RESEARCH ARTICLE



First record of the genus *Dialarnaca* Gorochov, 2005 from China, with description of two new species (Orthoptera, Gryllacrididae, Gryllacridinae)

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Abstract

In the present paper, *Dialarnaca* Gorochov, 2005 is recorded from China for the first time, with two new species of the genus described, *Dialarnaca longicerca* Shi & Bian, **sp. n.** and *Dialarnaca zhoui* Shi & Bian, **sp. n.** A key and a distribution map of the genus *Dialarnaca*, are provided.

Keywords

Gryllacrididae, Gryllacridinae, new record genus, Dialarnaca, new species, China

Introduction

Dialarnaca was first proposed by Gorochov (2005) with *Dialarnaca roseola* (type locality: Philippines, Mindoro Island, near Puerto Galera). Currently, except for the type species, no additional species was described (Eades et al. 2015). In this paper, the genus *Dialarnaca* is first recorded from China and two new species, *Dialarnaca longicerca* sp. n. (type locality: Hainan, Changjiang, Bawangling) and *Dialarnaca zhoui* sp. n. (type locality: Yunnan, Jinping, Pinghe), are described. A key to species and a distribution map are provided.

Material and methods

Specimens in this study were collected from tropical area of southern China. Morphological structures were examined and measured using Leica M205A stereomicroscope. Leica DFC 450 digital imaging system was used to obtain morphological images. The map was drawn using ArcGIS 10.2 based on the occurrence points. The specimens were deposited in the Museum of Hebei University, China.

All measurements of length are in millimetres. The following abbreviations were used for the specimen measurements: body w/wings – the distance from the apex of fastigium verticis to the apex of tegmina; body w/o wings – in male, the distance from the apex of fastigium verticis to the posterior margin of tenth abdominal tergite, in female, the distance from the apex of fastigium verticis to the apex of epiproct; pronotum – the straight-line distance from the anterior margin of pronotum to posterior margin; tegmen – the distance from the base of tegmen to apex; hind femur – the distance from the base of subgenital plate to the apex of ovipositor.

Taxonomy

Genus Dialarnaca Gorochov, 2005

Dialarnaca: Gorochov 2005: 821 (English translation by Entomological Review: 931).

Type species. Dialarnaca roseola Gorochov, 2005, by original designation.

Description. Body medium, form slender. Eyes kidney-shaped, prominent; ocelli small, inconspicuous. Humeral sinus of pronotum distinct. Tegmina and hind wings developed, far surpassing apices of hind femora; M vein of tegmina simple, free, not united with R vein. Fore coxae with one small spine; fore and middle femora unarmed on ventral surface, tibiae with five pairs of movable ventral spines (including a pair of apical spines); middle tibiae with an inner apical spine on dorsal surface. Hind femora with two rows of minute spines on ventral surface; tibiae with two rows of spines on dorsal surface, subapices with 1 pair of spines on ventral surface, apices with one pair of dorsal spines, the inner one obviously longer than outer one, and two pairs of ventral spines. Second and third abdominal tergites with two rows of transverse stridulatory teeth on lateral margins separately. MALE: ninth abdominal tergite without any hook, centre of posterior margin with a large tubercular process, the angular apex of which slightly directing downwards; tenth abdominal tergite in the form of transverse sclerite, posterior area projecting backwards, membranous, the apex with 1 pair of heavily sclerotized hooks, which curved upwards; subgenital plate variable with well-developed styli; genitalia entirely membranous. FEMALE: posterior area of seventh abdominal sternite projecting backwards; basal area of subgenital plate with numerous rugulae.

Diagnosis. The genus can be identified by the following characters: male ninth abdominal tergite without any process, posterior area of tenth abdominal tergite membranous with one pair of sclerotized apical hooks, which curved upwards. Because only one female is known, the diagnosis of the genus is insufficient.

Key to the species of Dialarnaca

1	Apical area of male cerci curly, styli shorter (0.23-0.24 mm), about 3.92-
	4.43 times shorter than the length of male subgenital plate along the mid-
	line <i>Dialarnaca longicerca</i> sp. n.
_	Male cerci straight, styli longer, about 2.33-2.47 times shorter than the
	length of male subgenital plate along the midline2
2	Posterior area of male subgenital plate slightly projected, posterior margin
	shallowly concave in the middle
_	Posterior area of male subgenital plate trapezoidal projected, posterior margin
	nearly straight

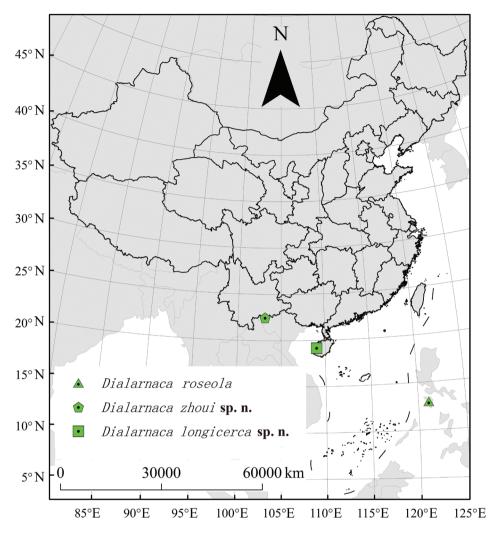
Dialarnaca longicerca Shi & Bian, sp. n.

http://zoobank.org/329CD64A-FCCF-4FDD-AD33-84D37D974C72 Map 1, Figs 1–11, 18–19

Type material. Holotype: male, pinned, China, Hainan, Changjiang, Bawangling, 26 May 2014, coll. by Jiao Jiao. Paratypes: 1 male and 1 female, pinned, China, Hainan, Changjiang, Bawangling, 13 July 2010, coll. by Ming Qiu and Rui-Lian Li.

Diagnosis. This species differs from the *Dialarnaca roseola* Gorochov, 2005 in body green, male cerci longer and apical area curled, posterior margin of male subgenital plate slightly concave in the middle, styli shorter.

Description. Male. The following characters are in addition to those given in the generic description. Fastigium verticis broad, about 1.5–1.7 times as wide as scape (Fig. 2). Eyes ovoid; ocelli inconspicuous. Scape about as long as length of eyes, pedicel approximately half as long as scape (Fig. 2). Anterior margin of pronotum projected in the middle, posterior margin almost truncate, lateral lobes longer than high (Figs 1, 3). Hind femora with 5–6 spines on internal margin of ventral surface, external margin with 6–8 spines; tibiae with 5–6 spines on internal margin and seven spines on external margin of dorsal surface. Apical area of ninth abdominal tergite with 1 tubercular process in the middle, which slightly directing downwards; posterior margin of tenth abdominal tergite with one pair of long triangular hooks in the middle, which curved upwards, its apices directing forwards (Figs 4–6, 18–19). Cerci about 4.3–4.4 mm, longer than in other species of the genus, apical area curly, apices obtuse (Fig. 5). Subgenital plate broader than long, anterior margin nearly straight, posterior margin slightly concave in the middle; styli about 0.23–0.24 mm, shorter than in other species of the genus, cylindrical, located on lateral margins of subgenital plate near apex (Fig. 4).



Map 1. Distribution of *Dialarnaca* species.

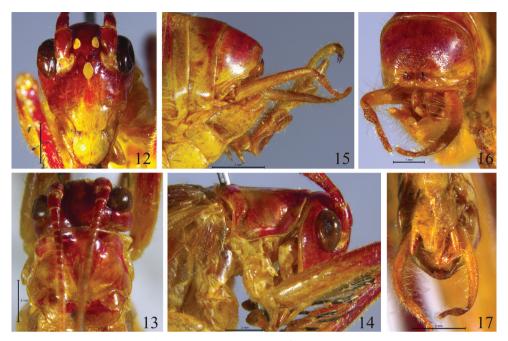
Female. Differs from male in following characters: cerci slender, apices acute. Seventh abdominal sternite long, both sides of four fifths apical area slightly concave, posterior area projecting backwards, centre of posterior margin slightly concave (Figs 10–11). Subgenital plate longer than broad, basal area semimembranous, with abundant fine stripes, posterior margin obtuse-angular. Ovipositor longer than hind femora, distinctly upcurved, apices obliquely roundly cutting (Fig. 10).

Coloration. Body green. Eyes black-brown. Apices of hooks of tenth abdominal tergite blackish.

Measurements (mm). Male: body w/wings 33.2–34.0, body w/o wings 18.7–20.5, pronotum 4.5–5.0, tegmen 28.7–29.2, hind femur 11.8–12.4; female: body w/



Figures 1–11. *Dialarnaca longicerca* sp. n.: **1–6** male **7–11** female. **1**, **7** head and pronotum in dorsal view **2**, **8** head in frontal view **3**, **9** head and pronotum in lateral view **4**, **11** apex of abdomen in ventral view **5**, **6** apex of abdomen in ventro-lateral view **10** apex of abdomen in lateral view.



Figures 12–17. *Dialarnaca zhoui* sp. n., male. **12** head in frontal view **13** head and pronotum in dorsal view **14** head and pronotum in lateral view **15** apex of abdomen in lateral view **16** apex of abdomen in apical view **17** apex of abdomen in ventral view.

wings 34.0, body w/o wings 21.2, pronotum 5.3, tegmen 28.0, hind femur 11.7, ovipositor 14.0.

Distribution. China (Hainan).

Etymology. The name is derived from the longer cerci of male.

Dialarnaca zhoui Shi & Bian, sp. n.

http://zoobank.org/085D18ED-EC36-490F-8786-BB88548DA126 Map 1, Figs 12–17, 20–21

Type material. Holotype: male, pinned, China, Yunnan, Jinping, Pinghe, 12 June 2009, coll. by Fu-Ming Shi.

Diagnosis. This species differs from *Dialarnaca roseola* Gorochov, 2005 and *Dialarnaca longicerca* Shi & Bian, sp. n. by: the posterior area of male subgenital plate trapezoidal projected, styli located on lateral margins near middle area of subgenital plate. In *Dialarnaca roseola*, posterior area of male subgenital plate slightly projected, centre of which with 1 shallow concavity. It can be distinguished from *Dialarnaca longicerca* sp. n. by the shape of male cerci and subgenital plate.

Description. Male. Fastigium verticis broad, about 1.5 times as wide as scape. Eyes ovoid; ocelli conspicuous. Scape about three-quarters length of eye, pedicel about half as



Figures 18–21. Hooks of male tenth abdominal tergite in *Dialarnaca* spp. 18–19 *Dialarnaca longicerca* sp. n. 20–21 *Dialarnaca zhoui* sp. n. 18, 21 apical view 19, 21 lateral view.

long as scape (Fig. 12). Anterior margin of pronotum slightly projected, posterior margin almost truncate, ventral margin of lateral lobes undulated (Figs 12–13). Hind femora with 7–9 pairs of spines on ventral surface, tibiae with 4–5 pairs of spines on dorsal surface. Posterior margin of ninth abdominal tergite projecting backwards, centre tubercular; posterior margin of tenth abdominal tergite with 1 pair of short, triangular hooks in the middle, the apices slightly directing forwards in lateral view (Figs 15–16, 20–21). Cerci approximately 3.9 mm, conical, nearly straight, apices obtuse (Figs 16–17). Subgenital plate longer than broad, anterior margin almost straight; styli long (about 0.94 mm), cylindrical, located on lateral margins near middle area of subgenital plate (Fig. 17).

Female. This species is known only from the holotype.

Coloration. Body reddish yellow. Labrum yellow, eyes brown, ocelli yellow. Spines of all legs black.

Measurements (mm). Male: body w/wings 42.0, body w/o wings 23.7, pronotum 6.5, tegmen 35.5, hind femur 18.3.

Distribution. China (Yunnan).

Etymology. This species is named in honour of Dr. Shan-Yi Zhou who provided much assistance in collecting specimens.

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References

Gorochov AV (2005) Contributions to the fauna and taxonomy of the Stenopelmatoidea (Orthoptera) of Indochina and some other territories: VI. Entomologicheskoe Obozrenie 84(4): 806–825. [In Russian; English translation: Entomological Review 85(8): 918–933]
Eades DC, Otte D, Cigliano MM, Braun H (2015) Orthoptera Species File. Version 5.0/5.0. http://Orthoptera.SpeciesFile.org [accessed 20–July–2015]

RESEARCH ARTICLE



Beetle and plant arrow poisons of the Jul'hoan and Haillom San peoples of Namibia (Insecta, Coleoptera, Chrysomelidae; Plantae, Anacardiaceae, Apocynaceae, Burseraceae)

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Abstract

The use of archery to hunt appears relatively late in human history. It is poorly understood but the application of poisons to arrows to increase lethality must have occurred shortly after developing bow hunting methods; these early multi-stage transitions represent cognitive shifts in human evolution. This paper is a synthesis of widely-scattered literature in anthropology, entomology, and chemistry, dealing with San ("Bushmen") arrow poisons. The term San (or Khoisan) covers many indigenous groups using so-called 'click languages' in southern Africa. Beetles are used for arrow poison by at least eight San groups and one non-San group. Fieldwork and interviews with Jul'hoan and Haillom hunters in Namibia revealed major differences in the nature and preparation of arrow poisons, bow and arrow construction, and poison antidote. Jul'hoan hunters use leaf-beetle larvae of *Diamphidia* Gerstaecker and *Polyclada* Chevrolat (Chrysomelidae: Galerucinae: Alticini) collected from soil around the host plants *Commiphora africana* (A. Rich.) Engl. and *Commiphora angolensis* Engl. (Burseracaeae). In the Nyae Nyae area of Namibia, Jul'hoan hunters use larvae of *Diamphidia nigroornata* Ståhl. Larvae and adults live above-ground on the plants and eat leaves, but the San collect the underground cocoons to extract the mature larvae. Larval hemolymph is mixed with saliva and applied to arrows. Haillom hunters boil the milky plant sap of *Adenium bohemianum*

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Schinz (Apocynaceae) to reduce it to a thick paste that is applied to their arrows. The socio-cultural, historical, and ecological contexts of the various San groups may determine differences in the sources and preparation of poisons, bow and arrow technology, hunting behaviors, poison potency, and perhaps antidotes.

Keywords

Hunting, indigenous knowledge, ethno-entomology, Bushmen, arrows

Introduction

Archery appears relatively late in human history and is thought to represent a cognitive shift in human behavior, social organization, and tool-making in the Middle and Late Stone Age (Sisk and Shea 2009; Lombard and Phillipson 2010; Wadley 2011, 2013). Hunting requires great knowledge in observation, intelligence, planning, and skills; hunting technologies also require intensive attention to the environment, materials, learning, and skills (Lombard 2015). Though inadequately studied and poorly understood, the use of poisons on arrows to increase lethality must have occurred shortly after early humans developed bow hunting methods. Today, archery persists in a few indigenous communities around the world, e.g., the Pumè in Venezuela (Greaves 1997); Haddad in Chad (Nicolaisen 2010); Ache in Paraguay (Hill and Hurtado 1989), Hadza in Tanzania (Woodburn 1970; Marlowe 2010), some native North American Indians; and various San communities in southern Africa. Although archery was likely very important to the biological and cultural evolution of humans (Shea 2006; Backwell et al. 2008; Evans 2012) we are losing the opportunity to understand this crucial period because these 'hunter-gatherer' groups, with men responsible for hunting animals and women responsible for gathering fruits, nuts, berries, and tubers, have become progressively more sedentary and the ancient practices are disappearing worldwide.

This paper concerns the arrow poisons used by the Southern African San. The term San (also known as Khoisan, Basarwa, or "Bushmen") covers many indigenous groups using so-called 'click languages' in southern Africa (Barnard 1992; Smith et al. 2000; Hitchcock et al. 2006; Fig. 1; see our Materials and methods below for further notes on San nations). In Africa, the origin of projectile points currently is dated to ~64,000–60,000 years ago, with the oldest from Sibudu Cave, South Africa (Lombard and Phillipson 2010; Lombard 2011). Some of the earliest reported arrowheads are carved bone projectile points that date to ~24,000 years ago, excavated from Border Cave, South Africa (d'Errico et al. 2012; Mitchell 2012). Ancient African rock paintings provide evidence of the use of arrows for hunting and conflict (Vinnicombe 1976). Poison arrows are discussed in ancient mythologies (e.g., Odysseus' helleborepoisoned darts in The Iliad, Homer ~800 BCE, see Scott 1923 and Cupid's arrow in Ovid's Metamorphoses, see Kline 2000) and in ancient religious texts (e.g., the Rig Veda from India (1100-1700 BCE), see Bisset and Mazars 1984). Theophrastus documented use of poison arrows in Africa in the 4th century (Sharples, Huby, and Fortenbaugh 1995).



Figure 1. Map showing contemporary distribution of major San groups in southern Africa (prepared by Marieka Brouwer Burg).

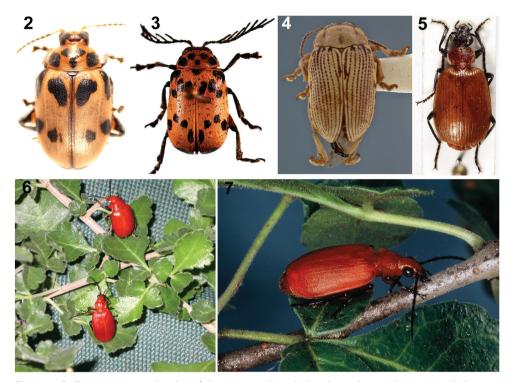
The most commonly used poisons across cultures are extracts from single plants or mixtures of plants (Neuwinger 1996, 1998). South American Indians in the Orinoco Basin use curare, extracted from plants (Loganiaceae: *Strychnos* L.; Menispermaceae: *Chondrodendron* Ruiz et Pavón, *Sciadotenia* Miers (Wintersteiner and Dutcher 1943). Poison dart frogs (Anura: Dendrobatidae) are used by the indigenous Chocó in Colombia (Myers et al. 1978); the frogs secure poison from their insect, mite and millipede prey (Clark et al. 2005; Daly et al. 2005).

Wikar (1779) is the first report of arrow poisons in southern Africa, one made from a "poison worm" by Hottentots along "the Great River" (called Groote River then and the Orange or Gariep River today), and the other made from a milky sap extracted from a tree (*Euphorbia virosa* Willd, Euphorbiaceae). Hunting with poison arrows continues in southern Africa today among a number of different San groups (Fig. 1, Map). The San are a diverse set of peoples, estimated today at 113,000, residing in six southern African countries: Angola, Botswana, Namibia, South Africa, Zambia, and Zimbabwe (Hitchcock et al. 2006; Sapignoli and Hitchcock 2013; Lee 2013). Some San groups still practice limited hunting and gathering, depending on their living conditions, population densities, technology, and the legal context in which they are operating. San use several hunting techniques: pursuit hunting on foot with bows and arrows, spears, or clubs; running down game animals and then dispatching them ("persistence hunting"; see Attenborough 2002; Liebenberg 2006, 2007); hunting from ambush, sometimes with bows and arrows or spears; mounted hunting, usually on horses but sometimes on donkeys, driving animals toward waiting hunters; and hunting with dogs. Noli (1993) provides a comprehensive review of archery in southern Africa. Hunting with guns is rare among most San. In general, the San hunt small game with traps and snares and use poison arrows on large game—antelope, buffalo, cheetah, eland, elephant, gazelle, giraffe, impala, lion, puku, springbok, warthog, wildebeest, and zebra (Campbell (1964, 1968a, b; Parker and Amin 1983; Marks 1977).

Schapera (1925) reviewed the plants, snakes, spiders, and two beetles, Diamphidia simplex Péringuey (now D. nigroornata Stål) and Blepharida evanida (Baly) (now B. vittata (Baly), used for Bushmen arrow poisons; he noted geographic variation in poison formulae and that only the Kalahari Bushmen used the beetles. John Marshall (1958a: 378) reported, "There are four kinds of poison—a root which is rarely used, two grubs, and the pod of a tree. One of the two kinds of grubs is the larva of an unidentified beetle that lives in a bush; the other is the larva of *D. simplex* (now *D. nigroornata*) that lives in certain marula trees (Anacardiaceae: Sclerocarya birrea (A. Rich.) Hochst.). The beetle's identity, however, is complicated by the presence of still a third beetle that apparently lives on the grub of *Diamphidia* complex...Lastly, still a fourth insect—small and hairy...." This third beetle has been identified as Lebistina Motschulsky (Carabidae: Lebiini) whose larva is a parasitoid, killing off the host chrysomelid larva as it develops. Koch (1958) indicated the involvement of multiple insect species belonging to various genera and families; he wrote that "results of all previous knowledge.....will have to be revised" (p 53). During the last 200 years, various sources of poison have been implicated (Table 1). Ethnographic data from Jul'hoansi residing at Tsodilo in the period 1960-2013 indicate that Jul'hoan hunters used Diamphidia poison mixed with Sansevieria juice (Robbins et al. 2012:9, Fig. 2). Robbins et al. (2012:15) summarizes ethnographic research that arrow poisons are derived from the pupae of three beetles that feed on Commiphora africana (A. Rich.) Engl. (Burseraceae) plants-Diamphidia nigroornata (Stål), Diamphidia vittalipensis [sic] (correct name D. vittatipenis Baly), and Diamphidia formalis [sic] (correct name D. femoralis (Gerstaecker)).

Today, the San's bow-and-arrow hunting and attendant tracking knowledge have a mythical status, but the facts of the poison sources and preparations are unclear. Several factors contribute misconceptions, outright errors, and ambiguous information about San arrow poisons. First, the use of the term "Bushmen" for diverse San tribes obscures apparent geographic variation in poison sources, recipes, and preparations. Second, insect taxonomists have rarely been involved in specimen identifications. Third, chemists analyzed specimens with presumed taxonomic identifications and left no specimen vouchers to confirm the species involved.

In this paper, we synthesize the anthropological, entomological, and chemical literature about San arrow poisons. Based on our fieldwork, we report arrow poison sources, their preparation and use, bow and arrow construction, and poison antidotes for the Jul'hoan San in north east Namibia and the Haillom San at Etosha National



Figures 2–7. Arrow-poison beetles of the San people and their host plants (photos: CS Chaboo, or indicated if otherwise). 2 *Diamphidia nigroornata* Ståhl (=*D. simplex* Péringuey, =*D. locusta* Fairmaire), Namibia (Chrysomelidae) 3 *Polyclada* sp. (Chrysomelidae) 4 *Blepharida* sp., Kenya (photo: C Smith, USNM) 5 *Lebistina* sp. (Carabidae) 6 *Diamphidia femoralis* (above) and its predator-parasitoid enemy, *Lebistina* (below), on *Commiphora* plant in South Africa (photo: K Ober) 7 *Lebistina sanguinea* (Boheman) adult beetle on a *Commiphora* plant in South Africa (photo: E. Grobbelaar, SANC, ARC-PPRI).

Park, Namibia. These two ethnic groups represent the largest San groupings in Namibia (Biesele and Hitchcock 2011; Dieckmann et al. 2014). We also summarize what is known about beetle poison use in seven other San groups—the G|ui, G||ana, G||olo, Kua, Naro, Tsila, and X'ao-ll'aen. We note arrow poison by one non-San group—Valley Bisa in Zambia (Marks 1977). Our paper supplements ethno-entomological documentation of the G|ui and G||ana in and around the Central Kalahari Game Reserve (see Fig. 1 map) and the Naro in Ghanzi, Botswana (Nonaka 1996).

Materials and methods

We synthesize literature from anthropology, botany, chemistry, and entomology to develop a better picture of the arrow poisons used by the San in southern Africa. We present novel data and images (Figs 2–17) based on our collective field observations with two distinct San groups, the Jul'hoansi in the Tsumkwe District of northeastern

Indigenous group	Location	Poison (by genus)	Source/Researcher
Basarwa (Naro, G ui,	Bostwana: Ghanzi; Namibia	Beetle: D. nigroornata	De la Harpe et al. 1983; Woollard et al. 1984; Woollard 1986; Kann 1989
G ana, !Ko, !Xóõ)	Botswana	Beetle: D. nigroornata	Koch 1958; Heinz 1966, 1973; Steyn 1971; Heinz and Maguire 1974; Main 1987; Woollard et al. 1984; Woollard 1986
Batwa	Central African Congo Basin	Plants: Eythrophylaeum guineense G.Don (Caesalpiniaceae), Palisota barteri Hook (Commelinaceae) Combretum sp. (Combretaceae)	Parke 1888; Holmes 1888
- u»	Karoo	[Plant: "black wax" [description appears to match <i>Adenium</i> poison]	Stow 1905
Bushmen	Namibia: Grootfontein	Beetle: D. simplex (now D. nigroornata)	Händel and Gildemeister 1912
	Namibia	Beetle: <i>Lebistina</i> sp.	Koch 1958; Mebs et al. 1982
G ui (=Gcwi)	Botswana: Central Kalahari Game Reserve	Beetle: Diamphidia simplex (now D. nigroornata)	Campbell 1968a; Silberbauer 1972, 1981a; Nonaka 1996
	Botswana: Central Kalahari Game Reserve	Beetle: Polyclada flexuosa	Marshall Thomas 1959; Gakelebone, pers. comm.; Sesana pers. comm.
G ana	Botswana: Central Kalahari Game Reserve	Beetle: D. simplex (now D. nigroornata)	Campbell 1968a, b; Nonaka 1996; Gakelebone, pers. comm.; Sesana pers. comm.
G olo	Bostwana: Central Kalahari Game Reserve	Beetle: D. simplex (now D. nigroornata)	Silberbauer 1981a, pers. comm.
Hai om (=Heikum)	Namibia: Etosha Nat. Pk.	Plant: Adenium bohemianum (tuber)	Dieckmann 2007; this paper
Hottentots	? Kaukauveld	Beetle: Diamphidia spp.	Trommsdorff 1911
	Namibia: Otjozondjupa	Beetle: Diamphidia sp.	Böhm 1897; Marshall 1958a, 1976; Lee 1979; Mebs et al. 1982; de la Harpe et al.1983; Green 1998; Chaboo 2011; Robbins et al. 2012
	Namibia: Nyae Nyae	Beetle: P. flexuosa	Oswalt 1973; Green 1998; Leffers 2003
Ju hoansı (= !Kung)	Namibia: Nyae Nyae	Beetle: D. simplex (now D. nigroornata)	Schapera 1925; Breyer-Brandwijk 1937
	Namibia: Nyae Nyae	Beetle: Blepharida evanida	Lewin 1912a, 1923
	Namibia: Gobabis	Beetle: D. nigroornata, D. simplex	Steyn 1957; Bijlsma and De Waard 1957

Table 1. Summary of southern African San groups using poisons on hunting arrows and the source of the poison.

Indigenous group	Location	Poison (by genus)	Source/Researcher
	Botswana	Beetle: Diamphidia sp.	Robbins et al. 2012
	Botswana	Beetle: Diamphidia sp.	Starcke 1897
	Botswana: Tsodilo	Beetle: D. nigroornata, D. vittalipensis [sic] (=D. vittatipennis), D. formalis [sic] (=D. femoralis)	Robbins et al. 2011
		Beetle: D. nigroornata, Diamphidia spp.	Vierich 1981; Hitchcock 1982
		Beetle: Diamphidia spp.	Bartram 1997; Hitchcock & Ebert pers. obs.
Kua	Bostwana	Beetle: Polyclada sp.	Valiente-Noailles 1993
		Beetle: D. simplex (now D. nigroornata), D. nigroornata	Valiente-Noailles 1993; Bartram 1997
Naro (=Nharo, Naron) Botswana, Namibia	Botswana, Namibia	Beetle: Diamphidia sp.	Bleek 1928; Steyn 1971; Guenther 1986; Alan Barnard, Mathias Guenther, Maria Sapignoli, pers. comm.
Shua	Botswana, Zimbabwe	2.	This paper
Tshwa	Botswana, Zimbabwe	4	This paper
Tsila	Botswana: Kweneng	Beetle: D. nigroornata	Vierich, pers. comm.
Valley Bisa	Zambia	Plant: Acokanthera sp.	Marks 1977
≠X'ao-ll'aen (=Makaukau, Auen)	Botswana, Namibia	Beetle: Diamphidia sp.	Tobias 1957; Alan Barnard, Mathias Guenther, Maria Sapignoli, pers. comm.

Namibia, and the Hai||om in northern and central Namibia (see Barnard 1992: 29–61 for Ju|'hoansi and Barnard 1992: 213–219 for Hai||om). Individual data is indicated by author initials [i.e., Caroline S. Chaboo (CSC), Andrea Weeks (AW), Megan Biesele (MB), and RK Hitchcock (RKH)]. Additional collecting of *Diamphidia* and *Polyclada* and their host plants, *Sclerocarya* (Fig. 8) and *Commiphora* (Fig. 9), was done by CSC and a colleague, E. Grobbelaar (Agricultural Research Council, Plant Protection Research Institute, Biosystematics Division), in South Africa.

Symbols in San languages. The San languages reported on here are characterized by sounds that are called clicks. This article is concerned primarily with the Jul'hoansi and the Hai||om (see Lee 2013) and the UN-sponsored site, Written in the Sand, 2015). They have four clicks in their languages; the symbols for these clicks used throughout this text are as follows:

/ (|) Dental click as in G|ui ‡ (‡) Alveolar click as in N‡a Jaqna ! Alveopalatal click (as in !Kung) // (||) Lateral click (as in G||ana).

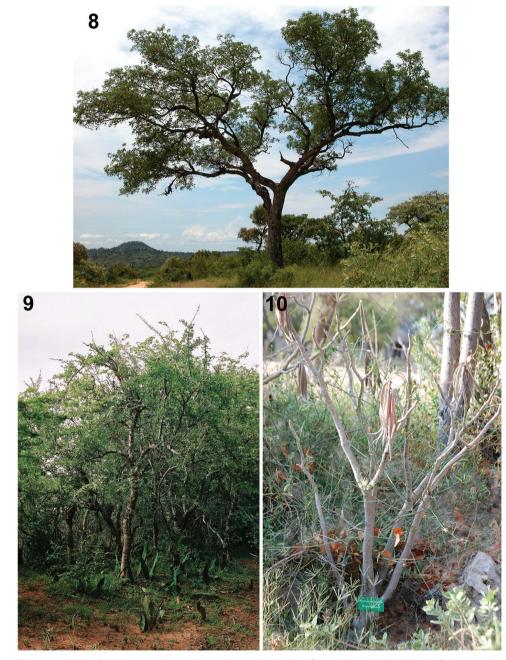
San words for aspects of the poisons and their preparation are available in linguistic dictionaries (see Tanaka 1978; Dickens 1994; Visser 2003).

Data collection. In addition to the Ju|'hoansi, our literature survey revealed beetle poison use by seven other San groups—G|ui, G||ana, G||olo, Kua, Naro, Tsila, and \pm X'ao-||'aen. We summarize these data below. Insect inventories were conducted by CSC in expeditions to Botswana, Namibia, and South Africa (2005–2007), including a field study for three weeks with Hai||om and Ju|'hoan communities in Namibia in October 2007. Hitchcock worked among the Ju|'hoansi in 1987–2015 and Hai||om in 2011–2012. Biesele has extensive experience among the Ju|'hoansi from 1970 to the present.

The landscape of our study. Throughout this manuscript, we refer to the Kalahari. The Kalahari Desert is a basin-shaped plateau extending over northern South Africa, from eastern Namibia, across most of Botswana to southwest Zambia, and southern Angola (Encyclopaedia Britannica 2015). Our data is drawn from our experiences with different communities in different parts of this vast region and our map (Fig. 1) illustrates contemporary distributions of major San groups that have been studied in southern Africa. In this paper we focus mainly on the Jul'hoansi and the Haillom. The former are found in both Namibia (Tsumkwe District) and Botswana (North West District, Ngamiland), and the latter are found in Odangwa, Cunene, and Otjozondjupa Regions. Some groups are not shown because of the history of forced removals of people from their ancestral lands and the small population sizes. An accurate sociolinguistic map of historic and contemporary distributions of southern African peoples is fraught with problems but will be developed as our research expands.

The environmental settings of Nyae Nyae (Namibia) and Tsodilo-Dobe-/Xai/Xai (Botswana) is Kalahari sandveld and consists of tree-bush savanna and pans where

17



Figures 8–10. 8 *Sclerocarya birrea* (Anacardiaceae), South Africa (photos: CS Chaboo) **9** *Commiphora africana* (Burseraceae), South Africa, with *Sanseviera* (Dracaenaceae) at base (photo: E Grobbelaar) **10** *Adenium bohemianum* (Apocynaceae) used as arrow-poison by Hai||om around Etosha National Park, Namibia.

water collects in the rainy season (Yellen and Lee 1976; Marshall 1976: 82–91; Lee 1979: 87–115; Thomas and Shaw 2010). The climate of the area is semi-arid, with a 4–6 month summer rainy season and moderate to cool winters with no rainfall (Yellen and Lee 1976; Thomas and Shaw 2010). Rainfall at Tsumkwe averages 450 mm per annum (range 219.8–627.8 mm; Namibia Meteorological Service data for 1984–2010). One of the unique features of this region is that there are between 15 and 25 permanent waterholes in the *molapos* (lowland areas) that lie between east-west trending sand dunes. Some of these waterholes are pans that are fed either by springs or by rainfall (Marshall 1976: 64; Yellen and Lee 1976: 36). As Yellen (1977: 21–22, 30–31) notes, the pattern in the distribution of dunes and *molapos* or *mekgacha* (low depressions between dunes) is important, as it provides different resource areas within relatively short distances that can be exploited by resident San populations.

Interviews with Hai||om, Namibia. Since 1954 the Hai||om have not been permitted to hunt in Etosha National Park, their original designated homeland. Subsequent displacement, settlement and shifting away from traditional ways have the consequence that hunters are rare and difficult to locate. Seven senior former hunters were interviewed within Etosha National Park, or on private farms south of Etosha, between 18–22 October 2007: Jan Tsumeb, Daniel Apia, Katison Khomob, Willem Dauxab, Fritz Khamuab, Abram Geesep, and Jakes Kamaxab. Interviews lasted several hours and involved a seated conversation and walks to collect specimens. Hunting nowadays is illegal; most informants said they were unaware of any active traditional hunters, but recalled their own hunting days or that of their fathers and uncles. Three elderly male Hai||om informants discussed their own hunting in their younger days, and pointed out traditional plants within the park. No poisons or arrows were prepared during the Hai||om interviews (this would have been illegal).

Interviews with Ju|'hoansi, Namibia. The Ju|'hoan communities together form a politically self-regulated body in the Nyae Nyae Conservancy. The region is part of the savanna biome, and is ecologically arid with brush or grass, almost no trees, and ranges from flat to gently hilly (Mendelsohn et al. 2009). Temperatures can be below freezing during winter and over 100°F in summer. The Ju|'hoansi live in small grass huts or rondavels (round adobe constructions with thatched roofs). Communities comprise 10–100 people living semi-permanently in some 36 villages around or near boreholes used for water. They are scattered throughout the area within one or more days of walking, the most common form of travel regionally. Today, men are still hunters where allowed and women are still the primary gatherers but more commonly both men and women carry out subsistence farming of maize, melons, beans, pumpkins, and other crops and some care for domestic animals and poultry.

The three-person field team, led by CSC, traveled to Tsumkwe (19°35'34.99 S, 20°30'07.99 E) in 2007, and then spent two weeks travelling to 10 villages scattered in the Nyae Nyae Conservancy. In each village, current and former hunters were interviewed, with questions presented by CSC in English and translated by team members (in German, Afrikaans, and Oshiwambo) or by native San speakers (three cases). Hunters are traditionally male; we did not encounter or hear of female hunters. With-

in 30 minutes of our arrival, most community members had surrounded our group, inserting comments from time to time, the senior women in particular correcting or debating details.

Twelve hunters were interviewed in Nyae Nyae Conservancy: Leon ‡oma Tsamkao, Tsumkwe Lodge; Trechie (‡Nlundi Village, Aha hills, 9–10 Oct 2007); Andreas (N|ama Village, 11 Oct 2007); Xushe Sao (N|ama Village, 11 Oct 2007); David Sao Iui (N|ama Village, 11 Oct 2007); /aice N!aucu (Xamsa Village, 11 Oct 2007); |aice ‡oma (Tambuti Village, 11.Oct.2007); G|aq'o ‡oma (Tambuti Village, 11.Oct.2007); N!aici Kaqece (Makuri Village, 12.Oct.2007); Kaqece Ikaece (Makuri Village, 12.Oct.2007); N!aici Kaqece (Makuri Village, 12.Oct.2007); and N!aici ‡oma (Tsumkwe Lodge, 14.Oct.2007). Interviews were conducted over one or two days. Each involved an initial interview, followed by a walk in the desert with the informants to look for the host plants and beetles; digging up beetle larvae (Fig. 11); returning to camp to prepare arrow poisons (Figs 16–17); and complete the interview. Each poison and arrow preparation session produced 10–20 arrows [>150 arrows observed in total]. Some reports indicate the Jul'hoan word for the poison beetle is "Nga" or "N'gwa" (Livingstone 1858; Livingstone and Livingstone 1865; Schapera 1925; Breyer-Brandwijk 1937; Woollard et al. 1984), but our informants indicated that the word is "kua".

Author MB has worked among the Jul'hoansi since 1970, and served as director of the Nyae Nyae Development Foundation of Namibia from 1988–1992. She and RKH collected data about hunting and the use of poison from 46 people in 1987, 1992, 1995, 2001, and 2011–2014.

Interviews with Ju|'hoansi, Bostwana. RKH collected data from 56 interviews in Dobe, /Xai/Xai, Tsodilo in the years 1976, 1978–1982, 1985, 1988, 1992, 1995, 1997, 1999–2000, 2005, and 2011–2013. Hunters' names are omitted here to protect their identities.

Interviews with G|ui, G||ana, Kua, and Tsila, Bostwana. RKH has conducted >140 interviews in about 15 visits (1976–2013) with these communities from the central and eastern Kalahari, many specifically on hunting. These data were collected in the Central Kalahari Game Reserve or in the resettlement sites outside the Reserve.

Taxonomic identifications. Due to the diversity of scientific names for plants and beetles used herein, our generic names are abbreviated to avoid confusion (Aca. = *Acacia*; Ade. = *Adenium*; Aco. = *Acocanthera*; Bob. = *Bobgunnia*; Comm. = *Commiphora*; Euph. = *Euphorbia*; Sans. = *Sansevieria*; Scl. = *Sclerocarya*).

Hai||*om poison plant.* Many former hunters indicated the poison plant on multiple separate occasions as *Adenium bohemianum* Schinz (Apocynaceae) (Fig. 10), which they call *!kores.* They confirmed the plant from photographs in our regional plant guides or by pointing out planted specimens in nearby gardens, including labeled plants in the educational garden of the Research Unit, Etosha National Park. Several members of the Apocynaceae are the source of latex, particularly from the roots, that are boiled and used as indigenous arrow poisons across Africa (Karimi 1973; Omino and Kokwaro 1993). For example, *Adenium obesum* (Forssk.) Roem. and Schult. is used as both a fish and arrow poison (Watt and Breyer-Brandwijk 1962; Gerhadt and Steiner 1986) and



Figures 11–17. Arrow-poison beetles of the Jul'hoansi, Tswumke Conservancy, Namibia (photos: CS Chaboo). **11** Typical collecting for beetle cocoons at base of a *Commiphora* shrub in the drip line **12** Ostrich egg-shell full of cocoons of *Diamphidia nigroornata* ab. *locusta* **13** Parasitoid carabid larva (left) and *Diamphidia* larva (right) extracted from collected cocoons **14** Cleaned 4th instar *Diamphidia* larva extracted from collected in cocoon **16** Squeezing the contents of leaf beetle larvae onto giraffe bone to prepare arrow poison **17** Typical hunting implements, quiver, bow, fire-sticks, and arrows.

an undetermined *Adenium* species is used as an arrow poison by the Hadza of Tanzania (Bartram 1997). Plant taxonomic names used herein follow the online catalogue of plant names, PlantZAfrica (http://pza.sanbi.org/). The two chrysomelid host plants are identified as belonging to the Burseraceae, using Steyn's (2003) key: *Commiphora africana* (A.Rich.) Engl. (poison-grub *Commiphora* which has true thorns) and *Commiphora angolensis* Engl. (sand *Commiphora* which lacks thorns).

Beetle identifications and vouchers. CSC obtained beetle specimens in several ways: receiving gifts of cocoons from informants from their stored supplies, collecting them with informants on bush walks, and purchasing containers from hunters' stored supplies (e.g., Fig. 12). More than 5,000 cocoons were accumulated by CSC during field-work in Namibia; she also conducted nightly light-trapping to sample flying adults. Five hundred cocoons were dissected in the field to determine the beetle species and their life stages.

Beetle species were identified by examination of types and as part of a taxonomic review of specimens from museum collections in France, Germany, South Africa, and the USA. The chrysomelid beetle species in the Namibian Jul'hoan arrow-poison case is *Diamphidia nigro-ornata* Ståhl (Figs 13–15; see Bryant 1942). Chrysomelid taxonomy follows Biondi and D'Alessandro (2012) who distinguished *Diamphidia* and *Polyclada* on the basis of antennal morphology—filiform in *Diamphidia* and pectinate or flabellate in males or serrate in females of *Polyclada*. Many synonyms for species of these genera appear in the historical literature. Heikertinger and Csikii (1940) is the last catalog of alticine flea beetles, but the last reviser of these species names was Bryant (1942) who indicates these synonyms for *D. nigroornata*: *Diamphidia lesnei* Achard, *Diamphidia locusta* Fairmaire, and *Diamphidia simplex* Péringuey.

Dissected cocoons revealed mostly larvae, some pupae, and some adults of leaf beetles. About 5% of the coccoons held only mature parasitoid carabid larvae (Carabidae: Lebiini; Fig. 13); but no adult carabids were found so we cannot be certain this is *Lebistina*. Carabid taxonomy follows the online catalog of Anichtchenko (2015).

Beetle vouchers are deposited in the collections of the National Museum of Namibia (NMWN, Windhoek), the American Museum of Natural History (AMNH, NYC), Agricultural Research Council, Plant Protection Research Institute, South African National Collection of Insects(ARC-PPRI, SANC, South Africa), and the University of Kansas Entomology collection (SEMC, KS, USA). John Irish, National Botanical Research Institute, Namibia, confirmed the identity of the plants.

Results

Our cross-disciplinary synthesis of historial literature, reports of anthropologists, and our own collective fieldwork in southern Africa indicates that beetle arrow poison is used by seven San groups—the G|ui, G||ana, G||olo, Naro, Kua, and Tsila in Botswana, and the Hai||om in Namibia. Two San groups, the Shua and Tshwa from the north-eastern Kalahari of Botswana and Zimbabwe, do not use arrow poisons. One San group, the Hai||om, uses a plant poison. The Valley Bisa in Zambia is a non-San group that uses beetle arrow poison. Our research focused primarily on two large San groups, Hai||om and Ju|'hoansi, in Namibia but we assemble data for other smaller communities. Kiema (2010: 22–36) used the generic term Kua to refer to G|ui, G||ana, G||olo, Tsila, and all of the groups in the Central Kalahari region (our Fig. 1 map does not indicate a location of the G||olo as we have not found maps with this information). We follow the usage of Hitchcock (1978), Vierich (1981), and Valiente-Noailles (1993) who restrict the term Kua to the people of the eastern and southeast parts of the Central Kalahari. Since these diverse San nations are so poorly known, we briefly summarize the location, contemporary status, and knowledge of arrow poisons below.

The G|ui and G||ana, Botswana (Fig. 1). They live nowadays in the Central Kalahari Game Reserve, Botswana. Both groups have been the subject of forced evictions after the Botswana government removed them from the Central Kalahari in 1997 and in 2002 (Hitchcock et al. 2011). Modern G|ui and G||ana, have become progressively more sedentary (Osaki 1984, 2001; Ikeya 2001; Tanaka 2014). Some do still hunt with the aid of bows and poisoned arrows, although this has decreased significantly due to governmental restrictions. Nonaka (1996) report that G|ui, G||ana, and Naro use *D. simplex* (= *D. nigroornata*) for their arrow poison, but it is not clear how she identified the beetle species.

Campbell (1968a) briefly described Glui and Gllana hunting with poison arrows. The arrows were lightweight, constructed in three detachable sections, and with little flight that necessitated the hunter getting close to his target. Campbell (1968a) indicated that poison was obtained from the pupae of *D. simplex* (= *D. nigroornata*), which were crushed and glued to the sinew around the haft of the arrow with plant gum. The arrow head was then dried over hot coals. This may be the earliest record of beetle poison use by Glui. Campbell (1968a, b) reported that fresh poison worked faster, but that arrows were only active for about six months. Since the beetles are supposedly available seasonally (-2 months), the G|ui apparently had no poison for part of the year. Silberbauer (1965, 1972, 1981a, b) provided more details about the Gluicocoon collection, poison from the larvae of D. simplex (= D. nigroornata), bow and arrow materials, and poison preparation. These broadly resemble those used by other San, but certain details raise doubts. We note the extended life cycle of Diamphidia, with a long underground phase, which permits digging up larvae and pupae at any time of the year; this cast doubt on Campbell's reports (1968a, 1968b) that G|ui had no poison for part of the year. We also wonder about 'flaming the arrowhead', which should theoretically deactivate certain toxins (Nonaka 1996).

