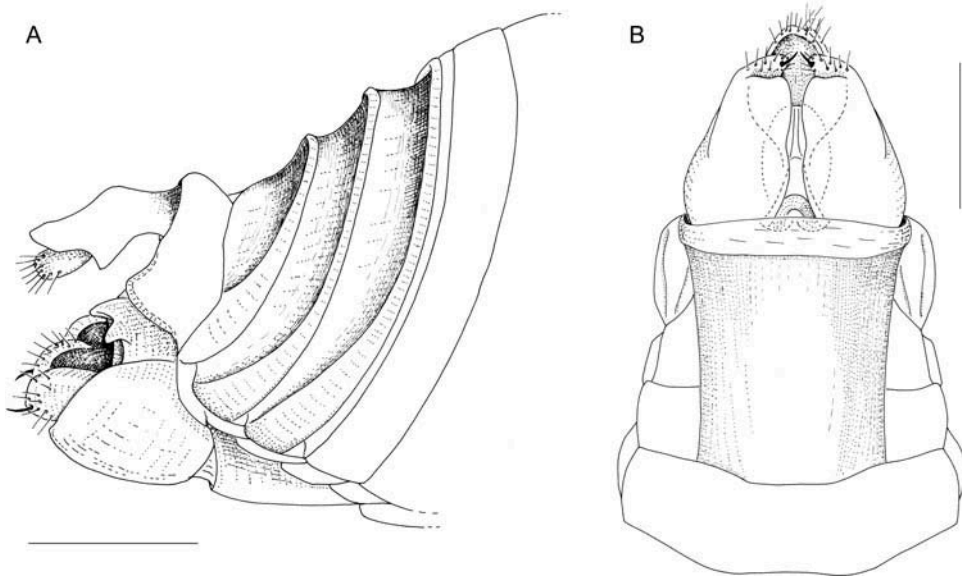
Figure 8. External female genitalia, *in situ*. (A) Right lateral aspect; (B) ventral aspect. Scale bar 0.5 mm.
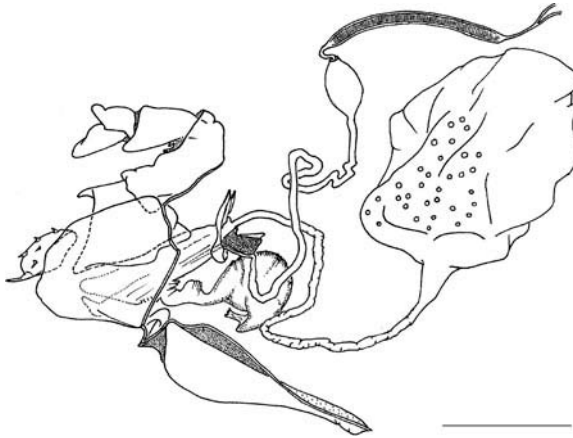
Figure 9. Internal female genitalia, dissected, right lateral aspect. Scale bar 0.5 mm.

wings), enclosing between them the bursa copulatrix ductus. Spermathecal ductus receptaculi running anteroventrally to the ventral wings; both ducts running inside the aliferum joining ventrally the dorsal wall of the vestibulum. Vagina opening anteriorly into the vestibulum at the base of the aliferum. Common oviductus as usual, branched anteroventrally but directed caudad. Lateral sides of sternite VII shortly produced posteriorly, not forming any rod-like arm, reaching gonocoxae VIII ventrally.

Diagnosis

Tsingya gen. nov. can be readily distinguished from all other meenoplid genera by the combination of the following characters: large body size (c.10–11 mm including tegmina), tegmina with fusion of claval veins near middle, both claval veins with two rows of sensory pits proximally of fusion, and fork of Sc + R and M at c. midlength of Sc + R.

In addition to the tegmina venation, the new genus differs significantly from other known meenoplid taxa by the configuration of the head capsule, the male genitalia (shape of genital segment, anal tube and paramere) and female genitalia (aliferum).