Thomas (1959: 94–97) described the arrow poison preparation of people she terms the Gwikwe (=G|ui). The poison was derived from grubs, extracted from underground cocoons; she drew attention to the similarity of the life cycle with that of *D. simplex* (= *D. nigroornata*), as used by the Ju|'hoansi. She described two different colored pupae in these cocoons, which the Gwikwe regarded as male (a small, yellow, black-headed pupa with poison only in the legs) and female (a larger orange pupa with poison throughout the body). She may have been observing different stages of matu-

rity of the 4th instar larva of the chrysomelid and the *Lebistina* parasitoid. This poison was applied directly to the arrow shaft.

In the Central Kalahari, according to our G|ui and G||ana informants, the beetle that is used for arrow poison is *Polyclada flexuosa* (Baly). The larvae and adults feed on the leaves of marula trees (*S. birrea*) (Jumanda Gakelebone, Roy Sesana, pers. comms. 2011–2013); pupation is likely to be in the soil around the host as in other species we have studied.

The Kua, Botswana (Fig. 1). The Kua (~7,500 people) practice part-time foraging and sedentary agro pastoralism; many work as herders with local cattle owners, and are dependent on government drought feeding and destitution relief programs (Vierich 1981). Their hunt involves poison from the "nymph" of *Polyclada* associated with *S. birrea* (Valiente-Noailles 1993) and of *D. nigroornata* known from *C. africana* (Valiente-Noailles 1993; Bartram 1997). Valiente-Noailles (1993) described Kua poison preparation, with 8–12 grubs squashed together with saliva on a mortar, then smeared unto the binding behind the arrowhead. The arrow was then air-dried. Bartram (1997: 326–327) wrote only of a *Diamphidia* species from a *Commiphora* host, but specified the rubbing of larval tissue directly onto the arrow shaft, which was then heated to dry. Observations of Kua in the eastern-Kalahari in 1975–1976, by Hitchcock and Ebert, revealed that they made poison from beetles and from 'spider's nests' (Hitchcock and Ebert, field data); they assumed that the beetle identification was *D. nigroornata*. Vierich (pers. comm. 2014) indicates that alternative plants were used when beetles were unavailable, however she did not confirm the identity of these plants.

In the east-central Kalahari, arrow poisons were used until the late 20th century. James Chapman, who visited Nkawane in this area in 1852, notes that the Bushmen there used bows, arrows and spears (Chapman 1971). He noted that the Bushmen killed elephants with spears, but he does not say whether or not poisons were used in elephant hunting. Based on observations made in 1850 in the eastern Kalahari, Schulz and Hammar (1897: 84) indicated that Bushmen used arrow poison "obtained from the juice of poisonous herbs and roots" and poisonous snakes.

The Naro (Nharo, Naron), Botswana and Namibia (Fig. 1). The Naro (~8,000 people) are a Khoe-speaking people that form the largest and most diverse set of San populations in western Botswana, stretching westwards into Namibia (Bleek 1928; Barnard 1976; Guenther 1986). They are located on the harder Ghanzi Ridge, but they are also found working on farms in northern Ghanzi and south of Ghanzi (Barnard 1992: 134–155). They use *Diamphidia* beetles for arrow poison (Bleek 1928; Steyn 1971; Guenther 1986; Nonaka 1996), but how the beetles were identified is not specified.

The Tsila, Botswana. The Tsila (~500 people) are found in the Central Kalahari Game Reserve, in the Northern Kweneng District and the eastern Central District. Vierich (pers. comm. 2014) observed their use of arrow poison derived from *D. ni-groornata* and an unidentified plant.

The Tshwa and Shua, Botswana and Zimbabwe. Ethno-historic evidence suggests that poisoning of arrows is uncommon among these San groups, living in the north-eastern Kalahari. Hodson (1912: 227) made the following observation "The Bushmen

in this district are called Mashuakue, their headman being Kotama . . . They do not use the bow and poison arrow so common with Bushmen in the far Kalahari, but carry long assegaais [light spear], with which they stalk game. Some have rifles and are good shots at a close distance." Detailed fieldwork with Tshwa and Shua (about 4,000 people), beginning in 1975, revealed that spears were the most common weapon used, along with clubs and guns of various kinds (Crowell and Hitchcock 1978; Hitchcock and Bleed 1997; Hitchcock et al. 2014). Tshwa who were forcibly moved to the eastcentral Kalahari in the 1950's by Bamangwato cattle owners, picked up the use of bows and poisoned arrows from the neighboring Kua (Hitchcock 1978).

The Valley Bisa, Zambia. Marks reported on his 1973 observations of Valley Bisa hunts in Zambia (1977, pers. comm.). Hunters stalked up to large game before letting an arrow fly, a distance that was further than that for shotguns and even rifles. Their tactic was to stay slightly beyond the species 'flight distance' (distance before the prey flees), force the herd into a smaller space, and then arc the arrow to fall within the anticipated space. They did aim to get closer to some individual mammals (e.g., warthog). The arrows only had to lance the animal to get poison into the blood stream, but the wounded prey normally did not move very far away. Marks found that hunters used two different types of arrows for mammals and for birds, both poisoned with an extract made of pods and roots from an *Acokanthera* sp. (Apocynaceae; identified by biologists at University of Zambia; Marks 1977).

The $\pm X'ao-\parallel'aen$ (=Makaukau, Auen), Botswana and Namibia. The $\pm X'ao-\parallel'aen$ San (~7,000 people) are sometimes called Makaukau or Auen (Schapera 1930: 33). They are found in the northern and southern parts of Ghanzi District (Groot Laagte, Kuke, D'Kar, Hanahai), Botswana and into the Omaheke region, eastern Namibia (Otjinene, Skoonheld, Donkerbos, Gobabis). The $\pm X'ao-\parallel'aen$ use *Diamphidia* beetles for arrow poison (Maria Sapignoli, Job Morris, pers. comms., 2012, 2013, 2014).

The Haillom (=+Akhoe) in Namibia. The Haillom (11,000–15,000 people) is the largest and most widely distributed San population in Namibia (Widlok 1999; Dieckmann 2007; Koot 2013; Dieckmann et al. 2014; Hitchcock 2015). They Haillom comprise different sociolinguistic groups according to linguists, anthropologists, and to the Haillom themselves (Hahn et al. 1928; Dieckmann 2007: 112, Table 4.1) and generally speak the Haillom language, part of the Khoe family of languages (Rapold and Widlok 2008). The Haillom and ‡Akhoe were affected significantly by South West African and later Namibian policy relating to conservation and hunting. Etosha, which is considered by the Haillom to be their ancestral homeland, was declared off limits in 1954 by the Department of Nature Conservation (Dieckmann 2007: 189-199; Suzman 2004; Friederich 2014: 60-69; Hitchcock 2015). Hunting laws restricted Haillom and ‡Akhoe hunting practices. The vast majority of Haillom today have mixed economic systems, combining a small amount of foraging with wage labor, some gardening, and food obtained from the government of Namibia as part of social safety net programs. Hunting is not done openly but relatively few Haillom continue to hunt with bows and poisoned arrows (Widlok 1999; Dieckmann 2007; Peters et al. 2009; Kadison Khomob, pers. comm., 2012).

The Ju|*'hoansi in Namibia.* The Ju|'hoansi represent one of the earliest-diverging lineages of modern humans (Knight et al. 2003; Tishkoff et al. 2009; Mitchell 2010a; Pickrell et al. 2012; Schlebush et al. 2012) and are therefore some of the best-documented peoples on the planet as they have been studied intensively and over a long period, since the early 1950s (Marshall and Ritchie 1984; Marshall 2003; Marshall 1976: Lee and DeVore 1968; Lee 1968, 1978, 2013). Although they may not be the only, or the best model, of human's hunting and gathering past, in some ways their history is very enlightening. Most Ju|'hoansi retain their language, culture, and many of their traditions till today. They have been able to secure some of their land and resources through advocacy, working with the Namibian government and non-governmental organizations (Biesele and Hitchcock 2011; Lee 2013). The Ju|'hoansi are the only indigenous people in Africa who still have the right to hunt for subsistence purposes using their traditional weapons. Some Ju|'hoansi continue to hunt with poisoned arrows, and they attempt to teach their young about finding poison materials, preparing the poison, and putting it on arrows. The Ju|'hoansi are, therefore, well-placed for the investigation of the use of arrow poisons.

San hunting. Bushmen tracking culture is well documented (Stander et al. 1997; Liebenberg 2000, 2001; Biesele and Barclay 2001). Indeed, San trackers were employed by opposing colonial militia in various conflicts (Lee and Hurlich 1982; Gordon and Douglas 2000; Guenther 2005). San participated also in fighting, sometimes using bows and arrows. One of the biggest fears of people with whom they had conflicts, such as settlers, was being struck by a poisoned arrow (Gordon and Douglas 2000; Hitchcock, Sapignoli, and Babchuk 2015). Lee (2003: 115) observed that a man hit with a poison arrow died, despite incisions made around the point of arrow entry to drain the poison. The most common weapon in family quarrels, suicides, homicides, and warfare has been poisoned arrows. The victim can die within one day if the wounded limb is not amputated (J. Marshall 1958b; newspaper citations). In addition to hunting for food, hunting has much prestige in the San community (Wiessner 2002; Marshall 1961, 1976; Lee 1972, 1979, 2013) and hunters are respected highly. Arrows are seen as having social and religious significance among 19th and 20th century San peoples in southern Africa (Wiessner 1983, 1984; Deacon 1992). Hunters learn how to make bows, arrows and poisons from older relatives (Wiessner 1983, 1984) and children use smaller bows and arrows in play. Today, poisoned arrows may be shared or traded among hunters (Lee 1984; L. Marshall 1976; CSC observations with Namibian Jul'hoan informants) and are used as a ritual gift between husband and wife, who can form marital hunting partnerships (Biesele and Barclay 2001). Women can own arrows and thus, sometimes oversee meat distribution.

Hunts can last several days depending on the animal's size and the slow paralysis by the poison. The tracks and spoor of the fleeing animal helps the hunter decide to immediately start stalking or return to the community to gather materials (e.g., water, food) and other men to help with the hunt. Animal tracks and dung inform the hunter about the size (size of footprint), species (nature of print), age (depth of foot print), wound (one side of foot prints heavier than other size), and travelling direction of the prey (Campbell 1968a; Liebenberg 2001; Lee 2003).

Biology of arrow poison beetles

Beetles from the following genera appear in the literature as the source of a "Bushmen" arrow poison (Table 1):

Chrysomelidae (leaf beetles): Galerucinae: Alticini (flea beetles): Blepharida-group:

- *Diamphidia* Gerstaecker (17 described species in genus; Biondi and d'Alessandro 2012; example Fig. 2)
- *Polyclada* Chevrolat (16 described species in genus; Biondi and d'Alessandro 2012; example Fig. 3)
- *Blepharida* Chevrolat (only from the subgenus *Blepharidina* Bechyné) (73 described species in genus; example Fig. 4)

Carabidae (ground beetles): Lebiini:

Lebistina Motschulsky (12 described species in genus; examples Figs 5-7).

Prathapan and Chaboo (2011) summarized the life cycle, biology and known host plants of the Blepharida-group. Blepharidines typically have large colorful adults (~1 cm); eggs are deposited in clusters on host plants, coated with fecal material; larvae that feed on host plant leaves, retain a fecal coat and eventually descend to the ground where they form a sandy underground cocoon; here they remain in a suspended larval stage, ready for pupation. The cycle from egg to adult can span 2-4 years; the underground phase is prolonged as a probable adaptation to unpredictable rainfall. Blepharidines tend to show generic-level specialization on certain plant families—Anacardiaceae, Apocynaceae, Burseraceae, Caesalpiniaceae, Clusiaceae, Eleaocarpaceae, Fabaceae, Lythraceae, Meliaceae, Moraceae, Theaceae, and Verbenaceae. Field reports of Diamphidia and Polyclada agree with the general blepharidine life cycle (Koch 1958; J. Marshall 1958a). Silberbauer indicated that the G wi San were knowledgeable about some details of the beetle life cycle (larvae, migration to the drip line of host plants for pupation), but they were less informed about the adults, even mistaking them for shield bugs (Hemiptera: Pentatomidae; Silberbauer 1981). CSC confirmed that most cocoons are found at the drip line of *Commiphora* host plant shrubs in Namibia (Fig. 11).

Arrow poison of the Ju|'hoansi, Nyae Nyae, Namibia. Locating host plants. Informants indicated that they learnt about the locations of *Commiphora* host plants from older hunters. Once the low-branching *Commiphora* shrubs are located, the hunter initiates a new hole at the leaf-drop (=drip line) margin of the shrub; in some cases, ditches of previous digs (past years) were still apparent and our informant jumped into the 1m deep ditch and extended the ditch to encircle the plant. We observed some ditches forming a complete moat around plants. Ju|'hoan traditionally use a wooden digging stick (e.g., of the widespread Kalahari Christmas tree, *Dichrostachys cinerea* (L.) Wight & Arn. (Fabaceae) (Leffers 2003), but metal pipes are more commonly used today. Green (1998: 5) reported that Ju|'hoan hunters "take measures to protect Marula trees by building fire breaks around them during the dry season" and that the indigenous word for the larva is "loan/aqro". *Sclerocarya birrea* (marula) was indicated as the host plant of *Polyclada*, one of the arrow poison beetles (Leffers 2003), but CSC found none of these trees in the Nyae Nyae conservancy. *Collecting poison beetles*. The hunter sifts the loosened sand with his fingers, straining out the ~1 cm long, ovalshaped cocoons (Figs 11–13, 15). When sufficient cocoons have been collected into an ostrich egg shell (Fig. 12) or plastic container, the hunter returns home.

Beetle poison preparation. What follows is our typical observation compiled after 12 interviews with hunters who each made their poison with our observation. First, he arranges his tools, stabilizing an old giraffe or kudu knuckle bone with the concave surface facing upwards in the sand in front of him and placing the beetle cocoons nearby. A small fire is lit; traditionally a fire stick was used, usually made of Commiphora pyracanthoides Engl. (Burseraceae) (Leffers 2003), but nowdays a cigarette lighter is used. He breaks open a cocoon and taps out the single larva; non-larval forms (adults, pupae) are discarded. The larva is then rolled between his fingers, loosening the inner tissues from the integument. Using a stick as a pestle, he rubs hard against the skin to loosen tissue, then extracts it to mix on the bone mortar (Fig. 16); about 10 larvae are used per arrow. He chews the bark of Acacia mellifera (Vahl) Benth. (Fabaceae) to produce saliva which is mixed with the larval tissue and hemolymph. Published accounts of similarly chewed extracts list the plants used as: Aca. mellifera, Asparagus sp. (Asparagaceae), the bark of Boscia albitrunca (Burch.) Gilg & Gilg-Ben. (Capparaceae) (Leffers 2003), and Ziziphus mucronata Willd. (Rhamnaceae) (Roodt 1993). A bean of Bobgunnia madagascariensis (Desv.) J.H.Kirkbr. & Wiersema (Fabaceae) is heated over the fire, cooled, and added to the poison mixture. An unidentified toxic bean (J. Marshall 1958a) and the bean of Bob. madagascariensis (Leffers 2003) appear as ingredients in some poison recipes. Jul'hoan informants at Xai Xai in Botswana told Hitchcock that they use the juice of Sansevieria plants to improve the poison.

CSC observed that the 'beetle paste' of *D. nigroornata* larva is applied with a twig to the dried sinew that fastens the arrowhead to the wooden shaft; the hunter never touches the poison mixture. The arrows are then propped up against a log or hung up to air dry, and stored in a quiver made of the bark of the root of *Acacia luedertizii* Engl., False umbrella thorn (Fabaceae) (Leffers 2003). Finally, the hunter cleans his hands with loose sand. Different San groups squeeze *Diamphidia* beetle tissue directly onto the shaft of the arrow (see photographs in Campbell 1968a and Chaboo et al. 2007). Hunters indicated that cocoons or prepared poison arrows may be traded with hunters in other communities.

Literature sources reported that saliva made by chewing the bark of *Dicerocaryum* eriocarpum (Decne.) Abels (devil's thorn) (Pedaliaceae) or the leaf of *Sansevieria ae-thiopica* Thunb. (Asparagaceae), are used to moisten the poison if it dries out (Leffers 2003: 87). The efficacy of the poison has been reported to last from three months (Green 1998) to two years (Clark 1975). Lee (1979: 137) reported that the high initial potency declines over time, and is essentially harmless after a year. Others report it to decline seasonally (Hitchcock et al. 2015).

Ju 'hoan bow and arrows. Arrows are constructed of grass reed (shaft), metal (arrowhead, blade), sinew for tying (from kudu), and glue (resin of *Aca. mellifera* obtained by damaging the bark) or beeswax (/aice ‡oma, pers. comm., Tambuti Village, 12 Oct. 2007). Bows are made from the wood of *Grewia flava* DC (Malvaceae). Leffers (2003: 34, 187) indicates that the shaft is from grass, *Andropogon gayanus* Kunth (Poaceae), and the glue is gum from *Terminalia sericea* Burch. ex DC. (Combretaceae).

Preparation for the hunt. CSC did not interview hunters about personal preparations before a hunt or special charms to accompany them. It is known that some rituals are performed to protect the hunter, improve his focus, and increase the hunt's success. Leffers (2003) reports applications of plant extracts, including powders from roasted fruits and stems of *Ceropegia distincta* N.E.Br. subsp. *lugardae* (N.E.Br.) H.Huber (Apocynaceae), *Pavonia burchellii* (DC.) R.A.Dyer (Malvaceae) and chewing of plants (he also indicates a *Maerua* Forssk. sp. (Capparaceae)). He also reports avoidance of, or throwing sand at, plants of *Orbea huillensis* (Heirn) Bruyns (Apocynaceae), so as not to spoil the hunt (Leffers 2003: 150).

Anti-venoms for beetle poison. The following are considered as anti-venoms: a melon (informant Xushe Sao, 11 October 2008); liquid from *Sans. aethiopica* (Asparagaceae) (Leffers 2003: 170); and gemsbok cucumber, *Acanthosicyos naudinianus* (Sond.) C. Jeffrey (Cucurbitaceae) (Leffers 2003: 25).

Beetle poison chemistry and effect. After the earliest report by Wikar (1779) of insect and plant poisons and soon after by Paterson (1789) of snake and plant poisons, a century followed of murky identifications of the San poison. Almost 60 years later, Livingstone (1858: 189) added more details about the insect and plant poisons he observed; one involved a caterpillar ("N'gwa") squeezed onto the arrow and allowed to dry and the other was milky sap of a Euphorbia L. (Euphorbiaceae) (cited also by Stow 1905). Andersson (1861) reported that poisoned arrows were used in fights with the Ovambo and Ovaquangari, in addition to hunting. Baines (1864) was the first to determine that the "caterpillar" reported by travellers was actually the larva of a beetle that the San squeezed unto arrows. Livingstone and Livingstone (1865) mentioned and illustrated arrows with plant and animal poisons of different peoples along the Zambesi. Passarge (1907) mentioned poison sticks, with "a lump of acacia gum drenched in arrow poison"; in this same text, he also reported two different poisons that were physically distinguishable as a dark-brown mass from a plant and light-brown dots of larval body fluid. Cornell (1920) mentioned Kalahari Bushmen arrow poisons derived from spiders, insects, a *Euphorbia* plant, and putrefying vertebrate corpses (death by lockjaw).

The next century saw different chemists examining residues on arrows or extracts of specimens sent to them and testing for hemolytic and toxic activity on various cells, tissues and live animals—fishes, frogs, birds (pigeons, sparrows), mice, cats, dogs, goats, rabbits, guinea pigs, and sheep (Böhm 1897; Starcke 1897; Heubner 1907; Händel and Gildemeister 1912; Lewin 1912a, 1923; Stigand 1913; Lewin 1923; Schapera 1925; Hall and Whitehead 1927; Pawlowsky 1927; Breyer-Brandwijk 1937; Steyn 1957; Bijlsma and De Waard 1957; Kündig 1978; De la Harpe and Dowdle 1980; Mebs et al. 1982; De la Harpe et al. 1983; Woollard et al. 1984; Kao et al.

1989; Jacobsen et al. 1990). Scientific attempts to verify the identity and nature of diamphotoxin, the identity of the beetles and their life stages, the host plants, and the recipes of poison preparation were unevenly documented, and led to further confusion about what was the poison being used by which San group. Schinz (1891) was first to observe the larval association with the host plant, C. africana. He sent beetle specimens to the French coleopterist, Fairmaire, who described it as a new species, Diamphidia locusta (Fairmaire, 1893), which is now considered a chromatic form of D. nigroornata (see Bryant 1942). Later, Schultze (1907: 663) indicated "worms" at the roots of Commiphora dinteri Engl. Lewin (1912a) reported that Bushmen and Hottentots used a kind of caterpillar, combined with extracts of a *Euphorbia* species and Lewin (1912b) reported *B. evanida* (Baly) and *Blepharidella lewini* Weise as possible sources of arrow poison. Rarely, a few field researchers provided more reliable information. For example, Trommsdorff's (1911) fieldwork in "Kaukaufeld....with Hottentots" provided the first photographic illustration of three beetle species (adults and larvae) used for poison. No taxonomic identification was given in the text, but the adult beetles in their photograph plates have filiform antennae and are thus Diamphidia species. By 1864, the general view was that a beetle was involved (Baines 1864).

As chemists explored the nature of the poison, the taxonomy for the poison also evolved. Shaw et al. (1963) was the first major synthesis about the sources, preparation and the chemistry of 'Bushmen' arrow poisons. In addition to Steyn's (1949) ~ 300 poisonous plants known from South Africa, they reported 16 different plant species in the genera *Acokanthera* G.Don, *Adenium* Roem. & Schult., *Euphorbia* L., *Haemanthus* L., *Hyaenanche* Lamb. & Vahl, *Pachypodium* Lindl., *Swartzia* Schreb., *Solanum* L., *Strophanthus* DC., and *Strychnos* L., and 15 different animal-derived arrow poisons, obtained from beetles, scorpions, spiders, and snakes that were used as arrow poisons by different 'Bushmen' groups from Central to southern Africa.

The beetle poison has been identified as a protein and referred to as a toxalbumin (Shinz and Böhm 1894; Böhm 1897; Starcke 1897; Breyer-Brandwijk 1937), diamphidia toxin (Breyer-Brandwijk 1937), and diamphotoxin (De la Harpe et al. 1983). Its effect has been explained as interfering with cell membrane by modulating calcium concentration (Kündig 1978), causing an influx of Ca²⁺ ions (Jacobsen et al. 1990); the affected animal exhibits massive hemolysis, convulsions, paralysis, then death (De la Harpe and Dowdle 1980; Mebs et al. 1982). Because of the high toxin concentration in the "pupa" compared to that in the adult, De la Harpe et al. (1983) suggested that diamphotoxin must have some functional role in this life stage, but it was unclear how autolysis was prevented. Diamphotoxin protein may be similar to toxic insect proteins found in tiger moths (Rothschild et al. 1970; Hsiao et al. 1980) and to leptinotarsin from the beetle, Leptinotarsa Chevrolat (Hsiao and Fraenkel 1969; Snyder 1971; Parker 1971, 1972; Satin et al. 1978; Hsiao 1978; McClure et al. 1980; Madeddu et al. 1985a, b; Miljanich et al. 1988). Leptinotarsa (subfamily Chrysomelinae) is phylogenetically distantly related to the galerucine *Blepharida*-group. The protein, leptinotarsin, also kills animals. It is unknown if leptinotarsin and diamphotoxin are related—evolutionarily, biogenetically, structurally, or in effects. Kann (1989) developed a protocol to purify diamphotoxin to facilitate the sequencing of its amino acid structure, but indicated the need to refine the protocol to obtain larger pure samples. At this point, a comprehensive and systematic approach to examining all life stages of all the *Blepharida*-group beetles for similar toxic activity will be useful to understanding the origin and biology of this remarkable protein.

Is the Lebistina parasitoid a source of arrow poison? This African carabid genus comprises 12 described species (Anichtchnko 2007–2014). Carabidae are commonly called ground beetles because they are generally ground-dwellers; however, Lebistina belongs to the tribe Lebiini, an evolutionary branch that has evolved a free-living first instar larva (technically called a triungulin). The lebiine first instar larva searches for host prey, attaches to it for feeding and in so doing becomes an ectoparasitoid which eventually kills its host (see Weber et al. 2008). Koch (1958) identified six different species of Coleoptera in the cocoons dug up by the "Bushmen" and suggested that the host plant, chrysomelid herbivores, and the Lebistina parasitoid formed trophic chains, where the "composition of the toxins and degree of toxicity may differ in each of these six [beetle] species". It is remarkable, but not unknown, that some insects appropriate offensive or toxic chemicals from their prey. Koch's (1958) concept has been perpetuated in the literature, implying that the San consider the parasitic *Lebistina* larva as more toxic than its chrysomelid host (e.g., Mebs et al. 1982; Lindroth 1971; Valiente-Noailles 1993; Neuwinger 1996). Koch (1958) indicated that only 1% of the chrysomelid cocoons collected contained a Lebistina larva. In our fieldwork, we dissected 500 Diamphidia cocoons and found mainly chrysomelids (many larvae, few pupae, few adults), few spiders, and only three carabid larvae (Fig. 13). Our Jul'hoan informants used only chrysomelid larvae for poison preparation, discarding chrysomelid pupae and adults, and any other species. Chemistry assessments of Lebistina have not been done. Given the low level of parasitoidism that we observed, we conclude that it is very unlikely that the San use such rare larvae for poison and we will not discuss *Lebistina* as a poison source further.

Arrow poison of the Hailom, in and around Etosha National Park, Namibia

Andersson (1856) indicated that the Ovaherero used milky-white, gummy extracts of *Euph. candelabrum* as poison on their arrows, whereas the Hill-Damaras used these extracts to poison pools where game animals drank (e.g., buffalo, p. 242). Böhm (1890) analyzed an extract of *Ade. bohemianum* that was sent to him in Leipzig, Germany—identified as the arrow poison of the Bergdamara from north Damaraland and the Ovambo in Kaoko. The Bergdamara bought the plants from the Ovambo, who called it 'exuja.' Böhm (1890) extracted and crystallized a poisonous glucoside from this 'exuja,' for which he coined the term 'echujin' and described it as a genuine resin. He tested its effects on frogs, rabbits, cats, and a dog, all of which died. This led him to conclude that 'echujin' was a cardiac poison, like digitalis. Böhm's (1890) report is the only one we found showing the trade or sale of poison between different ethnic communities of San.

Dornan (1925) and Schapera (1925) indicated that various "Bushmen" groups used several different plant species in the genera, *Acokanthera*, *Haemanthus*, *Buphane*, and *Euphorbia*, depending on geographic location. Livingstone and Livingstone (1865) mention poisoned arrows throughout their narrative and illustrated them (p. 466); they described the poison of natives in the upper cataracts of the Zambesi as an extract ("kombi) from the plant *Strophanthus* that felled most game except elephant and hippopotamus. We found Sands et al. (2011) to be the only recent indication of *Strophanthus* as a poison, used by the **‡** Hoan in the western Kweneng District, Botswana.

Hall and Whitehead (1927) studied the bows, arrows, and moving film of Hai||om, collected by CE Cadle on his 1925 Denver African Expedition. They reported the plant poison to be that from *Euphorbia*, but suggested that the Hai||om may use different poisons (p 55). They scraped the poison off the arrows and followed Fuller's (1920) protocols for studying another deadly toxin, namely strophanthin. The extracts they prepared killed frogs and cats; further chemical analyses conducted targeted alkaloids and glucosides. They referred to the poison as "ouabain" but the reason for this is unclear as they did not conduct comparative chemistry with other ouabain arrow poisons, known to be widely used in Africa (Burton 1856; Castellani and Chalmers 1919; Clark et al. 1975; Maitai et al. 1973).

Our finding of *Ade. bohemianum* as the source of Hai||om arrow poison confirms three previous reports (Steyn 1957; Neuwinger 1996; Peters et al. 2009). Steyn (1957) indicated that the Bushmen he worked with were aware of the chrysomelid larvae, but considered this poison to kill prey too quickly. They apparently preferred the slower-acting poison from *Ade. bohemianum*, but Koch (1958) was unable to confirm this. Our Hai||om informants had never heard about the beetles and laughed about the "Bushmen" (Ju|'hoan) using such [silly] things. They also did not mention ouabain as a plant poison.

Given the findings of poison on hunting implements at Sibudu Cave, an intriguing data point comes from Stanford (1909) which may be the only account of poison prepration of the San living the Drakensberg Mountains, South Africa. The San chief prepared poison by boiling the root of a shrub with the bark of a tree in a clay pot for several days. The Drakensberg area has over 35,000 cave paintings (Mitchell and Smith 2009), but no San were believed to live there. Today, there is a group in the Drakensberg Mountain region, the Abatwa (Zulu word for San) who believe that they are descendants of the San who lived in the region in the 19th century (Francis 2009; Prins 2009).

Plant poison preparation. Among the seven hunters interviewed, only one eventually admitted to hunting illegally and showed us his hunting gear—including poisoned arrows. According to our seven informants, tubers of *Ade. bohemianum* are dug out, cut into pieces, and the inner plant tissue is scraped into a cup using an animal bone. This is then boiled for "a long time" until it becomes a thick black glue that is applied to the arrows. In addition to our observations, other methods of poison preparation and application appear in the literature. Grubs are dried, ground and mixed with saliva or plant sap (Stigand 1913) or living larvae are squeezed to apply the entrails directly to the arrow-head (Breyer-Brandwijk 1937; Chaboo et al. 2007).

Discussion

Our discussion is organized around three topics below: bow and arrow technology, Jul'hoan beetle poison (source and pharmacology), and Hai||om plant poison (source and pharmacology).

Comparison of Namibian San bows and arrows. It is beyond the primary focus of this paper to discuss San arrow technology in detail, however it is important to pay attention to subtle aspects of design that might inform which poison source was adopted by the community. The use of poisons to increase the lethality of arrows and increase the success of a hunt must surely have impacted the design of bows and arrows, and therefore has implications for human cultural evolution. Hall and Whitehead (1927) found that the arrows of three San groups in Namibia—Haillom, Jul'hoan and Ovachimba (= ova-Himba) were made of different woods and other materials; they have different sizes and weights (Goodwin 1945; Clark 1975). The arrow poison was visible as a thin shellac on the Haillom arrows, but not on the Jul'hoan arrows. The Haillom bows and arrows came in two sizes, both being larger and heavier than those of the Jul'hoan. We found Jul'hoan arrows to have a three-part construction, matching Hall and Whitehead's (1927) description; our informants indicated that the metal arrowhead (as opposed to carved stone of past times) entered the prey, and the other two parts detached and fell to the ground on impact-thus notifying the hunter that his arrow had hit the prey. Marshall Thomas (1959) commented that the arrow release was different between the Jul'hoansi and the Gwikwe, suggesting subtle differences in archery styles, however Deacon (1984) proposed that stylistic differences may be a modern phenomenon.

We observed some modern impacts on Jul'hoan bows and arrows (Fig. 17). Wood and stone arrowheads were replaced a long time ago by arrowheads crafted from metal (Wiessner 1983; Robbins et al. 2012). We observed nails and fencing wires being pounded into arrowheads. In one community we saw an old can being used to mix the poison, instead of the traditional giraffe knuckle bone. Several hunters were using PVC pipe containers, instead of bark-derived quivers; Bartram (1997) also mentioned plastic quivers. Some hunters remarked on the efficiency of a gun, but indicated a preference for arrows because they were quiet and did not startle the animals, causing them to run away.

In their illustrated description of Hai||om arrows, Hall and Whitehead (1927) noted that there were two sizes made from the wood of *Grewia* (Malvaceae) or *Cordia* (Boraginaceae) (Peters et al. 2009), with partially stripped feathers on the shafts. Peters et al. (2009) reported three different-sized Hai||om arrowheads, one of which is poisoned with the boiled latex of *Ade. bohemianum*. None of the Hai||om we interviewed admitted to hunting with guns but Widlok (1999) reported instances of Hai||om poaching with guns on commercial farms along the northern border of the Etosha National Park. Gun hunting is not common among the Namibia San for various reasons—guns are hard to come by; hunting with guns is illegal in much of Namibia; it is difficult to obtain ammunition; and people often prefer quieter hunting methods.

Source of beetle poison. The life stages used by the San to obtain their poison have been reported as the larva and pupa, but all the past chemists who worked with material did not collect the specimens themselves and could not distinguish larva from pupa (e.g., De La Harpe et al.'s (1983) photograph of a "pupa" is actually a larva). Breyer-Brandwijk (1937) found that both larvae and cocoons show chemical activity, suggesting that the larva secretes poison in its cocoon. De la Harpe et al. (1983) also indicted lower concentrations of diamphotoxin in the adult. It is possible that all the beetle life stages have diamphotoxin, but the unevenness of historical studies raise uncertainty about both the identity of the beetle and the identity of the active ingredient. The synthesis of diamphotoxin is unexplored; chrysomelids could either sequester chemicals from their host plants, using them as precursors, or manufacture the chemicals de novo. Both Burseraceae and Anacardiaceae have diverse secondary chemicals (Daly et al. 2011; Pell et al. 2011) and have well-documented ecological interactions with blepharidine beetle species (e.g., Becerra 1993, 2004). The accuracy of past species determinations is questionable; none of the chemical work acknowledges how beetles were identified and no specimen vouchers were retained. Castellani and Chalmers (1919: 180) proposed the actual killing agent to be the microbes growing in the rotting larvae of *D. simplex* (= *D. nigroornata*), e.g., tetanus carried on arrows elsewhere (Hall and Whitehead 1927). These ideas, along with the confusing taxonomy of Blepharida, Diamphidia, and Polyclada, leave open questions about which species and genera are poisonous.

Based on our specimen collections of larval, pupal and adult stages (we did not collect egg stages) with the Ju'hoansi San at Nyae Nyae, we determine those beetles as *Diamphidia nigroornata*. Bryant (1942) indicates several species names as synonyms of *D. nigroornata*. Other researchers have photographed poison beetles used in the Nyae Nyae region and which are a different species from our sample. Thus, several *Diamphidia* species are used for poison.

Morphology-based revisions of these genera are now underway to test species concepts. Molecular methods are required to link different life stages with adults, to identify the larvae being used as poison. Linking the life stages and the host plants is crucial to clarifying which beetle is being used by which local San community.

Effect and pharmacology of beetle poison. The corpus of chemical studies of the last 200 years point to a highly toxic basic peptide, called a toxalbumin (Böhm 1897; Hall and Whitehead 1927), and diamphotoxin (coined by De la Harpe et al. 1983) that only works by entering the blood stream (Marshall 1958b: 379) and affects cell membrane permeability and electrolyte balance (e.g., De la Harpe et al. 1983), causes tissue hypoxia (Kao et al. 1989), neurotoxicity (Starcke 1897; Woollard et al. 1984), rapid and severe lysis of red blood cells, and hemoglobinuria (excessive loss of red blood cells through urine). One early outcome is a slow paralysis (Breyer-Brandwijk 1937) then death by renal failure, but the cause of death apparently varies according to the injection site, absorption rate, and dosage. Chemical analyses and equipment have changed a lot since many of the historical studies were done. Modern analyses and comprehensive targeting of the various beetles, along with the host plants, would

help greatly in unambiguously answering outstanding questions and doubts about the San arrow poison beetles.

Comparison of diamphotoxin and leptinotoxin. The speed, impact, and lethal nature of diamphotoxin recalls another toxic leaf beetle molecule, leptinotoxin, isolated from adults of *Leptinotarsa haldemani* Rogers in North America (Chrysomelidae: Chrysomelinae) (Crosland 1982; Crosland et al. 1984; Maddedu et al. 1985a, b; Miljanich et al. 1988). Chemists working on diamphotoxin and leptinotoxin in the mid-1980's were apparently unaware of each other's work, and did not compare these two protein toxins from relatively closely-related beetle taxa. Leptinotoxin seems to target calcium channels and is neurotoxic. Diamphotoxin on the other hand kills by hemolysis with a combination of tissue hypoxia and neurotoxicity. A comprehensive modern chemical analysis must be done to discern any relationship in genesis, molecular structure, and mode of action between leptinotoxin and diamphotoxin.

Beetles are known for other potent chemistry. For example, cantharidin or "Spanish fly", extracted from meloid beetles, *Lytta vesicatoria* (L.) (Meloidae) (inaccurately referred to as *Cantharis vesicatoria* (Cantharidae) in some publications), was known to the ancient Chinese and Greeks as an aphrodisiac (Karras et al. 1996; Moen et al. 2001). Such toxic chemicals in beetles play a central role in the formation of parasitic and mimicry relationships, e.g., between true *Cantharis* and *Lytta* and the secondary toxicity of their predators, such as poison frogs and birds (Dumbacher et al. 2004; Clark et al. 2005). Some predators appropriate offensive or toxic chemicals from their prey: dart frogs in Colombia (Myers et al. 1978), tiger keel back snake in Japan (Hutchinson et al. 2007), poison rat in Somalia (Kingdom et al. 2011), and poison birds in New Guinea (Dumbacher et al. 2004). As a parasitoid, *Lebistina*, could be sequestering chemicals of its hosts, *Diamphidia* and *Polyclada*; their similar body form and coloration certainly suggest a model of Müllerian or Batesian mimicry (Fig. 6).

San ethno-entomology. In addition to the beetle poison, the San collect and eat other insects, but reports are scattered. We did not conduct a complete ethno-entomological inventory of the Haillom and Jul'hoan as we believe that the degree of settlement and diversion from their traditional nomadic lifestyle would probably distort such data. However, we summarize here what other insects are used by the San. These are collected and eaten, dependent on seasonal outbreaks and swarming: certain caterpillars (e.g., Mopane worms (Saturniidae: Gonimbrasia belina Westwood = now Imbrasia belina) (Roodt 1993; Leffers 2003) and other lepidopteran species (Passarge 1907); grasshoppers (see Samuel Daniel's 1805 painting in Preston (1989); Passarge 1907; Marshall J. 1958a; Marshall L. 1961; Osaki 2001); termites (Bleek 1928; Bjerre 1958; Peters et al. 2009); sugary lerps secreted by jumping plant lice (Psyllidae) (Livingstone 1858: 182); locusts (Peters et al. 2009); bee honey (Marshall Thomas 1959; Peters et al. 2009); click beetles (Lee 1972); and winged ants (Stanford 1909; Lee 1972; Marshall Thomas 1959). Some insects are eaten roasted-caterpillars and grasshoppers (Passarge 1907; Chaboo, pers. observ.) and termites (Bleek 1928). The African honeybee is aggressive, so honey collection is an activity that is approached with caution (Marshall Thomas 1959). Fieldwork is needed to determine the full selection of insects that different San groups utilize as food sources.

Source of Hailor plant poison. The angiosperm genus Adenium Roem. and Schult. (Apocynaceae) comprises five species: A. bohemianum Schinz, A. multiflorum Klotzsch, A. obesum (Forssk.) Roem. and Schult., A. oleifolium Stapf, and A. swazicum Stapf. All species are limited to sub-Saharan Africa with the exception of A. obesum whose range extends into the Arabian Peninsula and Socotra. Four Adenium species, as currently circumscribed by Plazier (1980), have relatively narrow geographic ranges in southern or tropical East Africa (A. bohemianum, A. multiflorum, A. oleifolium, and A. swazicum). However, taxonomists prior to Plazier (1980) have treated three of these species as varieties of either A. obesum (A. multiflorum, A. oleifolium) or A. bohemianum (A. swazicum). Moreover, the wide distribution of A. obesum spurred a number of heterotypic species descriptions in the past and those names are now considered taxonomic synonyms (e.g., A. honghel, A. somalense) yet they remain in use, albeit incorrectly. Consequently, one may be prevented from verifying which Adenium species a particular ethnographer, natural historian or chemist reported or investigated, even if the identification was made correctly, due to the malleable taxonomic species concepts in this genus.

At least 29 different glycosylated cardenolides ("glycosides") have been isolated from *Adenium* species (Yamauchi and Abe 1990), and some have well-documented effects on cardiac cells and are referred to as cardiac glycosides. These include, but are not limited to, digitalin (=gitoxigenin 3-O-glucosyldigitaloside), honghelin (=digitoxigenin b-D -thevetoside), and somalin (=digitoxigenin b-D-cymaroside). Like *Adenium* species names, cardenolide nomenclature contains synonyms that are used interchangeably by authors, making cross-comparisons a challenge (Harbourne et al. 1999). Phytochemical description of species may be overly general; for instance, stating that a species contains "digitoxigenin" does not indicate the component sugar that modifies the cardenolide and is not a precise chemical reference. Yamauchi and Abe (1990) reported two pregnanes from *Ade. obseum* (neridienone A and 16,17-dihydroneridienone); these steroid-derived compounds are similar to animal hormones such as cortisol.

The angiosperm genus *Acokanthera* G. Don (Apocynaceae) comprises five species: *Aco. schimperi* (DC.) Schweinf., *Aco. oppositifolia* (Lam.) Codd, *Aco. laevigata* Kupicha, *Aco. rotundata* (Codd) Kupicha, and *Aco. oblongifolia* (Hochst.) Codd. All species are limited to East Africa, with the exception of *Aco. schimperi*, which ranges from tropical East Africa into the Arabian Peninsula. *Acokanthera oppositifolia* ranges from tropical East Africa to the south-eastern coast of South Africa. The remaining three species have narrower ranges that overlap with that of *Aco. oppositifolia*. The nomenclatural history of these taxa is too lengthy to be summarized here, although two illegitimate names bear explication. The name *Aco. ouabaio* (alternatively spelled *Aco. wabajo*) is a synonym of *A. schimperi*; its epithet is both a European adaptation of the Somali word for this taxon (Kupicha 1982), and is the basis for the name given to the highly toxic cardiac glycoside extracted from this and other *Acokanthera* species—ouabain. The name *Aco. longiflora* is a synonym of *Aco. oppositifolia*; publications enumerating other

cytotoxic cardiac glycosides (acovenoside A, acolongifloroside K) from the genus use this name (Kingston and Reichstein 1974; Cassels 1985).

The angiosperm genera Sclerocarya (Spondoideae; Anacardiaceae) and Commiphora (Bursereae; Burseraceae) derive from closely-related families of resinous, woody trees and shrubs that produce a range of toxic phenolic compounds and terpenoids respectively. These compound mediate plant-herbivore interactions. One compound, alkylcatechol (e.g., urushiol) may cause severe allergenic responses in vertebrates, especially humans, but acute toxicity of these compounds appears to be limited to invertebrates. Sclerocarya birrea is commonly cultivated for its edible fruit and bark whose decoction is used for medicinal purposes. As a member of the Spondoideae, it lacks the toxic phenolic compounds (e.g., biflavonoids, alkylcatechols and alkylresorcinols) (Aguilar-Ortigoza and Sosa 2004) that mediate insect interactions as they do in other anacardiaceous genera (e.g., Calophya and Schinus, Burckhardt and Basset 2000). Nevertheless, reports of the "insecticial" properties of its leaves, bark, and fruits do suggest that Scl. birrea has effective chemical defenses, such as high-levels of tannins or flavonoids, that have been documented in its tissues (Prinsloo and Street 2013). Commiphora species including Comm. africana and Comm. angolensis, produce gum-oleoresins in stem, leaf, and fruit tissues, that may contain a range of volatile and non-volatile compounds, predominantly terpenoids, with well-documented biological activities (Langenheim 1994). Volatile compounds documented for Commiphora, such as the monoterpenes pinene and limonene, the sequiterpene cadiene, and the phenolic compound eugenol, are known to be toxic to insects (Langenheim 1994, 2003). The resins of some species, including that of Comm. africana, are used by indigenous people to repel termites and ticks. Other compounds have an effect on human physiology: sesquiterpenes that interact with the brain's opiate pathways producing an analgesic effect, and guggulsterones lower the blood lipid content. Phytochemical assays of Commiphora species have uncovered a range of unexpected compounds, including phellamurin, which is a dihydroflavonal that mediates butterfly oviposition on Rutaceae (Ma et al. 2005).

What is ouabain? Different authors have used 'ouabain' to describe the toxic latex from plant sources—Acokanthera, Haemanthus, Buphane, and Euphorbia (Arnott 1853; Burton 1856; Hilton et al. 1865; Bolton 1906; Castellani and Chalmers 1919; Fuller 1920; Hall and Whitehead 1927; Reichstein 1965; Cassels 1985). The term is widely used in Africa, from the southern San to the Maasai in Kenya. There is even a plant with the specific name Acokanthera ouabaio (Franch. et Poiss.) Cathel. and there are compounds called "ouabain equivalents" (Neuwinger 1974a, b). Acokanthera trees and shrubs are a widely-used source of arrow poison and some species are known to have several cardenolides (e.g., Kingston and Reichstein 1974); ouabain may be a cardiac glycoside. In western Zimbabwe, the Matopos Bushmen make arrow poisons from Aco. oppositifolia (David Cummings, pers. comm. 2014). Acokanthera is also used by the Bemba and the Gwembe Tonga in Zambia (Ted Scudder, pers. comm. 2014) and Bushmen in southern Zimbabwe, the bark of the root of Aco. oppositifolia is used as a poison and as a means of ensuring that the poison stays on their arrow or spear. Aco. oppositifolia is more widespread in southern Africa than *Aco. oblongifolia*, which is limited to coastal areas. *Acokanthera schimperi* ranges from Bulawayo to Plumtree, western Zimbabwe. Both the Ndebele and Bushmen in western Zimbabwe claimed that their ancestors used *Aco. oppositifolia* and *Aco. schimperi* for poisoning projectiles (Parry 2007; Hitchcock et al. 2014). Some Bushmen also said that they used snake poison (e.g. from mamba, cobra, and puff adder) combined with *Aco. oppositifolia* and *Aco. schimperi* as a binding agent. The efficacy of the poison is varied; some informants said that arrow poison took 'a few minutes to a few hours' to kill a springbok or impala, from 8–10 hours to kill an eland, and 1–3 days for a giraffe. Parker and Amin (1983) report that the Wata, from the Tsavo area, Kenya, use *Acokanthera*-poisoned arrows to hunt elephants.

Potential pharmacology of San arrow poisons. It is fair to ask if highly toxic compounds like diamphotoxin, Adenium extracts, and other indigenous poisons have pharmaceutical potential. The San have experience with pharmaceutical bio-prospecting. They are known to chew pieces of the Hoodia "cactus" plant (Apocynaceae: Hoodia gordonii (Masson) Sweet ex Decne., 1844) to suppress hunger and thirst for long treks. In 1997, the South African Council for Scientific and Industrial Research (CSIR) licensed the UK-based company, Phytopharm, to develop a natural drug. Phytopharm then worked with Pfizer to commercialize and market a drug with the active ingredient, P57. The international outcry led the South African San Council to a court battle with these companies, and eventually to a landmark agreement to share profits with the San Hoodia Benefit Trust (Kahn 2002; www.scienceafrica.co.za/2003/may/san. htm, accessed 25 July 2014). Thus, any exploration of the pharmacology of arrow poisons must be discussed with the San community.

Conclusions

Under a harsh and drying climate across southern Africa, the San emerged and diversified into numerous distinct communities. Their survival has depended on a profoundly intimate knowledge of their environment-the distribution of all resources (water, tubers, animals) and the availability of the few material resources they keep (e.g., plants for temporary huts, digging sticks, bows and arrows; ostrich eggs for water and pupae; sources of poisons). Under specific local conditions, isolated communities appear to have developed their own specialized poison use and preparation. We have confirmed the species and life stages used as arrow poisons for two San groups, Haillom and Jul'hoan, and documented their poison preparation methods. Ethnological data collection such as ours, including the collection of terms in the local vernacular, can open new avenues of research about variations in ecology, fauna and flora. Differences in material culture, due to individual/group style and/or area-specific patterns, sensu Wiessner (1983, 1984), may apply to bow and arrow construction and poison preparation. Through this prism we should also expect variations, innovations, and evolution in music, dance, stories, self-decoration, and material culture. However, we propose that the ecological boundaries of the poison cultural practices are severely demarcated,

and the poison beetle practice may be strongly conserved, because of the crucial role it plays in food acquisition.

The hunter-gatherer phase of human evolution originated about seven million years ago, and today persists in a few cultures that are fast disappearing under the wheels of modern life. Bow and arrow hunting, a hallmark of hunter-gatherer living, is considered obsolete by some and has become illegal, neglected, or abandoned. Today hunting with traditional weapons is legally permitted only in the Nyae Nyae Conservancy, Namibia. The loss of San cultural knowledge is a proxy for multiple losses—of the environmental context of certain practices (e.g., which plants are nutritious, deadly, or medicinal), of languages, and in transformation of technology (e.g., from blow-darts to guns). Active Hai||om hunters are rare, reflecting their historical eviction from their Etosha homeland in 1954 (Suzman 2004; Dieckmann 2007) and the illegal status of their traditional hunting. Ju|'hoan traditional hunting is maintained today because they have a self-governing conservancy where they can hunt. In these two San communities knowledge is not being passed on to younger generations to sustain future practices.

While the term "San" describes many indigenous groups that share tongue-clicking languages, it is important to keep in mind that there are many sub-cultural differences among these communities. Such subtle differences exhibit the richness of indigenous human societies, provide insight into key innovations in early human behavior, and reflect the ecological context that drives the origins and diversification of traditions and practices. Confusing nomenclature of San communities, their plants and plant compounds, and the beetles and beetle compounds has led to errors in identifications and communication among scientists within and across disciplines. Although these San communities live short distances apart, their arrow poisons are diverse, pointing to an incredibly intimate knowledge of their environment. The discovery of arrow poisons was a significant evolutionary step for humankind, yet we may be facing the last opportunity to document arrow-poison use in southern African hunter-gatherer societies.

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References

- Aguilar-Ortigoza CJ, Sosa V (2004) The evolution of toxic phenolic compounds in a group of Anacardiaceae genera. Taxon 53: 357–364. doi: 10.2307/4135614
- Andersson CJ (1856) Lake Ngami or Explorations and Discovery during Four Years of Wanderings in Wilds of South-Western Africa. Harper and Brothers Publishers, New York, 521 pp.
- Andersson CJ (1861) The Okawango River, a Narrative of Travel, Exploration and Adventure. Harper and Brothers Publishers, London, 414 pp.
- Anichtchnko A (Ed.) (2007–2015) Carabidae of the World. http://carabidae.org/ [accessed 13 July 2015]
- Attenborough D (Presenter) (2002) Life of Mammals. Film, BBC Natural History Unit and Discovery Channel. http://www.youtube.com/watch?v=826HMLoiE_o
- Backwell L, d'Errico F, Wadley L (2008) Middle Stone Age bone tools from the Howiesons Poort layers, Sibudu Cave, South Africa. Journal of Archaeological Science 35(6): 1566–1580. doi: 10.1016/j.jas.2007.11.006
- Baines T (1864) Explorations in South-West Africa, being an account of a journey in the years 1861 and 1862 from Walvisch Bay, on the western coast, to Lake Ngami and the Victoria Falls. Longman, Green, Longman, Roberts and Green, London, 535 pp.
- Baldwin WC (1863) African hunting from Natal to the Zambesi, including Lake Ngami, the Kalahari Desert, etc. from 1852–1860. Harper and Row, New York, 387 pp.

- Barnard A (1976) Nharo Bushman Kinship and the Transformation of Khoi Kin Categories. PhD Dissertation, University of London.
- Barnard A (1992) Hunters and herders of Southern Africa: A comparative ethnography of the Khoisan Peoples. Cambridge University Press, New York, Cambridge, 349 pp. doi: 10.1017/CBO9781139166508
- Bartram LE Jr (1997) A comparison of Kua (Botswana) and Hadza (Tanzania) bow and arrow hunting. In: Knecht H (Ed.) Projectile Technology. Plenum Press, New York, 321–343. doi: 10.1007/978-1-4899-1851-2_13
- Becerra JX (1993) Synchronous coadaptation in an ancient case of herbivory. Proceedings of the National Academy of Sciences 100(22): 12804–12807. doi: 10.1073/pnas.2133013100
- Becerra JX (2004) Ecology and evolution of New World *Blepharida*. In: Jolivet P, Santiago-Blay J, Schmitt M (Eds) New contributions in biology of the Chrysomelidae. Kugler Publications, The Hague, 137–143.
- Biesele M, Barclay S (2001) Jul'hoan women's tracking knowledge and its contribution to their husband's hunting success. In: Tanaka J, Ichikawa M, Kimura D (Eds) African Hunter-Gatherers: Persisting Cultures and Contemporary Problems. African Study Monographs, Supplementary Issue 26: 67–84.
- Biesele M, Hitchcock R (2011) The Jul'Hoan San of Nyae Nyae and Namibian independence: Development, democracy, and indigenous voices in southern Africa. Berghahn Books, New York, 269 pp.
- Bijlsma UG, de Waard F (1957) 'n Pylvergif van die Boesmans in Suid Afrika. South African Medical Journal 31: 115–118.
- Biondi M, D'Alessandro P (2012) Afrotropical flea beetle genera: a key to their identification, updated catalogue and biogeographical analysis (Coleoptera, Chrysomelidae, Galerucinae, Alticini). ZooKeys (Special issue) 253: 1–158. doi: 10.3897/zookeys.253.3414
- Bisset NG, Mazars G (1984) Arrow poisons in south Asia. Part 1. Arrow poisons in ancient India. Journal of Ethnopharmacology 12(1): 1–24. doi: 10.1016/0378-8741(84)90084-9
- Bjerre J (1958) Kalahari Atomidens Stenalder. Carit Andersens Forlag, Copenhagen, 227 pp.
- Bleek DF (1928) The Naron: A Bushman tribe of the central Kalahari. Cambridge University Press, Cambridge, 67 pp.
- Böhm R (1890) Ueber das Echujin. Ein Beitrag zur Kenntniss der afrikanishen Pfeilgifte. Archiv für Experimentelle Pathologie und Pharmakologie 26: 165–176.
- Böhm R (1897) Ueber das gift der larven von *Diamphidia locusta*. Archiv für Experimentelle Pathologie und Pharmathologie 38: 424–427. doi: 10.1007/bf01824739
- Bortels A (1994) A cation-selective channel induced by two protein fractions from the larval haemolymph of the Colorado potato beetle, *Leptinotarsa decemlineata*. Physiological Entomology 7: 370–386.
- Breyer-Brandwijk MG (1937) A note on the Bushman arrow poison, *Diamphidia simplex* Péringuey. Bantu Studies 11: 279–284. doi: 10.1080/02561751.1937.9676056
- Burckhardt D, Basset Y (2000) The jumping plant-lice (Hemiptera, Psylloidea) associated with Schinus (Anacardiaceae): systematics, biogeography and host plant relationships. Journal of Natural History 34(1): 57–155. doi: 10.1080/002229300299688

- Burton RF (1856) First Footsteps in East Africa: Or, an exploration in Harar. Longman, Brown, Green, and Longmans, London, 648 pp. [available via Project Gutenburg]
- Bryant GE (1942) New species of *Polyclada* (Coleoptera, Halticinae) from Africa. Proceedings of the Royal Entomological Society of London (series B) 11: 161–165. doi: 10.1111/ j.1365-3113.1942.tb00716.x
- Campbell AC (1964) A few notes on the Gcwi Bushmen of the Central Kalahari Desert, Bechuanaland. Nada 9(1): 39–47.
- Campbell AC (1968a) Gcwi Bushmen: Some notes on hunting with poisoned arrows. Botswana Notes and Records 1: 95–96.
- Campbell AC (1968b) Central Kalahari Game Reserve: II. African Wildlife 22: 321.
- Cassels BK (1985) Analysis of a Maasai arrow poison. Journal of Ethnopharmacology 14: 273–281. doi: 10.1016/0378-8741(85)90094-7
- Castellani A, Chalmers AJ (1919) Manual of Tropical Medicine, 3rd edn. Bailliere, Tindall and Cox, London, 2425 pp. doi: 10.5962/bhl.title.84653
- Chaboo CS (2011) Defensive behaviors in leaf beetles: from the unusual to the weird. In: Vivanco JM, Weir T (Eds) Chemical Biology of the Tropics: an interdisciplinary approach. Springer-Verlag, Berlin, Heidelberg, 59–69. doi: 10.1007/978-3-642-19080-3_4
- Chaboo CS, Grobbelaar E, Larsen A (2007) Fecal ecology in leaf beetles: novel records in the African arrow-poison beetles, *Diamphidia* Gerstaecker and *Polyclada* Chevrolat (Chrysomelidae: Galerucinae). The Coleopterists Bulletin 61(2): 297–309. doi: 10.1649/0010-065X(2007)61[297:FEILBN]2.0.CO;2
- Chapman J (1971) Travels in the Interior of South Africa 1849–1863. Hunting and Trading Journeys from Natal to Walvis Bay, and Visits to Lake Ngami and Victoria Falls. In: Tabler EC (Ed.) AA Balkema, Cape Town, 451 pp [Vol. 1], 480 pp [Vol. 2].
- Clark JD, Philips JL, Staley PS (1975) Interpretations of prehistoric technology from ancient Egyptian and other sources (Part I) Ancient Egyptian bows and arrows and their relevance for African prehistory. Paléorient 2(2): 323–388.
- Clark JD (1975) Interpretations of prehistoric technology from ancient Egyptian and other sources (Part II) – Prehistoric arrow forms in Africa as shown by surviving examples of the traditional arrows of the San Bushmen. Paléorient 3: 127–150. doi: 10.3406/ paleo.1975.4193
- Clark VC, Raxworthy CJ, Sierwald P, Fisher BL (2005) Convergent evolution of chemical defense in poison frogs and arthropod prey between Madagascar and the Neotropics. Proceedings of the National Academy of Sciences of the United States of America 102: 11617–11622. doi: 10.1073/pnas.0503502102
- Cohen DR (2009) Histories of the Subaltern from the Kalahari's Fringe, Botswana. PhD Thesis, University of California, Berkeley, CA, 285 pp.
- Cornell FC (1920) The glamour of prospecting: Wanderings of a South African prospector in search of copper, gold, emeralds, and diamonds. T. Unwin Fisher, London, 334 pp.
- Crosland RD (1982) Purification and characterization of LPT-h, a protein that opens presynaptic calcium channels. PhD Thesis, University of California, Berkeley, CA, 139 pp.

- Crosland RD, Hsiao TH, McClure WO (1984) Purification and characterization of beta-leptinotarsin-h, an activator of presynaptic calcium channels. Biochemistry 23(4): 734–741. doi: 10.1021/bi00299a023
- Crowell AL, Hitchcock R (1978) Basarwa ambush hunting in Botswana. Botswana Notes and Records 10: 37–51.
- Heikertinger F, Csikii E (1940) Pars. 166: Chrysomelidae: Halticinae I. In: Schenkling (Ed.) Coleopterum Catalogus. W. Junk, S'Gravenhage, 635 pp.
- Daly D, Harley C, Martínez-Habibe M-C, Weeks A (2011) Burseraceae. In: Kubitzki K (Ed.) The Families and Genera of Vascular Plants (Vol. 10). Springer-Verlag, New York, 76–104.
- Daly JW, Spande TF, Garrafo HM (2005) Alkaloids from amphibian skin: a tabulation of over eight-hundred compounds. Journal of Natural Products 68(10): 1556–1575. doi: 10.1021/np0580560
- Deacon J (1984) Later Stone Age people and their descendants in southern Africa. In: Klein RG (Ed.) Southern African prehistory and paleoenvironments. A.A. Balkema, Rotterdam, 221–228.
- Deacon J (1992) Arrows as Agents of Belief amongst the /Xam Bushmen. South African Museum, Cape Town, 21 pp.
- De la Harpe JH, Dowdle EB (1980) Isolation and characterization of diamphotoxin. South African Journal of Science 76: 428.
- De la Harpe JH, Reich E, Reich KA, Dowdle EB (1983) Diamphotoxin the arrow poison of the !Kung bushmen. Journal of Biological Chemistry 258(19): 11924–11931.
- d'Errico F, Backwell LR, Villa P, Degano I, Lucejko J, Bamford M, Higham T, Colombini MP, Beaumont P (2012a) Early evidence of San material culture represented by organic artifacts from Border Cave, South Africa. Proceedings of the National Academy of Sciences 109(33): 13214–13219. doi: 10.1073/pnas.1204213109
- Dickens P (1994) English-Jul'hoan, Jul'hoan-English Dictionary. Rudiger Koppe Verlag, Koln, Germany, 371 pp.
- Dieckmann U (2007) Hai||om in the Etosha region. A history of colonial settlement, ethnicity and nature conservation. Bab Publications, Basel, 398 pp.
- Dieckmann U (2009) Born in Etosha: Homage to the Cultural Heritage of the Hai||om. Legal Assistance Centre, Windhoek.
- Dieckmann U, Thiem ME, Dirx E, Hays J (2014) 'Scraping the Pot: San in Namibia Two Decades after Independence. Legal Assistance Centre and Desert Research Foundation of Namibia, Windhoek, 650 pp.
- Dornan SS (1925) Pygmies and Bushmen of the Kalahari: An account of the hunting tribes inhabiting the Great Arid Plateau of the Kalahari Desert, their precarious manner of living, their habits, customs and beliefs, with some reference to Bushman art, both early and of recent date, and to the neighbouring African tribes. Seeley, Service and Co, London, 318 pp.
- Dumbacher JP, Wako A, Derrickson SR, Samuelson A, Spande TF, Daly JW (2004) Melyrid beetles (Choresine): A putative source for the batrachotoxin alkaloids found in poison-dart frogs and toxic passerine birds. Proceedings of the National Academy of Sciences 101(45): 15857–15860. doi: 10.1073/pnas.0407197101
- Encyclopaedia Britannica (2015) Encyclopaedia Britannica Inc. http://www.britannica. com/place/Kalahari [accessed July 10 2015]

- Evans AE (2012) Arrow poisons in the Palaeolithic? Proceedings of the National Academy of Sciences USA 109(48): e32902. doi: 10.1073/pnas.1213860109
- Fairmaire L (1893) Coleopteres de l'Ouganghi, recueillis par Crampel. Annales de la Société entomologique de France 37 62: 133–156.
- Francis M (2009) Silencing the Past: Historical and Archaeological Colonization of the Southern San in KwaZulu-Natal, Southern Africa. Anthropology Southern Africa 32(3–4): 106–116. doi: 10.1080/23323256.2009.11499985
- Fuller HC (1920) Chemistry and analysis of drugs and medicine. John Wiley and Sons, New York, 1072 pp.
- Furth DG (1992) The new world *Blepharida* group, with a key to genera and description of a new species (Coleoptera: Chrysomelidae). Journal of the New York Entomological Society 100(2): 399–414.
- Gerhadt K, Steiner M (1986) An inventory of a coastal forest in Kenya at Gedi National Monument including a checklist and a nature trial: Report from a minor field study. Swedish University of Agricultural Sciences, Uppsala, 52 pp.
- Goodwin AJH (1945) Some historical Bushman arrows. South African Journal of Science 41: 429–443.
- Gordon RJ, Douglas SS (2000) The Bushman Myth: The Making of a Namibian Underclass. 2nd edn. Westview Press, Boulder, CO, 342 pp.
- Greaves RD (1997) Hunting and multifunctional use of bows and arrows: Ethnoarchaeology of technological organization among Pumé hunters of Venezuela. In: Knecht H (Ed.) Projectile technology. Plenum, New York, London, 287–320. doi: 10.1007/978-1-4899-1851-2_12
- Green SV (1998) The bushman as an entomologist. Antenna 22(1): 4–8.
- Guenther M (Ed.) (2005) Kalahari and Namib Bushmen in German South West Africa: Ethnographic Reports by Colonial Soldiers and Settlers. Rudiger Koppe Verlag, Koln, 268 pp.
- Guenther MG (1986) The Nharo Bushmen of Botswana: Tradition and Change. Helmut Buske Verlag, Hamburg, 224 pp.
- Hahn C, Vedder H, Fourie L (Eds) (1928) The native tribes of South West Africa. South West African Administration, Cape Town.
- Hall IC, Whitehead RW (1927) A pharmaco-bacterologic study of African poisoned arrows. Journal of Infectious Diseases 41: 51–69. doi: 10.1093/infdis/41.1.51
- Harbourne JB, Baxter H, Moss GP (Eds) (1999) Phytochemical Dictionary: a handbook of bioactive compounds from plants. Taylor and Francis, London, 976 pp.
- Heinz HJ (1966) The Social Organization of the !Ko Bushmen. M.A. Thesis, Department of Anthropology, University of South Africa, Pretoria, South Africa.
- Heinz HJ (1973) Bere: A Balance Sheet. Occasional Paper No. 4. Department of Pathology, University of Witwatersrand, Johannesburg, South Africa.
- Heinz HJ, Maguire B (1974) The ethno-biology of the !Ko Bushmen. Occasional Paper No. 1. Botswana Society, Gaborone, 53 pp.
- Heubner W von (1907) Über das pfeilgift der Kalahari. Archiv für experimentelle Pathologie und Pharmakologie 57: 358–366.

- Hill K, Hurtado AM (1989) Hunter-Gatherers of the New World. American Scientist 77(5): 436–443.
- Hitchcock RK (1978) Kalahari Cattle Posts: A regional study of hunter-gatherers, pastoralists, and agriculturalists in the Western Sandveld Region, Central District, Botswana. Two volumes. Government Printer, Gaborone, Botswana, 709 pp.
- Hitchcock RK (1982) The Ethnoarcheology of Sedentism: Mobility Strategies and Site Structure among Foraging and Food Producing Populations in the Eastern Kalahari Desert, Botswana Ph.D. dissertation, University of New Mexico, Albuquerque, 402 pp.
- Hitchcock RK (2015) Authenticity, identify, and humanity: The Hai||om San and State of Namibia. Anthropological Forum 25(3): 262–284. doi: 10.1080/00664677.2015.1027658
- Hitchcock RK (in press) Hunters-gatherers, herders, agropastoralists, and farm workers:
 Hai||om and Ju|'hoansi San and their neighbors in Namibia in the 20th and 21st centuries.
 In: Ikeya K, Hitchcock R (Eds) Hunter-Gatherers and Their Neighbours in Asia, Africa, and South America. Senri Ethnological Studies, Osaka.
- Hitchcock RK, Begbie-Clench B, Murwira A (2014) The San of Zimbabwe: An Assessment Report. Government of Zimbabwe, Harare, International Work Group for Indigenous Affairs, Copenhagen, and Open Society Initiative for Southern Africa, Johannesburg, 134 pp.
- Hitchcock RK, Bleed P (1997) Each according to need and fashion: Spear and arrow use among San hunters of the Kalahari. In: Knecht H (Ed.) Projectile Technology. Plenum Press, New York, 345–368. doi: 10.1007/978-1-4899-1851-2_14
- Hitchcock RK, Sapignoli M, Babchuk W (2011) What about Our Rights? Settlements, Subsistence, and Livelihood Security among Central Kalahari San and Bakgalagadi. International Journal of Human Rights 15(1): 67–87. doi: 10.1080/13642987.2011.529689
- Hitchcock RK, Sapignoli M, Babchuk WA (2015) Settler Colonialism, Conflict, and Genocide: Interactions between Hunter-Gatherers and Settlers in Kenya and Zimbabwe and Northern Botswana. Settler Colonial Studies 5(1): 40–65.
- Hitchcock RK, Sapignoli M, Main M, Babchuk WA (2015) The Politics and Economics of Community-Based Natural Resource Management in /Xai/Xai, Ngamiland, Botswana. African Study Monographs 36(4): 211–260.
- Hitchcock RK, Yellen J, Crowell AL, Gelburd D, Osborn AJ, Crowell AL (1996) Subsistence hunting and resource management among the Jul'hoansi of northwestern Botswana. African Study Monographs 17(4): 153–220.
- Hitchcock RK, Ikeya K, Biesele M, Lee RB (Eds) (2006) Updating the San: Image and Reality of an African People in the 21st Century. Senri Ethnological Studies 70. National Museum of Ethnology, Osaka, Japan, 236 pp.
- Holmes EM (1888) The arrow poisons of the pygmies (Part II) Identification of the material. In: Holmes EM (Ed.) My Personal Experiences in Equatorial Africa: As Medical Officer of the Emin Pasha Relief Expedition. C. Scribner, New York, 315–319. [Reprinted 2011, Ullan Press, 628 pp]
- Homer (~800 B.C.E.) The Odyssey. Perseus Project, Tufts University, Boston, MA. http:// www.gutenberg.org/ebooks/26275 [Project Gutenberg, accessed July 9 2015]

- Homer (~800 B.C.E.) The Iliad. Available via the Perseus Project, Tufts University, Boston, MA. [accessed July 9 2015]
- Hsiao TH (1978) Comparative studies on haemolymph protein toxins of *Leptinotarsa* beetles. In: Rosenberg P (Ed.) Toxins: animal, plant and microbial: 5th International Symposium proceedings. Pergamon Press, Oxford, 675–688.
- Hsiao T, Fraenkel G (1969) Properties of leptinotarsin, a toxic haemolymph protein from the Colorado potato beetle. Toxicon 7: 119. doi: 10.1016/0041-0101(69)90074-9
- Hsiao TH, Hsiao C, Rothschild M (1980) Characterization of a protein toxin from dried specimens of the garden tiger moth (*Arctia caja* L.). Toxicon 18: 291. doi: 10.1016/0041-0101(80)90008-2
- Hutchinson DA, Mori A, Savitzky AH, Burghardt GM, Wu X, Meinwald AJ, Schroeder FC (2007) Dietary sequestration of defensive steroids in nuchal glands of the Asian snake *Rhabdophis tigrinus.* Proceedings of the National Academy of Sciences 104(7): 2265–2270. doi: 10.1073/pnas.0610785104
- Ikeya K (2001) Some Changes among the San under the Influence of Relocation Plan in Botswana. In: Anderson DG, Ikeya K (Eds) Parks, Property, and Power: Managing Hunting Practice and Identity Within State Policy Regimes. Senri Ethnological Studies No. 59. National Museum of Ethnology, Osaka, Japan, 183–198.
- Jacobsen TF, Sand O, Bjøro T, Karlsen HE, Iversen JG (1990) Effect of Diamphidia toxin, a Bushman arrow poison, on ionic permeability in nucleated cells. Toxicon 28: 435–44. doi: 10.1016/0041-0101(90)90082-I
- Kahn T (2002) Bushmen to share gains from 'slimming cactus'. Science and Development Network. http://www.scidev.net [accessed 26 July 2006]
- Kann N (1989) Further purification of the Basarwa arrow poison. Unpublished manuscript on file with the Kalahari Peoples Fund, Austin, Texas, 21 pp.
- Kao CY, Salwen MJ, Hu SL, Pitter HM, Woollard JMR (1989) *Diamphidia* toxin, the bushman's arrow poison: possible mechanism of prey-killing. Toxicon 27: 1351–1366. doi: 10.1016/0041-0101(89)90067-6
- Karimi M (1973) The arrow poisons. East African Literature Bureau, Nairobi, 97 pp.
- Karras DJ, Farrell SE, Harrigan RA, Henretig FM, Gealt L (1996) Poisoning from "Spanish fly" (cantharidin). American Journal of Emergency Medicine 14(5): 478–483. doi: 10.1016/S0735-6757(96)90158-8
- Kiema K (2010) Tears For My Land: A Social History of the Kua of the Central Kalahari Game Reserve, Tc'amnqo. Mmegi Publishing House, Gaborone, 171 pp.
- Kline AS (2000) Ovid's *Metamorphoses*. http://ovid.lib.virginia.edu/trans/Ovhome.htm [accessed July 10 2015]
- Kingdon J, Agwanda B, Kinnaird M, O'Brien T, Holland C, Gheysens T, Boulet-Audet M, Vollrath F (2011) A poisonous surprise under the coat of the African crested rat. Proceedings of the Royal Society B 279(1729): 675–680. doi: 10.1098/rspb.2011.1169
- Kingston DG, Reichstein T (1974) Cytotoxic cardenolides from Acokanthera longiflora Stapf. and related species. Journal of Pharmaceutical Sciences 63(3): 462–464. doi: 10.1002/ jps.2600630337

- Knight A, Underhill PA, Mortensen HM, Zhivotovsky LA, Lin AA, Henn BM, Ruhlen M, Mountain J (2003) African Y Chromosome and mtDNA divergence provides insight into the history of click languages. Current Biology 13: 464–473. doi: 10.1016/S0960-9822(03)00130-1
- Koch C (1958) Preliminary notes on the coleopterological aspect of the arrow poison of the Bushmen. South African Biological Society. Pamphlet 20: 49–54.
- Koot SP (2013) Dwelling in Tourism: Power and Myth amongst Bushmen in Southern Africa. African Studies Collection Volume 54. African Studies Centre, Leiden, The Netherlands, 310 pp.
- Kündig H (1978) The pharmacology of *Diamphidia* arrow poison. PhD Thesis, Department of Pharmacology, University of Witwatersrand, Johannesburg, 180 pp.
- Kupicha FK (1982) Studies on African Apocynaceae: the genus Acokanthera. Kew Bulletin 37(1): 41–67. doi: 10.2307/4114719
- Langenheim JH (1994) Higher plant terpenoids: a phytocentric overview of their ecological roles. Journal of Chemical Ecology 206: 1223–1280. doi: 10.1007/BF02059809
- Langenheim J (2003) Plant resins: Chemistry, evolution, ecology, ethnobotany. Timber Press, Portland, 586 pp.
- Lawry S, Begbie-Clench B, Hitchcock RK (2012) Hai||om Resettlement Farms: Strategy and Action Plan. Windhoek: Ministry of Environment and Tourism and Millennium Challenge Corporation, September, 2012, 105 pp.
- Lee RB (1968) What hunters do for a living, or, how to make out on scarce resources. In: Lee RB, DeVore I (Eds) Man the Hunter. Aldine, Chicago, 30–48.
- Lee RB (1972) The !Kung Bushmen of Botswana. In: Bicchieri MG (Ed.) Hunters and gatherers today, a socioeconomic study of eleven such cultures in the twentieth century. Holt, Rinehart and Winston, New York, 327–368.
- Lee RB (1978) Ecology of a contemporary San people. In: Tobias PV (Ed.) The Bushmen: San hunters and herders of southern Africa. Human and Rousseau, Cape Town, 94–114.
- Lee RB (1979) The !Kung San: Men, Women, and Work in a Foraging Society. Cambridge University Press, Cambridge, 556 pp.
- Lee RB (2013) The Dobe Jul'hoansi. 4th edn. Wadsworth Cencage Publishing, Belmont, CA, 294 pp.
- Lee RB, Hurlich S (1982) From Foragers to Fighters: South Africa's Militarization of the Namibian San. In: Leacock E, Lee RB (Eds) Politics and History in Band Societies. Cambridge University Press, Cambridge, 327–345.
- Lee RB, DeVore I (Eds) (1968) Kalahari Hunter-Gatherers. Studies of the !Kung San and their neighbors. Harvard University Press, Cambridge, 408 pp.
- Leffers A (2003) Gemsbok bean and Kalahari truffle: traditional plant use by Ju|'hoansi in north-eastern Namibia. Gamsberg MacMillan Publishers, Windhoek, 202 pp.
- Lewin L (1912a) Uber die Pfeilgifte der Bushmanner. Zeitschrift für Ethnologie Bd 44(5): 831–837.
- Lewin L (1912b) *Blepharida evanida*, cin neuer Pfeilgiftkafer. Archiv für experimentelle Pathologie und Pharmakologie 69: 60–66.
- Lewin L (1923) Die Pfeilgifte. Verlag von Johann Ambrosius Barth, Leipzig, 517 pp.

- Liebenberg L (2000) A photographic guide to tracks and tracking in southern Africa. Struik, Cape Town, 144 pp.
- Liebenberg L (2001) The art of tracking: the origin of science. David Philip, Cape Town, 176 pp.
- Liebenberg L (2006) Persistence Hunting by Modern Hunter Gatherers. Current Anthropology 47(6): 1017–1025. doi: 10.1086/508695
- Liebenberg L (2008) The relevance of persistence hunting to human evolution. Journal of Human Evolution 55(6): 1156–1159. doi: 10.1016/j.jhevol.2008.07.004
- Lindroth CH (1971) Disappearance as a protective factor: a supposed case of Batesian mimicry among beetles (Coleoptera: Carabidae, Chrysomelidae). Entomologica Scandinavica 2(1): 41. doi: 10.1163/187631271x00031
- Livingstone D (1858) Missionary travels and researches in South Africa including a sketch of sixteen years' residence in the interior of Africa. John Murray, London, 732 pp.
- Livingstone D, Livingstone C (1865) A narrative of an expedition to the Zambesi. J. Murray, London, 608 pp.
- Lombard M (2011) Quartz-tipped arrows older than 60,000 ya. Journal of archaeological Science 38: 1918–1930. doi: 10.1016/j.jas.2011.04.001
- Lombard M (2015) Hunting and Hunting Technologies as Proxy for Teaching and Learning During the Stone Age of Africa. Cambridge Archaeological Journal 25(4): 877–887. doi: 10.1017/S0959774315000219
- Lombard M, Phillipson L (2010) Indications of bow and stone tipped arrow use 64,000 years ago in KwaZulu-Natal, South Africa. Antiquity 84(325): 635–648. doi: 10.1017/S0003598X00100134
- Ma J, Jones SH, Hecht SM (2005) A dihydroflavonol glucoside from *Commiphora africana* that mediates DNA strand scission. Journal of Natural Products 68: 115–117. doi: 10.1021/ np0400510
- Madeddu L, Pozzan T, Robello M, Rolandi R, Hsiao TH, Meldolesi J (1985a) Leptinotoxin-h action in synatosomes, neurosecretory cells, and artificial membranes: stimulation of neurotransmitter release. Journal of Neurochemistry 45(6): 1708–1718. doi: 10.1111/j.1471-4159.1985.tb10526.x
- Madeddu L, Saito I, Hsiao TH, Meldolesi J (1985b) Leptinotoxin-h action in synaptosomes and neurosecretory cells. Stimulation of neurotransmitter release. Journal of Neurochemistry 45(6): 1719–1730. doi: 10.1111/j.1471-4159.1985.tb10527.x
- Main M (1987) Kalahari: Life's variety in dune and delta. Southern Book Publishers, Cape Town, 265 pp.
- Maitai CK, Muraguri N, Patel HA (1973) A survey on the use of poisoned arrows in Kenya during the period 1964–1971. East Africa Medical Journal 50: 100–104.
- Marean CW, Assefa Z (2005) The Middle and Upper Pleistocene African Record for the Biological Origins of Modern Humans. In: Stahl AB (Ed.) African Archaeology: A Critical Introduction. Blackwell Publishing, Malden, Massachusetts, 93–129.
- Marks S (1977) Hunting Behavior and Strategies of the Valley Bisa in Zambia. Human Ecology 5(1): 1–36. doi: 10.1007/BF01880256
- Marlowe FW (2010) The Hadza: Hunter-gatherers of Tanzania. University of California Press, Berkeley and London, 325 pp.

- Marshall J (1958a) Huntsmen of Nyae Nyae: The !Kung still practice Man's oldest craft. Part II. Natural History 67: 291–309, 376–395.
- Marshall J (Producer) (1958b) The Hunters (film). Wilmette: Films Incorporated. Center for Documentary Educational Resources, Watertown, MA.
- Marshall J (2003) A Kalahari Family (film). Documentary Educational Resources, Watertown.
- Marshall J, Ritchie C (1984) Where are the Ju|Wasi of Nyae Nyae? Changes in a Bushman Society: 1958–1981. Communications No. 9, Center for African Area Studies, University of Cape Town. University of Cape Town, Cape Town, 187 pp.
- Marshall L (1961) Sharing, talking, and giving: Relief of social tensions among !Kung Bushmen. Africa 31: 231–249. doi: 10.2307/1157263
- Marshall L (1976) The !Kung of Nyae Nyae. Harvard University Press, Cambridge, MA, 433 pp. doi: 10.4159/harvard.9780674180574
- Marshall Thomas E (1959) The harmless people. Secker and Warburg, Ltd., London, 250 pp. [Reprinted 1988 & 2006, Africa South Paperbacks, Cape Town.]
- McClure WO, Abbot BC, Baxter DE, Hsiao TH, Satin LS, Siger S, Yoshino J (1980) Leptinotarsin: a new toxin neurotoxin that stimulates acetylcholine release. Proceedings of the National Academy of Sciences 77(2): 1219–1223. doi: 10.1073/pnas.77.2.1219
- Mebs D, Brünning F, Pfaff N, Neuwinger HD (1982) Preliminary studies on the chemical properties of the toxic principle from *Diamphidia nigro-ornata* larvae, a source of Bushman arrow poison. Journal of Ethnopharmacology 6(1): 1–11. doi: 10.1016/0378-8741(82)90068-X
- Mendelsohn J, Jarvis A, Roberts C, Robertson T (2009) Atlas of Namibia: A Portrait of the Land and its People. 3rd edn. Sunbird Publishers, Cape Town, South Africa, 260 pp.
- Miljanich GP, Yeager RE, Hsiao TH (1988) Leptinotarsin-D, a neurotoxic protein evokes neurotransmitter release from, and calcium flux into, isolated electric organ nerve terminals. Journal of Neurobiology 19(4): 373–386. doi: 10.1002/neu.480190405
- Mitchell PJ (2010a) Genetics and Southern African Prehistory: An Archaeological View. Journal of Anthropological Sciences 88: 73–92.
- Mitchell PJ (2010b) Making History at Sehongong: Soal and the Last Bushman Occupants of His Shelter. Southern African Humanities 22: 149–170.
- Mitchell PJ (2012) San Origins and Transition to the Later Stone Age: New Research from Border Cave, South Africa. South African Journal of Science 108(11/12): 1–2. doi: 10.4102/sajs.v108i11/12.1447
- Mitchell P, Smith B (Eds) (2009) The Eland's People: New Perspectives in the Rock Art of the Maloti-Drakensberg Bushmen: Essays in Memory of Patricia Vinnicombe. Witwatersrand University Press, Johannesburg, 386 pp.
- Moen L, Shwayder T, Chang M (2001) Cantharidin revisited: a blistering defense of an ancient medicine. Archives of Dermatology 137: 1357–1360.
- Morton F, Hitchcock RK (2013) Tswana hunting: Continuities and changes in the Transvaal and Kalahari after 1600. South African Historical Journal. doi: 10.1080/02582473.2013.855809
- Myers CW, Daly JW, Malkin B (1978) A dangerously toxic new frog (*Phyllobates*) used by Embera Indians of western Colombia, with discussion of blowgun fabrication and dart poisoning. Bulletin of the American Museum of Natural History 161(2): 307–366.

- Nedved R (2014) On the complexity of the Urbanizaiton Process of the Bushmen: Cas Study on the !Xung in the Grootfontein Area in Namibia. Urban People /Lide Mesta 16(2): 169–194.
- Neuwinger HD (1974a) Afrikanische Pfeilgifte I. Naturwissenschaftliche Rundschau 27(9): 340–349.
- Neuwinger HD (1974b) Afrikanische Pfeilgifte II. Naturwissenschaftliche Rundschau 27(10): 385–402.
- Neuwinger HD (1996) African Ethnobotany: poisons and drugs. Chapman Hall, Heidelberg, 941 pp.
- Neuwinger HD (1998) Alkaloids in arrow poisons. In: Roberts MF, Wink M (Eds) Alkaloids: Biochemistry, Ecology, and Medical Applications. Plenum Press, New York, 45–88. doi: 10.1007/978-1-4757-2905-4_3
- Nicolaisen I (2010) Elusive hunters: The Haddad of Kanem and the Bahr el Ghazal. Aarhus University Press, Aarhus, 522 pp.
- Noli HD (1993) A technical investigation into the material evidence for archery in the archaeological and ethnographical record in Southern Africa. Unpublished Ph.D. thesis, University of Cape Town, 252 pp.
- Nonaka K (1996) Ethnoentomology of the Central Kalahari San. African Study Monographs Supplementary Issue 22: 29–46.
- Omino EA, Kokwaro JO (1993) Ethnobotany of Apocynaceae species in Kenya. Journal of Ethnopharmacology 40: 167–180. doi: 10.1016/0378-8741(93)90065-D
- Osaki M (1984) The social influence of change in hunting technique among the Central Kalahari San. African Study Monographs 5: 49–62.
- Osaki M (2001) Reconstructing the recent history of the G|wi and G||ana Bushmen. African Study Monographs, Supplementary Issue 26: 27–39.
- Ovid. Metamorphoses. English Translation by AS Kline, available at http://ovid.lib.virginia. edu/trans/Ovhome.htm [accessed 1 October 2014] and at the Internet Classics Archive, Massachusetts Institute of Technology, MA, http://classics.mit.edu/Ovid/metam.html
- Oswalt WH (1973) Habitat and Technology: The Evolution of Hunting. Holt, Rinehart, and Winston, New York, 191 pp.
- Parke TH (1888) The arrow poisons of the pygmies. Part I. Description of the material. pp. 308–315. In: My personal experiences in Equatorial Africa: As medical officer of the Emin Pasha Relief Expedition. C. Scribner, New York. [Reprinted 2011, Ullan Press, 628 pp.]
- Parker I, Amin M (1983) Ivory Crisis. Chatto and Windus Ltd., London, 184 pp.
- Parker RA (1971) A comparison of heamolymph proteins in two species of *Leptinotarsa* beetles. Journal of Insect Physiology 17: 1689–1698. doi: 10.1016/0022-1910(71)90064-3
- Parker RA (1972) A comparison of the toxic protein in two species of *Leptinotarsa*. Toxicon 10: 79–80. doi: 10.1016/0041-0101(72)90094-3
- Parry E (2007) Arrow poisons. Zimbabwean Prehistory 27: 52-58.
- Passarge S (1907) Die Buschmanner der Kalahari [The Bushman of the Kalahari]. Translated by Wilmsen EN (Ed.) The Kalahari Ethnographies (1869–1898) of Siefried Passarge. Research in Khoisan Studies 13: 127–218. Rüdiger, Köppe, Verlag, Köln, 332 pp.
- Paterson W (1789) A narrative of four journeys into the country of the Hottentots and Caffaria, in the years 1777, 1778, 1779. J. Johnson, London, 205 pp.

Pawlowsky EN (1927) Giftiere und ihre Giftigkeit. Gustav Fischer, Jena, 466 pp.