Etymology

The genus name honours the Tsingy de Bemaraha National Park in western Madagascar, characterized by its acutely eroded, sharp-bladed "tsingy" limestone pinnacle karst.

Remarks

With regard to the internal structures of the female genitalia, the aliferum (Bourgoin 1997) deserves special attention. The aliferum is a complex of sclerotized formation(s) in the dorsal wall of the posterior vagina forming a more or less tubular structure that encompasses the bursa copulatrix ductus, and also in most cases (but not all: e.g. *Anorhinosia* Bourgoin 1997), the spermatheca, and which separates them from the vagina. It is a particularly common structure observed in all meenoplid genera, of both subfamilies Kermesiinae and Meenoplinae (but also in several kinnarid planthopper genera: *Adolenda* Distant, 1911, *Bashgultala* Dlabola, 1957, *Emeljanopleroma* Koçak, 1986, *Nesomicrixia* Emeljanov, 1984, *Southia* Kirkaldy, 1904 and *Oeclidius* Van Duzee, 1914) and is diverse in its configuration according to the taxa studied. In *Tsingy*a gen. nov. the sagittal medioventral lamina is separated into two ventral wings. The unpaired dorsal lamina is absent. The morphological origin of this structure is unclear: at least it is formed by the fusion of the basal apodeme of gonapophyses IX with the posterovaginal process, probably also with parts of the gonospiculum (Bourgoin 1993).

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Tsingya clarkei Hoch and Wessel sp. nov.
(Figures 1–9)

</div>

Description

Habitus. Unusually large meenoplid, tegmina long, steeply tectiform, small compound eyes, pale bodily pigmentation.

Body length. Anterior margin of head to distal margin of tegmina. Males. 10.0–10.6 mm (*n* = 2). Female. 11.5 mm (*n* = 1). Tip of head to distal margin of anal segment. Males. 6.9–7.0 mm (*n* = 2).

Colouration (Figure 1). Body pale (white) throughout, except for compound eyes, these pigmented lightly red; tegmina translucent, venation white.

Configuration and proportions of head and thorax incl. legs, tegmina and wings as described for the genus (Figures 2 and 3).

Male genitalia. (Figures 4–7). Genital and anal segments as described for the genus. Parameres with ventral branch more strongly developed, dorsal branch differentiated into a strong, finger-shaped process bent medially, and a short, stout, apically blunt appendage, densely beset with setae, directed laterodorsally. Aedeagus with dorsal and ventral processes arising from a short, wide common base: dorsal trilobate process forming a half-pipe, with median part hood-shaped, distally subacute with phallotreme located medially at apex, phallotreme exposed ventrally; lateral lobes apically rounded, in lateral aspect slightly surpassing median lobe; ventral aedeagal process tongue-shaped, dorsally at base concave, distally taeniform, narrow, apically acute, its tip curved dorsally.

Female genitalia. (Figures 8 and 9). As described for the genus.

Diagnosis

Tsingy clarkei sp. nov. is characterized by a unique combination of characters pertaining to the male genital structures: parameres bifurcate with ventral branch more strongly developed, aedeagus with a dorsal, trilobate process forming a half-pipe, and phallotreme situated medially at apex and a ventral, tongue-shaped, taeniform and apically acute process.

Etymology

The species is named in honour of the collector, Arthur Clarke (Honorary Research Associate in the School of Zoology, University of Tasmania) in Hobart, Tasmania (Australia), ardent cave explorer, dedicated cave ecologist and biospeleologist, reliable caving buddy and good friend.

Distribution

Known only from Anjohy Manitsy (translates as "Cold Cave") in the southernmost Petit Tsingy ("Little Tsingy") section of the Tsingy de Bemaraha National Park east of Bekopaka, just north of the Manambolo River, in western Madagascar. Likely to be a narrow range endemic, *T. clarkei* is known only from Madagascar.

Ecology

Clarke (2003) reported that some substantial trees occur in the dense thickets of vegetation formed in the canyons and fault grabens between the elevated blocks of pinnacle karst. However, above the caves the karst surface is generally devoid of large

trees and almost barren. Among the perilously razor sharp karren flutes, the surface vegetation in the tsingy itself is unique with many endemic xerophytic and/or water storage plants. Although the Bemaraha tsingy receives torrential downpours in the wet season, very little water remains on the surface and in the dry season the only moisture for 6–7 months is the nightly dew, so the karst is essentially an arid environment for much of the year. The "arid" flora of the Bemaraha karst surface typically includes cactiform succulents such as *Euphorbia* and *Cynanchum*, numerous bulbous stemmed plants or trees that hold water in their internal pith (e.g. *Pachypodium, Adenia* and the occasional baobab), the many thorned, narrow or spiny leafed xerophytic or xerophilous species such as *Pandanus* and *Dracaena* and the unusual leafless plants such as *Commiphora* with its photosynthesizing trunks and branches (Clarke 2003).

Access to the enclosed cave collection site involved passing through a lushly forested canyon, before commencing a traverse of 40–50 m along a narrow 1.0–1.5m wide, 30–40m high diaclase (roofless cave) rift with abundant tree roots. The entrance elevation (altitude) of the diaclase is approximately 130 m above sea level. Among the green-leafed foliage in the canyon and in the outer extremities of the diaclase, a number of vertebrate species were observed, including three smaller species of lemur: the common brown lemur *Eulemur fulvus*, the grey mouse lemur *Microcebus murinus* and a large nocturnal species the Milne-Edwards' weasel lemur *Lepilemur edwardsi* and several reptiles. Along with one of the leaf-tailed *Uroplatus* geckos, three species of chameleons were noted; two species of *Brookesia*, *Brookesia ebenaui* and *Brookesia perarmata*, and the much longer Malagasy Giant Chameleon *Furcifer oustelati*. A colubrid snake *Madagascarophis colubrinus occidentalis* was also spotted in a *Pandanus* tree (A. Clarke, unpublished records, pers. comm.).

In the subdued daylight/twilight inner reaches of the Anjohy Manitsy diaclase rift heading into the roofed cave, several specimens of a locally known so-called nocturnal butterfly (a noctuid moth) were found on the rift walls. In the outer twilight section of the cave, two species of land snails were seen among tree roots and rootlets on the moist sandy floor: *Kalidos griffithshauchleri* (Ariophantidae) and *Acroptychia bathiei* (Cyclophoridae). Two frogs were observed in this same outer part of cave: the grey-legged, red and brown-backed *Mantella betsileo* (Mantelidae) and a speckled brown frog, possibly the Mascarene Ridged Frog *Ptychadena mascareniensis* (Ranidae). In this outer twilight zone, there was also a dark brown coloured flatworm 12–14 cm long, with broadly flattened bulbous head, which may possibly predate on the cavernicolous species including the planthoppers. All three specimens of *Tsingya clarkei* were found in the inner high humidity dark transition zone of the cave, collected from the subterranean roots of an unidentified surface tree and from smaller rootlets in clay soil adjacent to the cave wall. Among the other cave-dwelling invertebrates in Anjohy Manitsy, there were unidentified species of depigmented isopods, entomobryid springtails and millipedes.

Remarks

With 10.0–11.5 mm in length, *Tsingya clarkei* sp. nov. is the largest known meenoplid to date.

Material examined

Holotype male: MADAGASCAR, Anjohy Manitsy, Petit Tsingy, Tsingy de Bemaraha, east of Bekopaka, western Madagascar, May 2003, Arthur Clarke leg., MNHN.

Paratypes. 1 male, 1 female, same data as holotype, MNHN.

Discussion

Tsingya clarkei – a true troglobite?

The configuration of external morphology of *T. clarkei* raises the question whether or not the species is a true troglobite, i.e. restricted to subterranean habitats. Although compound eyes are present, they appear comparatively smaller than is usually observed in epigean meenoplids, and the occelli display a light red pigmentation. Body pigmentation is strongly reduced: body, legs and venation of tegmina are entirely white. These traits are common in troglobitic planthoppers (Hoch 1994, 2002). In contrast, the tegmina and wings do not show any sign of reduction: *T. clarkei* is almost certainly capable of flight. Interestingly, among the legs, the forelegs are longest, due to elongate femora (see also supporting on-line material). Whether the elongation of the forelegs is correlated with cave adaptation, or is a plesiomorphic trait shared with an (extant or extinct) epigean relative remains unclear.