- Pell S, Mitchell K, Lobova JD, Miller AJ (2011) Anacardiaceae. In: Kubitzki K (Ed.) The Families and Genera of Vascular Plants. Springer-Verlag, New York, 10, 7–50.
- Peters J, Dieckmann U, Vogelsang R (2009) Losing the spoor: Hai||om animal exploitation in the Etosha region. In: Grupe G, McGlynn G, Peters J (Eds) Tracking Down the Past: Ethnohistory meets archaeozoology. Documenta Archaeobiologiae. Jahrbuch der Staatssammlung für Anthropologie und Paläoanatomie München 7. Verlab Marie Leidorf, Rahden/Westf., 103–185.
- Pickrell JK, Patterson N, Barbieri C, Berthold F, Gerlach L, Güldemann T, Kure B, Mpoloka SW, Nakagawa H, Naumann C, Lipson M, Loh P-R, Lachance J, Mountain J, Bustamante CD, Berger B, Tishkoff SA, Henn BM, Stoneking M, Reich D, Pakendorf R (2012) The Genetic Prehistory of Southern Africa. Nature Communications 3: 1143. doi: 10.1038/ncomms2140
- PlantZAfrica (2015) South Africa National Biodiversity Institute. http://pza.sanbi.org/ [accessed July 9 2015]
- Plazier AC (1980) A revision of *Adenium* Roem. and Schult. and of *Diplorhynchus* Welw. ex Fic. and Hiern (Apocynaceae). Mededelingen Landbouwhogeschool 80(12): 1–40.
- Prathapan KD, Chaboo CS (2011) Biology of *Blepharida*-group flea beetles with first notes on natural history of *Podontia congregata* Baly 1865, an endemic flea beetle from southern India (Coleoptera: Chrysomelidae: Galerucinae: Alticini). ZooKeys 157: 95–130. doi: 10.3897/zookeys.157.1472
- Preston D (1989) Suid-Afrikaanse Geskiedenis in Beeld. Bion Books, Cape Town, 192 pp.
- Prins F (2009) Secret San of the Drakensberg and Their Rock Art Legacy. Critical Arts 23(2): 198–2008. doi: 10.1080/02560040903016917
- Prinsloo G, Street RA (2013) Marula [Sclerocarya birrea (A.Rich) Hochst]: A review of traditional uses, phytochemistry, and pharmacology. In: Juliani H, Simon JE, Ho C-T (Eds) African Natural Plant Products. Vol II: Discoveries and Challenges in Chemistry, Health and Nutrition. ACS Symposium Series, American Chemical Society, Washington, DC, 19–32. doi: 10.1021/bk-2013-1127.ch002
- Rapold CJ, Widlok T (2008) Dimensions of variability in Northern Khoekhoe Language and Culture. Southern African Humanities 20: 133–161.
- Reichstein T (1965) Chemische Rassen in Acokanthera. Planta Medica 13: 382–399. doi: 10.1055/s-0028-1100132
- Robbins LH, Campbell AC, Murphy ML, Brook GA, Mabuse A, Hitchcock R, Babuts G, Mmolawa M, Stewart KM, Steele TC, Klein RG, Appleton CC (2009) Mogapelwa: Archaeology, Paleoenvironment, and Oral Traditions at Lake Ngami, Botswana. South African Archaeological Bulletin 64(189): 13–32.
- Robbins LH, Campbell AC, Brook GA, Murphy ML, Hitchcock RK (2012) The antiquity of the bow and arrow in the Kalahari Desert: Bone points from White Paintings Rock Shelter, Botswana. Journal of African Archaeology 10(1): 7–20. doi: 10.3213/2191-5784-10211
- Roodt V (1993) The Shell field guide to the common trees of the Okavango Delta and Moremi Game Reserve. Shell Oil, Gabarone, Botswana, 110 pp.
- Rothschild M, Riechstein T, von Euw J, Aplin R, Harmon RRM (1970) Toxic Lepidoptera. Toxicon 8: 293. doi: 10.1016/0041-0101(70)90006-1

- Sands B, Chebanne A, Shah S (2011) Hunting terminology in =/Hoan. Paper presented at the International Symposium on Khoisan languages and linguistics, 11–13 July 2011, Riezlern/Kleinwalsertal.
- Sapignoli M, Hitchcock R (2013) Indigenous Peoples in Southern Africa. The Round Table: The Commonwealth Journal of International Affairs 102(4): 355–365. doi: 10.1080/00358533.2013.795013
- Satin LS, Siger A, Abbot BC, Hsia TM, McClure WO (1978) Leptinotarsin: quantized release of acetylcholine at the rat neuromuscular junction. Abstracts, Society for Neuroscience 4: 584.
- Schapera I (1925) Bushman Arrow Poisons. Bantu Studies 2: 199–214. doi: 10.1080/02561751.1923.9676184
- Schapera I (1930) The Khoisan peoples of South Africa: Bushmen and Hottentots. Routledge and Kegan Paul, Ltd., London, 312 pp.
- Schinz H (1891) Deutsch-Südwestafrika, Forschungsreisen durch die deutschen Schutzgebiete Groß- Nama- und Hereroland, nach dem Kunene, dem Ngamisee und Kalahari, 1884–1887 (German South West Africa: Research Expedition of Herero and Nama Country, the Kunene Region, Lake Ngami and the Kalahari-1884–1887).
- Schinz H, Böhm R [in Fairmaire] (1894) Ueber das Pfeilgift de Kalixari-San. Biologisches Zentralblatt 14(10): 337–339.
- Schlebusch CM, Skoglund P, Sjodin P, Gattepaille LM, Hernandez D, Jay F, Li S, De Jongh M, Singleton A, Blum MBB, Soodyall H, Jakobson M (2012) Genomic Variation in Seven Khoe-San Groups Reveals Adaptation and Complex African History. Science 338: 374–379. doi: 10.1126/science.1227721
- Schmidt S (2015) South African /Xam Bushman Traditions and Their Relationships to Further Khoisan Folklore. Ruediger Koeppe Verlag, Cologne, 251 pp.
- Schultze L (1907) Aus Namaland und Kalahari. Gustav Fischer, Jena, 752 pp.
- Schulz A, Hammar A (1897) The New Africa: A journey up the Chobe and down the Okovango Rivers, a record of exploration and sport. William Heinemann, London, 406 pp.
- Scott JA (1923) Poisoned arrows in Homer. Classical Journal 23: 619–620.
- Sharples RW, Huby PM, Fortenbaugh WW (1995) Theophrastus of Eresus: Sources on Biology. Brill, Leiden, 273 pp.
- Shaw EM, Woolley PL, Rae FA (1963) Bushman arrow poisons. Cimbebasia 7(2): 2-41.
- Shea JJ (2006) The origins of lithic projectile point technology: Evidence from Africa, the Levant, and Europe. Journal of Archaeological Science 33: 823–846. doi: 10.1016/j. jas.2005.10.015
- Silberbauer GB (1972) The G/wi Bushmen. In: Bicchieri MG (Ed.) Hunters and gatherers today, a socioeconomic study of eleven such cultures in the twentieth century. Holt, Rinehart and Winston, New York, 271–326.
- Silberbauer GB (1981a) Hunter and habitat in the Central Kalahari Desert. Cambridge University Press, Cambridge, 330 pp.
- Sisk ML, Shea JJ (2009) Experimental use and quantitative performance analysis of triangular flakes (Levallois points) used as arrowheads. Journal of Archaeological Science 36: 2039–2047. doi: 10.1016/j.jas.2009.05.023

- Smith A, Malherbe C, Guenther M, Berens P (2000) Bushmen of Southern Africa: Foraging Society in transition. Ohio University Press, Athens, 112 pp.
- Snyder AK (1971) A study of the physiological effects of leptinotarsin. PhD Thesis, University of Illinois, Urbana, 83 pp.
- Stander PE, Ghau II, Tsisaba D, Oma II, VI || (1997) Tracking and the Interpretation of Spoor: A Scientifically Sound Method in Ecology. Journal of the Zoological Society of London 242: 329–341. doi: 10.1111/j.1469-7998.1997.tb05805.x
- Stanford WE (1909–1910) Statement of Silayi with reference to his life among the Bushmen. Transactions of the Royal Society of South Africa 1: 435–440. doi: 10.1080/00359191009520056
- Stapleton T (2015) Warfare and Tracking in Africa, 1952–1990. Pickering and Chatto Publishers, London.
- Starcke F (1897) Ueber die Wirkung des Giftes Larven von *Diamphida locusta* (Pfeilgift der Kalachari). Archives für experimentelle Pathologie und Pharmakologie 38: 428–446.
- Steyn DG (1949) Vergiftiging van Mens en dier met gifplante, voedsel en drinkwater. Van Schaik, Pretoria, 264 pp.
- Steyn DG (1957) The bushman arrow poison. South African Medical Journal 31: 119–120.
- Steyn HP (1971) Aspects of the Economic Life of Some Nomadic Nharo Groups. Annals of the South African Museum 56(6): 275–322.
- Steyn M (2003) Southern Africa Commiphora. United Lithoa, Arcadia, 92 pp.
- Stigand AG (1913) Notes on Ngamiland. Transactions of the Royal Society of South Africa 3: 379–391. doi: 10.1080/00359191309519705
- Stow GW (1905) The native races of South Africa: A History of the Intrusion of the Hottentots and Bantu into the Hunting Grounds of the Bushmen, the Aborigines of the Country. Swan Sonnenschein and Co., Ltd., London, 618 pp.
- Suzman J (1999) "Things from the Bush": A Contemporary History of the Omaheke Bushmen. Basel Namibia Studies Series 5. P. Schlettwein Publishing, Basel, Switzerland, 246 pp.
- Suzman J (2004) Etosha Dreams: An historical account of the Hai||om predicament. Journal of Modern African Studies 42(2): 221–238.
- Tanaka J (1978) A San Vocabulary of the Central Kalahari: G//ana and G/wi Dialects. Institute for the Study of Languages and Cultures of Asia and Africa (ILCAA), University of Tokyo, Tokyo, 158 pp.
- Tanaka J (2014) The Bushmen: A Half Century Chronicle of Transformations in Hunter-Gatherer Life and Ecology. Transpacific Press, 296 pp.
- Thomas DSG, Shaw PA (2010) The Kalahari environment. Cambridge University Press, Cambridge, 325 pp.
- Tishkoff SA, Reed FA, Friedlaender FR, Ehret C, Ranciaro A, Froment A, Hirbo JB, Awomoyi AA, Bodo J-M, Doumbo O, Ibrahim M, Juma AT, Kotze MJ, Lema G, Moore JH, Mortensen H, Nyambo TB, Omar SA, Powell K, Pretorius GS, Smith MW, Thera MA, Wambebe C, Weber JL, Williams SM (2009) The Genetic Structure and History of Africans and African Americans. Science 324: 1035–1044. doi: 10.1126/science.1172257
- Tobias PV (1957) Bushmen of the Kalahari. Man 57: 33-40. doi: 10.2307/2794792

- Trommsdorff H (1911) Experimentale Untersuchung ueber eine von Buschleten zum vergiften der Pfeilspitz benutzte Käferlarve. Archiv für Schiffs- und Tropen. Hygiene 15(19): 617–630.
- Valiente-Noailles C (1993) The Kua: Life and soul of the Central Kalahari Bushmen. A.A. Balkema, Amsterdam, 232 pp.
- Vierich HD (1981) The Kua of the Southeastern Kalahari: a study in the socio-ecology of dependency. PhD Thesis, University of Toronto, Toronto, 363 pp.
- Vinnicombe P (1976) People of the Eland: Rock Paintings of the Drakensberg Bushmen as a Reflection of their Life and Thought. Natal University Press, Pietermaritzburg, 284 pp.
- Visser, Hessel (2003) Naro Dictionary: Naro-English, English-Naro. 4th edn. Naro Language Project and Gaborone, Ghanzi, Botswana, Printing and Publishing Company, Botswana.
- Wadley L (2013) Recognizing complex cognition through innovative technology in Stone Age and Paleolithic sites. Cambridge Archaeological Joural 23(2): 163–183. doi: 10.1017/ S0959774313000309
- Watt JM, Breyer-Brandwijk M (1962) The medicinal and poisonous plants of Southern and Eastern Africa. E and S Livingstone, 2nd edn, Edinburgh, 1457 pp.
- Weber DC, Saska P, Chaboo CS (2008) Carabid beetles, parasitoid. In: Capinera J (Ed.) Encyclopedia of Entomology, 2nd edn. Kluwer Academic Publishers, Dordrecht, The Netherlands, 35–37.
- Widlok T (1999) Living on Mangetti: 'Bushman' autonomy and Namibian Independence. Oxford University Press, Oxford, 291 pp.
- Wiessner P (1983) Style and information in Kalahari San projectile points. American Antiquity 48(2): 253–276. doi: 10.2307/280450
- Wiessner P (1984) Reconsidering the behavioral basis for style: A case study among the Kalahari San. Journal of Anthropological Archaeology 3: 190–234. doi: 10.1016/0278-4165(84)90002-3
- Wiessner P (2002) Hunting, healing, and Hxaro exchange: A long term perspective on !Kung (Ju|'hoansi) large game hunting. Evolution and Human Behavior 23: 407–436. doi: 10.1016/S1090-5138(02)00096-X
- Wilmsen EN (1989) Land Filled with Flies: A Political Economy of the Kalahari. University of Chicago Press, Chicago, 420 pp.
- Wilmsen EN (Ed.) (1997) The Kalahari ethnographies (1896–1898) of Siegfried Passarge. Nineteenth century Khoisan and Bantu-Speaking peoples. Rudiger Koppe Verlag, Koln, Germany, 332 pp.
- Wikar HJ (1779) The journal of Hendrik Jacob Wikar. With an English translation by A.W. van der Horst and the journals of Jacobus Coetsé Jansz: (1760) and Willem van Reenen (1791) with an English translation by Dr. E. E. Mossop. Dr. E.E. Mossop (Editor, with footnotes). The Van Riebeeck Society, Cape Town, 1935.
- Wintersteiner O, Dutcher JD (1943) Curare alkaloids from *Chondodendron tomentosum*. Science 97(2525): 467–470. doi: 10.1126/science.97.2525.467
- Woodburn J (1970) Hunters and gatherers: The material culture of the nomadic Hadza. British Museum, London, 59 pp.

- Woollard J (1986) The active chemical components of the Basarwa arrow-poison. Botswana Notes and Records 18: 139–141.
- Woollard JMR, Fuhrman AA, Mosher HS (1984) The Bushman arrow toxin, Diamphidia toxin: Isolation from pupae of *Diamphidia nigro-ornata*. Toxicon 22(6): 937–946. doi: 10.1016/0041-0101(84)90185-5
- Written in the Sand (2015) Written in the Sand. UNESCO'S Division for Cultural Policies in the Sector for Culture. http://www.san.org.za/terms.php [accessed July 10 2015]
- Yamauchi T, Abe F (1990) Cardiac glycosides and pregnanes from *Adenium obesum* (Studies on the constituents of *Adenium*. I). Chemical and Pharmaceutical Bulletin 38(3): 669–672. doi: 10.1248/cpb.38.669
- Yellen JE (1977) Archaeological approaches to the present: Models for reconstructing the past. Academic Press, New York, 259 pp.
- Yellen JE, Lee RB (1976) The Dobe-|Du|Da environment: Background to a hunting and gathering way of life. In: Lee RB, DeVore I (Eds) Kalahari Hunter-Gatherers: Studies of the !Kung San and their neighbors. Harvard University Press, Cambridge, MA, 27–46. doi: 10.4159/harvard.9780674430600.c4

RESEARCH ARTICLE



Systematic review of the firefly genus Scissicauda (Coleoptera, Lampyridae, Amydetinae) from Brazil

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Abstract

The Amydetinae genus *Scissicauda* McDermott, 1964 is reviewed and redescribed. We describe *S. balena* **sp. n.** from Brazil as new, and provide illustrations of the structural features and a key to species of both sexes.

Keywords

Amydetini, Neotropical Region, Psilocladina

Introduction

The subfamily Amydetinae is a little known firefly group distributed predominantly in South America. Molecular data identified Lampyrinae as sister to Amydetinae (Bocakova et al. 2007, Viviani 2011, Amaral et al. 2014), though the circumscription of the subfamily remained unaddressed due to limited taxon sampling of the studies. Phylogenetic relationships of Amydetinae genera sensu McDermott (1966) has not been clarified yet. The monophyly of Amydetinae has been challenged by Jeng (2008, unpublished), whose analyses involved morphological characters, concluding that the subfamily is polyphyletic.

Most Amydetinae share a complex antennal morphology in the males, except some species of *Vesta*, whose antennae are often serrate. Most of the females remain undescribed. McDermott (1966) assigned Amydetinae to subfamily level, keeping its subgroups as subtribes: Amydetina, Vestina and Psilocladina, the latter with five genera including *Scissicauda*. He supposedly retained these subtribes under Amydetini, although not explicitly quoting this tribe in his catalogue (1966). Though such Psilocladina has been challenged (Jeng 2008, unpublished), we refer to McDermott (1966) subdivisions as to the latest comprehensive study.

McDermott (1964) established *Scissicauda* as a replacement name for the monotypic *Schistura* Olivier, 1911 because it was preoccupied by a balitorid fish genus, *Schistura* McClevelland, 1838 (*cf.* McDermott 1966). *Scissicauda* is easily distinguishable from all other lampyrids by the strongly indented pygidium. Currently, only males of the type species, *S. disjuncta* (E. Olivier, 1896), from Rio de Janeiro, Brazil are known. Here we present a review of the genus, redescribe the type species *S. disjuncta*, and provide the female description for the first time, together with phenological data for a population in the Serra dos Órgãos Mountain Range (Rio de Janeiro, Brazil). We also propose *Scissicauda balena* sp. n. as new and provide a key to species of the genus.

Material and methods

The holotype of *S. disjuncta* was loaned from the Natural History Museum in Paris (MNHN, A. Taghavian). Other specimens were examined in the Museu de Zoologia de São Paulo, São Paulo, Brazil (MZSP, S. Casari) and Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ, M. L. Monné). Additional specimens of *S. disjuncta* were obtained in the Serra dos Órgãos mountain range (Teresópolis municipality, Rio de Janeiro State, Brazil), using monthly sampled Malaise traps (flight interceptor), arranged in seven transects along an elevation gradient in 850–2030m, separated by approximately 200m distance. Totally, 84 Malaise traps were installed there and operated for a one year period (06/2013-06/2014). Specimens were stored in 92% ethanol and are housed at Coleçao José Alfredo Pinheiro Dutra, Universidae Federal do Rio de Janeiro (DZRJ, J. R. Mermudes). The specimens of *Scissicauda balena* sp. n. were loaned from The Natural History Museum, London (BMNH, M. Geiser).

Terms for structural features follow Jeng et al. (2011), Zaragoza (1995) and Silveira and Mermudes (2013, 2014a, 2014b); Crowson (1938, 1944) for metendosternite nomenclature; and Kazantsev and Perez-Gelabert (2008) for female genitalia. For taxonomic treatment we follow McDermott (1966), which is the most recent species catalogue of Lampyridae. Specimens had the abdomen dissected and boiled in 10% KOH. This clearing procedure was also applied to two entire specimens of the type species. The morphology was examined using a stereomicroscope and photographs were made with the Leica Application Suite CV3 Auto-montage Software.

Taxonomy

Amydetinae Olivier, 1907 Psilocladina McDermott, 1964

Scissicauda McDermott, 1964

Scissicauda McDermott, 1964: 10, 39; 1966: 87. *Schistura* Olivier, 1911:51 (*nec Schistura* McClevelland, 1838 Actinopterygii). *Aethra* Laporte, 1833 (partim). Olivier *in* Wytsman 1907: 16; Blackwelder 1944: 353. *Lychnuris* Motschulsky, 1853 (partim). McDermott 1966 (*quid pro quo*). *Schistura* Olivier, 1911: 51; McDermott 1964: 10, 39.

Type species. Lucidota disjuncta Olivier, 1896, by monotypy.

Diagnosis. Antenna 11-segmented, compressed, filliform to flabellate, uniramose (while biramose in *Psilocladus* and *Pollaclasis*), with dense, upright bristles, rami atmost twice longer than antennomere body, attached basally (distally in *Ethra*). Antennal sockets large, two thirds of frontal width, close-set, reniform, antennifer process distinct. Occiput as wide as one third head width. Apical maxillary palpomere lanceolate. Apical labial palpomere securiform. Pronotum semilunate, with a marginal row of gross, deep punctures. Abdominal terga with posterior angles progressively produced and acute. Tibial spurs present. Tarsomere I 2× longer than II, II 2× longer than III, III of subequal length as IV. Tarsomere IV bilobed, lobes reaching two thirds of length of tarsomere V. Male sternum IX retracted under VIII. Aedeagus with phallus consisting of a dorsal plate basally fused to parameres, symmetric, projected dorsolaterally toward apex; ventral plate with lateral margins sinuose, weakly sclerotized; parameres symmetric, apically rounded, with a ventrobasal process rudimentary or extended beyond phallus.

Redescription. Head (Figs 1–15, 44–45, 53–54, 59) entirely covered by pronotum (Figs 1, 2, 42, 51, 67); almost $2\times$ as wide as long, slightly longer than high (Figs 4–7); lateral margins slightly convergent posteriad (Fig. 4). Frons slightly prominent dorsally, swollen (Fig. 6). Antennal sockets reniform, of two thirds frons width; antennifer process conspicuous (Fig. 7). Vertex somewhat convex, with two posterior parasagittal indentations (Fig. 4). Antenna 11-segmented, scape constricted basally, pedicel almost as long as wide and constricted medially, antennomeres III–X serrate to flabellate (males of *S. disjuncta*), compressed, subequal in length, with dense, upright bristles, lamellae long and slender, subequal in length, apical antennomere slightly longer than subapical one (Figs 10, 42, 54, 68). Frontoclypeus slightly curved (Fig. 7). Labrum connected to frontoclypeus by a membranous suture; $2\times$ as wide as long, anterior margin evanescent (Fig. 4).

Mandibles long and slender, monotonically arcuate, apex acute, internal tooth absent, external margin sparsely setose in basal ¹/₂, with a basal wisp of bristles up to half its length (Figs 14, 15). Maxilla with cardo well-sclerotized; stipe oblong in ventral view, posterior margins truncate, well-sclerotized, palpi 4-segmented; palpomere III triangular; IV lanceolate, with internal margin covered with minute, dense bristles, almost 3× longer than III (Fig. 7). Labium with mentum well-sclerotized and bristled, completely divided sagit-tally; submentum sclerotized and bristled, subcordiform, elongate; palpi 3-segmented, palpomere III securiform (Fig. 5). Gular sutures almost indistinct; gular bar transverse, 2× as wide as submentum minimal width. Occiput piriform, as wide as one third posterior width (Fig. 9). Tentorium long and slender, almost as high as half head high, projected internally almost on the half of its length, strongly curved backwards (Figs 11–13).

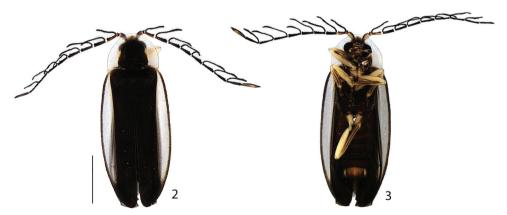
Thorax (Figs 16–29, 46, 55, 56, 70). Pronotum semilunar, posterior angles acute; disc subquadrate in dorsal view, notably convex, regularly punctured, punctures small and bristled; with a line of distinct deep marginal punctures; pronotal expansions well-developed, anterior expansion maximal length almost half as long as disc, posterior expansions straight; slightly wider than humeral distance (Figs 16, 46, 55, 70). Hypomeron longer than high (Figs 18, 56). Prosternum 4× as wide as its major length; slightly constricted parasagitally (Fig.17). Proendosternite clavate, slightly longer than prosternal process minimal width (Fig. 20). Mesoscutellum with posterior margin rounded (Fig. 21). Elytra ellipsoid, almost 5× as long as wide, pubescent, secondary pubescence absent, with a line of conspicuous punctures all over sutural and lateral margins (Fig. 25).

Hind wing well-developed, posterior margin sinuose, 2× as long as wide, r3 almost as long as r4, radial cell 2× wider than long, almost reaching anterior margin, costal row of setae inconspicuous (Fig. 26); CuA, crossvein absent, mp-cu crossvein present; RP + MP_{1,2} of three fourths r4 length, almost reaching distal margin, J indistinct (Fig. 26). Allinotum slightly wider than long, lateral margins slightly convergent posteriad, posterior margin straight; prescutum extending slightly less than half metascutum length (Fig. 21); rounded area of scutum weakly sclerotized, scutum-prescutal plates sclerotized, extending ridges almost up to posterior margin; metascutellum glabrous. Mesosternum weakly sclerotized, acute medially, attached to metasternum by a suture almost as wide as mesosternum (Fig. 22). Mesoepimeron attached to metasternum by membrane (Fig. 22). Mesosternum/mesanepisternum suture inconspicuous (Fig. 22). Mesanepisternum /mesepimeron suture conspicuous (Fig. 22). Metasternum oblique and strongly depressed by mesocoxae, anterior medial keel prominent up to anterior one third, discrimen indistinct, lateral margins divergent posteriad up to lateral-most part of metacoxa, then convergent posteriad posterior margin bisinuose (Fig. 22). Femur slightly shorter than tibia (Fig. 28). Tibial spurs present (Fig. 28). Tarsomere I 2× longer than II, II 2× longer than III, III subequal in length to IV, IV bilobed, lobes reaching two thirds V length (Fig. 29). Mesendosternum with two parasagittal projections directed outwards, irregularly alate (Fig. 26). Metendosternum spatulate, 2× longer than wide, median projection acute anteriad, with two lateral laminae (Fig. 27).

Abdomen (Figs 21, 23, 30–41, 47–50). Tergum I with anterior margin membranous (Fig. 21), laterotergite membranous, polygonal in shape, with sparse

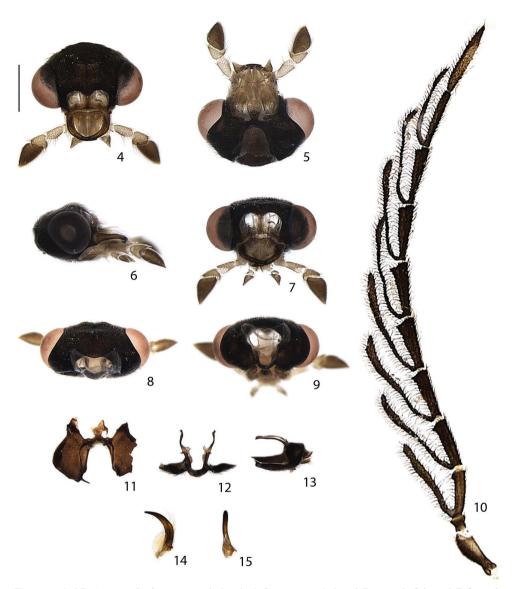


Figures 1. Scissicauda disjuncta, holotype and labels.



Figures 2–3. Scissicauda disjuncta, male habitus 2 dorsal 3 ventral. Scale bar: 2.0 mm (2–3).

bristles (Fig. 23); spiracle obliquely attached to thorax, more vertically (Fig. 21). Terga II–VII with posterior angles progressively produced and acute posteriad, posterior margins progressively bisinuose (Fig. 30). Sterna II–VIII visible (Fig. 31). Spiracles dorsal, at almost half sterna lenghts (Fig. 30). Sternum VIII with larval lanterns elongate (Figs 33–58).



Figures 4–15. *Scissicauda disjuncta*, male head. 4–9 overview 4 dorsal 5 ventral, 6 lateral 7 frontal 8 posterior 9 occipital 10 antenna, frontal 11–13 tentoria, detail. 11 dorsal 12 frontal 13 lateral 14–15 mandible 14 dorsal 15 internal view. Scale bar: 0.5 mm (4–15).

Male. Syntergite consisting of paired lateral plates convergent posteriad (putatively tergite IX or paraproct), median transversal suture absent (Figs 34, 35, 61, 62). Sternum IX asymmetric, posterior margin acute. Aedeagus with phallus consisting of a dorsal plate basally fused to parameres, symmetric, medially grooved, projected dorsolaterally toward apex (Figs 36–38, 41, 63, 64); ventral plate with lateral margins



Figures 16–20. *Scissicauda disjuncta*, prothorax. 16 dorsal 17 ventral 18 lateral 19 frontal 20 posterior. Scale bar: 0.5 mm (16–20).

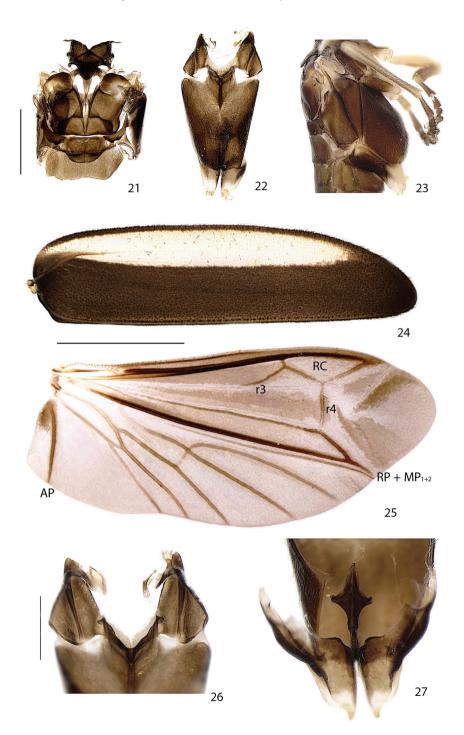
sinuose, weakly sclerotized; parameres symmetric, apically rounded, with a ventrobasal process rudimentary or projected and extended beyond phallus (Figs 40, 65, 66).

Female. Sternum VIII as long as wide, spiculum ventrale long and slender, three fourths sternum length (Fig. 47). Internal genitalia with a large and somewhat rounded spermatophore-digesting gland anteriad to the common oviduct (Fig. 50). Valvifers free, twisted basally, $3 \times$ coxite length; coxites medially fused, coxital baculi well-developed, sclerotized, divergent basally; styli minute, sclerotized; proctiger indistinct (Fig. 49).

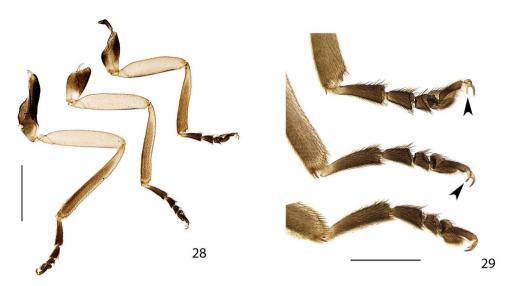
Remarks. Concerning the etymology for the generic name, McDermott (1964) did not refer explicitly to the meaning of *Scissicauda*, neither did Olivier (1911) for *Schistura. Scissi* is putatively derived from the English word scissor, which in turns refer to the old French *cisoires* and the Latin *caedo*, *caesus*; and *cauda*, a Latin word for the pygydium (Brown, 1956) (see Figs 30, 32). *Scissicauda* is of a feminine gender.

Key to species (both sexes)

 Elytron with sutural margin brown to blackish-brown (Figs 1–2, 42); hypomeron constricted posteriad (Fig. 18); male antennae flabellate (Fig. 10); lateral margins of female terminal sternum convergent posteriad, indented medially (Fig. 43) (BRAZIL: *Rio de Janeiro*) *Scissicauda disjuncta* (Olivier, 1896)
 Elytron with sutural margin pale yellow (Figs 51, 67); hypomeron rather bisinuose (Fig. 56); male antennae serrate, without branches (Fig. 54); female terminal sternum rounded (Fig. 68) (BRAZIL: *Espírito Santo*)



Figures 21–27. *Scissicauda disjuncta*, pterothorax and associated structures. 21 dorsal 22 ventral 23 lateral 24 elytron, ventral frontal 25 right wing 26 mesoendosternum, posterior 27 metaendosternum, dorsal. Scale bar: 1.0 mm (21–23); 2.0 mm (24–25); 0.5 mm (26–27). RC radial cell.



Figures 28–29. *Scissicauda disjuncta*, male legs. **28** anterior view of right legs **29** detail of tarsus and claw teeth. Scale bar: 1.0 mm (**28**); 0.5 mm (**29**). Arrows: claw teeth.

Scissicauda disjuncta (E. Olivier, 1896)

Figs 1-50

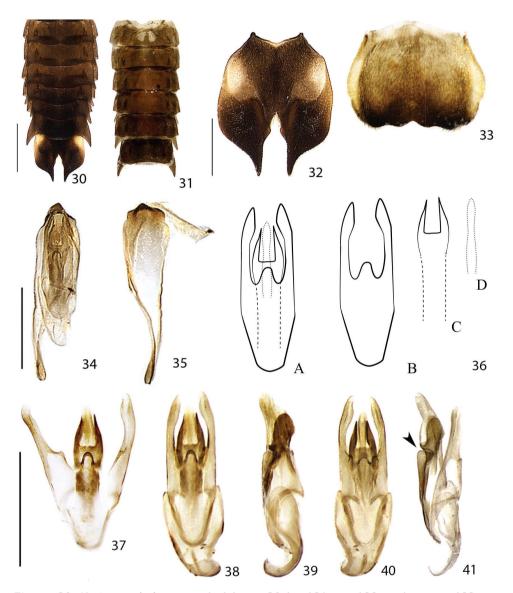
Lucidota disjuncta Olivier, 1896: 1.

Aethra disjuncta (Olivier, 1896). Olivier in Wytsman, 1907: 16; Blackwelder 1944: 353. Schistura disjuncta (Olivier, 1896). Olivier 1911: 51; McDermott 1964: 10, 39. Lychnuris disjuncta (Olivier, 1896); McDermott 1966 (quid pro quo). Scissicauda disjuncta (Olivier, 1896). McDermott 1964: 10, 39; 1966: 87.

Type material. Holotype (Fig. 1) male (MNHN), without locality data (although Olivier 1911 reported the species from Rio de Janeiro). Bearing the labels: 1) green and rectangular, handwriting *Lucidota disjuncta* E. Oliv.; 2) white and rectangular, printed, *Specimen typicum originale auctoris* Ern. Olivier.; 3) white and square, handwriting, Fry.

Material examined. BRAZIL. *Rio de Janeiro*. Rio de Janeiro, without other data, 1 male, 2 females, Fry coll. (BMNH); Petrópolis, P. N. Serra dos Órgãos, 25/11/2012, Mermudes & Mattos col. (DZRJ); Teresópolis, P. N. Serra dos Órgãos, 15/XII/2014, A. Katz col. (DZRJ), ~1100m, 14-17/I/2015, L. Silveira col. (DZRJ), 18/XII/2014, 1 female, V.A.C WILSON col. (DZRJ), 1050m, XII/2013, Malaise trap, 1 male, 2 females, R. Monteiro col. (DZRJ), 1050m, I/2014, Malaise trap, 2 females, R. Monteiro col. (DZRJ), 1050m, II/2014, Malaise trap, 2 females, R. Monteiro col. (DZRJ), 2600, 2000,

Diagnosis. Males with antennae flabellate (Fig. 10) (filiform in *S. balena* sp. n.), anterior pro and mesoclaws bifid (Fig. 29) (entire in *S. balena* sp. n.), phallus dorsal plate strongly rounded basally, phallic groove at apical one third, strongly curved



Figures 30–41. *Scissicauda disjuncta*, male abdomen. 30 dorsal 31 ventral 32 pygidium ventral 33 sternum VIII ventral 34 terminalia, dorsal 35 syntergite and sternum IX, dorsal 36 schematic drawing of aedeagus, dorsal A paramerae and phallum B paramerae, dashed lines show basal part of dorsal plate C Phallic dorsal plate, dashed lines show basal part D ventral plate 37 dissected phallum and paramerae, dorsal 38–41 aedeagus 38 dorsal, 39 lateral 40 ventral 41 lateral view, dissected. Scale bar: 1.0 mm (30–31); 0.5 mm (32–33); 0.5 mm (34–35); 0.5 mm (37–41). Arrow: phallic groove.

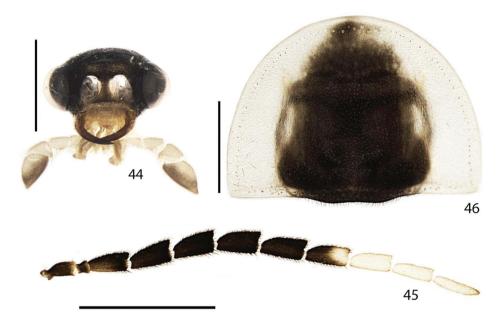
(subtruncate basally, phallic groove at half its length, moderately curved in *S. balena* sp. n.); ventral plate at least 2× phallobase length (slightly shorter than phallobase in *S. balena* sp. n.); parameres ventrobasal process rudimentary (Figs 36–41) (digitiform,



Figures 42-43. Scissicauda disjuncta, female habitus. 42 dorsal 43 ventral. Scale bar: 2.0 mm (42-43).

extending slightly beyond ventral plate, shorter than paramere itself in *S. balena* sp. n., Figs 63–66). Female sternum VIII constricted at posterior one third, indented medially (Fig. 43) (rounded in *S. balena* sp. n., Fig. 68).

Description. Colour pattern. Integument from entirely brown to blackish -brown, scape and pedicel yellowish-brown (Figs 1, 2), legs with trochanters, femora and tibial base yellowish, tibiae progressively darkening toward apex (Fig. 3). Prothorax with translucent to slightly pale yellow peripheral semicircular margin, sometimes bearing orangish vittae (Fig. 2), hypomeron antero-dorsally yellowish (Fig. 18). Elytra

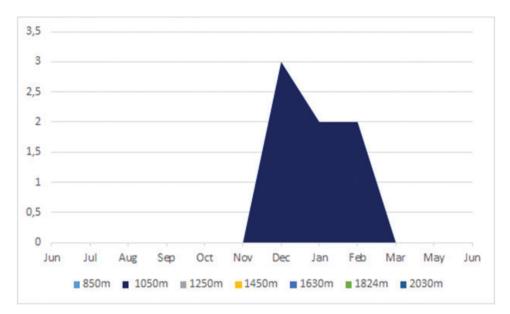


Figures 44–46. *Scissicauda disjuncta*, female. 44 head, frontal 45 antenna 46 pronotum, dorsal. Scale bar: 1.0 mm (44); 2.0 mm (45); 1.0 mm (46).



Figures 47–50. *Scissicauda disjuncta*, female. **47** sternum VIII **48** pygidium, dorsal **49** external genitalia **50** internal genitalia. CO = common oviduct, SDG = spermatophore digesting gland. Scale bar: 1.0 mm (**47–49**); 1.0 mm (**50**).

with pale yellow lateral-longitudinal vittae (Figs 1–3, 24), sutural margin and outer lateral line brown to blackish-brown. Sternum VII with lateral margins yellowish (Fig. 33). Pygidium with anterior angles yellowish (Figs 30, 32).



Graphic 1. For the period of Jun/2013–Jun/2014, *S. disjuncta* was sampled at 1250m of elevation and had an abundance peak in the rainy season, between the November–February in the Serra dos Órgãos mountain range.

Male. Antennae (Fig. 10) with scape constricted basally, pedicel almost as long as wide and constricted medially; antennomeres III–X subequal in length, slightly serrate and basally flabellate, lamellae almost 2× as long as antennomeres, except for branch X, which is one third longer than antennomere; antennomere XI filiform, slightly longer than previous one. Pronotum 1.3× wider than long (Figs 1–3, 16–18). Abdominal sternum II with two median close-set vitreous spots (Fig. 31), sternum VIII with posterior margin trisinuose (Fig. 33). Sternum IX abruptly constricted anteriad at half its length, one third longer than aedeagus (Figs 34–35). Phallus dorsal plate strongly rounded basally, phallic groove at apical one third, strongly curved; ventral plate slightly shorter than phallobase; parameres ventrobasal process rudimentary (Figs 36–41).

Female. Antennomeres III–XI compressed, subequal in length, antennomeres III–X serrate (Figs 42–34, 45). Sternum VIII as long as wide (Fig. 43), constricted at posterior one third, indented medially. Spiculum ventrale long and slender, three fourths sternum length. Sclerotized part of internal genitalia with a large and somewhat rounded spermatophore-digesting gland anteriad to common oviduct. Bursa plate and median oviduct plate absent. Valvifers free, twisted basally, 3× longer than coxite; coxites medially fused, coxital baculi well-developed, sclerotized, divergent basally; styli minute, sclerotized; proctiger indistinct (Figs 47–50).

Biology. Active during daytime, on moisty days. In our experimental design (Jun/2013–Jun/2014), individuals were only collected between December and February, when there is a local increase in pluviosity (Graphic 1). Our results suggest that *S*.

disjuncta breeds during the rainy seasons, possibly in low montane forests. Otherwise, although it could in principle be a sampling artifact, it could also mean that the species has a patchy distribution.

Remarks. McDermott (1966:87) quoted *Lychnuris disjuncta* referring it to Olivier 1899: 91, but in this paper there is no reference to such a name. However, on page 90, there is a *Lychnuris adjuncta* Olivier, 1899, which is not quoted under *Lychnuris* in his catalogue (McDermott 1966). Therefore we consider the citation a *quid pro quo*. Regarding the etymology of the specific name, the author did not mention a meaning for *disjuncta*, which is a Latin expression for apart, separate. We tentatively associate it with the separated corners of the pygidium.

Scissicauda balena Silveira, Mermudes & Bocakova, sp. n. http://zoobank.org/3626185C-4C9A-49AD-B2C2-B079D85D7927 Figs 51–72

Type material. Holotype (Figs 51–66, 71) male, Brazil: Espírito Santo, [n] 6521, Descourtils [leg.], coll. Fry 1905-100 (BMNH). **Paratype** (Figs 67–70, 72) female, Brazil, the same data (BMNH).

Diagnosis. Males with antennal lamellae absent (Fig. 54) (present in *S. disjuncta*, Fig. 10), anterior pro and mesoclaws entire (bifid in *S. disjuncta*), phallus dorsal plate subtruncate basally, phallic groove at half of its length, moderately curved (strongly rounded basally, phallic groove at apical one third, strongly curved in *S. disjuncta*); ventral plate at least 2× phallobase length (slightly shorter than phallobase in *S. disjuncta*); parameres ventrobasal process digitiform, extending slightly beyond ventral plate, shorter than paramere itself (Figs 63–66) (process rudimentary in *S. disjuncta*, Figs 36–41). Females with sternum VIII rounded (Fig. 68) (constricted at posterior one third, indented medially in *S. disjuncta*, Fig. 43).

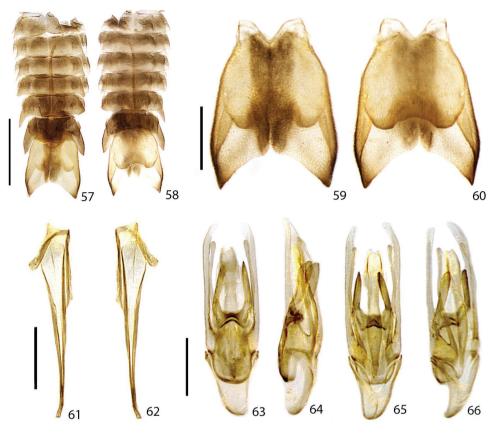
Etymology. The specific name *balena* is a Latin expression for whale, whose tail resembles the pygidium of this species. The name is formed as a noun in apposition.

Description. Colour pattern. Integument overall blackish-brown, with scape brownish (Fig. 54); antennomeres VIII–XI and sternum VIII entirely yellowish (Figs 52, 68). Pronotum largely yellowish at sides and slenderly anterior at the disc, with paired yellow parasagittal vittae (Figs 55, 70); hypomeron translucent, with anterodorsal margin yellowish (Fig. 56). Elytron with pale yellow lateral-longitudinal and sutural vittae (Fig 51, 67). Sternites, trochanters and femorae yellowish, tibiae and tarsi dark-brown (Fig. 52, 68). Abdominal sternites yellowish posteriad (Fig. 52, 68). Pygidium laterally and medially dark-brownish (Fig. 52).

Male. (Figs 51–56, 57–66). Scape constricted basally, pedicel almost as long as wide and constricted medially, antennomeres III–X cylindrical, impressed and not-flabellate (Fig. 54). Pronotum 1.5× wider than long (Fig. 55). Elytra with epipleural maximal width as wide as disc width (Fig. 51). Sternum VIII with posterior margin emarginate (Fig. 60). Sternum IX gradually convergent anteriad, almost 2× longer



Figures 51–56. *Scissicauda balena* sp. n., holotype male. **51–52** habitus **51** dorsal **52** ventral **53** head, frontal **54** antenna, dorsal **55–56** prothorax **55** dorsal **56** lateral. Scale bar: 2.0 mm (**51–52**); 1.0 mm (**53**); 1.0 mm (**55–56**).



Figures 57–66. *Scissicauda balena* sp. n., male abdomen. 57–58 abdomen 57 dorsal 58 ventral 59 syntergite dorsal 60 sternum IX ventral. segment VIII 61 pygidium, dorsal 62 sternum VIII, ventral 63–66 aedeagus 63 dorsal 64 lateral 65 ventral 66 oblique. Scale bar: 2.0 mm (57–58); 1.0 mm (59–60); 1.0 mm (61–62); 0.5 mm (63–66).

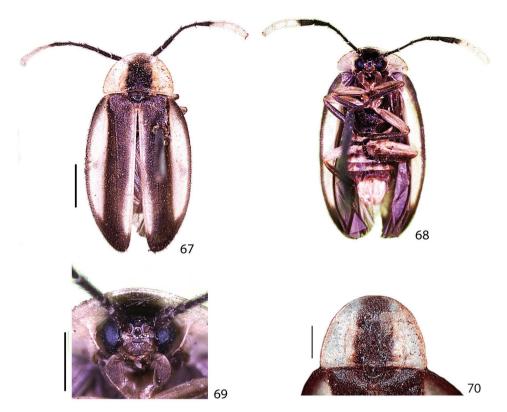
than aedeagus (Figs 61–62). Phallus dorsal plate subtruncate basally, phallic groove at half of its length, moderately curved; ventral plate at least 2× of phallobase length; parameres ventrobasal process digitiform, extending slightly beyond ventral plate, shorter than paramere itself (Figs 63–66).

Female. Sternum VIII rounded, indented medially (Fig. 68).

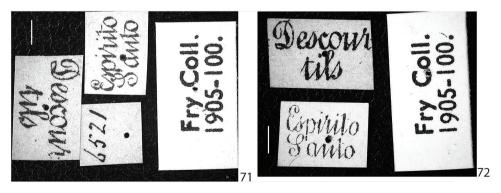
Discussion

Systematics

Scissicauda has flabellate antennae, mandibles arcuate ("normal mandibles" *auctorum*), elytral secondary pubescence absent, and abdominal spiracles dorsally-oriented, all of



Figures 67–70. *Scissicauda balena* sp. n., paratype female. 67–68 habitus 67 dorsal 68 ventral 69 head, frontal 70 pronotum dorsal. Scale bar: 2.0 mm (67–68); 1.0 mm (69); 1.0 mm (70).