The latter two traits may be explained by the characteristics of the environment: the habitat consists of narrow vertical rifts and crevices, some of which are roofed and some connect to the surface, creating an extended transition zone, where varying temperature and humidity levels of the surface are still felt; roots in long strands dangle from the ceiling (A. Clarke, personal communication, used with permission). To exploit these as a food resource and to orientate within a, probably vertically shifting, optimum humidity zone, it may be mandatory for *T. clarkei* to maintain the capability of rudimentary vision and flight. It is conceivable that the elongate forelegs further facilitate orientation, and serve as an auxiliary antennae and/or enhance the perception of intraspecific communication signals which in planthoppers are transmitted as vibrations via the substrate (Hoch & Wessel 2006). Although little is known about the biology, reproductive behaviour and life history of *T. clarkei*, it is here provisionally classified (according to the definitions suggested by Sket 2008, see also Ruffo 1957) as being at least eutroglophile (i.e. an essentially epigean species able to maintain a permanent subterranean population), if not troglobiont (i.e. obligate cave dweller, completion of life cycle underground mandatory). Nymphs whose association with adults inside the caves would further corroborate this assumption have hitherto not been found.

Tsingya clarkei – a "true relict"?

The present distribution of *T. clarkei* – endemic to Madagascar, only known from one cave – indicates that the species is restricted to a specialized environment and confined to a small area. Whether it is indeed a "true relict" or a cavernicolous representative of an extant epigean lineage cannot be decided at the present moment. Little is known about the epigean Fulgoromorpha fauna of Madagascar, with only a few publications dedicated to the Meenoplidae (Synave 1953, 1957). No comprehensive taxonomic treatment of the Meenoplidae of Madagascar has been undertaken,

and for the whole Afrotropical Region, there is only a single recent revision of the genus *Afronisia* Wilson (1988).

Which factors drove the evolution of cave-adapted planthoppers on Madagascar?

The distribution of *T. clarkei* coincides with one of the areas of microendemism as recognized by Wilmé et al. (2006) based on the distribution of modern Malagasy vertebrates: the northwestern part of the island (Wilmé et al. 2006: "center of endemism 8, N Tsiribihina, W Bétsiboka"). This area includes the limestone karst of Bemaraha as well as the karst of Namoroka, the type locality of the troglobitic cixiid *Typhlobrixia namorokensis*. The model suggested by Wilmé et al. (2006) explains patterns of speciation by the influence of Quaternary palaeoclimatic fluctuation: in Madagascar low elevation habitats experienced cooler and drier conditions than did those at higher elevations where orographic precipitation allowed for the continuous support of river systems and associated forest ecosystems. It therefore acted as hydrological buffers, providing potential corridors for retreat to higher elevations, while habitats with low elevation water sources were apparently more prone to ecological shifts, increased levels of aridification, perhaps resulting in habitat fragmentation and isolation.

This model appears plausible to also explain adaptation of epigean planthoppers to subterranean environments in Madagascar and in fact complies with the "classical" *climatic relict hypothesis sensu* Vandel (1964) and Barr (1968). Increasing levels of aridity on the surface might have forced adult planthoppers to seek an alternative habitat with more adequate or sufficient humidity, such as in more sheltered and moist crevices or caves, for feeding and oviposition, and/or prompted immatures to not leave the nymphal habitat (leaf litter or soil) for adult moult, but search for food and mating partners in underground environments. At present, it is unclear whether the shift to a permanent life underground was indeed triggered by deteriorating conditions on the surface (with survival and subsequent cave-adaption of troglophilic populations; i.e. in allopatry), or by the exploitation of a novel food resource, roots inside caves, as suggested by the *adaptive shift hypothesis*, which provides an alternative model explaining cave adaptation by parapatric speciation (Howarth 1981, 1986, 1987; Howarth & Hoch 2012). Unfortunately, the degree of troglomorphy is not a reliable indicator for the age of the cavernicolous lineage, as it does not necessarily correlate with cave age, as has been shown for cave planthopper models in Hawaii and Australia (Wessel et al. 2007).