Figures 71–72. Scissicauda balena sp. n., labels. 71 holotype 72 paratype. Scale bar: 2.0 mm (71–72).

which are features of the Amydetinae. The long and diffused antennal branches are features of the Psilocladina. A unique feature amongst the Psilocladina is the abdominal sternum VIII covering sternum IX. However, Psilocladina was deemed polyphyletic on the most comprehensive phylogenetic analysis for the Lampyridae (Jeng 2008). Phallus with ventral plate is a condition found in other lampyrids as the Luciolinae (Ballantyne et al. 2011), Ototretinae (Janisova and Bocakova 2012), Photurinae (Rosa 2007) and *Amydetes* Illiger, 1807 (Silveira and Mermudes 2014a). However, several other taxa lack it, as Lampyrinae: Lampyrini (Geisthardt, 1982), Cratomorphini and Photinini (Zaragoza, 1995), and Pleotomini (Jeng et al., 2006). Phallus dorsally fused to parameres is a derived condition in the phylogenetic analysis of Jeng (2008) based on morphological characters, the most comprehensive for the lampyrids. This condition is also found in some Lampyrinae, Photurinae and Amydetinae, putatively as an evolutionary convergence, supported by its low consistency index (CI=0,15, Jeng 2008). The fused phallus cannot articulate with the parameres, being thus articulated only with the phallobase.

Finally, *S. disjuncta* share remarkable similarities on reproductive morphology with some taxa considered basal amongst the Lampyridae (Bocakova et al. 2007, Stanger-Hall et al. 2007), such as: some Photurinae taxa, *e.g. Presbyolampis* spp. (*cf.* Kazantsev and Perez-Gelabert 2008), and *Photuris* (*cf.* Rosa 2007 for male genitalia; L. Silveira dissected some females of this genus); as well as some Luciolinae taxa (reviewed by Ballantyne 1987), especially for the female internal genitalia, that of *S. disjuncta* being quite similar to *Luciola* Laporte, 1833 (South et al. 2008) and *Aquatica* Fu et al. 2010 (Fu et al. 2012), although lacking bursa and median oviduct plates. Even though its knowledge is still incipient, future phylogenetic evaluation and functional morphology of the firefly female genitalia would certainly enhance lampyrid taxonomy.

Sexual dimorphism

We describe for the first time the females of *Scissicauda disjuncta* and *S. balena* sp. n., detailing especially the female internal tract, which is inedit for South American taxa and also for the Psilocladina as a whole. Other psilocladina taxa with known females are *Psilocladus* Blanchard, 1846 and *Pollaclasis* Newman, 1838, both genera showing virtually no secondary sexual dimorphism. In *Scissicauda*, secondary sexual dimorphism is stronger in *S. disjuncta*, where only the males have long lamellae and teethed pro and mesoclaws. *S. balena* sp. n. is dimorphic only in abdominal segments VIII and beyond. Besides the slightly greater size of the females in both *Scissicauda* species, there are no other noteworthy dimorphic character.

Sexual selection and possible function of the pygidium in the genus

We suggest male pygidium is involved in reproduction. This could be either working as a clamp, or by enhancing female fecundity. Clamping structures allow prolonged copulation, which is generally assumed to ensure paternity by preventing other males to access - and thus fertilize the eggs of the female (Wing et al. 1993). The evidence that male pygidium may work as a clamp is that anterior angles of female pygidium, which should attach male abdomen, are sclerotized. Alternatively, male reproductive structures may stimulate females while mating, and thus increase fertilization and/or oviposition rates. It was shown that in polyandric systems, female choice can promote male genitalic diversification (Arn-qvist 1998), although the *modus operandi* is still disputed (Hosken and Stockley 2004). Furthermore, structures involved in mating are generally species-specific (which is the case in *Scissicauda*) and evolve fast (Eberhard 2004), often as a consequence of sexual selection (Hosken and Stockley 2004), and may promote reproductive isolation either by structural or sensory lock-and-key, thus avoiding hybridization (Masly 2012). Future field observations and detailed histological studies would be useful to test these hypotheses.

Endemism

Although similar sampling efforts have been made in other montane areas of the Rio de Janeiro State (notably the Serra da Mantiqueira formation), *Scissicauda* was only collected in the Serra dos Órgãos (Petrópolis and Teresópolis municipality). However, the holotype of *S. disjuncta* is reported from Rio de Janeiro (Olivier 1896), which could be related to the city or the state (which includes the aforementioned municipalities). Thus, we assume that *S. disjuncta* is restricted to the Serra dos Órgãos low montane forests, and could have occurred also in the Tijuca Forest, although no specimens collected there were found in any of the entomological collections studied. *S. balena* sp. n. is described from Espírito Santo State, Brazil, lacking more precise locality data.

Acknowledgements

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References

Amaral DT, Arnoldi FGC, Rosa SP, Viviani VR (2014) Molecular phylogeny of Neotropical bioluminescent beetles (Coleoptera: Elateroidea) in southern and central Brazil. Luminescence 29(5): 412–422. doi: 10.1002/bio.2561

- Arnqvist G (1998) Comparative evidence for the evolution of genitalia by sexual selection. Nature 393(6687): 784–786. doi: 10.1038/31689
- Ballantyne LA (1987) Lucioline Morphology, Taxonomy and Behaviour: A Reappraisal (Coleoptera, Lampyridae). Transactions of the American Entomological Society 113: 171–188.
- Ballantyne L, Fu XH, Shih CH, Cheng CY, Yiu V (2011) *Pteroptyx maipo* Ballantyne, a new species of bent-winged firefly (Coleoptera: Lampyridae) from Hong Kong, and its relevance to firefly biology and conservation. Zootaxa 2931: 8–34.
- Blackwelder RE (1944) Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America. United States National Museum Bulletin 185: 189–341.
- Brown RW (1956) Composition of scientific words. Smithsonian Institution Press, Washington, 882 pp.
- Crowson RA (1938) The metendosternite in Coleoptera: a comparative study. Transactions of the Royal Entomological Society of London 87(17): 397–415. doi: 10.1111/j.1365-2311.1938.tb00723.x
- Crowson RA (1944) Further studies on the metendosternite in Coleoptera. Transactions of the Royal Entomological Society of London 94(2): 273–310. doi: 10.1111/j.1365-2311.1944. tb01220.x
- Eberhard WG (2004) Rapid divergent evolution of sexual morphology: comparative tests of antagonistic coevolution and traditional female choice. Evolution 58(9): 1947–1970. doi: 10.1111/j.0014-3820.2004.tb00482.x
- Geisthardt M (1982) Beitrag zur Kenntnis der Gattung *Nyctophila* Olivier, 1884 (Coleoptera, Lampyridae). Annales historico-naturales Musei nationalis hungarici 74: 115–128.
- Hosken DJ, Stockley P (2004) Sexual selection and genital evolution. Trends in Ecology & Evolution 19(2): 87–93. doi: 10.1016/j.tree.2003.11.012
- Janisova K, Bocakova M (2012) Revision of the subfamily Ototretinae (Coleoptera: Lampyridae). Zoologischer Anzeiger 252: 1–19. doi: 10.1016/j.jcz.2012.01.001
- Jeng ML, Branham MA, Yang PS (2006) Revision of the Neotropical genus *Roleta* (Coleoptera: Lampyridae). Insect Systematics and Evolution 37(2): 227–239. doi: 10.1163/1876-31206788831100
- Jeng ML (2008) Comprehensive phylogenetics, systematics, and evolution of neoteny of Lampyridae (Insecta: Coleoptera). PhD thesis, University of Kansas, Lawrence, Kansas.
- Jeng ML, Branham MA, Engel M (2011) A second species of *Oculogryphus* (Coleoptera, Lampyridae), with notes on the phylogenetic affinities of the genus. ZooKeys 97: 31–38. doi: 10.3897/zookeys.97.1223
- Kazantsev SV, Perez-Gelabert DE (2008) Fireflies of Hispaniola (Coleoptera: Lampyridae). Russian Entomological Journal 17(4): 367–402.
- Masly JP (2012) 170 years of "lock-and-key": genital morphology and reproductive isolation. International Journal of Evolutionary Biology 2012: 1–10. doi: 10.1155/2012/247352
- McDermott FA (1964) The taxonomy of the Lampyridae (Coleoptera). Transactions of the American Entomological Society 90: 1–72.
- McDermott FA (1966) Lampyridae. In: Steel WO (Ed.) Coleopterorum Catalogus Supplementa. Pars 9 (editio secunda). W. Junk, S'Gravenhage, 149 pp.

- Olivier E (1896) Descriptions de nouvelles especes de Lampyrides du Musee de Tring. Novitates Zoologicae III: 1–3.
- Olivier E (1899) Revision des coléoptères lampyrides des Antilles et description des especes nouvelles. Bulletin de la Société zoologique de France 24: 87–92.
- Olivier E (1907) Coleoptera. Fam. Lampyridae. Genera Insectorum 53: 1-74.
- Olivier E (1911) Révision des Lampyrides. Revue scientifique du Bourbonnais et du centre de la France 24: 39–58.
- Rosa SP (2007) Description of *Photuris fulvipes* (Blanchard) immatures (Coleoptera, Lampyridae, Photurinae) and bionomic aspects under laboratory conditions. Revista Brasileira de Entomologia 51(2): 125–130. doi: 10.1590/S0085-56262007000200001
- Silveira LFL, Mermudes JRM (2013) Memoan ciceroi gen. et sp. n., a remarkable new firefly genus and species from the Atlantic Rainforest (Coleoptera: Lampyridae). Zootaxa 3640(1): 79–87. doi: 10.11646/zootaxa.3640.1.6
- Silveira LFL, Mermudes JRM (2014a) Systematic review of the firefly genus *Amydetes* Illiger, 1807 (Coleoptera: Lampyridae), with description of 13 new species. Zootaxa 3765(3): 201–248. doi: 10.11646/zootaxa.3765.3.1
- Silveira LFL, Mermudes JRM (2014b) *Ybytyramoan*, a new genus of fireflies (Coleoptera: Lampyridae, Lampyrinae, Photinini) endemic to the Brazilian Atlantic Rainforest, with description of three new species. Zootaxa 3835(3): 325–337. doi: 10.11646/zootaxa.3835.3.2
- South A, Sota T, Abe N, Yuma M, Lewis SM (2008) The production and transfer of spermatophores in three Asian species of Luciola fireflies. Journal of Insect Physiology 54: 861–866. doi: 10.1016/j.jinsphys.2008.03.008
- Viviani VR, Amaral D, Prado R, Arnoldi FG (2011) A new blue-shifted luciferase from the Brazilian Amydetes fanestratus (Coleoptera: Lampyridae) firefly: molecular evolution and structural/functional properties. Photochemical and Photobiological Sciences 10: 1879–86. doi: 10.1039/C1PP05210A
- Wing SR, Lloyd JE, Hongtrakul T (1983) Male competition in *Pteroptyx* fireflies: Wing-cover clamps, female anatomy, and mating plugs. Florida Entomologist 66(1): 86–91. doi: 10.2307/3494553
- Zaragoza CS (1995) La familia Lampyridae (Coleoptera) en la Estación de Biología Tropical "Los Tuxtlas", Veracruz, México. Universidad Nacional Autónoma de México, México: Publicaciones Especiales del Instituto de Biología 14, 93 pp.

RESEARCH ARTICLE



Review of Afraustraloderes rassei Bouyer, 2012: description of its female and a new species of Pixodarus Fairmaire, 1887 (Coleoptera, Cerambycidae, Prioninae)

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Abstract

The original description of *Afraustraloderes rassei* Bouyer, 2012 included a female that is now recognized as a separate species belonging to the genus *Pixodarus* and here described as *P. spiniscapus* sp. n. The true female of *A. rassei* has also been obtained recently and is, therefore, here described. The synonymy of *P. exasperatus* with *P. nyassae*, proposed earlier by Santos Ferreira (1980), is here supported. Conversely, the earlier inclusion of *A. rassei* in the tribe Hopliderini is rejected, on the basis of a key set of characters established by Quentin and Villiers (1972, 1975). *Afraustraloderes rassei* appears to be restricted to the Cape Floral Region, exhibiting larval development in trunks and roots of dead Proteaceae plants. Conversely, *P. spiniscapus* has so far only been recorded in the eastern part of South Africa and appears to be associated with bushveld vegetation.

Keywords

Hopliderini, new species, Cape Floral Region, South Africa

Introduction

Afraustraloderes rassei Bouyer, 2012 was originally described based on a small collection of three males and one female from South Africa. Bouyer (2012) acknowledged that the two sexes were morphologically very different, but decided nevertheless to describe them as the male and female of a new species and new genus. This was on the grounds that both exhibited a pronounced spine on the internal margin of the first antennomere, which is a unique character not shared with any other known Hopliderini, the tribe to which he assigned the new species.

The male and female specimens represented in the photos of Figures 1 and 2 in Bouyer (2012), show several distinct differences. The holotype male was purchased at an unspecified entomological fair, and was collected in "Matrosberg" [sic], probably Matroosberg in the Western Cape Province, in 2003. Two paratype males were included in the original description, both from Joubertina in the Eastern Cape Province. The "allotype female", however, is a specimen reportedly collected in Oribi Gorge, KwaZulu-Natal Province in 1989.

In 2006, one of the authors (EG) was working on the collection of the late Richard Watmough, a well-known South African entomologist who passed away in 2005 (Allsopp 2005). Upon his death, his private insect collection was bequeathed to the Mountain Club of South Africa, which in turn donated it to the South African National Collection of Insects (SANC), Pretoria. Three specimens resembling the female "*A. rassei* allotype" of Bouyer (2012) were discovered in this collection during 2013, two males and one female. This revealed that the initial assumption that the female belonged to the same species (*A. rassei*) was incorrect, and that this specimen, and those discovered in the Watmough collection, represented a new prionine species. This prompted further searches in the Joubertina fynbos area, in an attempt to find the yet undescribed female of *A. rassei*. One adult female and five more males were obtained in December 2014, by rearing larvae collected in the field during 2013. This now allows for a full review of the species, including the description of the correctly recognised female *A. rassei* and the placement of the original "female allotype" within a new species of *Pixodarus* Fairmaire, 1887.

Materials and methods

Adult specimens of *A. rassei* were obtained either through direct searching of burnt and dead logs/roots of Proteaceae in the fynbos vegetation or by rearing their larvae in a controlled, closed environmental room in Port Elizabeth, about 170 km from the Joubertina collection locality. Larvae were collected in an advanced stage of development and maintained in the logs in which they were found in closed plastic crates, in darkness and at ambient temperature. Logs were left lying in a horizontal position with minimal manipulation and moistened by spraying rainwater on the outer surface once a month. Specimen length was measured from the anterior margin of the head to the elytral apex and the width was measured at the widest point of the elytra. Photos of set specimens were taken using either a Canon EOS 5D camera fitted with a Canon MP-E 65 Macro 2.8–1.5× objective or a Canon PowerShot G11 with automatic macro setting. The background was removed from the photos using Microsoft Word 2010 (Picture Tools), to increase clarity of resolution. Combine ZP Image Stacking Software by Alan Hadley (alan@micropics.org.uk) was used to obtain z-stacking composite images. *In situ* photos were taken using a Ricoh CX1 camera with macro setting.

Terminology used to describe the male genitalia follows the standard work of Ehara (1954) and is complemented with more recent views as reported in Hubweber and Schmitt (2006, 2010) and Lin and Li (2012).

Holotype label data is quoted verbatim. Collections are abbreviated as follows: SANC, South African National Collection of Insects (Pretoria, South Africa); NHMO, Natural History Museum (Oslo, Norway); ABPC, Anders Bjørnstad Private Collection (Skien, Norway); RPPC, Renzo Perissinotto and Lynette Clennell Private Collection (Port Elizabeth, South Africa); TBPC, Thierry Bouyer Private Collection (Chênée, Belgium); NDPC, Norbert Delahaye Private Collection (Plaisir, France); TGPC, Thierry Garnier Private Collection (Montpellier, France). Geographical abbreviations are as follows: RSA, Republic of South Africa; ECA, Eastern Cape Province, RSA; GAU, Gauteng Province, RSA; MPU, Mpumalanga province, RSA.

Four observations of the new *Pixodarus* species were located on the citizen science platform iSpot (Silvertown et al. 2015) and incorporated in this study. Stable, permanent copies, using WebCite (Eysenbach and Trudel 2005), were created on 03 July 2015. Their URLs are given in the Additional records section for this species.

Taxonomic account

Genus Afraustraloderes Bouyer, 2012

Type species. Afraustraloderes rassei Bouyer, 2012

When Bouyer (2012) described the genus *Afraustraloderes* he assigned it to the tribe Hopliderini Thomson, 1864. The reason for this seems to be due to the incorrect assumption that it was the male of a female which obviously belongs to the Hopliderini.

The tribe Hopliderini was revised by Quentin and Villiers (1972, 1975). They provided several morphological characteristics for recognizing the group, first as a subtribe of the Callipogonini Thomson, 1861 (Quentin and Villiers 1972), later as a tribe of its own (Quentin and Villiers 1975). The most important of these are listed below and numbered here for easy reference:

- 1. eyes strongly emarginate, but not embracing antennal tubercle;
- 2. eyes widely separated dorsally;
- 3. antennae as long as or exceeding the body length in males;

- 4. antennae gradually becoming more slender distally;
- 5. scape very short;
- 6. 3rd antennomere very long;
- 7. anterior coxal cavities open posteriorly;
- 8. prosternal process pointed;
- 9. metathoracic episterna usually truncate apically, without posterior constriction;
- 10. tibiae apically spined;
- 11. pronotal disc distinctly punctate;
- 12. lateral margins of pronotum each bearing five spines;
- 13. anterior border of pronotum with a silky tuft on each side of the 'neck';
- 14. head strongly declivous, resulting in mandibles not being visible in dorsal view.

Afraustraloderes has some of these characteristics: *viz.* items 1, 2, 5, 7, 13 (partly) and 14. But it does not exhibit the majority of the features listed above: *viz.* nos. 3, 4, 6, 8, 9, 10, 11, 12. Regarding no. 9, although the metathoracic episterna are truncate apically, there is an evident constriction near the distal end. Regarding no. 10, there are the usual two spurs between the end of the tibia and the base of the tarsus, but there are no apical teeth or spines on the tibiae themselves. Regarding no. 11, there is micro-punctation on the disc of the male, but not in the female. Thus, from the above analysis it can be concluded that *Afraustraloderes* does not belong in the tribe Hopliderini. We propose that this genus be removed from the Hopliderini and regarded as Prioninae *incertae sedis*.

Afraustraloderes rassei Bouyer, 2012

Figures 1-4, 7-8

Afraustraloderes rassei Bouyer, 2012: 214

Material examined. Paratypes: 1♂ RSA, ECA, Joubertina (33°53'10" S, 23°50'18" E), 18 Dec 2009, M Villet and R Smith leg (RPPC); 1♂, same locality, but 25 Dec 2010, R Perissinotto and L Clennell (TBPC). Other material: 1♂, same locality as paratype, but Oct 2010, found dead on the ground, Rodger Smith leg (RPPC); 1♀, same locality, but 28 Dec 2014, found dead inside dead *Protea* log, R Perissinotto and L Clennell (RPPC); 5♂ 1♀, same locality, bur reared from larvae in Port Elizabeth, adults emerged 23 Dec 2014-7 Jan 2015 (ABPC, NDPC, NHMO, RPPC, SANC, TGPC).

Description of the female. *Size.* 29.6–31.5 mm long including pygidium, 11.5–12.2 mm wide (maximum width at metacoxae).

Head. Mandibles relatively short and broad with foveolate base, distal part short, shiny and weakly arcuate with pointed apex, cutting edge with a small tooth near base; maxillary and labial palpi with terminal segments terete and slightly truncate at apex; galeae much shorter than palpi and covered in rufous bristles; clypeus with long stiff rusty brown bristles directed anteriorly; frons very uneven; antennal tubercles moderately



Figure 1. Afraustraloderes rassei &, 33 mm A dorsal habitus B ventral habitus (Photos: Lynette Clennell).

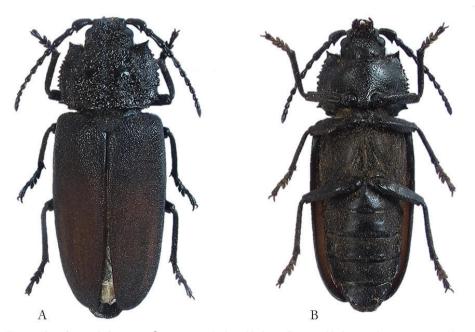


Figure 2. Afraustraloderes rassei $\stackrel{\bigcirc}{_{+}}$, 31.5 mm A dorsal habitus B ventral habitus (Photos: Lynette Clennell).



Figure 3. Afraustraloderes rassei \bigcirc **A** ovipositor in dorsal view (length segment 8+9: 6 mm) **B** apical section of ovipositor enlarged (Photos: Anders Bjørnstad).

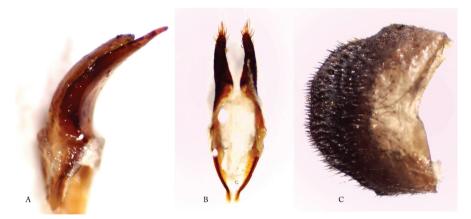


Figure 4. *Afraustraloderes rassei*, male genitalia **A** median lobe, apex of ventral (above) + dorsal (below) plates, semi-lateral view **B** tegmen, ventral view **C** anal tergite, dorsal view (Photos: Anders Bjørnstad).

raised, with strongly uneven, deeply sculptured surface; eyes small, finely facetted with deep emargination dividing each eye into subequal lobes, with lower lobe almost reaching gula; vertex strongly uneven and deeply sculpted, with poorly defined median depression.

Antenna. Short and slender, only reaching slightly beyond humeri of elytra; with scape as longest antennomere, finely punctate with a narrow base gradually widening distally and ending in apical spine on posterior margin; antennomeres 2–10 with circular cross-section, exhibiting narrow base but widened apically; 11th antennomere slightly compressed; pedicel very short, 3rd antennomere almost as long as scape, antennomeres 4–11 subequal in length.

Pronotum. Distinctly transverse, with disc deeply sculpted by irregular reticulations and foveolations; two strongly uneven, raised areas with smooth and shiny surface present about halfway between anterior and posterior margin; anterior margin with fringe of short, black setae curled around base of head, but slightly longer and straight on either side of head, without forming a marked 'brush'; lateral margins with many (15–20) short teeth, foremost tooth much stronger than others and directed forwards, last tooth on each side, near posterior corner, much larger and sharper than the rest.

Scutellum. Broadly tongue-shaped to triangular, with finely reticulate surface.

Elytron. Shallowly reticulate basally, sculpture becoming less distinct towards rounded apices; humeri smoothly rounded.

Legs. Short and slender; femora only slightly thickened at middle, hardly projecting beyond lateral borders of elytra; tibiae nearly straight, only slightly curved in basal part; tarsi with first tarsomere slightly longer than others, noticeably so in metatarsi.

Pygidium. Tergite 8 long, protruding beyond elytral apices.

Ventral surface. Base of maxilla punctate and shiny; submentum transversely ridged; gula glabrous, deeply punctate/reticulate/foveolate, but posterior part raised, exhibiting black bristles and less sculpture; prosternum shiny, transversally strongly convex, punctate, glabrous and with ligulate prosternal process bent dorsally at apex; proepimeron only weakly punctate, glabrous, not reaching prosternal process (i.e. procoxal cavities open); mesosternum punctate and with longitudinal median furrow, with soft black pubescence, exhibiting mesial depression just in front of mesocoxae; mesosternal process short, strongly excavate, resulting in bifurcate apex; mesocoxae moderately raised; metasternum transversally strongly convex, with median furrow increasing in depth posteriorly; whole metasternum and mesepisterna covered by soft, sparse blackish pubescence; metathoracic episterna posteriorly narrowed and truncate; all five visible abdominal sternites subequal in length, densely, but shallowly punctate, glabrous in median part, increasingly pubescent laterally with very short and soft whitish bristles; last visible sternite with evenly rounded posterior margin.

Ovipositor. Abdominal segments 8 + 9 (Figure 3A) are fully extended, and together measure 6 mm. They telescope into segment 7 when retracted (Hutcheson 1980). Figure 3B shows an enlarged photo of the apical portion of the ovipositor with coxites and styli. The strong sclerotization is consistent with an ovipositor characteristic of Cerambycidae that lay their eggs beneath bark, and is typical of the subfamily Prioninae, as opposed to the unsclerotized ovipositors of Cerambycinae, Lepturinae and Lamiinae (cf. e.g. Hubweber and Schmitt 2010: 40 Fig. 2).

Remarks. *Sexual dimorphism.* The morphological differences between the sexes are largely confined to the anterior parts of the thoracic segments. The most noticeable difference lies in the appearance and structure of the pronotum. Although the outline is quite similar in both male and female. The pronotal disc of the male has an even, matte surface, while that of the female has a very irregular lustrous surface (Figure 2A). The male pronotum is mostly shallowly irrorate or punctate, with three deep depressions: two large lateral ones, elliptic in outline; and a smaller dot-like pit medially (Figure 1A). Conversely, the female pronotum is heavily and deeply sculptured, with two irregular smooth and raised areas in about the same position as the elliptic depressions of the male (Figure 2A).

Ventrally the male prosternum and proepimera have a relatively smooth surface, with only a shallow microstructure giving a matte appearance (Figure 1B), while the same parts in the female are strongly punctate and shiny (Figure 2B). The punctate prosternal process of the female is wider than the corresponding finely sculptured process of the male. Sexual dimorphism is also clearly expressed in the shape and structure of the mesosternum: where the female has a shiny mesial concavity anterior to the mesocoxae (Figure 2B), the male has a matte and finely punctate convexity with a low irregular, shiny median ridge (Figure 1B). The anterior border of the mesosternum, hidden beneath the prosternal process, is shallowly excavate in the female, but bluntly convex in the male. The bifurcate mesosternal process is quite prominent in the female, but much less so in the male.

As usual, the visible abdominal sternites are transversally more convex in the female than in the male (Figures 2A and 2B). Also, the pygidium is long and protruding in the female, but hardly visible in dorsal view in the male. The posterior border of the ultimate visible sternite is evenly rounded in the female, but weakly truncate in the male. Finally, unlike in most other Prioninae there is very little difference in the shape and length of the female and male antennae (Figures 1A and 1B).

Male genitalia. Bouyer (2012) in his original description of A. rassei pictured the male genitalia with lateral and dorsal views of the tegmen and 'penis' (median lobe), including the two sclerotized plates of the internal sac. The accompanying description was, however, very brief and limited in detail. A more comprehensive description is hereby given. Median lobe 4 mm long, strongly arcuate with apophyses (median struts, paired lamellae) rather short, constituting only c. 35% of total length of median lobe (Figure 4A); apophyses weakly sclerotized, becoming nearly transparent towards their truncate apices; ventral plate (ventral lobe of median lobe or "ventral edge of the median orifice" sensu Ehara 1954) very long with a sharply pointed apex, length surpassing the bilobed dorsal plate; ventral plate strongly sclerotized, dorsal plate much less so; median foramen not elongate; tegmen 4 mm long, strongly sclerotized (black almost throughout); parameres quite long, constituting one third of total tegmen length; apical brush with setae much shorter than parameres; ringed part gradually curved, not geniculate, arms converging (Figure 4B). The shape and structure of the anal tergite has in some studies proven to be of great diagnostic value (e.g. Adlbauer 1998). The anal tergite of the male A. rassei (Figure 4C) is black, about 1.5 times wider than long, moderately vaulted and with a truncate, but not emarginate, posterior border. The tergite is provided with a dense cover of black, short, stiff, very acute setae.

Genus Pixodarus Fairmaire, 1887

Type species. Hoplideres nyassae Bates, 1878

In their revision of the African and Madagascan Hopliderini (then referred to as subtribe Hopliderina), Quentin and Villiers (1972) cautioned strongly in their preamble about treating this group carefully: "due to the extreme variability of a number of characters" (l.c. p. 258). As examples of this extreme variability, they listed characters like the longitudinal furrow of the head, the length and number of spines on the antennae and

antennomeres, the shape, sculpture and number of lateral spines on the pronotum, the spines and denticulation of the humeral and posthumeral margins of the elytra, and the pubescence on the ventral surface and tibiae.

In spite of these cautionary remarks, Quentin and Villiers (1972) described a new species of *Pixodarus*, *P. exasperatus*, based on very subtle characters. These included the raised parts of the pronotal vermiculations being glossy or not, variations in shades of reddish-brown to black in the colour of the elytra, as well as small differences in elytral length/width ratios.

Pixodarus nyassae is known from RSA and Mozambique northwards to Zimbabwe and Malawi, while *P. exasperatus* occurs in Tanzania, southern Kenya and the eastern part of the Democratic Republic of Congo (Quentin and Villiers 1972). During the course of this study, the authors have examined a number of specimens from RSA and Mozambique, as well as from Tanzania. We find great variation in all diagnostic characters mentioned both in the southern and the northern populations, and these variations strongly overlap. We therefore endorse the earlier proposal of Santos Ferreira (1980) to synonymize *P. exasperatus* with *P. nyassae*.

On the other hand, the female erroneously included in the description of *A. rassei* by Bouyer (2012) represents a new species of *Pixodarus* and, together with the recently obtained male, is described as a new species below.

Pixodarus spiniscapus Bjørnstad & Grobbelaar, sp. n. http://zoobank.org/88E28DA9-EBA6-482D-BEC3-CEFCC6B4EF80 Figures 5–7

Type material. Holotype ♂: SOUTH AFRICA: GAU, Florauna, Pretoria 25°41'20"S, 28°09'30"E, XII.1985, R.H. Watmough (SANC). Paratypes: 1♀: same data as holotype, XI.1989 (SANC); 1♂: same data as holotype, XII.1987 (ABPC); 1♀: RSA, GAU, Magaliesberg, SSW Hekpoort, 25°54'58"S, 27°35'51"E, 21-30.XI.2012, M. Shanahan (SANC).

Material excluded from type series due to insufficient data. 1 (3: A69 [no further data] (SANC).

Additional records (iSpot). 1♂: RSA, GAU, Roodepoort, Walter Sisulu National Botanical Garden (26°05'21"S, 27°50'40"E), 05 Nov 2012, A Hankey, http://www.webcitation.org/6ZkmxK0on; 1♀: RSA, GAU, Randburg, Curro Aurora Private School, school grounds (26°04'48"S, 27°56'06"E), 30 Oct 2014, A Hankey, http://www.webcitation.org/6ZknFLtcm; 1♂: RSA, MPU, Presidentsrus (25°45'33"S, 29°19'05"E), 31 Oct 2014, R Bate, light trap, http://www.webcitation.org/6ZknAyhMq; 1♀, ditto, but 14 Nov 2014, http://www.webcitation.org/6ZknGm829.

Description. *Size.* Male: 31.5–33.7 mm long, 12.5–13.4 mm wide (maximum width at metacoxae); female: 33.9-34.0 mm long, 13.0-13.7 mm wide (maximum width at metacoxae).

Head. Mandibles black, short and stout with deeply punctate base and strongly hooked apex; maxillary palpi tetramerous, labial palpi trimerous, basal segment of



Figure 5. *Pixodarus spiniscapus* sp. n. holotype ♂, 31.5 mm **A** dorsal habitus **B** ventral habitus (Photos: Karsten Sund).

maxillary palpi extremely short and appearing 3-segmented; shape and size of the two types of palpi very similar, both shiny and brown with long, stiff, yellow setae, terminal segments hyaline in apical third and abruptly truncate; frons short, deeply concave, bordered by lateral ridges formed as continuation of mandibular bases; antennal tubercles prominent, separated by a narrow depression which continues well past the eyes posteriorly, then disappears gradually on vertex; yellowish to orange arcuate to curled bristles present on most surface areas, particularly well-developed along above mentioned depression; entire fronto-dorsal surface heavily sculpted with irregular irrorations and foveolations; eyes finely facetted, sinuately emarginate resulting in smaller dorsal eye lobe and larger suborbicular ventral lobe, emargination itself densely pubescent; genae very short.

Antenna. Scape almost wedge-shaped, gradually widening distally from narrow base, slightly compressed, with marked apical spine on proximal side; pedicel very short (< 1/5 length of scape); antennomere 4 noticeably shorter than 3 and 5 in male, not in female; antennomeres 3 and 5–10 of subequal length in male; last antennomere longest by far, more than 1.5 times length of preceding; antennomeres 3-9 + 11 of sub-



Figure 6. *Pixodarus spiniscapus* sp. n.: paratype ♀, 33 mm **A** dorsal habitus **B** ventral habitus (Photos: Karsten Sund).

equal length in female, only antennomere 10 slightly shorter; antennomeres 1–3 punctate in both male and female, segment 4 transitional and last 7 antennomeres only very finely micropunctate; antennomeres 2–4 practically terete, from segment 5 onwards increasingly flattened and with weak lateral tooth apically; apical segment sharply carinate; antenna reaching approximately 4/5 of elytral length or slightly longer in male, only about ½ or slightly longer in female.

Pronotum. Distinctly transverse, length/width ratio of pronotal disc (lateral spines excluded) approximately 0.6; anterior margin straight to shallowly concave, posterior margin slightly convex medially; three stout spines present laterally on either side, two straight spines at edge of anterior margin and at posterior corner respectively, one strongly curved spine between previous two and pointing posteriorly; few irregular small teeth between first and second spine; pronotal disc irregularly folded and foveate to shallowly vermiculate, elevated parts shiny; sparse yellowish- to rusty brown and somewhat curly pubescence covering much of surface, particularly dense along anterior margin.



Figure 7. *Pixodarus spiniscapus* sp. n. male genitalia **A** tegmen, ventral view **B** median lobe (Photos: Anders Bjørnstad and Karsten Sund).

Scutellum. Shield-like, pubescent and finely punctate.

Elytron. Dark brown, and rather elongate, ratio elytral length:combined elytral width at metacoxae varying between 1.9 and 2.3; surface distinctly costate, with three costae normally visible at least in part; humeri rounded and weakly marked; post-humeral lateral margin bent outwards and upwards, forming a miniature "gutter"; posterior sutural corner sharply angled, or exhibiting small tooth, otherwise lateral margin evenly rounded; shallow vermiculations in subscutellar part, gradually becoming finely punctate laterally and posteriorly; basal parts sparsely covered with short yellowish pubescence, gradually becoming less conspicuous posteriorly; greatest elytral width in female about half way down the elytron, distinctly wider than in male.

Legs. Profemora with a somewhat scabrid dorsal surface, ventral face punctate; meso- and metafemora smooth and lustrous dorsally; tibiae straight with short rusty brown pubescence, all widening towards the apex, with two short spurs on proximal side and blunt tooth on distal side; all tarsomeres on all legs of subequal length.

Ventral surface. Gula strongly concave and densely punctate in anterior part, transversely undulate in posterior part; prosternum pubescent, distinctly convex with anterior border strongly thickened; prosternal process ligulate with apex bent dorsally; procoxal cavities open; mesosternum punctate and pubescent, very short; mesosternal process short with median furrow, bifurcate apically; metasternum strongly convex, pubescent, finely punctate and glossy; all five visible abdominal sternites of subequal length, finely punctate, pubescent and glossy; last visible sternite with rounded to weakly truncate posterior border in female, weakly concave in male; epipleura well developed in correspondence with dorsal gutter-like extension of elytral margin.



Figure 8. Typical habitat of *Afraustraloderes rassei*, with fynbos vegetation regrowth after fire on the slopes of the Langkloof mountains near Joubertina (Photo: Lynette Clennell).



Figure 9. *Afraustraloderes rassei* $\stackrel{\circ}{\sim}$ specimen in its natural habitat assuming "defensive position", Joubertina 25 Dec 2010 (Photo: Lynette Clennell).

Male genitalia. Median lobe (sensu Ehara 1954, Hubweber and Schmitt 2010; otherwise commonly referred to as just "aedeagus" or "penis", e.g. Bouyer 2012) with heavily sclerotized acuminate ventral edge of median orifice (= ventral plate sensu Lin and Li 2012, but usually referred to as 'ventral lobe'); dorsal edge of median orifice (dorsal plate/'dorsal lobe') rounded with emarginate apex, only slightly shorter than ventral edge, and distinctly less sclerotized; basal apophyses (sensu Hubweber and Schmitt 2010; in Ehara 1954 as "median struts") long and strap-shaped, constituting more than 60% of total length of median lobe; median foramen not elongate; tegmen reddish-brown to brown, indicating medium sclerotization (Hubweber and Schmitt 2006); parameres (lateral lobes) long and slender and widening slightly apically, with brush of setae, shorter than the parameres; pouch-like appendage on internal side at base of each paramere; tegminal ring with converging geniculated arms.

Etymology. The name '*spiniscapus*' refers to the prominent apical spine present on the first antennomere or scape.

Remarks. Pixodarus spiniscapus sp. n. differs from P. nyassae (Bates, 1878) (syn. P. exasperatus Quentin and Villiers, 1972) in several diagnostic characters. Unlike P. nyassae, P. spiniscapus has costate elytra and these are also more elongate than in P. nyassae. Its ratio of elytral length: combined width at humeri varies from 1.9 to 2.3, while it ranges between 1.7 and 1.9 in *P. nyassae*. The first antennomere, in particular, has a distinct apical spine in *P. spiniscapus*, while it is unarmed in *P. nyassae*. Furthermore, in *P.* spiniscapus most of the pronotal disc and elytral surfaces have a yellowish pubescence, which is lacking in *P. nyassae*. The pronotum in *P. spiniscapus* has three lateral spines on either side, while there are usually five in *P. nyassae*. There are also significant genitalic diagnostics. While the median lobe of *P. spiniscapus* is very similar to that of *P. nyassae*, the ventral edge of the median orifice (ventral plate) in particular has an acuminate apex longer than that of *P. nyassae*. In the terminology of Ehara (1954: 65), that of *P.* spiniscapus would classify as 'sharply pointed' (l.c. Fig. 4), while that of *P. nyassae* looks more like 'strongly projected' (l.c. Fig. 7). The dorsal edge of the median orifice ('dorsal lobe') in *P. spiniscapus* has a more deeply emarginate apex than in *P. nyassae*. The tegmen has parameres with setae confined to the widened apical part in *P. spiniscapus*, but in *P. nyassae* the apical part is not noticeably wider than the basal part, and the setae cover a larger part of the surface.

Discussion

This study shows that the two sexes originally described as belonging to the same species, *A. rassei*, actually represent two very different species. The unique characteristics of the genus *Afraustraloderes* are also highlighted, revealing the unlikelihood of it belonging to the tribe Hopliderini. According to the analysis undertaken by Quentin and Villiers (1972), this tribe is a coherent systematic group with no obvious outliers. The main reason used by Bouyer (2012) for including *Afraustraloderes* in the Hopliderini was its perceived association with what is now known as the female of a true *Pixodarus*. However, *Afraustraloderes* is something that cannot be compared closely with anything else, at least on the African continent, and may even constitute a tribe of its own. A phylogenetic study, including molecular analyses, is thus required to resolve the systematic position of this genus.

The habitat and ecology of *A. rassei* are also unusual for a prionine – both adults and larvae have so far only been found in fynbos vegetation (Figure 7), with a distribution range apparently restricted to the Fynbos Biome. Most specimens have been collected on the slopes of the Langkloof-Tsitsikamma mountain range in the Joubertina area of the Eastern Cape Province, at an altitude of approximately 650 m. The holotype described by Bouyer (2012) reportedly originates from Matroosberg, which is located at the entrance of the Hex River Valley, near Worcester in the Western Cape Province. The two localities are approximately 400 km apart, but both are well within the Fynbos Biome (Mucina and Rutherford 2006).

Among the fynbos vegetation, adults and larvae of A. rassei were found on or inside trunks, branches and upper roots of dead Protea and Leucadendron species (Proteaceae) and also Hakea sericea Schrad. and J.C.Wendl., which is an alien invasive plant in the same family, introduced into South Africa from southeastern Australia in the 19th century (Rebelo 2001). All adults were found during the daytime, perched on branches or crawling at the base of dead plants. They exhibit very sluggish movements and when disturbed assume a carabid-like defence position, raising their abdomen above the ground and pointing the pygidium in the direction of the would-be predator (Figure 8). They raise the abdomen, then continuously lower and raise it in a pumplike movement, when disturbed. It is possible that they mimic the behaviour of beetles of the genus Termophilum Basilewsky, 1950 (Carabidae: Harpalinae), which are quite common in the area and which spray powerful chemical concoctions, based on formic acid, towards potential predators as a deterrent (Scholtz and Holm 1985). It is not yet known whether adults are also active at night, but light trapping undertaken in the area on several occasions during the period 2010-2014 failed to provide any evidence that the species may be nocturnal and/or attracted to light.

Larval stages of *A. rassei* were first collected in December 2010, but were small, < 15 mm long, and did not survive to the next season in captivity. By December 2013, larvae observed in their natural habitat had reached an average size of 30–50 mm and were able to survive in captivity, with a few eventually pupating and emerging as adults in December 2014–January 2015. Others are currently completing their life cycle in the laboratory. As the fynbos area where larvae were monitored had been burned by a veld fire in the winter of 2009, it would appear that larvae may take about 6–7 years to complete their development to imago. Thus, it seems likely that this reflects the cycle of natural fire burning in the fynbos vegetation of this region (Van Wilgen et al. 1992). This will provide a regular, new supply of dead plants at a rate comparable to that of the beetle life cycle.

Unfortunately, very little is known about the habitat and biology of *Pixodarus spiniscapus*, as all known specimens are accompanied by essential data only. It is most likely that the specimens collected by RH Watmough in the Florauna suburb of Pretoria were attracted to the light at night, as this is the typical behavior shown by the other

known species of the genus *Pixodarus* (RP, pers. observ.), as also confirmed by the iSpot observations. The predominant vegetation of the Magaliesberg slopes, where the bulk of the type specimens of *P. spiniscapus* were collected, is of the Gold Reef Mountain Bushveld type (Mucina and Rutherford 2006). Specimens recorded on iSpot occur in Rand Highveld Grassland which has an intrusion of Loskop Mountain Bushveld along the river course about 13 km to the north (Presidentsrus which lies alongside the river); Gold Reef Mountain Bushveld (Walter Sisulu National Botanical Garden); and Egoli Granite Grassland (Randburg, grounds of the Curro Aurora Private School) (Mucina and Rutherford 2006). The specimen erroneously included as "allotype female" in the description of *A. rassei* by Bouyer (2012), was reportedly from the Oribi Gorge area of KwaZulu-Natal. However, one of the authors (RP) has collected cerambycids intensively in the Oribi Gorge Nature Reserve over the past 15 years, including by light trapping at night, and has never encountered this species. Given that the specimen was acquired at an unspecified fair and carries no collector's name, it is possible that the locality reported in the data label may be erroneous.

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References

- Adlbauer K (1998) Revision der Gattung *Taurotagus* Lacordaire (Coleoptera, Cerambycidae, Cerambycini). In: Ebermann E (Ed.) Arthropod Biology: Contributions to Morphology, Ecology and Systematics. Biosystematics and Ecology Series 14: 333–363.
- Allsopp E (2005) In Memoriam: Dr Richard Henry Watmough. Rostrum, Newsletter of the Entomological Society of Southern Africa 66: 1–4.
- Bates H (1878) New genera and species of longicorn Coleoptera. Entomologist's Monthly Magazine 14: 272–274.
- Bouyer T (2012) Description d'un nouveau genre et d'une nouvelle espèce d'Hopliderini d'Afrique du Sud (Coleoptera, Cerambycidae, Prioninae). Lambillionea 112(3): 213–217.