Insular gigantism

Relative to all other meenoplid taxa known, which generally range between 4 and 8 mm maximum, *T. clarkei* exhibits an exceptionally large body size (up to 11.5 mm). That islands can support species or populations of gigantic (or dwarf) forms of mainland relatives is a well-known biological phenomenon. Initially triggered by the description of Pleistocene pygmy elephants from Cyprus (Bate 1902), Foster (1964) investigated insular effects on the body size of mammals and Van Valen (1973, p. 35) finally coined the term "island rule". The island rule states (relating to mammals) that small animals isolated on islands become bigger (island gigantism), while large animals become smaller (island dwarfism). In case of *Tsingya* the

gigantism, which is clearly autapomorphic for the taxon, falls under island/insular gigantism or autapomorphic giantism (Gould & MacFadden 2004). Recently, another bigger epigean planthopper from the family Achilidae was described from Madagascar (Bourgoin & Soulier-Perkins 2006).

A physiological basis of this rule in terms of resource availability is discussed by McNab (1999): endotherms isolated on islands show a decrease in body mass in response to smaller resource abundance, or an increase because a resource is added or the absence of competition. To date several hypotheses (summarized in Gould & MacFadden 2004) have been advanced to explain this complex phenomenon, which can be summarized as a relaxation of predation or competition pressures and random genetic drift (Keogh et al. 2005); however, all studies in support of these rules reveal a very strong bias towards vertebrates.

Although the petit tsingy limestone may appear connected as a block of rock and its contained karst biospace may be locally contiguous (Clarke 1997a), the cave where *T. clarkei* was discovered is effectively an isolated area (island) in the various sections of Tsingy karst, already endemic and isolated areas within the island of Madagascar, a hot spot of endemic taxa (Myers et al. 2000). It is obvious that these successive very particular conditions (i.e. essentially "an island on an island on an island") have strongly influenced the evolution of the taxa. In these very special biotopes, removal of some constraints might have occurred, whereas a large and unused food resource through the extraordinary developed root system has become available.

Perspectives for the cavernicolous fauna of Madagascar: the need for inventory and conservation of subterranean environments

Tsingy de Bemaraha Strict Nature Reserve, the type locality of *T. clarkei*, is also home to numerous species of birds, reptiles and mammals, including lemurs, all of which are considered rare and endangered and it has therefore been classified a UNESCO World Heritage Centre (http://whc.unesco.org/en/list/494). Madagascar with its extensive karst areas is rich in caves (Juberthie & Decu 2001) and presumably also rich in cave planthopper habitat. Intensified efforts to explore the subterranean biome will doubtlessly reveal the existence of additional cave-dwelling planthopper taxa, and may eventually add Madagascar to the list of hot-spots of cave-planthopper diversity – next to the Canary Islands, Australia and Hawaii (see information in Hoch 2002).

Obligately cave-dwelling organisms are highly specialized ecologically (Howarth 1983) and often have small geographic ranges. Hence the karst biospace is extremely vulnerable to habitat degradation and loss (Clarke 1997a, 1997b, 1997c). It is therefore mandatory that cavernicolous species be added to the list of target taxa for conservation which currently focuses on plants and epigean macrofauna (chameleons, frogs, geckos, lemurs) and where insects are concerned, on ants and butterflies (Kremen et al. 2008).

It is hoped that increasing information on subterranean habitats such as caves and their specialized, endemic and narrow range faunas, which make up an important element of Madagascar's microendemic biota will result in the recognition of regions rich in caves and karst biospace as high-priority conservation areas (Kremen et al. 2008), eventually to be included in legal designation for the expansion of the current reserve network.

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Supplemental material

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