- Ehara S (1954) Comparative anatomy of male genitalia in some Cerambycid beetles. Journal of the Faculty of Science, Hokkaido University. Ser. VI Zoology 12: 61–115.
- Eysenbach G, Trudel M (2005) Going, going, still there: using the WebCite service to permanently archive cited web pages. Journal of Medical Internet Research 7(5): e60. doi: 10.2196/jmir.7.5.e60
- Fairmaire LMH (1887) Coléoptères des Voyages de M. G. Révoil chez les Somâlis et dans l'intérieur du Zanguebar. Annales de la Société Entomologique de France, Paris (6) 7: 277–368.
- Hubweber L, Schmitt M (2006) Parameres similarities and differences in Chrysomelidae and Cerambycidae (Coleoptera). Bonner zoologische Beiträge 54(4): 253–259.
- Hubweber L, Schmitt M (2010) Differences in genitalia structure and function between subfamilies of longhorn beetles (Coleoptera: Cerambycidae). Genetica 2010: 37–43. doi: 10.1007/s10709-009-9403-x
- Hutcheson JA (1980) *Arhopalus ferus* (Coleoptera: Cerambycidae): structure and function of the female reproductive system. New Zealand Journal of Zoology 7: 417–424. doi: 10.1080/03014223.1980.10423795
- Lin M, Li D (2012) Description of a new species of *Glenea* from Tibet, China (Coleoptera, Lamiinae, Saperdini). ZooKeys 216: 5–11. doi: 10.3897/zookeys.216.3360
- Mucina L, Rutherford MC (2006) The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria, 807 pp.
- Quentin RM, Villiers A (1972) Révision des Hoploderina africains et malgaches (Col. Cerambycidae Prioninae). Annales de la Société Entomologique de France (NS) 8(2): 257–289.
- Quentin RM, Villiers A (1975) Insectes Coléoptères Cerambycidae Parandrinae et Prioninae. Faune de Madagascar 40: 1–251.
- Rebelo T (2001) Proteas: A Field Guide to the Proteas of Southern Africa. Fernwood Press, Vlaeberg (RSA), 240 pp.
- Santos Ferreira GW (1980) The Parandrinae and the Prioninae of Southern Africa (Cerambycidae, Coleoptera). Memoirs van die Nasionale Museum, Bloemfontein 13: 1–335.
- Scholtz CH, Holm E (Eds) (1985) Insects of Southern Africa. Butterworths, Durban, 502 pp.
- Silvertown J, Harvey M, Greenwood R, Dodd M, Rosewell J, Rebelo T, Ansine J, McConway K (2015) Crowdsourcing the identification of organisms: A case-study of iSpot. ZooKeys 480: 125–146. doi: 10.3897/zookeys.480.8803
- Van Wilgen BW, Bond WJ, Richardson DM (1992) Ecosystem management. In: Cowling RM (Ed.) The Ecology of Fynbos: Nutrients, Fire and Diversity. Oxford University Press, Cape Town, 345–371.

RESEARCH ARTICLE



Three new species of *Tricimba* Lioy from the West Palaearctic region (Diptera, Chloropidae)

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Citation: Kubík Š, Barták M, Civelek H (2016) Three new species of *Tricimba* Lioy from the West Palaearctic region (Diptera, Chloropidae). ZooKeys 558: 95–107. doi: 10.3897/zooKeys.558.6930

Abstract

Tricimba rudolfi Kubík, **sp. n.** (Czech Republic, Portugal), *Tricimba chalupi* Kubík, **sp. n.** (Czech Republic), and *Tricimba dursuni* Kubík, **sp. n.** (Turkey) are described and illustrated. First records of *Tricimba kaplanae* Dely-Draskovits, 1983 from Corsica and *Tricimba hungarica* Dely-Draskovits, 1983 from Turkey are listed.

Keywords

Diptera, Acalyptratae, Oscinellinae, taxonomy, new records, Corsica, Czech Republic, France, Portugal, Turkey

Introduction

The genus *Tricimba* was erected by Lioy (1864). Species belonging to this genus may be distinguished from the remaining genera of the extant Palaearctic Oscinellinae by the presence of three or five more or less deeply impressed longitudinal grooves on the scutum, equipped with criss-cross arrangement of stiff micro-setulae. Fig. 19 in von Tschirnhaus and Hoffeins (2009) demonstrated such grooves in the fossil sister

genus Protoscinella Hennig. Beschovski (1981) divided the genus Tricimba (only species from the Palaearctic Region) into three subgenera - Tricimba s. str., Nartshukiella Beschovski, and Schumanniella Beschovski, but those subgenera were not accepted by Ismay (1991) in the most thorough study of the genus Tricimba. With convincing arguments in that article he only defined species groups. Moreover Beschovski erroneously stated that the type species Schumaniella setulosa did not have two separate male cerci but instead both were fused to a mesolobus. However, a mesolobus is omitted in his figure of the genitalia, possibly as the cerci were damaged during dissection. M. von Tschirnhaus stated in his own material that the species has typical cerci similar to T. cincta (Meigen, 1830). Dely-Draskovits (1983) revised the Palaearctic species of the genus. The larvae of several species are associated with fungi (Ševčík 2010) and several authors before him observed the same. Other species have been reared from rotting grasses and fruits (von Tschirnhaus 1982: 122) and T. sulcella (Zetterstedt, 1848) developed in exposed dead snails (von Tschirnhaus 1992). The genus Tricimba is widely distributed in all faunal realms and it is the only extant genus within the Chloropidae which was identified already in Baltic and Dominican amber (Tertiary) (von Tschirnhaus and Hoffeins 2009). In the Palaearctic region 23 described valid species occur: T. albiseta Dely-Draskovits, 1983, T. apicalis (von Roser, 1840) T. bimarginata Sabrosky, 1979, T. brachyptera (Thalhammer, 1913), T. cincta (Meigen, 1830), T. curvata Sabrosky, 1961, T. freidbergi Dely-Draskovits, 1983, T. heratica Dely-Draskovits, 1983, T. humeralis (Loew, 1858), T. hungarica Dely-Draskovits, 1983, T. japonica Dely-Draskovits, 1983, T. kaplanae Dely-Draskovits, 1983, T. lineella (Fallen, 1820), T. magna Dely-Draskovits, 1983, T. meridiana Dely-Draskovits, 1983, T. minima (Vanschuytbroeck, 1945), T. paraalbiseta Dely-Draskovits, 1983, T. parasetulosa Dely-Draskovits, 1983, T. pulla Dely-Draskovits, 1983, T. setulosa (Becker, 1903), T. stigma Kanmyia, 1983, T. submagna Dely-Draskovits, 1983 and T. sulcella (Zetterstedt, 1848). T. bimarginata was added to the Palaearctic Region (Portugal) only recently by Ebejer and Andrade (2015). Further eight Palaearctic taxa are synonyms: T. aristolochiae, T. delpinii, T. flavipila, T. fungicola, T. maculifrons, T. opacifrons, T. punctifrons, T. trisulcata [and spinigera, a Nearctic syn. of T. lineella]). (Duda 1932-1933; Sabrosky 1961; Beschovski 1981; Dely-Draskovits 1983; Kanmiya 1983; Deeming and Al-Dhafer 2012; Nartshuk 2013). Three additional species of this genus are added here.

Material and methods

The studied material is deposited in the collections of the Czech University of Life Sciences, Prague (CULSP).

The genitalia were macerated in 10% KOH (24 hours, room temperature) and later stored together with the specimens on plastic tags and fixed with butyl-methacrylate copolymer of methyl-methacrylate, xylene. The genitalia were photographed by means of an Olympus E-41 digital camera mounted on an Olympus BX51 compound microscope and images were edited with the computer software Quick Foto micro 2.3 provided with Deep focus 3.1. Each image resulted usually from combining 7-15 layers. Images were improved by means of Adobe Photoshop and they served as models for outline of hand drawn illustrations; details were added by direct observing the genitalia. Individual species were photographed by means of a Nikon D300 digital camera mounted on an Nikon SMZ-U microscope and images were edited with the computer software NIS-Elements 3.0. Each image resulted usually from combining 15 layers. Images were improved by means of Adobe Photoshop. The morphological terms used here follow Merz and Haenni (2000). Abbreviations: f1,2,3 = fore, mid, hind femur, t1,2,3 = fore, mid, hind tibia. The length of the ocellar triangle was measured from the posterior margin of the posterior ocelli to the apex of the main part of the ocellar triangle. The head width was expressed as the distance of the widest points of the compound eyes. The head length was measured from the level of the posterior of the head horizontally to the level of the foremost extension of the anterior margin of frons or eye (depending what is most extending), excluding the antenna. The frons length was measured from posterior margin of posterior ocelli to the anterior margin of frons, the width across the dorsal posterior corners of the eye where the frons is the widest. In many species the number of orbital setae is difficult to judge as the setae are scarcely differentiated from the interfrontal setulae. The length of the scutum was measured from the level of the anterior margin to the base of scutellum, its width as the distance between the widest lateral points anterior of the wing base. All measurements (including body length) were taken from dry specimens (therefore the actual length may differ). The body length of males were measured from the antennal base to the hind end of the epandrium.

We were not able to compare the new species with all described species from the adjacent zoogeographical regions, Oriental, Afrotropical and Nearctic. Some Palaearctic *Tricimba* species are known also from tropical Africa (Deeming and Al-Dhafer 2012), the Oriental and/or Nearctic Regions: *bimarginata, cincta, humeralis, lineella, setosa, setulosa,* and *stigma.* The Afrotropical species *T. africana* (l.c.) occurs also in South Yemen, belonging to the Afrotropics while North Yemen is Palaearctic, and Oriental species in India occur near to the Palaearctic Afghanistan.

Systematic treatment

Tricimba Lioy, 1864

Tricimba Lioy, 1864: 1125. Type species: *Oscinis lineella* Fallén, 1820: 8 by designation Enderlein 1911: 207.

Note. The 15 generic synonyms of the genus were listed chronologically by Nartshuk (2012).

Tricimba rudolfi Kubík, sp. n.

http://zoobank.org/F8F5770C-CDB9-4535-8CE5-848F71224D9F Figs 1–3

Holotype male. Czech Republic, Moravia, Horní les u Lednice, 29.vi.1997, leg. R. Rozkošný. Holotype is in good condition.

Paratypes. 1 male, same data as the holotype, 1 male and 1 female: CZ Moravia, Podyjí NP, Nad Šobesem, Malaise trap, 2.vi.–2.vii.2003, leg. Š. Kubík, 1 male and 1 female, **Portugal**, Valhelhas, 500m, near river, SW+PT [= sweeping vegetation and yellow pan water traps], 40°24'10"N, 7°24'16"W, 16.–17.vii.2009, leg. M. Barták.

Distribution. Czech Republic, Portugal

Date of occurrence. June–July.

Diagnosis. Tricimba rudolfi Kubík sp. n. is similar to T. lineella. The main characters distinguishing these two species are as follows: Tricimba rudolfi has scutellum longer than wide, flat and triangular. Dorsal side has sharp margin and two rows of small pale setulae. Apical scutellar setae are divergent. Tricimba lineella has scutellum wider than long, more rounded and convex, without sharp margin on upper side. Apical scutellar setae convergent.

Description. Male. Head wider than long. Frons about as wide as long, slightly concave, brownish black, brownish yellow on anterior 1/4, lateral margins almost parallel, anterior margin slightly produced anteriorly to anterior margin of eye. All setae and setulae pale. Frons with sparse setulae. Ocellar tubercle scarcely raised above level of remainder of frons. Ocellar triangle well developed, occupying 1/2 wide of frons posteriorly, extending almost 1/2 distance between anterior ocellus and anterior margin of frons, dusted with light grey microtoment. Ocellar setae small, upright and convergent, postocellar setae as long as ocellar setae, convergent. Outer vertical setae slightly longer than ocellar, inner vertical small. Altogether 6-7 thin and short orbital setae developed. Pedicel yellow. First flagellomere yellow, darkened on dorsal margin and base of arista. Arista thin, brown with pubescence as long as its basal diameter. Face yellow with keel between antennae, vibrissal angle projecting before margin of eye. Eye deeper than long, long axis nearly vertical. Gena broader than fore tibia, yellow, dusted, lower margin brownish yellow with two rows of pale setulae. Postgena dark, dusted, as broad as lower part of gena. Occiput dark brown, dusted, with one row of pale occipital setae. Proboscis brown. Palpus yellow, narrow, with pale yellow setulae.

Scutum slightly longer than broad, dark brown and gray microtrichose, with 5 longitudinal deeply impressed grooves along acrostichal and dorsocentral lines and laterally from the latter ones. Notopleural setae 1+1. Anepisternum, katepisternum, and anepimeron dark brown and microtrichose except a shiny anterior lower margin of anepisternum and anterior margin of katepisternum. Scutellum (Fig. 1) longer than broad, flat, triangular, brown and dusted. Upper side with sharp margin and this with two rows of short pale setulae. Three pairs of short pale marginal setae each on a minute tubercle. Divergent apical pair slightly longer than lateral setae. Subscutellum developed, black, dusted dorsally and shining ventrally.

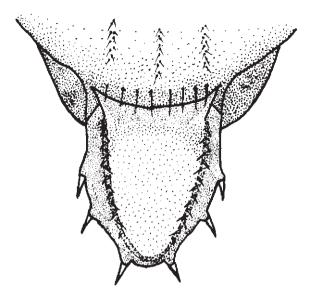


Figure 1. Tricimba rudolfi Kubík, sp. n. (holotype): scutellum dorsal view.

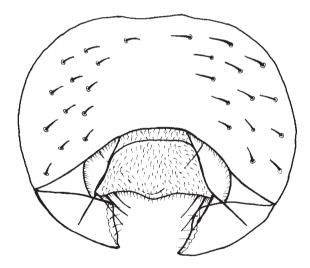


Figure 2. Tricimba rudolfi Kubík, sp. n. (holotype): epandrium posterior view.

Legs yellow, t3 with narrow brown band in middle. Wings hyaline with brown veins, R_{2+3} , R_{4+5} and M_{1+2} almost parallel, second costal section as long as third costal section. Halter whitish yellow. Abdomen dark brown. Epandrium as in Fig. 2.

Length: 1.5-2 mm.

Female. Similar to male. Cercus dark brown with pale setulae.

Etymology. named in honour of Professor Rudolf Rozkošný (Brno), collector of the holotype.



Figure 3. Tricimba rudolfi Kubík, sp. n. (holotype): body lateral view.

Tricimba chalupi Kubík, sp. n.

http://zoobank.org/47A10964-219F-4938-BA91-9606CCBA0C63 Figs 4, 5

Holotype male. Czech Republic, Moravia, Podyjí NP, Terasy mixed wood, 460 m, MT [= Malaise trap], 48°53'22"N, 15°50'18"E, 2.vii.–9.viii.2003, leg Š. Kubík and M. Barták. Holotype is in good condition but mid leg missing on left side.

Paratypes. 2 males, same data as holotype.

Distribution. Czech Republic

Date of occurrence. July-August.

Diagnosis. *Tricimba chalupi* Kubík, sp. n. belongs to the group of thirteen Palaearctic very similar former *Nartshukiella* species which are difficult to separate. The main characters distinguishing this species are as follows: dark species with all setae and setulae black and with large bevelled cerci (Fig. 4).

Description. *Male.* Head wider than long. Frons as wide as long, posterior half dark brown to black, dusted, anterior half brownish yellow, slightly concave, lateral margins parallel. All setae and setulae dark. Frons with irregular dark setulae, pale setulae occur only in front part of frons. Ocellar tubercle scarcely raised above level of remainder of frons. Ocellar triangle large, occupying more than half of posterior margin of frons, lateral margins slightly convex, main part extending more than halfway between anterior ocellus and anterior margin of frons, dusted with light grey microtoment, with one row of dark setulae along lateral margin. Ocellar setae as long as the distance between ocelli, upright and convergent, postocellar setae longer than ocellar setae, convergent. Outer

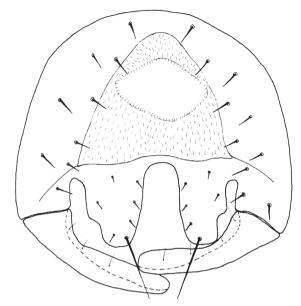


Figure 4. Tricimba chalupi Kubík sp. n. (holotype): epandrium posterior view.



Figure 5. Tricimba chalupi Kubík, sp. n. (holotype): body lateral view.

vertical setae as long as postocellar setae, inner vertical smaller, as long as ocellar setae, 9–10 dark orbital setae, posterior five of them longer and stronger then the anterior ones. Antennae yellow, first flagellomere rounded. Arista thin, brown with pubescence of equal length as its basal diameter. Face yellow, vibrissal angle slightly projecting before anterior margin of eye. Eyes with scattered short ommatrichia, deeper than long, long axis vertical. Gena slightly broader than fore tibia in middle, yellow, dusted, with one row of pale long setulae. Postgena dark brown, dusted, slightly narrower than gena. Occiput dark and dusted. Proboscis and palpus yellow with pale setulae.

Scutum slightly longer than broad, black and dusted with gray microtrichosity, with three grooves of punctuations along acrostichal and dorsocentral lines, lateral groove not developed, 1+2 notopleural setae. Anepisternum black and dusted with gray microtrichosity, anepimeron similarly dusted as anepisternum, but posteroventrally with small shiny spot, katepisternum dark brown with dorsal half shiny and ventral gray dusted. Scutellum as long as broad, flat, rounded, black and dusted with gray microtrichosity, brownish yellow only on apical third. Three pairs of black marginal setae. Apical setae as long as half of scutellum and convergent, lateral short, one third as long than apical. Subscutellum developed, black, dusted dorsally, shining ventrally.

Legs yellow, f1-f3 with narrow brown band in middle. Wings hyaline with dark brown veins. Second costal section longer than third. Halter whitish yellow.

Epandrium as in Fig 4.

Length: 2–2.5 mm

Female. Unknown.

Etymology. Named in honour of our friend Tomáš Chalupa who popularized the National Park Podyjí.

Remarks. This species may be identified with difficulties in the key by Dely-Draskovits (1983) because significant differences are only present in male genitalia. We propose to modify couplet 31 of the key as follows:

31	Larger, body length 1.7–2.5 mm
31a	Cerci short and rounded, body gray-brown, body length 1.7mm
31b	Cerci large and bevelled (Fig. 4), body black, body length 2-2.5mm
32	Smaller, body length 1.4–1.5 mm

Tricimba dursuni Kubík, sp. n.

http://zoobank.org/1B61D35B-41DF-47A8-A681-015FA4AC6F08 Figs 6, 7, 10

Holotype male. Turkey, Akyaka, pasture, 4m, 37°03'08.9"N, 28°20'17.4"E, 16.–22. ix.2012 leg. Barták and Kubík. Holotype is in good condition.

Paratypes. 19 males and 2 females, same data as the holotype.

Distribution. Turkey.

Date of occurrence. September.

Diagnosis. *Tricimba dursuni* Kubík sp. n. belongs to the "extralimital taxon" (Ismay 1991: 303) together with *T. setulosa* and *T. parasetulosa* (phylogenetically first shifted here close to *setulosa*) in the Palaearctic Region. The main characters distinguishing these three species are as follows: frons brownish yellow on anterior half in *T. dursuni*, but darker, yellowish brown on anterior 1/3 in *T. setulosa* and 1/4 in *T. parasetulosa*. *Tricimba dursuni* has pale setulae on scutum, both *T. setulosa* and *T. parasetulosa* have dark setulae.

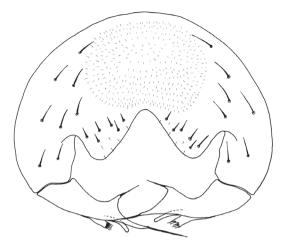


Figure 6. Tricimba dursuni Kubík, sp. n. (holotype): epandrium posterior view.

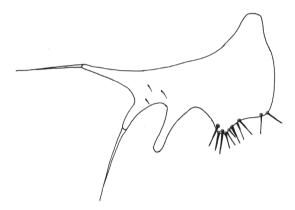


Figure 7. Tricimba dursuni Kubík, sp. n. (holotype): surstylus lateral view.

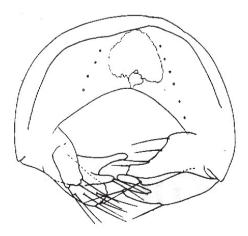


Figure 8. Tricimba setulosa: epandrium (after Beschovski 1981).

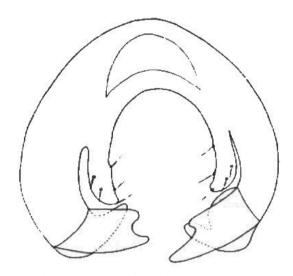


Figure 9. Tricimba parasetulosa: epandrium (after Dely Draskovits 1983).

Genitalia strikingly differ in all these three species: *T. dursuni* has surstylus with three long spurs and numerous black long setae on lower side (Figs 6–7), *T. setulosa* and *T. parasetulosa* have differently shaped surstylus (Figs 8–9).

Description. Male. Head longer than wide, as long as deep. Frons longer than wide, in front slightly concave, dark brown on posterior half, yellowish brown on anterior half, lateral margins parallel, anterior margin slightly produced before anterior margin of eye. All setae dark and setulae pale. Frons with sparse setulae. Ocellar tubercle scarcely raised above level of remainder of frons. Ocellar triangle well developed, occupying 2/3 width of frons posteriorly, extending almost ^{1/2} distance between anterior ocellus and anterior margin of frons, dusted with light gray microtrichosity. Ocellar setae small and convergent, postocellar seta as long as ocellar, convergent. Outer vertical setae slightly longer than inner vertical setae, 6-7 thin and small orbital setae, posterior four slightly longer than anterior. Pedicel yellow, first flagellomere yellow, darkened on dorsal margin and base of arista. Arista thin, brown, with pubescence subequal to its basal diameter. Face yellow, vibrissal angle not much projecting before margin of eye. Gena as broad as t3, yellow and dusted, lower margin with one row of pale setulae. Postgena ventrally dark, dusted, broader than gena. Occiput dark brown and dusted. Proboscis brown. Palpus yellow, narrow, with pale yellow setulae.

Scutum longer than wide, black, dusted with grey microtrichosity, with deeply impressed grooves and punctures. All setulae on scutum pale. Notopleural setae 1+2. Katepisternum, anepisternum and anepimeron dark brown and dusted. Scutellum longer than broad, flat, triangular, brown and dusted. Three pairs of black scutellar setae. Apical scutellar setae twice longer than lateral, black and convergent. Subscutellum developed, black, dusted dorsally, shining ventrally.



Figure 10. Tricimba dursuni Kubík, sp. n. (female paratype): body lateral view.

Legs yellow, t1, t2, t3, f2 and f3 with brown band in middle. Wings hyaline with dark veins, second costal section longer than third. Halter white.

Abdomen dark brown. Epandrium as in Figs 6-7.

Length: 1.5–2 mm.

Female. Similar to male.

Etymology. Named in honour of Oktay Dursun, our colleague and dipterologist from Mugla University, Turkey.

Other examined material. *Tricimba kaplanae* Dely-Draskovits, 1983: Corsica, 10 km W of Corte, 700m, Calacuccia env., 9.v.1993, 2 3, B. Mocek leg. This species has only been known from Israel. First record from the Corsica Isl.

Tricimba hungarica Dely-Draskovits, 1983: Turkey, Mugla, University campus, PT [= yellow and white pan water traps], 700m, 37°09'42"N, 28°22'21"E, 21.–24. ix.2012, 2Å, Barták and Kubík leg. This species has only been known from the Czech Republic, Hungary and Ukraine. First record from Turkey.

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References

- Beschovski V (1981) On the systematics of the genus *Tricimba* Lioy, 1864 (Diptera: Chloropidae). Reichenbachia, 21: 119–122.
- Deeming JC, Al-Dhafer HM (2012) Chloropidae from the Arabian Peninsula (Diptera: Cyclorrhapha). Zoology in the Middle East 58: 3–88. doi: 10.1080/09397140.2012.10648977
- Dely-Draskovits Á (1983) Revision der Typen der paläarktischen Arten der Gattung *Tricimba* Lioy, 1864 (Diptera, Chloropidae). Acta zoologica Academiae Scientiarum hungaricae 29: 327–355.
- Duda O (1932–1933) 61: Chloropidae. In: Lindner E (Ed.) Die Fliegen der paläarktischen Region, 6(1), 248 pp.
- Ebejer M, Andrade R (2015) The Chloropidae (Diptera, Brachycera) of mainland Portugal with description of a new species of *Lasiosina* Becker. Entomologist's monthly Magazine 151: 227–271.
- Enderlein G (1911) Klassifikation der Oscinisominen. Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin 1911(4): 185–244.
- Ismay JW (1993) Revision of *Tricimba* Lioy and *Aprometopis* Becker (Diptera: Chloropidae) from Australia and the Papuan Region. Invertebrate Taxonomy 7(2): 297–499. doi: 10.1071/IT9930297
- Kanmiya K (1983) A systematic study of the Japanese Chloropidae (Diptera). Memoirs of the entomological Society of Washington 11: 1–370.
- Lioy P (1864) I ditteri distribuiti secundo un nuovo metodo di classificazione naturale. Atti dell' imperiale Regio Istituto Veneto di Scienze, Lettere ed Arti (3) 9: 1087–1126.
- Merz B, Haenni JP (2000) Morphology and terminology of adult Diptera. In: Papp L, Darvas B (Eds) Contributions to a Manual of Palaearctic Diptera. Volume 1, Science Herald, Budapest, 21–51.
- Nartshuk EP (2012) A check list of the world genera of the family Chloropidae (Diptera, Cyclorrhapha, Muscomorpha). Zootaxa 3267: 1–43.
- Nartshuk EP (2013) Chloropidae. In: Pape T (Ed.) Fauna Europaea: Diptera Brachycera. Fauna Europaea version 2.6.2. http://www.faunaeur.org
- Sabrosky CW (1961) A report on Chloropidae and Milichiidae from Afghanistan (Diptera). Opuscula entomologica 26(1–2): 61–66.
- Ševčík J (2010) Czech and Slovak Diptera associated with fungi. Slezské zemské muzeum Opava, 112 pp.

- von Tschirnhaus M (1981) Die Halm- und Minierfliegen im Grenzbereich Land-Meer der Nordsee. Eine ökologische Studie mit Beschreibung von zwei neuen Arten und neuen Fang- und Konservierungsmethoden (Diptera: Chloropidae et Agromyzidae). Spixiana Supplement 6: 1–405.
- von Tschirnhaus M (1992) Minier- und Halmfliegen (Agromyzidae, Chloropidae) und 52 weitere Familien (Diptera) aus MALAISE-Fallen in Kiesgruben und einem Vorstadtgarten in Köln. Decheniana-Beihefte 31: 445–497, Taf. 13–15
- von Tschirnhaus M, Hoffeins C (2009) Fossil flies in Baltic amber insights in the diversity of Tertiary Acalyptratae (Diptera, Schizophora), with new morphological characters and a key based on 1,000 collected inclusions. Denisia 26: 171–212.

RESEARCH ARTICLE



Leinendera achaeta sp. n., a new species of robber fly from Brazil (Diptera, Asilidae, Asilinae)

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Abstract

The third species of the Neotropical genus *Leinendera* Carrera, 1945, *Leinendera achaeta* **sp. n**., is described from Rio Grande do Sul state, Brazil. The habitus, wing and male terminalia are described and illustrated, and a key to the three Brazilian species is provided.

Keywords

Asilus group, Neotropical, taxonomy

Introduction

Asilinae Latreille, 1802 is the most diverse subfamily of Asilidae, including 179 extant genera, and is distributed in all biogeographic regions, except Antarctica (Geller-Grimm 2004, Londt 2005, Vieira 2012a, Artigas and Vieira 2014, Vieira and Rafael 2014). Sixty-eight genera are recognized in the Neotropical Region, of which 20 occur in Brazil (Papavero 2009, Vieira 2012a, Artigas and Vieira 2014, Vieira and Rafael 2014). Carrera (1945) had distinguished his newly proposed genus

Leinendera through the presence of apical scutellar setae, wing with spots (of dense microtrichia) in apical third, and tergites with lateral marginal macrosetae.

Currently, the two valid species of *Leinendera* are restricted to the Neotropical Region (Fig. 1): *Leinendera rubra* Carrera, 1945 (Brazil: Rio de Janeiro and São Paulo states) and *Leinendera nigra* Vieira, 2012 (Brazil: Rio de Janeiro state) (Vieira 2012b).

In this work, the third species of *Leinendera*, from Rio Grande do Sul, Brazil, is described and illustrated, and a key to Brazilian species is provided.

Material and methods

This study is based on the examination of specimens housed in the following institutions: CESC–Coleção Entomológica de Santa Cruz do Sul, Santa Cruz do Sul, Brazil and INPA–Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil. Morphological terminology follows Cumming and Wood (2009), and antennal terminology follows Stuckenberg (1999).

The wing was detached from the body, placed in xylene for 30 minutes and then mounted in Canada balsam between coverslips. After drying, the cover slips were glued to the edge of a piece of thick paper, which was then pinned with the specimen. The techniques of Vieira (2012b) were used to examine the terminalia. After examination and illustration, the detached parts of the terminalia were placed in microvials with glycerin and pinned with their respective specimen.

The label data are cited in full, with the original spellings, punctuation, and dates. Information presented within square brackets are complementary data not included on the labels. Data from the same specimen, but from different labels, are separated by slashes (/). The map was generated with SimpleMappr.

Results

Leinendera Carrera, 1945

Diagnosis. Brown oblique stripe extending from the base of the wing to the base of the fore and mid coxae (Figs 2, 4, 16, 24); wing with spots (of dense microtrichia) in apical third (Figs 6, 7, 18, 26); tergites with lateral marginal macrosetae (Figs 2, 16, 24).

Leinendera achaeta sp. n. http://zoobank.org/D4EA37A5-B70E-4327-8ACB-EC943DAE1848 Figs 2–15

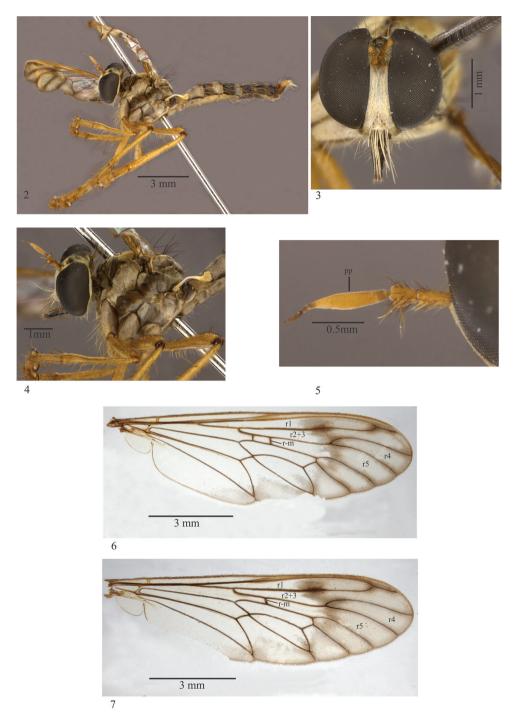
Diagnosis. Apical scutellar macrosetae absent; epandrium elongate, apical 1/3 triangular in lateral view (Figs 8–11); gonocoxite with an indentation on apical third of



Figure 1. Distribution of *Leinendera* species.

the inner margin (Figs 9, 10); hypandrium with distal margin straight, basal margin rounded (Fig. 12).

Male. Holotype. Body: Slender (Fig. 2). Head: Antenna (Fig. 5) with yellow scape and pedicel, with brown and yellow setae; yellow postpedicel with brown apex, and 16 times the length of first element of the stylus; stylus brown; second element of stylus five times the length of the first element. Vertex (Fig. 3) golden tomentose; ocellar tubercle brown tomentose with two brown, short, proclinate, ocellar setae; face and frons golden tomentose (Fig. 3), face moderately narrow (Fig. 3), lower facial margin silvery tomentose; gena dark-brown; pale yellow mystacal macrosetae (Figs 3, 4); occiput golden-brown tomentose; yellow occipital setae; 4-6 light brown postocular macrosetae; brown palpus with brown setae; apical setae of palpus longer than others;



Figures 2–7. *Leinendera achaeta* sp. n. (**2–6** Holotype male.). **2** Habitus, lateral view **3** Head, frontal view **4** Head & thorax, lateral view **5** Antenna, lateral view **6** Wing **7** Paratype wing. Abbreviations: pp: postpedicel.

light brown labrum, lacinia and postmentum, black labella and prementum; yellowish labial setae.

Thorax (Figs 2, 4). Antepronotum and postpronotum brown and golden tomentose; brown mesonotum; brown paramedian stripe, darker on anterior half; presutural and postsutural spots brown tomentose, area between spots grey tomentose; mesonotum grey tomentose laterally; brown scutellum with impressed rim, silvery tomentose; pleuron silvery tomentose with brown oblique stripe extending from base of wing to base of fore and mid coxae (Fig. 4). Chaetotaxy: Brown acrostichal setae; two brown notopleural macrosetae; one brown supra-alar macroseta and 1 brown supra-alar seta; one brown postalar macroseta; four brown, dorsocentral, presutural setae; four brown, dorsocentral, postsutural setae; apical scutellar macrosetae absent; one short, brown, discal scutellar seta; yellowish anatergal and katatergal setae; posterior meron + metanepisternum with yellow macroseta and pale yellow tuft of small setae on posterior margin.

Wing (Figs 6, 7). Hyaline basal 2/3, apical 1/3 extending to anal margin reaching anal cell with dense brown microtrichiae; dark brown veins; R_{2+3} slightly sinuous at the level of the R_4 and R_5 bifurcation; cell r4 narrower basally; without costal dilatation; R_4 and R_5 bifurcation beyond level of the discal cell apex; crossvein r-m before level of discal cell middle (Obs. the additional r-m on figure 6 is an anomaly); microtrichia on posterior margin arranged in two divergent planes; pale-yellow halter.

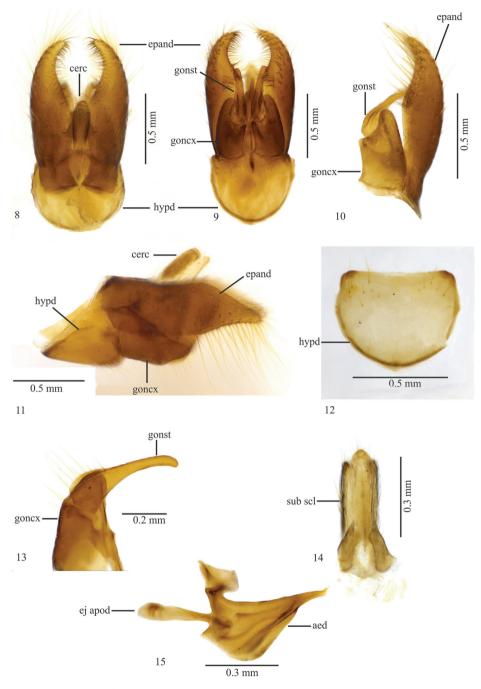
Legs (Figs 2, 4). Narrow, yellow; apex of all femora with dark brown ring. Chaetotaxy: Hind trochanter with 1 yellow macrosetae; fore femur with 4 yellow setae ventrally; mid femur with 1 yellow anterior macroseta, 2–3 yellow macrosetae anteroventrally, 2–3 yellow macrosetae posteroventrally and 1 yellow, posterior, preapical macroseta; hind femur with 2 yellow anterior macrosetae, 2–3 dorsal preapical macrosetae and 3 yellow macrosetae posteroventrally; fore tibia with 3 yellow long macrosetae laterally; mid tibia with 4 yellow long macrosetae anteroventrally, 1 yellow posterior macroseta and 2 yellow macrosetae posteroventrally; hind tibia with 3 yellow anterior setae, 2 yellow posterior setae, 1 yellow anteroventral seta and 3 yellow posteroventral setae; tarsomere with yellow setae and macrosetae; yellow empodium and pulvillus; claws with light brown basal half and black apical half.

Abdomen (Fig. 2). Brown. Dark brown tergites, except I–III light brown laterally; tergites III–VI with silvery tomentose spots laterally; tergites with yellow, lateral, marginal macrosetae. Light brown sternites, except dark brown V–VI.

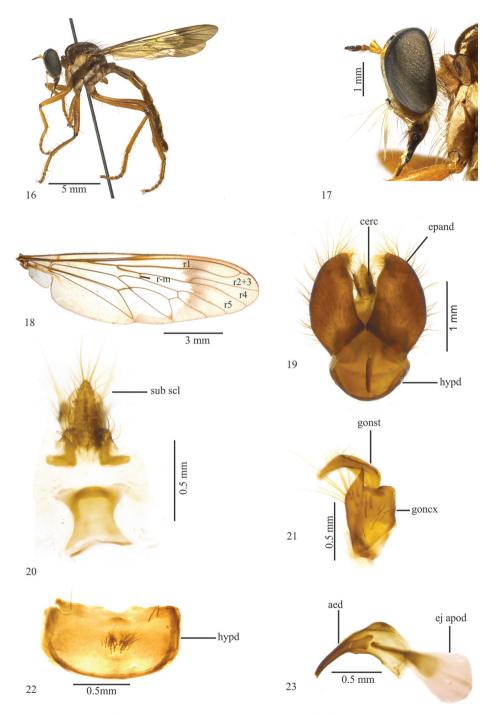
Terminalia (Figs 8–15). Light brown. Epandrium elongate, apical 1/3 triangular in lateral view (Figs 8–11); hypandrium with distal margin straight, proximal margin rounded (Fig. 12); gonocoxite with an indentation on apical third of inner margin (Figs 9, 10); gonostyle tapered and with rounded apex (Fig. 13); apex of subepandrial sclerite rounded (Fig. 14); ejaculatory apodeme narrow in lateral view (Fig. 15), aedea-gal sheath subtriangular in lateral view (Fig. 15).

Length: Body length 11.9 mm; wing length 10.9 mm.

Holotype condition: Right postpedicel and right hind tarsus lost. Detached wing mounted on microslides, terminalia placed in microvial with glycerin, both pinned with the specimen.



Figures 8–15. *Leinendera achaeta* sp. n. Holotype male. 8 Terminalia, dorsal view 9 Terminalia, ventral view 10 Epandrium, gonocoxite and gonostylus 11 Terminalia, lateral view 12 Hypandrium 13 Gonocoxite and gonostylus 14 Subepandrial sclerite 15 Aedeagus. Abbreviations: aed: aedeagus; cerc: cercus; ej apod: ejaculatory apodeme; epand: epandrium; goncx: gonocoxite; gonst: gonostylus; hypd: hypandrium; sub scl: subepandrial sclerite.



Figures 16–23. *Leinendera nigra* Vieira, 2012. Holotype male (modified from Vieira 2012). 16 Head, lateral view 17 Head, frontal view 18 Wing 19 Terminalia, dorsal view 20 Subepandrial sclerite 21 Gonocoxite and gonostylus 22 Hypandrium 23 Aedeagus. Abbreviations: aed: aedeagus; cerc: cercus; ej apod: ejaculatory apodeme; epand: epandrium; goncx: gonocoxite; gonst: gonostylus; hypd: hypandrium; sub scl: subepandrial sclerite.

Variation (n = 2): Size. Body length 11.5-12.4 mm; wing length 10.1-10.5 mm. Face silvery tomentose; mid femur with 1-3 yellow anterior macrosetae; mid tibiae with 3 yellow long macrosetae anteroventrally.

Female: Unknown.

Etymology. From the greek *achaeta*, a = absent and chaeta = bristles, referring to the absence of apical scutellar macrosetae.

Biology. All specimens of *L. achaeta* sp. n. were collected with Malaise traps placed in tobacco, *Nicotiana tabacum* L., plantations. The vegetation surrounding the tobacco plantations was composed mainly by grasslands and shrubs of small to medium size. No information about the prey is known.

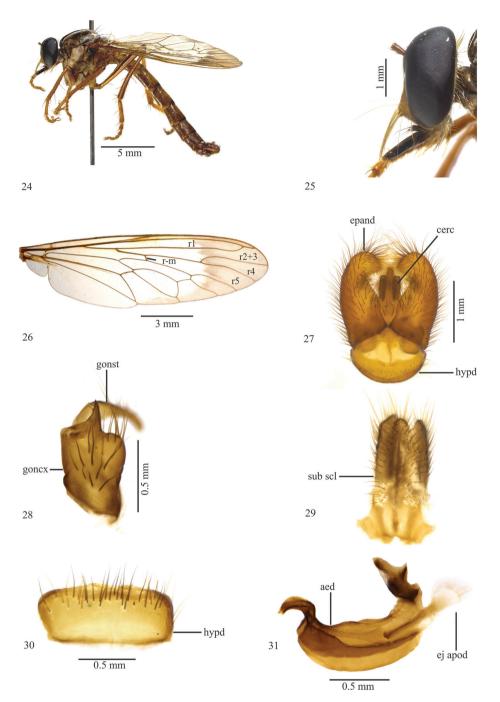
Discussion. Differs from the other two species of *Leinendera* by the absence of apical scutellar macrosetae and characters of the terminalia (Figs 2–15). When describing *Leinendera*, Carrera (1945) mentioned that the genus was distinct from *Glaphyropyga* by the presence of apical scutellar setae. However, that author described the taxon based on a single species and, with the inclusion of *L. achaeta* sp. n., this character can no longer be used in the diagnosis of the genus. Regardless, *L. achaeta* sp. n., *L. nigra* Vieira, 2012 and *L. rubra* Carrera, 1945 have a brown oblique stripe extending from the base of the wing to the base of the fore and mid coxae (Figs 16, 24), which could be used as a new diagnostic character for the genus, since it does not occur in any other closely related genus of Asilinae.

Type material. Holotype: BRA[ZIL], **RS** [**Rio Grande do Sul**], Santa Cruz do Sul, Premium 08/09, 21.02.2009, Armadilha de Malaise / N: 34378 L: 6 P: H: / Holotype *Leinendera achaeta* Vieira, Camargo, Köhler & Rafael sp. nov. (**male INPA**).

Paratypes: BRA[ZIL], **RS** [**Rio Grande do Sul**], Lagoão, 08.03.2009, Armadilha de Malaise / N: 29577 L: 108 Lote álcool: 23120 P: H: / Paratype *Leinendera achaeta* Vieira, Camargo, Köhler & Rafael (**1 male CESC**); BRA[ZIL], **RS** [**Rio Grande do Sul**], Vera Cruz, CTA 28.11.2008, Armadilha de Malaise / N: 29657 L: 143 Lote álcool: 16444-15 P: H: / Paratype *Leinendera achaeta* Vieira, Camargo, Köhler & Rafael (**1 male CESC**).

Distribution. Brazil: Rio Grande do Sul state.

Identification key to males of Leinendera



Figures 24–31. *Leinendera rubra* Carrera, 1945. Ordinary specimen male (modified from Vieira 2012). **24** Head, lateral view **25** Head, frontal view **26** Wing **27** Terminalia, dorsal view **28** Subepandrial sclerite **29** Gonocoxite and gonostylus **30** Hypandrium **31** Aedeagus. Abbreviations: aed: aedeagus; cerc: cercus; ej apod: ejaculatory apodeme; epand: epandrium; goncx: gonocoxite; gonst: gonostylus; hypd: hypandrium; sub scl: subepandrial sclerite.

Acknowledgments

To Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the PRONEX project, Edital 016/2006, Proc. 1437/2007, CNPq/PNPD Process nº: 560987/2010–2, CNPq Process nº: 401.243/2012–5, FAPEAM EDITAL N. 022/2013–FIXAM/ AM Process nº: 062.00745/2014, FAPEAM PAPAC, Edital 020/2013 (I Chamada) and FAPEAM edital 21/2011; and to Fundação de Amparo a Pesquisa do Estado do Rio Grande do Sul (FAPERGS) for fellowships (Proc. 10/0115–0 and 11/0473-3). Thanks to Dr. Torsten Dikow, Dr. Fritz Geller-Grimm and Lucas Cezar for valuable comments that greatly improved the manuscript.

References

- Artigas JN, Vieira R (2014) New genus and species of Neotropical robber flies (Diptera, Asilidae, Asilinae). Zootaxa 3774: 282–288. doi: 10.11646/zootaxa.3774.3.5
- Carrera M (1945) Estudo sobre os gêneros *Glaphyropyga* e *Senoprosopis* com descrição de novo gênero e novas espécies. Papéis Avulsos do Departamento de Zoologia 5: 175–192.
- Cumming JM, Wood DM (2009) Adult morphology and terminology. In: Brown BV, Borkent A, Cumming JM, Wood DM, Woodley NE, Zumbado MA (Eds) Manual of Central American Diptera, Volume 1. NRC Research Press, Ottawa, Ontario, 950 pp.
- Geller-Grimm F (2004) A world catalogue of the genera of the family Asilidae (Diptera). Studia dipterologica 10(2): 473–526.
- Londt JGH (2005) An annotated key to the genera of Afrotropical Apocleinae, with descriptions of six new genera (Diptera: Asilidae). Tijdschrift voor Entomologie 148: 39–62. doi: 10.1163/22119434-900000166

Papavero N (2009) Catalogue of Neotropical Diptera. Asilidae. Neotropical Diptera 17: 1–179.

- Vieira R (2012a) New distribution records of six species of Asilinae (Diptera, Asilidae) Latreille, 1802. Checklist 8: 779–781.
- Vieira R (2012b) A new species of *Leinendera* Carrera, 1945 (Diptera, Asilidae, Asilinae) from Brazil. Biota Neotropica 12(3): 1–7. doi: 10.1590/S1676-06032012000300003
- Vieira R, Rafael J (2014) *Longivena*, a new robber-fly genus from Brazil (Diptera, Asilidae, Asilinae). ZooKeys 443: 119–138. doi: 10.3897/zookeys.443.8324

CHECKLIST



Faunistic and bibliographical inventory of the Psychodinae moth-flies of North Africa (Diptera, Psychodidae)

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Abstract

All published records for the 49 species of moth flies known from North Africa are reviewed and discussed: Morocco (27 species), Algeria (33 species), Tunisia (18 species) and Egypt (five species). In addition, records of seven species of Psychodinae new to the fauna of Morocco are added, of which three are new mentions for North Africa (Table 1) and one is a new record for Egypt. *Telmatoscopus squamifer* Tonnoir, 1922 is transferred to the genus *Iranotelmatoscopus* Ježek, 1987, **comb. n**. *Satchelliella reghayana* Boumezzough & Vaillant, 1987 is transferred to the genus *Pneumia* Enderlein, 1935, **comb. n**. *Pneumia aberrans* Tonnoir, 1922 is transferred to the subgenus *Logima*.

Keywords

Moth-flies, Psychodinae, checklist, Rif, High Atlas, Morocco, Tunisia, Algeria, Egypt, North Africa

Introduction

Within Psychodidae, the Psychodinae form a highly derived subfamily containing the majority of psychodid species diversity. The world fauna of Psychodinae consists at present of approximately 2000 recognized and described species belonging to approximately 100 genera. Their taxonomy is not yet satisfactory; a universally-agreed, stable classification is still lacking for the world fauna, since different generic and tribal concepts are still followed by several authors (Vaillant 1971–1983, 1990; Duckhouse 1987; Wagner and Beuk 2002; Ježek and Van Harten 2005; Kvifte 2011).

Contributions to Psychodinae of Morocco are very fragmented and remain patchy; the first record in this area was by Tonnoir (1920) and the first study was that of Vaillant (1955). A few years later, the same author (Vaillant 1958) published on the Psychodinae in North Africa and their range in Europe. It took almost thirty years for another work on Psychodidae in southern Morocco; the survey in the High Atlas showed the presence of five species (Boumezzough and Vaillant 1986). As part of a national study on the biota of inland waters, Dakki (1997) conducted an initial inventory of Moroccan Psychodidae, in which ten species were listed as Psychodinae. A recent study (Ježek 2004) showed the presence of a new species of Psychodinae in Morocco; and in 2012 Omelková and Ježek described a new species from the High Atlas. For Algeria the study of Psychodinae started with Eaton (1894, 1896) who mentioned records on Algerian Psychodinae; in 1955 Satchell showed the presence of six new species for country. Later, Vaillant described many species from Algeria between 1971 and 1983. The only important Psychodinae reference from Tunisia is provided by Wagner (1987).

Concerning the Egyptian psychodids, Tonnoir (1920, 1922) recorded four species of Psychodinae.

In our study, a total of 674 specimens (109 larvae, 377 males and 188 females) collected at 47 sampling sites in Morocco and one in Egypt (Table 2) has provided 19 species (18 from Morocco and one from Egypt) and added seven unpublished species to the list of Moroccan Psychodinae: *Clogmia albipunctata* (Williston, 1893), *Psychoda cinerea* Banks, 1894, *Psychoda gemina* (Eaton, 1904), *Pericoma pseudexquisita* Tonnoir 1940, *Philosepedon humerale* (Meigen, 1818), *Pneumia nubila* (Meigen, 1818) and *Pneumia propinqua* (Satchell 1955), and one unpublished species to the Egyptian list: *Psychoda alternata* Say 1824. Of these, *Pericoma pseudexquisita* Tonnoir 1940, *Pneumia nubila* (Meigen, 1818) and *Psychoda gemina* (Eaton, 1904) are first records for North Africa. Locality photos are given in Figures 1, 2 and 3 (A, B, C and D).

Material and methods

Collecting

Six techniques have been used to collect Psychodinae: rearing larvae and pupae in the laboratory from collected substrates in the field; adults were collected with sweep net, adhesive papers impregnated with Ricin oil, malaise traps, light traps and aspirators. The early stages of Psychodids were obtained from the lotic and lentic habitats where they may be abundant. Larvae or/and pupae were collected from running (rivers, springs, streams) and standing waters (ponds, lagoons). The substratum was transported to the laboratory and organized on steel gauze net. This is put over a shallow watered dish and left for several days (Wagner 1997).



Figure 1. Moroccan habitat of *Pericoma pseudexquisita* Tonnoir, 1940: Oued Azila, mossy and rocky river in cedar forest with dominance of *Pteridium aquilinum* and *Rubus ulmifolius*. Photograph by HA.

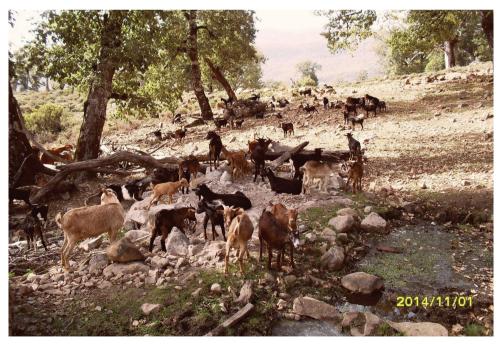


Figure 2. Moroccan habitat of *Pneumia nubila* (Meigen, 1818): Aïn Mâaze, spring with swampy shores, predominant vegetation: *Quercus canariensis, Rubus ulmifolius, Arbutus unedo, Erica arborea, Cistus populifolius, Luzula* sp. Photograph by HA.



Figures 3. Moroccan habitat of *Psychoda gemina* (Eaton, 1904): A Daya Fifi, bog on siliceous sol, predominant vegetation: *Quercus canariensis, Quercus pyrenaica, Cistus salviifolius, Euphorbia characias* B Oued Zarka, waterfall and pool with the dominance of moss covering the rocks C Oued Aâyaden, river of the high course on a limestone sol with dominance of *Pistachia lentiscus, Cistus* sp., *Nerium oleander* and moss on the roc D Douar Kitane, farm with *Arondo donax, Midicago sativa, Inula viscose* and mosses. Photographs by BB.

As the substratum dries out, larvae of Psychodidae fall down into the water and are extracted from the substrate and put into Petri dishes with some rewet substratum from their biotope. The top of the dishes is covered with fine gauze for aeration and the substratum is kept moist by regular water spraying, but not too wet. Larvae are difficult to control, because they bury into the substratum. However, they develop successfully into adults that can be collected by aspiring them from the dishes (pers. obs., approach modified from Wagner 1997). Adults were also collected with hand nets, sweeping through the vegetation preferably at sunset or directly with an aspirator below bridges at daylight. On the other hand, adults were also collected on sticky traps made of paper impregnated with Ricin, placed in different habitats: trees in the field, old urban and animal environments. Whatever the method used, all adult specimens were fixed in 70% ethanol in which they are left until identification. Some species were recognized at 40–80× magnification but for many species, it was necessary to prepare slides, mostly for the close identification of the male genitalia. The method followed was that used by Wagner (1997).

The authors sampled the Moroccan areas from March 2011 to May 2015 and BB captured the Egyptian material in the Nile River in April 2015.

All specimens collected and recorded are deposited in the collection of Diptera in the Laboratory of Ecology, Biodiversity and Environment, Faculty of Sciences, University Abdelmalek Essaâdi, Tétouan.

The following checklist summarizes the species presently known from North Africa. Those species which are new records for North Africa are marked with three asterisks (***), those new for Morocco or Egypt are marked with two asterisks (**) and the species which represent the first record in the Rif Mountains are signalized with one asterisk (*) (Table 1). Taxa are listed according to the classification scheme of Vaillant (1990), Wagner (1990) and Kvifte et al. (2011).

	Morocco	Algeria	Tunisia	Egypt
Bazarella atra (Vaillant, 1955)	X*	Х		
Berdeniella lucasii (Satchell, 1955)		Х		
Clogmia albipunctata (Williston, 1893)	X**	Х		Х
Clytocerus kabylicus Wagner, 1987		Х		
Iranotelmatoscopus numidicus (Satchell, 1955)		Х		
Iranotelmatoscopus squamifer (Tonnoir, 1922)				Х
Lepiseodina tristis (Meigen, 1830)		Х		
Mormia tenebricosa (Vaillant, 1954)	X*	Х	Х	
Mormia riparia (Satchell, 1955)		Х		
Mormia similis Wagner, 1987			Х	
Panimerus goetghebueri (Tonnoir, 1919)		Х	Х	
Panimerus thienemanni (Vaillant, 1954)	Х	Х	Х	
Paramormia ustulata (Walker, 1856)	X*	Х	Х	
Pericoma barbarica Vaillant, 1955	X*	Х	Х	
Pericoma blandula Eaton, 1893	Х	Х	Х	
Pericoma diversa Tonnoir, 1920	X*			
Pericoma exquisita Eaton, 1893	Х	Х	Х	
Pericoma granadica Vaillant, 1978	X*			
Pericoma latina Sarà, 1954	X*	Х		
Pericoma maroccana Vaillant, 1955	X*			
Pericoma modesta Tonnoir, 1922	Х	Х		
Pericoma pseudexquisita Tonnoir, 1940	X***			
Philosepedon beaucournui Vaillant, 1974		Х	Х	
Philosepedon humerale (Meigen, 1818)	X**	Х		
Pneumia nubila (Meigen, 1818)	X***			
Pneumia pilularia (Tonnoir, 1940)	Х	Х		
Pneumia propinqua (Satchell, 1955)	X**	Х		
Pneumia reghayana (Boumezzough & Vaillant, 1986)	Х			

Table 1. Species (in alphabetical order) of Psychodinae known from the North African countries. Libya has been omitted because no information exists in the literature from Libya.

	Morocco	Algeria	Tunisia	Egypt
Pneumia toubkalensis (Omelková & Ježek 2012)	X*			
Psychoda aberrans Tonnoir, 1922				Х
Psychoda (Falsologima) savaiiensis Edwards, 1928		Х		
Psychoda (Logima) albipennis Zetterstedt, 1850		Х	Х	
Psychoda (Logima) erminea Eaton, 1893		Х		
Psychoda (Psycha) grisescens Tonnoir, 1922	Х	Х	Х	
Psychoda (Psychoda) phalaenoides (Linnaeus, 1758)		Х		
Psychoda (Psychoda) uniformata Haseman, 1907	Х			
Psychoda (Psychodocha) cinerea Banks, 1894	X**	Х	Х	
Psychoda (Psychodocha) gemina (Eaton, 1904)	X***			
Psychoda (Psychomora) trinodulosa Tonnoir, 1922		Х		
Psychoda (Tinearia) alternata Say, 1824	X*	Х	Х	X**
Psychoda (Tinearia) efflatouni Tonnoir, 1922				Х
Psychoda (Tinearia) lativentris Berden, 1952			Х	
Telmatoscopus advena (Eaton, 1893)		Х		
Thornburghiella quezeli (Vaillant, 1955)		Х	Х	
Tonnoiriella atlantica (Satchell, 1953)		Х	Х	
Tonnoiriella paveli Ježek, 1999	Х			
Tonnoiriella pulchra (Eaton, 1893)	Х	Х		
Vaillantodes fraudulentus (Eaton, 1896)		Х	Х	
Vaillantodes malickyi (Wagner, 1987)			Х	

X***: new species for North Africa; X**: new species for Morocco or Egypt; X*: new species for the Rif Mountains.

Table 2. Sampling sites (in alphabetical order) harboring the species collected in Morocco and Egypt with localities, geographical coordinates and altitudes.

Site	Province, locality	ce, locality Geographical coordinates	
Rif Mts			
1. Aïn Bou Ghaba	Chefchaouen, Jbel Bou Bessoui	35°57.980'N/4°43.447'W	1638
2. Aïn Mâaze	Larache, Jbel Bouhachem	35°14.381'N/05°26.316'W	1294
3. Aïn Quanquben	Chefchaouen, Jbel Bou Bessoui	34°57.634'N/4°40.842'W	1596
4. Aïn Sidi Yahya	Berkan, Beni Snassen	34°48.370'N/2°32.408'W	541
5. Âounsar Aheramen	Chefchaouen, Majjou village	35°06.319'N/5°10.820'W	855
6. Cascade Ras El Ma	Chefchaouen, Majjou village	35°6.162'N/5°10.739'W	859
7. Daya Fifi	Chefchaouen, Fifi	35°06.873'N/5°11.338'W	856
8. Douar Derâa	Chefchaouen, Tanakoub	35°10.106'N/5°25.381'W	770
9. Douar Idrene	Chefchaouen, Oued Laou	35°24.942'N/5°12.593'W	460
10. Douar Ihermochene	Chefchaouen, Oued Laou	35°26.602'N/5°11.793'W	405
11. Douar Ikhlafene	Chefchaouen, Oued Laou	35°25.575'N/5°11.807'W	548
12. Douar Kitane	Tétouan, Kitane	35°32.412'N/05°20.393'W	52
13. Douar Mouklata	Tétouan, Mouklata	35°34.551'N/5°21.505'W	9

Site	Province, locality	Geographical coordinates	Altitude (m)
14. Douar Taria	Chefchaouen, Daradara	35°8.312'N/5°20.991' W	796
15. Oued Aâyaden	Chefchaouen, Majjou village	35°6.186'N/5°10.935'W	799
16. Oued Achekrade	Tétouan, Douar Aouzighen	35°22.931'N/5°20.364'W	642
17. Oued Ametrasse	Chefchaouen, Chrafate	35°05.014'N/5°5.130'W	828
18. Oued associé à daya Fifi	Chefchaouen, Fifi	35°00.041'N/5°12.166'W	1280
19. Oued Azila	Al hoceima, Jbel Tidghine	34°52.028'N/04°32.609'W	1601
20. Oued à 20 Km de Fifi	Chefchaouen, Fifi	35°02.077'N/5°12.083'W	1020
21. Oued Chrafate	Chefchaouen, Armoutah	35°04.14'N/5°06.66'W	900
22. Oued El Kanar	Chefchaouen, Beni Fenzar	35°10.083'N/5°01.133'W	220
23. Oued El Kanar	Chefchaouen, 2 km de Douar Assoul	35°17.233'N/4°59.639'W	52
24. Oued Farda	Chefchaouen, Akchour,	35°14.350'N/5°10.46'W	420
25. Oued Hachef	Tanger-Azilah	35°31.37'N/05°42.51'W	58
26. Oued Inesmane	Chefchaouen, Adeldal	35°08.595'N/5°05.100'W	1173
27. Oued Jnane en Niche	Jebha, village Jnane en Niche	35°17.040'N/4°51.479'W	46
28. Oued Kelâa	Chefchaouen, Akoumi	35°14.440'N/5°14.542'W	400
29. Oued Madissouka	Chefchaouen, Talassemtane	35°10.622'N/5°08.400'W	1367
30. Oued M'Hannech	Tétouan, Faculty of Sciences	35°33.650'N/5°21.751'W	8
31. Oued Nakhla	Chefchaouen, Koudiet Krikra	35°23.084'N/5°31.448'W	145
32. Oued Ouara	Chefchaouen, Ikadjiouene	35°03.987'N/5°14.005'W	680
33. Oued Ras El Ma	Chefchaouen, Chefchaouen ville	35°10.230'N/5°15.412'W	628
34. Oued Taïda	Larache, Taïda	35°22.099'N/5°32.297'W	494
35. Oued Talembote	Chefchaouen, Talembote	35°15.041'N/5°11.717'W	320
36. Oued Tazzarine	Chefchaouen, Beni Oualal	35°04.347'N/5°19.339'W	242
37. Oued Tiffert	Chefchaouen, Tiffert	35°11.012'N/5°07.573'W	1230
38. Oued Zarka	Tétouan, Zarka	35°31.211'N/5°20.477'W	128
39. Ruisseau Maison forestière	Chefchaouen, Parc National Talassemtane	35°08.076'N/5°08.262'W	1674
40. Seguia barrage Dar Chaoui	Tanger-Azilah, Dar Chaoui	35°31.27'N/05°43.46'W	47
Beni Snassen			
41. Cascade Grotte des Pigeons	Berkan, Beni Snassen	34°49.044'N/5°24.329'W	676
Middle Atlas Mts			
42. Aïn Vittel	Ifrane, Ifrane ville	33°32.87'N/5°6.616'W	1611
43. Gîte Aït Ayoub	Sefrou, Barrage Allal El Fassi	33°55.446'N/4°40.558'W	537
Central Plain (Costal region)			
44. Douar Aoulad Ali	Safi, Jemaâ Shaim	32°20.288'N/8°51.09'W	170
High Atlas Mts			
45. Cascade sur sol cuivreux	Al Haouz, Taddart	31°21.19'N/7°23.54'W	1607
46. Oued Reghaya	Marrakech, Asni	31°14.736'N/7°58.654'W	1189
Egypt			
47. Oued Nile	Nady Tajdif, Giza	30°3.511'N/31°13.013'E	26

Results

Tribe MARUININI Enderlein, 1937 Genus *TONNOIRIELLA* Vaillant, 1982

Tonnoiriella paveli Ježek, 1999

Literature records. Morocco: High Atlas, Anti Atlas (Ježek 1999).

Comment. Male described by Ježek (1999: 10–12). Species collected by sweeping on the bank of streams (on *Oleander*, *Ficus* and *Pteropsida*), on wet grassy rocky slopes and on sources in semidesert areas. Considered as mountainous species (Ježek 1999: 10–12).

Biology. Unknown.

Tonnoiriella pulchra (Eaton, 1893)

= Pericoma pulchra (Eaton, 1893); Vaillant 1955: 223

Literature records. Morocco (Wagner 1990); Algeria: Aurès (Vaillant 1955).

Biology. Species found in "madicole" habitat whose substrate consists on bare rock or lined by retaining algae by very few mineral particles, and in compact lime-stone crust "néoformation" (Vaillant 1955).

Tonnoiriella atlantica (Satchell, 1955)

= Pericoma atlantica Satchell, 1955; Satchell 1955

Literature records. Algeria: Fort National, El Biar (Satchell 1955), L'Hospice de Veillards, Bône (Satchell 1955); Tunisia: Oued Titria, Ain Sobah (Wagner 1987).

Comment. Male and female described by Satchell (1955: 112–113). **Biology.** Unknown.

Tribe PARAMORMIINI Enderlein, 1937 Genus *CLOGMIA* Enderlein, 1937

**Clogmia albipunctata (Williston, 1893)

= Telmatoscopus meridionalis (Eaton, 1894); Tonnoir 1920: 128–133.

= *Telmatoscopus albipunctatus* (Williston, 1893)

Literature records. Algeria: Boghari (Alger), Rocher Blanc (Tonnoir 1920, Satchell 1955); Egypt: Delta Barrage, Ghezireh (Tonnoir 1920, El-Badry et al. 2014).

New records. Morocco, Rif: Douar Kitane, 13/V/2014, 13, 299, 1/V/2015, 19, light trap; Douar Mouklata, 12/IV/2005, 5 larvae, suber net; Oued M'Hannech, 12/IV/2005, 333, 1/V/2015, 533, 799, aspirator; Central Plateau (Coastal region): Douar Aoulad Ali, 12/VII/2014, 133, sweep net, coll. Afzan and Belqat.

New site. Egypt, Oued Nile: 1-9/IV/2015, 3, 2, Malaise trap, coll. Belqat.

Comment. A complete description and full synonymy of *Clogmia albipunctata* (Williston, 1893) can be found in Ibañez-Bernal (2008).

Biology. Species reported, in central Europe in kitchens, bathrooms and hospitals (Oboňa and Ježek 2012). Full bionomies can be found in Boumans (2009), Boumans et al. (2009) and Werner (1997). Collected in the present study in synanthropic habitats and on plants such as *Oxalis*.

Genus LEPISEODINA Enderlein, 1937

Lepiseodina tristis (Meigen, 1830)

= Clogmia tristis (Meigen, 1830)

= Telmatoscopus tristis (Meigen, 1830); Vaillant 1972: 53-54

Literature record. Algeria (Vaillant 1972).

Biology. Species found in wet rot-holes and in an oak branch-end (Withers 1989). Larvae found in rotting wood or hole trees (Oboňa and Ježek 2012).

Genus IRANOTELMATOSCOPUS Ježek, 1987

Iranotelmatoscopus numidicus (Satchell, 1955)

= Telmatoscopus numidicus Satchell, 1955: 115

- = Panimerus numidicus (Satchell, 1955); Vaillant 1972: 78
- = Iranotelmatoscopus numidicus (Satchell, 1955); Ježek 1987: 6-8

Literature records. Algeria: Biskra (Satchell 1955), Vaillant (1972).

Comment. Original description of the species *Telmatoscopus numidicus* by Satchell (1955: 115–116).

Biology. Unknown.

Iranotelmatoscopus squamifer (Tonnoir, 1922), comb. n.

Telmatoscopus squamifer Tonnoir, 1922: 102

Literature record. Egypt: Shoubra (Tonnoir 1922).

Comment. *Telmatoscopus squamifer* is transferred to *Iranotelmatoscopus* based on the structure of the male genitalia, ascoids and wing venation, as judged from illustrations.

Biology. Unknown.

Genus PANIMERUS Eaton, 1913

Panimerus goetghebueri (Tonnoir, 1919)

- = Pericoma goetghebueri Tonnoir, 1919
- = Telmatoscopus (Panimerus) goetghebueri (Tonnoir, 1919); Satchell 1955: 119
- *Telmatoscopus goetghebueri* (Tonnoir 1919); Freeman 1950 (synonymy according to Vaillant 1972)
- = Panimerus goetghebueri (Tonnoir, 1919); Vaillant 1972: 71

Literature records. Algeria: Satchell (1955), Bône (Vaillant 1972); Tunisia: Hammam Bourguiba stream, Hammam Bourguiba, Oued Hammam Bourguiba Barbarian, Ain Sobah, Dum Djeddour, Oued Titria (Wagner 1987).

Comment. adults described by Vaillant (1972). **Biology.** Unknown.

Panimerus thienemanni (Vaillant, 1954)

- = Mormia thienemanni Vaillant 1954
- = Telmatoscopus thienemanii (Vaillant, 1954); Vaillant 1955: 85, 200-202
- = ? Panimerus maynei (Tonnoir, 1919); Vaillant 1972 (placed in synonymy)
- = *Panimerus thienemanni* (Vaillant, 1954); Vaillant and Withers 1992 (raised from synonymy)

Literature records. Morocco: High Atlas (Boumezzough and Vaillant 1986); Algeria: Djurdjura mountains (Satchell 1955), (Vaillant 1972; Vaillant and Withers 1992); Tunisia: Oued Maden (Wagner 1987).

Comment. Adults reared from larvae collected in the foam in Assif Reghaya by Boumezzough and Vaillant (1986: 237); detailed description of the adult given by Vaillant (1972).

The status of *Panimerus maynei* in North Africa is unclear. Vaillant (1954) described *Mormia thienemanni* from Algeria and later synonymized it with *P. maynei* (Vaillant 1972). However, Vaillant and Withers (1992) identified diagnostic differences between the type material of *P. maynei* and *P. thienemanni* and raised the latter species from synonymy. The records of *P. maynei* given by Satchell (1955), Boumezzough and Vaillant (1986) and Wagner (1987) are here assumed to represent *P. thienemanni*, although the material should ideally be revised.

Genus VAILLANTODES Wagner, 2001

Vaillantodes fraudulentus (Eaton, 1896)

- = Pericoma sp. Eaton, 1896
- = Pericoma fraudulenta Eaton, 1896
- = Xenapates fraudulenta (Eaton, 1896); Eaton 1904
- = Telmatoscopus fraudulentus (Eaton, 1896); Satchell 1955:116–118
- = Panimerus fraudulentus (Eaton, 1896); Vaillant 1972: 79
- = Jungiella fraudulenta (Eaton, 1896); Wagner 1987: 17–18
- = Vaillantia fraudulentus (Eaton, 1896); Wagner 1988: 10

Literature records. Algeria: Mt. Edough, l'Hospice de Vaillards (Bône), El Biar, Aine Souk, Forêt de Yakourene (Hakowen), Mustaph Superior (Satchell 1955); Tunisia (Wagner 1987).

Comment. Male and female described by Satchell (1955). **Biology.** Unknown.

Vaillantodes malickyi Wagner, 1987

= Jungiella malickyi Wagner, 1987: 18–19

Literature record. Tunisia: Hammam Bourguiba (Wagner 1987). Comment. Description of adult by Wagner (1987: 18–19). Biology. Unknown.

Genus PARAMORMIA Enderlein, 1935

- = Paramormia Enderlein, 1935: 248
- = Duckhousiella Vaillant, 1972: 54

*Paramormia ustulata (Walker, 1856)

= Pericoma ustulata Walker, 1856: 263

= Telmatoscopus limosus Vaillant, 1955: 85

= Duckhousiella ustulata (Walker, 1856); Vaillant 1972: 58

= Paramormia ustulata (Walker, 1856); Wagner 1990: 50

Literature records. Morocco: High Atlas (Vaillant 1955, 1972); Algeria: Djurdjura, Aurès, Petite-Kabylie (Satchell 1955, Vaillant 1955, 1972); Tunisia: Hammam Bourguiba stream, Oued Hammam Bourguiba Barbarian, Ain Drahan, Dum Djeddour, reservoir of Kasseb, Oued Maden (Wagner 1987).

New record. Morocco, Rif: Seguia barrage Dar Chaoui, 14/II/2013, 433, reared; Douar Kitane, 14/XI/2013, 233, adhesive papers, 24/III/2015, 13, malaise trap; Oued Jnane en Niche, 19/IV/2013, 433, sweep net, coll. Afzan and Belqat.

Comment. Detailed descriptions of adult, pupae and larvae given by Vaillant (1972: 58–59).

Biology. Larva and pupa can live in habitats with different levels of salinity in seaweed-heaps or near salt springs. Larvae can be found in rivers, sea shores, thermal springs, in crust of limestone dust, beneath stones, in moss and in moist earth (Vaillant 1971, 1972). Specimens collected by Ježek (1990a) occupy a large variety of habitats like, banks of outflows of ponds, moist pastures, swamps, steams and pools on margins of forest, arms of rivers, in biotopes with *Alnus, Salix, Populus, Aesculus, Pinus, Fraxinus* and others.

Genus TELMATOSCOPUS Eaton, 1904

Telmatoscopus advena (Eaton, 1893)

= Pericoma advena Eaton 1893, 1896

- = Telmatoscopus advenus Vaillant, 1972: 80
- = Panimerus havelkai (Wagner, 1975); syn. according to Kvifte (2014): 392
- = Telmatoscopus seguyi (Vaillant, 1990); syn. according to Kvifte (2014): 392

Literature record. Algeria: Fort National (Vaillant 1972).

Comment. Vaillant (1972) lists a single specimen that was captured and determined as *Pericoma advena*, but the identification must be considered as doubtful. A full synonymy is given in Kvifte (2014).

Biology. Species considered as a tree-breeder; found in sycamore with damp (no standing water) rot, approximately 1.5 m above ground, in elm trunk-base, very damp, but no standing water, in ash, birch, hole approximately 1.5 m. above ground, with some standing water (Withers 1989).

Tribe Mormiini Enderlein, 1937 Genus *MORMIA* Enderlein, 1935

*Mormia tenebricosa Vaillant, 1954

= Telmatoscopus tenebricosus Vaillant, 1955: 85; Vaillant 1974: 135

Literature records. Morocco: High Atlas (Vaillant 1955, 1974); Algeria: Aurès, Petite-Kabylie, Alger (Vaillant 1955, 1974); Tunisia: Hammam Bourguiba, Hammam Bourguiba stream, Ain Drahan, Oued Ain Bousabala, Oued Maden (Wagner 1987).

New record: Morocco, Rif: Oued Achekrade, 9/III/2014, 13, reared, coll. Afzan and Belqat.

Comment. Detailed description of adult, pupae and larvae (Vaillant 1974: 135–139).

Biology. In the present work, larvae were collected and reared by the authors at laboratory temperature; the emergence of the adult took 10 days.

Mormia similis Wagner, 1987

Literature records. Tunisia: Oued Hammam Bourguiba Barbarian (Wagner 1987). Biology. Unknown.

Mormia riparia (Satchell, 1955)

= Telmatoscopus (Mormia) riparius Satchell, 1955: 113–115

= Mormia riparia (Satchell, 1955); Vaillant 1975: 144

Literature records. Algeria: Bône, El Biar (Satchell 1955), (Vaillant 1975). Comment. Descriptions of the male (Satchell 1955: 113–115).

Tribe PERICOMAINI Enderlein, 1935 Genus *BAZARELLA* Vaillant, 1964

*Bazarella atra (Vaillant, 1955)

= Pericoma atra (Vaillant, 1955); Vaillant 1983: 337-339

Literature records. Morocco, High Atlas: Massif du Siroua (Vaillant 1955); Algeria: Aurès, Tlemcen, Djurjura, Petite-Kabylie, Massif des Aures (Vaillant 1955, 1983).

New records. Morocco, Rif: Oued Inesmane, 12/IV/2004, 1 larva, surber net; Oued Madissouka, 18/V/2014, 533, sweep net; Aïn Quanquben, 28/IV/2015, 333, 10 \bigcirc \bigcirc , sweep net; Aïn Bou Ghaba, 28/IV/2015, 1 \bigcirc , 4 \bigcirc \bigcirc , sweep net; Oued Aâyaden, 27/IV/2015, 2 \bigcirc \bigcirc , aspirator; High Atlas: Oued Reghaya, 07/V/2011, 8 larvae, surber net, coll. Afzan and Belqat.

Comment. Larvae, pupae and adults described by Vaillant (1983: 337–339). Species wrongly recorded as new for Morocco by Ježek (2004: 146–147).

Biology. Authors of this paper collected the material in rivers, springs and brook with cedar forest and *Rubus ulmifolius* as the predominant vegetation.

Genus BERDENIELLA Vaillant, 1976

Berdeniella lucasii (Satchell, 1955)

= Pericoma lucasii (Satchel, 1955); Satchell 1955: 111–112.

Literature records. Algeria: Coastal city Bône (Satchell 1955, Vaillant 1976). Comment. Adult described by Vaillant (1976: 188).

Genus CLYTOCERUS Eaton, 1904

Clytocerus kabylicus Wagner, 1987

= Clytocerus wollastoni Satchell, 1953; Satchell 1955: 107–109 (partim, misidentification)

Literature records. Algeria: El Biar (Wagner 1987: 14).

Comment. *Clytocerus wollastoni* Satchell, 1955 was recorded from Algeria by Satchell (1955), but according to Wagner (1987), these specimens were likely misidentified *C. kabylicus*. True *C. wollastoni* occurs only on Madeira.

Genus PERICOMA Walker, 1856

*Pericoma barbarica Vaillant, 1955

Literature records. Morocco: High Atlas (Vaillant 1955); Algeria: Aurès, Tlemcen, Edge of Tlemcen, Oued Safsaf, Constantine, Petite Kabylie (Vaillant 1955); Tunisia: Hammam Bourguiba stream, Ain Drahan (Wagner 1987: 13).

New record. Morocco, Rif: Oued Taïda, 17/IV/2013, 13, 19, reared; Douar Taria, 08/IX/2013, 433, adhesive papers; Cascade Grotte des pigeons, 5/XI/2014, 3333, sweep net, coll. Afzan and Belqat.

Biology. In the present work, the adults were collected from vegetation as, *Eucalyptus, Olea oleaster, Rubus ulmifolius, Crataegus monogyna, Nerium oleander, Chamae-* *rops* sp., and *Phragmites australis* by a waterfall. Adults were also reared at the laboratory temperature from larvae collected in a stony ground stream with brown algae and mosses. They emerged in 30 days.

Pericoma blandula Eaton, 1893

Literature records. Morocco: High Atlas (Boumezzough and Vaillant 1986; Ježek 2004), Rif (Ježek 2004); Algeria: Ruisseau des singes (Vaillant 1979); Tunisia: Hammam Bourguiba stream, Ain Drahan, Oued Sardouk, Oued Titria (Wagner 1987; Ježek 2004).

New site. Morocco, Rif: Oued Taïda, 17/IV/2013, 233, reared; Âounsar Aheramen, 10/V/2014, 933, 699, reared; Oued Beni Ouachekradi, 24/XI/2014, 233, 699, reared, Oued Aâyaden, 27/IV/2015, 633, aspirator; Cascade Ras El Ma, 27/IV/2015, 233, sweep net, coll. Afzan and Belqat.

Comment. Adults reared from larvae collected along the Assif Reghaya by Boumezzough and Vaillant (1986: 237); adult, larvae and pupa, habitat of different states and characteristics of *Pericoma blandula* of North Africa and Europe were described by Vaillant (1979: 239–240). Species wrongly recorded as new for Morocco by Ježek (2004: 147).

Biology. According to Duckhouse (1962) and Vaillant (1976), the larvae of *Pericoma blandula* can live in different habitats: in mosses which cover, the dead leaves present in the banks of springs and rivers, as well as in sand, mud and stones on the edge of large and small courtyards water. They also can be found in different substrates: granite, basalt and slate. Vaillant (1979) described in detail the larva.

*Pericoma granadica Vaillant, 1978

Literature records. Morocco: High Atlas (Boumezzough and Vaillant 1986).

New records. Morocco, Rif: Oued Taïda, 18/III/2011, 2 larvae, surber net; Oued Ametrasse, 16/V/2011, 9 larvae, surber net; Oued Ras El Ma, 17/V/2011, 2 larvae, surber net; Oued Farda, 28/III/2012, 113, 29 9, sweep net, reared; Oued Aâyaden, 27/IV/2015, 133, 3, sweep net; Middle Atlas: Aïn Vittel, 11/XII/2011, 43, 59 9, reared; High Atlas: Cascade sur sol cuivreux, 06/V/2011, 2 larvae, surber net; Oued Reghaya, 07/V/2011, 23, 19, sweep net, coll. Afzan and Belqat.

Comment. Adults reared from larvae collected in the foam in the site Assif Reghaya (Boumezzough and Vaillant 1986: 237–238).

Biology. Larvae extremely abundant in the foam that cover the walls of irrigation canals and exterior walls; adults obtained by breeding (Vaillant 1978). In the present paper, the eclosion at the temperature laboratory of several adults was registered at 2 days from pupae and 60 days from larvae. Adults were also collected by sweeping the vegetation mostly constituted by *Nerium oleander*, *Pistacia lentiscus* and *Rubus ulmifolius* near springs, streams and waterfall habitats.

Pericoma exquisita Eaton, 1893

= Pericoma minutissima Vaillant, 1963

= Pericoma petricola Vaillant, 1962

Literature records. Morocco: High Atlas, Rif (Ježek 2004); Algeria: Ježek (2004); Tunisia: Hammam Bourguiba stream, Oued maden, Oued Titria (Wagner 1987).

Biology. Larvae living on the banks of rivers; adults found on Crete and the islands of Evia in the Aegean (Vaillant 1978).

*Pericoma diversa Tonnoir, 1920

Literature record. Morocco: High Atlas (Vaillant 1978: 229).

New record. Morocco, Rif: Cascade Chrafate, 18/III/2015, 233, 19, reared, coll. Afzan and Belqat.

Comment. Description of larva, pupa and male by Vaillant (1978: 229).

Biology. Present in fast rivers, fit into the foams containing stones, in walls of natural or artificial waterfalls; as well as in bryophytes covering irrigation canals. In England, larvae were found at an altitude that does not exceed 1100 m; in Morocco it was collected at 2000 m (Vaillant 1978) and at 900 m in the present work.

*Pericoma latina Sarà, 1954

= Pericoma numidica Vaillant, 1955

Literature records. Morocco: High Atlas (Vaillant 1955); Algeria: Aurès, Tlemcen mountains (Vaillant 1978).

New record. Morocco, Rif: Cascade Chrafate, 18/III/2015, 2♂♂, reared; Oued Majjou, Nord Village Majjou, 19/03/2004, 1 larva; Oued Majjou, Majjou village, 19/03/2004, 17 larvae; Oued Kelâa, 04/V/2004, 29 larvae; Oued Talembote, 21/VI/2005, 4 larvae; Oued associé à daya Fifi, 16/VI/2005, 25 larvae; Oued Tiffert, 16/VI/2005, 3 larvae; Oued à 20 Km de Fifi, 16/VI/2005, 1 larva; Oued El Kanar, Beni Fenzar, 21/VI/2004, 1 larva, surber net, coll. Afzan and Belqat.

Comment. Detailed description of larvae, pupae and adults, reared from larvae (Vaillant 1978: 234–235).

Biology. Larvae particularly "petrimadicolous"; can be found also under the leaves soaked on the banks of sources. In the present work, the authors collected the larvae in diversified habitats, in streams, in arms of pounds and rivers, in waterfall. The reared adults were obtained at the temperature laboratory from larvae collected in a waterfall which abundant vegetation was: *Olea oleaster, Ficus carica, Rubus ulmifolius, Eucalyptus, Nerium oleander, Hedera maroccana* and *Ricinus communis.*

**Pericoma maroccana* Vaillant, 1955

= Pericoma numidica var. marocana Vaillant, 1955

Literature records. Morocco: High Atlas (Boumezzough and Vaillant 1986; Dakki 1997). New records. Morocco, Rif: Cascade Chrafate, 18/III/2015, 2♂♂, 2♀♀, sweep net; Ruisseau Maison forestière, 21/IV/2015, 1♂, sweep net, coll. Afzan and Belqat.

Comment. Species recorded from Tissaout in the High Atlas; it is endemic from Morocco.

Biology. The authors of the present paper collected the species on the branches of the vegetation around a waterfall and a streamlet. The localities with *Olea oleaster*, *Ficus carica*, *Rubus ulmifolius*, *Eucalyptus*, *Nerium oleander*, *Hedera maroccana*, *Ricinus communis*, *Abies marocana*, *Pinus negra*, *Pinus pinaster*, *Cedrus atlantica* and *Berberis hispanica*.

Pericoma modesta (Tonnoir, 1922)

= Pericoma numidica Vaillant, 1955 (syn. according to Vaillant 1978)

Literature records. Morocco: High Atlas: Boumezzough and Vaillant (1986); Algeria: Aurès, Djurdura, Constantine, Atlas de Blida, Ruisseau des singes, Camp-des-Chênes, Sidi-Madani, Alger (Vaillant 1955), Aegean, Djurdjura mountains (Vaillant 1978).

Comment. Adults reared from larvae collected in wet sand along the Assif Reghaya (Boumezzough and Vaillant 1986: 237). Detailed description of larvae and adults (Vaillant 1978: 226–227).

Biology. Unknown.

***Pericoma pseudexquisita Tonnoir, 1940

= Pericoma avicularia Tonnoir, 1940; Vaillant 1978: 233

New record. North Africa, Morocco, Rif: Oued Azila, 27.VI.2013, 733, 299, reared, coll. Afzan and Belqat.

Biology. Larvae living on pure rocky soil, in the foam and between the leaves. Adults observed throughout the summer season (Vaillant 1978). In the present work, adults were reared at the laboratory and the hatchings were obtained at the 10th and the 20th days. At the unique locality, the most abundant vegetation was formed by *Pteridium aquilinum* and *Rubus ulmifolius*, and the rocky substrate was covered by some mosses.

Genus THORNBURGHIELLA Vaillant, 1982

Thornburghiella quezeli (Vaillant, 1955)

= Pericoma quezeli (Vaillant 1955)

Literature records. Algeria: Petite-Kabylie, Camp-des-Chênes, Constantine, Atlas de Blida, Chabet-el-Akra Vaillant (1955); Tunisia: Aïn Draham (Vaillant 1983).
Comment. Detailed description of adult, pupa and larvae (Vaillant 1983: 326–328).
Biology. Unknown.

Genus PNEUMIA Enderlein, 1935

= Satchelliella Vaillant, 1979

***Pneumia nubila (Meigen, 1818)

= Satchelliella nubila (Meigen, 1818); Vaillant 1979: 270

New record. Morocco, Rif: Aïn Mâaze, 1/XI/2014, 1∂, sweep net, coll. Afzan and Belqat.

Biology. Larvae found in accumulations of dead, leaves decaying on the bottom of a tank near a stream, or on the banks of a marsh (Vaillant 1981). In the present work, the authors collected the unique adult by sweeping the vegetation formed essentially by *Quercus canariensis*, *Rubus ulmifolius*, *Arbutus unedo*, *Erica arborea*, *Cistus populifolius* and *Luzula* sp.

Pneumia pilularia (Tonnoir, 1940)

= Pericoma pilularia Tonnoir, 1940; Satchell 1955: 118

= Satchelliella pilularia (Tonnoir, 1940); Vaillant 1981: 277–278

Literature records. Morocco (Ježek 2004); Algeria: Djurdjura mountains (Satchell 1955). **Comment.** Description of larvae and adult (Vaillant 1981: 277–278).

Biology. Larvae common among the remaining plants on the banks of rheocrene springs, many madicole habitats and on limestone substrates (Vaillant 1981).

**Pneumia propinqua (Satchell, 1955)

= Pericoma propinqua Satchell, 1955; Satchell 1955: 109–111

= Satchelliella propinqua (Satchell, 1955); Vaillant 1979: 265–266

Literature records. Algeria: Village Tissadourt (Satchell 1955), Tissadourt, Algiers, Fort National in Kabylia (Vaillant 1979).

New Record: Morocco, Rif: Chrafate, 24/V/2013, 233, reared; Oued Zarka, 14/XI/2013, 233, reared, coll. Afzan and Belqat.

Comment. Description of the male (Satchell 1955: 109–111, Vaillant 1979), placement in *Pneumia* according to Omelková and Ježek (2012).

Biology. The authors of the present work reared the species at temperature laboratory; the emergence of the adults was registered after 30 days. The abundant vegetation at the localities was: *Olea oleaster, Ficus carica, Rubus ulmifolius, Eucalyptus, Nerium oleander, Hedera maroccana* and *Ricinus communis.*

Pneumia reghayana (Boumezzough & Vaillant, 1986), comb. nov.

= Satchelliella reghayana Boumezzough & Vaillant, 1986: 238–239; Dakki 1997: 87, 89

Literature records. Morocco: High Atlas (Boumezzough and Vaillant 1986, Dakki 1997).

Comment. Adults reared from larvae, description, differential diagnosis (Boumezzough and Vaillant 1986: 238–239). The species was overlooked by Omelková and Ježek (2012) in their catalogue of world *Pneumia* species and is here first recognized as a species of *Pneumia*.

Biology. Unknown.

*Pneumia toubkalensis (Omelková & Ježek, 2012)

Literature records. Morocco: High Atlas (Omelková and Ježek 2012).

New record: Morocco, Rif: Oued Aâyaden, 27/IV/2015, 433, sweep net; Aïn Ras El Ma, 27/IV/2015, 13, sweep net, coll. Afzan and Belqat.

Comment. *Pneumia toubkalensis* can be separated from *P. reghayana* on the presence of four digitiform sensilla laterosubapically and a microseta mediosubapically on the gonostyle.

Biology. The species was collected on a wall of a river of the higher course, on a limestone soil and mosses on the rock, and on a wall of a spring. The localities were dominated by *Pistachia lentiscus*, *Cistus* sp. and *Nerium oleander*.

Tribe PSYCHODINI Newman, 1834 Genus *PHILOSEPEDON* Eaton, 1904

**Philosepedon (Philosepedon) humerale (Meigen, 1818)

Psychoda humeralis Meigen, 1818; Eaton 1893, Satchell 1955: 119, Tonnoir 1919, 1922, Enderlein 1937, Freeman 1950, Jung 1956, Vaillant 1960

Literature record. Algeria (Satchell 1955).

New records. Morocco, Rif: Oued Hachef, 4/II/2013, 233, 19, reared; Cascade Ras El Ma, 27/IV/2015, 19, aspirator; Oued El Kanar, 2 km de Douar Assoul, 27/IV/2015, 13, aspirator; Oued Aâyaden, 27/IV/2015, 13, aspirator, coll. Afzan and Belqat.

Biology. Larvae growing in snail-shells; adults found in damp places (Ježek 1985). The authors of the present work collected the adults on walls of a river of the higher course and of a spring. The localities had a dominance of *Pistachia lentiscus*, *Cistus* sp. and *Nerium oleander*.

Philosepedon (Philosepedon) beaucournui Vaillant, 1974

Literature records. Algeria (Vaillant 1974); Tunisia: Oued Ain Bousabala, reservoir of Kasseb, Ain Drahan (Wagner 1987).

Comment. Description of adult from Algeria. Brief comparison between this species and *Philosepedon humerale* (Vaillant 1974: 116–117).

Genus *PSYCHODA* Latreille, 1796 Subgenus *Falsologima* Ježek and Van harten, 1996

Psychoda (Falsologima) savaiiensis (Edwards, 1928)

= Psychoda rarotongensis Satchell, 1953: 183–184

Literature record. Algeria (Satchell 1955).

Subgenus Logima Eaton

Psychoda (Logima) aberrans Tonnoir, 1922

Literature record. Egypt: Shoubra (Tonnoir 1922)

Comment. The species is transferred to subgenus *Logima* based on figures in Tonnoir (1922).

Biology. Unknown.

Psychoda (Logima) albipennis Zetterstedt, 1850

= Psychoda severini Tonnoir, 1922; Ježek, 1983: 214

Literature records. Algeria (Satchell 1955); Tunisia: Hammam Bourguiba stream, Ain Drahan (Wagner 1987).

Biology. Larvae living in various habitats: in the mud of tracks of both cattle and horses, dung, waste pipes drain devices out houses and on the trickling beds of sewage films, bathrooms (Wagner 1977).

Psychoda (Logima) erminea Eaton, 1893

Literature records. Algeria (Satchell 1955).

Biology. Larvae found on the margins of polluted ponds or reservoirs (Nielsen 1961), on banks of streams and drainage canals, swamps, periphery of ponds (Vaillant and Botosaneanu 1966); adults have been collected in localities shaded by *Alnus, Salix, Robinia, Sambucus, Pinus* and *Fraxinus*, with undergrowth with mostly *Geranium* and *Urtica* (Ježek 1983).

Subgenus Psycha Ježek, 1984

Psychoda (Psycha) grisescens Tonnoir, 1922

Literature records. Morocco: Rif (Ježek 2004); Algeria (Satchell 1955); Tunisia: Hammam Bourguiba stream (Wagner 1987).

New records. Morocco, Rif: Douar Kitane, 13/III/2014, 13° , 39° , sweep net, 20-22/IV/2015, 14 3° , light trap, 1/V/2015, 4 3° , light trap, 24/III/2015, 60 3° , 59° , malaise trap, H. Afzan and B. Belqat collectors; Middle Atlas: Gîte Aït Ayoub, 14/IV/2014, 23° , adhesive papers, coll. Afzan and Belqat.

Biology. Larvae found on banks of polluted brooks or in wet cow dung; adults collected in banks of a pond, on house windows, on the branches of coniferous trees and in gardens (Ježek 1990b).

Subgenus Psychoda s. str.

Psychoda (Psychoda) phalaenoides (Linnaeus, 1758)

Literature record. Algeria (Satchell 1955).

Biology. Adults found in several habitats: banks of mountain forest brooks, decaying organic matter in drainages, growth of alders, dry places, banks of rivers, springs on meadows, outflow from ponds and swamps with *Populus*, *Alnus*, *Picea*, *Fagus*, *Castanea*, *the* undergrowth with *Urtica*, *Petasites*, *Imoatiens*, *Ficaria*, *Grossularia*, *Ires*, *Rubus*, *Fragaria*, *Filipendula* and *Assarum* (Ježek 1990b).

Psychoda (Psychoda) uniformata Haseman, 1907

Literature record. Morocco: Rif (Ježek 2004).

Biology. Adults found in various habitats: banks of drainages, moist meadows, near arms of rivers, forest brooks pond, in dry bed of canal shaded by *Alnus*, *Fraxinus*, *Crataegus* and others (Ježek 1990b).

Subgenus Psychodocha Ježek, 1984

**Psychoda (Psychodocha) cinerea Banks, 1894

Literature records. Algeria (Satchell 1955); Tunisia: Hammam Bourguiba, Hammam Bourguiba stream, Oued Titria, Ain Drahan, Ain Sobah (Wagner 1987).

New records. Morocco, Rif: Oued Tazzarine, 17/V/2011, 333, 799, sweep net; Douar Taria, 08/IX/2013, 533, adhesive papers; Douar Kitane, 30/IV/2015, 233, light trap, 24/III/2015, 433, malaise trap; Oued Chrafate, 27/IV/2015, 233, 399, light trap, 27/IV/2015, 233, 599, aspirator, 28/IV/2015, 233, 299, sweep net; OuedAâyaden, 27/IV/2015, 233, sweep net; Beni Snassen: Cascade Grotte des Pigeons, 25/XI/2014, 13, reared, coll. Afzan and Belqat.

Biology. Larvae registered by several authors (in Ježek 1990b) in diversified habitats (in mud and moss, below stones and moist rock walls, in stagnant waters, in ducts of drainage machinery, on toilets, near banks, in food industry, cow excrements, hollows of trees, heaps of garden's rest, margins of periodical water reservoirs, etc.). Adults, also collected by several authors (in Ježek 1990b) in light traps, on branches of coniferous trees, in mixed forests, on banks of gutters, brooks, ponds, arms of rivers, in gardens, dirty toilets, etc. Authors of the present work collected the species in several habitats with predominant vegetation as: *Eucalyptus, Olea oleaster, Rubus ulmifolius, Crataegus monogyna, Nerium oleander, Chamaerops* sp., *Phragmites australis, Ficus carica, Hedera maroccana* and *Ricinus communis.*

***Psychoda (Psychodocha) gemina (Eaton, 1904)

New record. North Africa, Morocco, Rif: Daya Fifi, 30/III/2012, 333, 299, sweep net; Oued Zarka, 14/XI/2013, 833, 19 reared; Douar kitane, 20-22/IV/2015, 533, 1/V/2015, 533, light trap; Oued Aâyaden, 27/IV/2015, 133, aspirator, coll. Afzan and Belqat.

Biology. Larvae living in moist mud of paddocks, in manure, in waste pipes, on toilets, sewage work, water mains etc. (Jung 1956), among decayed leaves on the banks of pounds and near springs (Wagner 1977). Ježek (1990b) collected adults near mountain streams drainages, banks of river, inundated lowland forests, surroundings of sluices, moist places near dustbins, rills below railway bridges, spring areas with fallen trees, brooks in meadows, ponds and their outflows, swamps in forests, dry water reservoirs and dry cesspools.

In the present paper, the authors collected the species on both lotic and lentic habitats. The predominant vegetation in the localities were dominated by *Quercus canariensis*, *Quercus pyrenaica*, *Cistus salviifolius*, *Euphorbia characias*, *Arondo donax*, *Midicago sativa*, *Inula viscose* and mosses.

Subgenus Psychomora Ježek, 1984

Psychoda (Psychomora) trinodulosa (Tonnoir, 1992)

Literature records. Algeria (Satchell 1955).

Biology. Larvae developed in horse and cow excrement (Wagner 1977). Adults collected in areas of inundated forests, on banks of brooks and gutters, on moist pastures, near arms of rivers, rubbish heaps, at moist material, dry drainages, banks of ponds, spring areas and toilets (Ježek 1990b).

Subgenus Tinearia Schellenberg, 1803

*Psychoda (Tinearia) alternata Say, 1824

Literature records. Morocco: High Atlas: La Maire (Tonnoir 1920); Algeria (Satchell 1955); Tunisia: Oued Ain Bousabala (Wagner 1987).

New record: Morocco, Rif: Oued Nakhla, 18/III/2011, 7 , 59, sweep net; Oued Farda, 28/III/2012, 19, reared; Oued Ouara, 23/XI/2012, 19, reared; Oued Ametrasse, 11/VI/2012, 2, 49, reared; Oued Chrafate, 11/VI/2012, 12, 12, 16, 16, reared; Douar Derâa, 24/VIII/2013, 2, 59, adhesive papers; Douar Ihermochene, 06/V/2014, 9, 9, 99, adhesive papers; Douar Ikhlafene, 07/X/2013, 15, 109, 06/V/2014, 2, 69, adhesive papers; Douar Taria, 08/IX/2013, 4, 3, 119, adhesive papers; Douar Idrene, 4, 29, 6.X.2013, adhesive papers; Douar Kitane, 9/III/2014, 12, 20, 20, 9, light trap; Oued 2km deDouar Assoul, 27/IV/2015, 29, aspirator; Douar kitane, 1/V/2015, 50, 69 light trap; Oued Aâyaden, 27/IV/2015, 19, sweep net; Ruisseau Maison forestière, 21/IV/2015, 2, sweep net; Oued Mhannech, 5, 79, aspirator; Aïn Sidi Yahya, 26/XI/2014, 1, reared; Middle Atlas: Gîte Aït Ayoub, 14/IV/2014, 1, 19, adhesive papers, coll. Afzan and Belqat.

New record. Egypt, Oued Nile: 3∂∂, 1♀, 1-9/IV/2015, malaise trap, Belqat coll. Biology. The authors of this paper collected the species in varied habitats: rivers, streamlets and walls of homes in small countryside villages (light trap and adhesive papers). The localities whith Olea oleaster, Ficus carica, Rubus ulmifolius, Eucalyptus, Nerium oleander, Hedera maroccana, Ricinus communis, Abies marocana, Pinus negra, Pinus pinaster, Cedrus atlantica, Berberis hispanica, Pistacia lentiscus and Rubus ulmifolius.

Psychoda (Tinearia) efflatouni Tonnoir, 1922

Literature record. Egypt: Shoubra (Tonnoir 1922). Biology. Unknown.

Psychoda (Tinearia) lativentris (Berdén, 1952)

Literature record. Tunisia: Ain Drahan (Wagner 1987). **Comment.** Cited in Tunisia by Wagner (1987).

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References

- Boumans L (2009) De WC-motmug *Clogmia albipunctata*, een opvallend maar onopgemerkt element van onze fauna (Diptera: Psychodidae). Nederlandse Faunistische Medelingen 30: 1–10.
- Boumans L, Zimmer J-Y, Verheggen F (2009) First records of the 'bathroom mothmidge' Clogmia albipunctata, a conspicuous element of the Belgian fauna that went unnoticed (Diptera: Psychodidae). Phegea 37: 153–160.
- Boumezzough A, Vaillant F (1986) Quelques Diptères Psychodidae Psychodinae du Grand-Atlas marocain. Entomologiste 42(4): 237–239.
- Dakki M (1997) Etude Nationale sur la Biodiversité, Faune Aquatique Continentale. Rapport PNUE & Ministère d'environnement, Maroc., 117 pp.
- Duckhouse DA (1962) Some British Psychodidae (Diptera, Nematocera): description of species and discussion on the problem of species pairs. Transactions of the Royal Entomological Society of London 114: 403–436. doi: 10.1111/j.1365-2311.1962.tb01072.x

- Duckhouse DA (1987) A revision of Afrotropical *Setomima*, elucidation of their genealogical relationships and descriptions of other Afrotropical Psychodinae (Diptera: Psychodidae). Annals of the Natal Museum 28(2): 231–282.
- Eaton AE (1893) A Synopsis of British Psychodidae. Entomologist's Monthly Magazine 29: 5–8, 31–34, 120–130.
- Eaton AE (1894) The Geographical Distribution of Psychodidæ. Entomologist's Monthly Magazine 30: 22–24.
- Eaton AE (1896) Supplement to the Synopsis of British Psychodidae. Entomologist's Monthly Magazine 32: 70–76, 127–131, 202–211.
- Eaton AE (1904) New genera of European Psychodidae. Entomologist's Monthly Magazine 15: 55–59.
- Enderlein G (1935) Zur Klassifikation der Psychodinen. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1935: 246–249.
- Enderlein G (1937) Klassifikation der Psychodiden (Dipt.). Deutsche Entomologische Zeitschrift 4: 81–112.
- El-Badry A, Salem HKh, Edmardash YA (2014) Human urinary myiasis due to larvae of *Clog-mia (Telmatoscopus) albipunctata* Williston (Diptera: Psychodidae) first report in Egypt. Journal of vector Borne Diseases 51: 247–249.
- Freeman P (1950) Handbooks for the identification of insects, Diptera 2. Royal Entomologycal Society of London 9: 77–96.
- Ibañez-Bernal S (2008) New records and descriptions of Mexican moth flies (Diptera: Psychodidae, Psychodinae). Transactions of the American Entomological Society 134: 87–131. doi: 10.3157/0002-8320(2008)134[87:NRADOM]2.0.CO;2
- Ježek J (1983) Contribution to the taxonomy of the genus *Logima* Eat. (Diptera, Psychodidae). Acta entomologica Musei Nationalis Pragae 41: 213–234.
- Ježek J (1985) Contribution to the knowledge of a new subtribe Trichopsychodina (Diptera, Psychodidae) from Czechoslovakia. Acta Musei Nationalis Pragae 40B(1984): 65–92.
- Ježek J (1987) Results of Czechoslovak-Iran Entomological Expeditions to Iran: Iranotelmatoscopus hajiabadi gen.n., sp.n. (Diptera, Psychodidae) Palaearctic region. Acta Entomologica Musei Nationalis Pragae 42: 5–9.
- Ježek J (1990a) Contribution to the taxonomy of some genera of Paramormiine moth flies (Diptera, Psychodidae) with description of a new genus *Karakovounimerus*. Acta Entomologica Musei Nationalis Pragae 43: 129–157.
- Ježek J (1990b) Redescriptions of nine common palaearctic and Holarctic species of Psychodini End. (Diptera: Psychodidae). Acta Entomologica Musei Nationalis Pragae 43: 33–83.
- Ježek J (1999) Rare and new Palaearctic *Tonnoiriella*-species (Diptera, Psychodidae) Časopis Národního Muzea, Řada přírodovědná 168: 7–18.
- Ježek J (2004) New Faunistic Data of non-phlebotomine moth Flies (Diptera, Psychodidae) from the Palaearctic region. Dipterologica Bohemoslovaca Vol. 11. Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Biologia 109: 141–151.
- Ježek J, Van Harten A (2005) Further new taxa and little-known species of non-biting moth flies (Diptera, Psychodidae) from Yemen. Acta Entomologica Musei Nationalis Pragae 45: 199–220.

- Jung HF (1956) Beiträge zur Biologie, Morphologie und Systematik der europäischen Psychodiden (Diptera). Deutsche Entomologische Zeitschrift 3: 97–257.
- Kvifte GM (2011) Biodiversity studies in Afrotropical moth flies (Diptera: Psychodidae). Master thesis in biology – Biodiversity, Evolution and Ecology. University of Bergen, 102 pp.
- Kvifte GM (2014) Nomenclature and taxonomy of *Telmatoscopus* Eaton and Seoda Enderlein; with a discussion of parameral evolution in Paramormiini and Pericomaini (Diptera: Psychodidae, Psychodinae). Zootaxa 3878(4): 390–400. doi: 10.11646/zootaxa.3878.4.5
- Kvifte GM, Håland Ø, Andersen T (2011) A revised checklist of Norwegian moth flies (Diptera, Psychodidae). Norwegian Journal of Entomology 58: 180–188.
- Nielson BO (1961) Studies on the Danish Psychodidae (Diptera Nematocera). Entomologiske Meddelelser 31: 127–152.
- Oboňa J, Ježek J (2012) Range Expansion of the Invasive Moth midge *Clogmia albipunctata* (Williston, 1893) in Slovakia (Diptera: Psychodidae). Folia faunistica Slovaca 17: 387–391.
- Omelková M, Ježek J (2012) Two new species of *Pneumia* Enderlein (Diptera, Psychodidae, Psychodinae) from the Palaearctic region. Zootaxa 3180: 1–18.
- Satchell GH (1953) New and little known samoan Psychodidae and a new species from Rarotonga. Proceeding of the Royal Entomological Society of London (B) 22: 181–188. doi: 10.1111/j.1365-3113.1953.tb00042.x
- Satchell GH (1955) New and little known Algerian and Canary Island Psychodidae. Annals of the Natal Museum 13: 101–120.
- Tonnoir A (1919) Contribution á l'étude des Psychodidae de Belgique. Note préliminaire. Annales de la Société Entomologique de Belgique 59: 8–17.
- Tonnoir A (1920) Notes sur quelques Psychodidae africains. Revue Zoologique Africaine 8: 127–147.
- Tonnoir A (1922) Contribution à l'étude des Psychodidae d'Afrique (Dipt.). Bulletin de la Société entomologique d'Égypte 81–112.
- Vaillant F (1954) Trois nouveaux Psychodinae (Diptères) d'Algérie. Bulletin de la Société d'Histoire Naturelle d'Afrique du Nord 45: 89–94.
- Vaillant F (1955) Recherche sur la faune Madicole de France, de Corse et d'Afrique du Nord. Mémoire du National d'histoire Naturelle Série A. Zoologie. Tome XI, fascicule unique 233–246.
- Vaillant F (1958) Quelques espèces de *Pericoma* du groupe *unispinosa* Tonnoir. Revue Francaise d'Entomologie 25: 99–110.
- Vaillant F (1960) Les Larves de quelques espèces de *Telmatoscopus* et de *Pericoma* de la zone paléarcitique (Diptera, Psychodidae). Travaux du Laboratoire d'Hydrobiologie et de Pisciculture de l'Université de Grenoble 48–49(1957): 71–108.
- Vaillant F (1971–1983) 9d. Psychodidae-Psychodinae (not finished). In: Lindner E (Ed.) Die Fliegen der palaearktischenRegion. Stuttgart. Vols. 287, (1971), 1–48; 291, (1972), 49–78; 292, (1972), 79–108; 305, (1974), 109–142; 310, (1975), 143–182; 313, (1977), 183–206; 317, (1978), 207–238; 320, (1979), 239–270; 326, (1981), 271–310; 328, (1983), 311–357.
- Vaillant F (1990) Propositions pour une révision de la classification des Diptères Psychodidae Psychodinae. Bulletin de la Société Vaudoise des Sciences Naturelles 80: 141–163.
- Vaillant F, Botosaneanu L (1966) Notes sur les Psychodides (Diptera) des grottes. Lucr Inst. Speol. "Emil Racovitā" 5: 91–98.

- Vaillant F, Withers P (1992) Panimerus goodi sp. n. from Ireland, with a description of other members of the maynei complex (Diptera: Psychodidae). Irish Naturalists' Journal 24: 27–28.
- Wagner R (1977) Zur kenntnis der Psychodiden fauna des Allgäus (Diptera, Nematocera). Nachrichtenblatt der Bayerischen Entomologen 26: 23–28.
- Wagner R (1987) Tunesische Psychodiden (Diptera, Psychodidae). Entomofauna 8: 9–25.
- Wagner R (1988) Psychodiden (Diptera) der Kanarischen Inseln. Stuttgarter Beiträge zur Naturkunde Serie A (Biologie) 425: 1–14.
- Wagner R (1990) Family Psychodidae. In: Soós Á, Papp L (Eds) Catalogue of Palaearctic Diptera. 2. Psychodidae-Chironomidae. Akadémiai Kiadó, Budapest, 499 pp.
- Wagner R (1997) Diptera Psychodidae, Moth Flies. In: Nilsson A (Ed.) The aquatic Insects of North Europe 2, Apollo Books Aps., Kirkeby Sand 19, DK-5771 Stenstrup, 133–144.
- Wagner R, Beuk PLTh (2002) Family Psychodidae. In: Beuk PLTh (Ed.) Checklist of the Diptera of the Netherlands. KNNV Uitgeverij, Utrecht, 85–88.
- Walker F (1856) Insecta Britannica. Diptera. III. London, 352 pp.
- Werner D (1997) Studies on some moth flies (Diptera: Psychodidae) with the first record of *Clogmia albipunctata* in central Europe. Entomological News 108: 273–282.
- Withers P (1989) Some further records of Irish rot-hole moth-flies (Diptera: Psychodidae), with a first record for *Telmatoscopus Rothschildii*, and a Figure of The Male Terminalia of that species. Irish Naturalists' Journal 23: 16–17.

RESEARCH ARTICLE



A new species of Chaetaglaea (Lepidoptera, Noctuidae, Noctuinae, Xylenini), from eastern North America

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Abstract

Chaetaglaea tremula (Harvey) occurs through the Gulf States, from southern Florida, west to eastern Texas. Coastal populations, previously referred to *Chaetaglaea tremula* occurring from the Carolinas, at least as far north as Massachusetts and shoreline dunes in southwestern Ontario are recognized as distinct and described here as *Chaetaglaea rhonda*. Adults and genitalia are illustrated for *Chaetaglaea rhonda* and *Chaetaglaea tremula*.

Keywords

Chaetaglaea tremula, Chaetaglaea rhonda, dunes, taxonomy

Introduction

Since the early 1990s, the senior author has been studying the Lepidoptera of Pinery Provincial Park and adjacent areas of Lambton County, Ontario. As a result of this work, many undescribed species and new species for Canada, were found. One such species is *Chaetaglaea rhonda* sp. n., which is associated with sand cherry (*Prunus pumila* L.) on Lake Huron's foreshore dunes in Lambton County. This species was first discovered in Lambton County, by Ken Stead and Dr. Kirk Zufelt in 1993 and remains the only site at which *C. rhonda* is known to occur in Canada. At the time of its discovery in Canada, it was identified as *C. tremula*; however, although specimens from Florida, Louisiana, and Mississippi submitted to BOLD for DNA analysis are *C. tremula* (TL "Texas"), those from Ontario, coastal North Carolina, and coastal Massachusetts represent an undescribed sister species to *C. tremula*. In order that a name be available for biodiversity inventories and conservation work, we describe this new species as *Chaetaglaea rhonda*.

Materials and methods

Procedures for the dissection and preparation of genitalia and terminology for genital structures and wing markings follow that of Lafontaine (2004). Molecular variation was assessed based on the 658 bp 'barcode' region of the first subunit of the cytochrome oxidase (*cox1*) gene (Hebert et al. 2003). DNA was extracted from one leg removed from a dried specimen, sent to and processed at the University of Guelph through the Barcode of Life Data systems (BOLD; www.lepbarcoding.org). DNA extraction, amplification and sequencing protocols for the Barcode of Life initiative are detailed in Hebert et al. (2003). Molecular sequence data were compared with phylograms constructed using the neighbour-joining method, and distance calculations were performed using the Kimura 2-parameter (K2P) distance model as implemented on the BOLD website.

Systematics

Chaetaglaea rhonda sp. n.

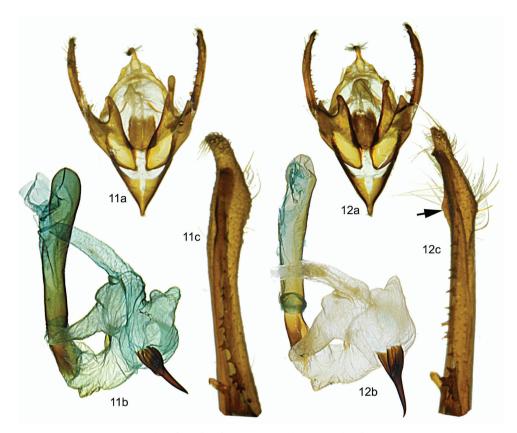
http://zoobank.org/4E3DF077-C472-476A-A6F3-863A8580448F Figs 1–3, 11, 13

Diagnosis. *Chaetaglaea rhonda* is closely related to *C. tremula* (Figs 4-10). There appears to be very little individual variation within populations of *C. rhonda*. At the type locality in Ontario, all specimens have a gunmetal gray forewing with concolourous subterminal band and dark gray-brown hindwing. However, significant variation is present between populations. In coastal North Carolina, specimens of C. rhonda are slightly larger (forewing length 21–22 mm vs. 18–19 mm) and the forewing is brick red with a slightly darker, browner hindwing (Fig. 3) than populations in Ontario. Among the reddish North Carolina specimens examined there appears to be little variation. *Chaetaglaea tremula* exhibits tremendous individual variation (Figs 4–10) with the forewing of *C. tremula* can be concolourous with the ground colour of the forewing or much paler. Due to this variation it is difficult to provide external characters that reliably separate the species; however, in *C. tremula*, the anal margin of the forewing normally has a pale beige line, bordered by a brick red fringe. In *C. rhonda*, the



Figures 1–10. Adults of *C. rhonda* and *C. tremula*. 1 *C. rhonda*, male, Port Franks, ON 2 *C. rhonda*, female, Port Franks, ON 3 *C. rhonda*, female, Carolina Beach State Park, NC 4–10 *C. tremula*, Ocala National Forest, FL.

ground colour of the forewing extends to the posterior margin, which is bordered by a distinct red fringe. Internally, in *C. tremula* the costal margin of the valve is produced dorsally to form a short, subapical pointed ridge (see Fig. 12c). In *C. rhonda* this sub-



Figures 11–12. Male gentalia of *C. rhonda* and *C. tremula.* **11** *C. rhonda*: **a** armature **b** aedeagus with vesica everted **c** tip of right valve **12** *C. tremula*: **a** armature **b** aedeagus with vesica everted **c** tip of right valve; arrow shows subapical ridge absent in *C. rhonda*.

apical ridge is absent. The dorsal processes of the sacculus are asymmetrical in both species, but are noticeably longer in *C. rhonda* (Fig. 11a) than *C. tremula* (Fig. 12a). The female genitalia of *C. rhonda* are roughly similar to those of *C. tremula*; however, the distal sclerotized section of the ductus bursae of *C. rhonda* (Fig. 13) is slightly longer and narrower than that of *C. tremula* (Fig. 14). DNA sequence data are congruent with the morphological data, showing that of the 658 COI base pairs examined, there is a 2.44% difference between *C. tremula* (Florida, Louisiana, and Mississippi) and *C. rhonda* (Ontario and North Carolina).

Description. Males and females similar. **Holotype.** Antennae filiform, ciliate; palpi red; head, vertex, prothoracic collar, thorax, and abdomen gray. Forewing length 19mm. **Dorsal forewing** glossy gunmetal gray (brick red in specimens from the Atlantic coast) with numerous black scales, costal and posterior margins red; darker gray antemedial and postmedial lines evenly concave from costa to vein CuA2, where both

lines turn slightly toward outer margin; subterminal line slightly lighter gray than ground colour, scalloped between veins below vein M3; between veins M3 and R5 line evenly convex, terminating closest to outer margin on vein R5 and then bending inward toward costa. Black scales occur along anterior margin of subterminal line forming a distinct black spot in cell M5; these black scales gradually fade between vein M5 and costa and below vein M1. Outer margin with a series of black dots between veins; orbicular and reniform spots poorly demarcated by thin gray lines; a black dot occurs in lower margin of reniform spot; fringe gray. Dorsal hindwing dark gray brown with concolourous fringe. Male genitalia. (Fig. 11) Uncus narrow, terminating in fine hook. Juxta more-or-less rectangular with concave dorsal margin. Sacculus with ventral triangular process and elongate, finger-like dorsal process, left process much longer than right. Valve excavated above sacculus, leaving elongate, narrow arm terminating in setose, bubble-like, membranous cucullus. Heavily sclerotized costal margin with row of medial teeth terminates in short, subapical claw. Ampulla of clasper finger-like, extends dorsally above costa of valve. Vesica bends ventrally to the right with small sclerite on dorso-anterior margin of bend and large, posterior, bulbous, thorn-like cornutus. Two small sub-basal diverticulae on right extend to anterior and posterior; apical diverticulum terminates in ductus seminalis, above which a globular subapical diverticulum on right splits into elongate dorsal and posterior arms; a bulbous diverticulum occurs on left and a short, bi-lobed diverticulum arises from ventral surface. Female genitalia. (Fig. 13) Ovipositor lobes pointed with scattered setae; sclerotized plates occur on ventral and dorsal surfaces of ductus bursae between ostium bursae and a 0.5mm unsclerotized section, after which a second pair of sclerotized plates occur anterior to appendix bursae; appendix bursae with a thickened, almost leathery wall, the surface of which is very lightly sclerotized on the ventral side; ductus seminalis arises on ventral surface of appendix bursae at corpus bursae; corpus bursae egg shaped with prominent ridges and four elongate signa.

Type material. Holotype male: Canada: Ontario, Port Franks, [Lambton County], 43.226 N 81.923 W, 17 ix 2015, J. Troubridge and K. Stead, in the Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Canada. **Paratypes:** 13 males, 11 females: same data as holotype.

Etymology. We take pleasure in naming this species to honour Rhonda Landry, who gave support and encouragement to the authors by providing us with good food, coffee and conversation. It is a noun in apposition.

Distribution. In Canada, this species is presently known only from dunes along the shore of Lake Huron in Lambton County, Ontario. In the United States, we have examined specimens from Carolina Beach State Park, New Hanover County, North Carolina. Additional specimens of *C. rhonda* have been submitted to BOLD for DNA analysis from the Frances A. Crane Wildlife Management Area, Barnstable County, Massachusetts, and Pine Knoll Shores, Carteret County, North Carolina. Each of these US sites are close to the Atlantic beaches and we expect that *C. rhonda* occurs in suitable habitats up and down the Atlantic seaboard.



Figures 13–14. Female gentalia of C. rhonda and C. tremula. 13 C. rhonda 14 C. tremula.

Acknowledgements

We thank Jeremy deWaard (Barcode of Life Initiative) for DNA analysis. We also thank Don Lafontaine, and Chris Schmidt, for their help and advice.

References

- Hebert PDN, Cywinska A, Balland SL, deWaard JR (2003) Biological identifications through DNA barcodes. Proceedings of the Royal Society B 270: 313–321. doi: 10.1098/ rspb.2002.2218
- Lafontaine JD (2004) Noctuoidea, Noctuidae (part): Noctuinae, Agrotini. The Moths of America North of Mexico, fasc. 25.1, The Wedge Entomological Research Foundation, Washington, DC, 385 pp.

RESEARCH ARTICLE



On the spider genus Arboricaria with the description of a new species (Araneae, Gnaphosidae)

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Abstract

The spider genus *Arboricaria* Bosmans, 2000 is redefined and an updated diagnosis given. The differences between *Arboricaria* and *Micaria* Westring, 1851 are discussed in detail. A key to all five species of the genus is provided. One new species, *Arboricaria zonsteini* **sp. n.** (\mathcal{O} Q), is described based on specimens from Kyrgyzstan and Azerbaijan. One new synonym is proposed: *A. koeni* Bosmans in Bosmans & Blick, 2000, **syn. n.** is assigned to *A. sociabilis* Kulczyński in Chyzer & Kulczyński, 1897. Data on the distribution of *Arboricaria* in Russia and adjacent countries are presented with references to the papers on local spider faunas.

Keywords

Spiders, Gnaphosidae, new species, taxonomy, Caucasus, Middle Asia

Introduction

Arboricaria was established by Bosmans and Blick (2000) to accommodate the Micaria subopaca species group as outlined by Wunderlich (1980: 249). Five species were included, three of which had been known earlier, A. cyrnea (Brignoli, 1983) (the type species), A. subopaca (Westring, 1861) and A. sociabilis Kulczyński in Chyzer & Kulczyński, 1897, and two further described as new: *A. koeni* Bosmans in Bosmans & Blick, 2000 and *A. brignolii* Bosmans & Blick, 2000.

Platnick (2014, latest version), in his World Spider Catalog, does not accept this genus, because the authors provided "no evidence whatever that these taxa constitute the sister group of all other *Micaria*, or that the remaining *Micaria* do not constitute a paraphyletic group from which a relatively autapomorphic subgroup has been artificially extracted, those changes are not followed here". The same concerns the current World Spider Catalogue (WSC 2015). *Arboricaria* is absent from the latest world gnaphosid revision as well (Murphy 2007), albeit it has never been synonymized with *Micaria*.

When preparing a review of the *Micaria* fauna of the former Soviet Union (Mikhailov 1987), I came across a specimen from Kyrgyzstan, Central Asia which showed a bifid male tibial apophysis and apparently represented a new species. Because its generic assignment seemed obscure at that time, this specimen was excluded from my 1987 paper. However, additional material has since become available from Azerbaijan, Caucasus.

The present contribution not only provides a description of that new species, but it also aims at clarifying the distinctions between two similar genera, *Micaria* Westring, 1851 and *Arboricaria* Bosmans, 2000, so as to provide a brief review of and a key to the known species of the latter genus. In addition to Mikhailov's (1987) faunistic review, data on the distribution of *Arboricaria* species in Russia and adjacent countries are provided. Since most of the species included in *Arboricaria* are well-known and properly described, e.g. by Wunderlich (1980) within *Micaria* and/or by Bosmans and Blick (2000) in *Arboricaria*, this paper requires no redescriptions to be made and can be reduced to a key, with only short remarks given for most of species.

Material and methods

Material of three species was examined in detail: *A. subopaca*, *A. sociabilis* and *A. zon-steini* sp. n. Specimens were examined using MBS-9 and Olympus stereo microscopes. All initial pencil sketches drawn on scale paper were subsequently inked and then digitized with Cintiq.

The following abbreviations are used below: ap – apically, Cb – cymbium, d – dorsally, F – femur, Mt – metatarsus, pl – prolaterally, Pt – patella, T – tarsus, Ti – tibia, IRSNB – Institut Royal des Sciences Naturelles de Belgique, Bruxelles, ZMMU – Zoological Museum, Moscow State University, Russia. All measurements are given in mm.

Only basic and necessary synonymies are given in the species reviews below, as a more detailed list is available in WSC (2015).

Data on the distribution of *Arboricaria* species in Russia and Azerbaijan are mostly previously unpublished (my unpublished card Catalogue of the Spiders of Russia and Adjacent Territories; see also Mikhailov 2012, 2013). Only well-figured descriptions and redescriptions as well as main synonyms are listed here.

Taxonomy

Arboricaria Bosmans, 2000

Bosmans, in Bosmans and Blick 2000: 460–461. Tuneva 2007: 250.

Type species. Micaria cyrnea Brignoli, 1983.

Composition. *Arboricaria* includes five known species listed above and one new species described below.

Despite not being followed on the world spider catalogues (see above), the original description of *Arboricaria* and its diagnosis both fully fit the provisions of the International Code of Zoological Nomenclature, especially Articles 13.1 and 67.4 (ICZN 1999), i.e., diagnostic characters are sufficient for recognizing the new genus, as well as the type species is properly indicated. So there are no formal grounds to reject the validity of *Arboricaria*.

According to the original diagnosis, the new genus "is very close to *Micaria* and differs by the more flattened, wider cephalothorax, the less spinate legs and the posteriorly truncate sternum. Males differ by the large tibial apophysis, bifid or curved, the bulging bulbus and the absence of the median apophysis (= Retinaculum in Wunderlich 1980), females by the large epigyneal fossa [= groove] with distinctly chitinized posterior margin". In addition, the *Micaria subopaca*-group is characterized by 0-2 distal-ventral spines on the cymbium, as well as the absence of ventral spines on tibiae and metatarsi I–II (Wunderlich 1980: 249).

Not all of the characters are equally important.

- 1. The width of the carapace is variable within the remaining *Micaria* (cf. Table 1 herein with table 1 in Wunderlich 1980). In *Micaria* sensu stricto, the carapace length/width index is 1.2–2.0.
- 2. The same concerns the size of the tibial apophysis (for large ones in *Micaria*, see figs 29a, 31a, in Wunderlich 1980), not bifid in *Micaria*, as well as in *Arboricaria subopaca*.

Species/Sex	Index	Source	
Arboricaria zonsteini sp. n., 👌	1.29-1.31	Present paper	
<i>Arboricaria zonsteini</i> sp. n., ♀	1.4	Present paper	
A. brignolii Bosmans & Blick, 2000, 👌	1.32-1.33	Bosmans and Blick 2000	
A. brignolii Bosmans & Blick, 2000, ♀	1.35, 1.46	Bosmans and Blick 2000	
A. koeni Bosmans in Bosmans & Blick, 2000, \circlearrowleft	1.33-1.37	Bosmans and Blick 2000	
<i>A. koeni</i> Bosmans in Bosmans & Blick, 2000, \bigcirc	1.42	Bosmans and Blick 2000	
A. cyrnea (Brignoli, 1983), 👌	1.35-1.36	Bosmans and Blick 2000	
A. cyrnea (Brignoli, 1983), 4	1.47	Bosmans and Blick 2000	
<i>A. subopaca</i> (Westring, 1861), ∂,♀	1.25-1.35	Wunderlich 1980	

Table 1. Carapace length/width index in Arboricaria species.

- A median apophysis is absent or almost absent in *Micaria rossica* Thorell, 1875, wholly absent both in *M. utahna* Gertsch, 1933 and *M. medica* Platnick & Shadab, 1988.
- 4. An analysis of leg spination (see table 1 in Wunderlich 1980: 250–251) shows that *Arboricaria* species fall within the range of *Micaria* variability, yet close to its marginal part.
- 5. The shape of the posterior part of the sternum is clearly different in *Micaria* and *Arboricaria* (see Figs 1–5).

Therefore, the above diagnosis of *Arboricaria* must be adjusted. This genus is indeed close to *Micaria*, but differs in the following characters that together allow recognizing the genus: a posteriorly truncate sternum in both sexes, a bulging bulbus and a missing median apophysis, a chiefly bifid tibial apophysis, a large epigynal groove with distinctly chitinized posterior margins in females. At least, the shape of bulbus and bifid apophysis can be regarded as apomorphic characters. All these characters constitute *Arboricaria* as a monophyletic and sister-group to other *Micaria*. An extended description of *Arboricaria* is available in Bosmans and Blick (2000).

The distribution pattern of *Arboricaria* is mostly Mediterranean and on the mountain regions of central Asia, although *A. subopaca* extends to most of the Palearctic.

Micaria Westring, 1851

Remarks. Type species. *Micaria fulgens* (Walckenaer, 1802), originally described as *Aranea fulgens*.

Diagnosis. Gnaphosids of the "*Micaria*-group" (Murphy 2007), differing from *Arboricaria* by the more or less ovoid, posteriorly not truncate sternum in both sexes, the ovoid, not bulging bulbus with a mostly present median apophysis, the palpal tibial apophysis, sometimes poorly expressed, not bifid in males, the epigynal groove in females, if present, without distinctly chitinized posterior margins.

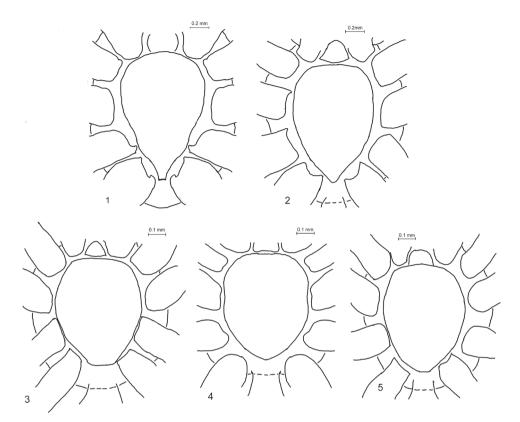
Composition. 101 species (WSC 2015).

Distribution. Holarctic. Other records require confirmation.

An analysis of the new *Micaria* species described from the Palaearctic since Bosmans and Blick (2000), all listed in WSC (2015), shows no match with *Arboricaria* characters. Therefore, despite the previous neglect of *Arboricaria*, no new species of this genus have been described within *Micaria sensu lato* since 2000. In addition, all extra-Holarctic records of *Micaria* are doubtful; these species most likely belonging to other genera or even families (Murphy 2007).

Key to Arboricaria species

1	Males	2
_	Females	6



Figures 1–5. Sternum in *Micaria* and *Arboricaria*. 1 *M. formicaria*, male 2 *M. fulgens*, female 3 *A. subopaca*, female 4 *A. zonsteini* sp. n., male 5 *A. zonsteini* sp. n., female.

2	Tibial apophysis not bifurcate (see fig. 35b in Wunderlich 1980); complex of
	other male diagnostic characters of Arboricaria present
_	Tibial apophysis bifurcate
3	Branches of tibial apophysis of equal or subequal length4
_	Branches of tibial apophysis different in length
4	Embolus wide and large, rising over bulbus (Figs 17-20)A. sociabilis
_	Embolus thin, lying directly on apical surface of bulbus (Fig. 6)
5	Inner branch of tibial apophysis ca 3 times longer than outer branch; maxi-
	mum width of embolus closer to 1/4 of bulbus width (see figs 24 & 25 in
	Bosmans and Blick 2000)
_	Inner branch of tibial apophysis ca 2 times as long as outer branch; maximum
	width of embolus closer to 1/2 of bulbus width (see figs 28 & 29 in Bosmans
	and Blick 2000)
6	Lateral edges of epigynal groove divergent (see fig. 59 in Wunderlich 1980).
_	Lateral edges of epigynal groove parallel or convergent

7	Lateral edges of epigynal groove parallel (see fig. 30 in Bosmans and Blick
	2000)
_	Lateral edges of epigynal groove convergent
8	Spermathecae shorter than epigynal groove; spermathecae not reaching the
	latter's fore edge (Figs 10–11) A. zonsteini sp. n.
_	Spermathecae long, reaching fore edge of epigynal groove or even exceeding it 9
9	Hind edge of epigynal groove straight (see fig. 26 in Bosmans and Blick
	2000)
_	Hind edge of epigynal groove protruding backwards (see fig. 60a in Wunder-
	lich 1980 and fig. 34 in Bosmans and Blick 2000; fig. 60b-c in Wunderlich
	1980 refers to A. brignolii, see below)A. sociabilis

Description

Arboricaria zonsteini sp. n.

http://zoobank.org/D362E1C2-E41A-4AAF-AECA-C4F3FAFC6CA0 Figs 5–11

Material. Holotype \Diamond (ZMMU Ta-7739), Kyrghyzstan, env. of Frunze (now Bishkek), ca 42°52-54'N, 74°33-40'E, 30.03.1983 (S.L. Zonstein & S.V. Ovtchinnikov). Paratypes, Azerbaijan, Apsheron Peninsula: 1 \Diamond (ZMMU Ta-7740), Baku City, environs of Lake Ganly-Gyol, ca 40°22'N, 49°48'E, shrub branch, 21.05.1996 (E. Huseynov); 1 \heartsuit (ZMMU Ta-7741), Baku City, Botanical Garden, 40°21'20"N, 49°49'46"E, pine trunk, 13.06.1996 (E. Huseynov); 1 \heartsuit (ZMMU Ta-7742), Mardakyany, 40°29'32"N, 50°08'20"E, stone wall, 1.06.1996 (E. Huseynov).

Name. Honours Sergei L. Zonstein, arachnologist, now living in Israel, earlier in Kirghizia (= Kyrgyzstan).

Diagnosis. The new species differs by a combination of the following characters: Males: equally long branches of tibial apophysis with thin embolus lying on apical surface of bulbus; Females: convergent edges of epigynal groove with moderately long spermathecae, the latter being shorter than the groove, the former not reaching the fore edge of the latter.

Description. Male (holotype; measurements of paratype in brackets). Carapace length 1.20(1.05), width 0.93(0.80), ratio 1.29(1.31). Carapace and leg femora reddish brown, in holotype carapace darker, other podomeres, especially metatarsi and tarsi, straw-coloured.

For leg measurements, see Table 2.

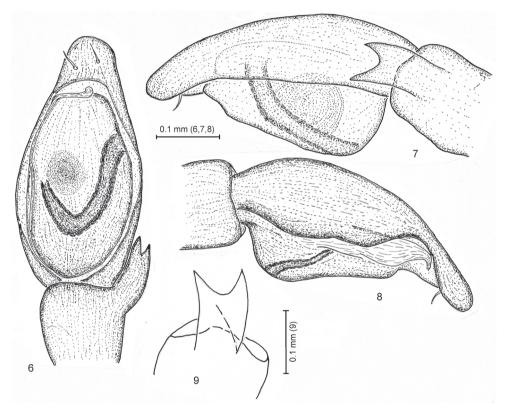
Leg spination: F I d 1, pl 1, F II–IV d 1, Ti III–IV pl 1(ap), Mt III v 2(1.2, 2.2), Mt IV v 1.1.1.2 (1.1.2).

Abdomen length 1.63(1.60), width 0.93(0.93), ratio 1.76(1.72), dark brown, with transverse band of white bristles, broken in the middle.

Palpus as in Figs 6–9. Length of palpomeres (holotype): F 0.37, Pt 0.21, Ti 0.16, Cb 0.50. Cymbium longer than femur, rounded in apical part, with 2 ventral-dis-

Leg/Article	F	Pt	Ti	Mt	Т
Ι	0.79(0.75)	0.46(0.40)	0.69(0.58)	0.57(0.45)	0.50(0.40)
II	0.79(0.73)	0.41(0.40)	0.63(0.55)	0.56(0.45)	0.51(0.40)
III	0.64(0.60)	0.36(0.30)	0.49(0.40)	0.53(0.40)	0.37(0.30)
IV	0.81(0.78)	0.43(0.38)	0.79(0.65)	0.79(0.58)	0.43(0.40)
Total	3.03(2.86)	1.66(1.48)	2.60(2.18)	2.45(1.88)	1.81(1.50)

Table 2. Leg measurements of male Arboricaria zonsteini sp. n.



Figures 6–9. *Arboricaria zonsteini* sp. n., right male palp. **6** ventral view **7** retrolateral view **8** prolateral view **9** tibial apophysis, schematically.

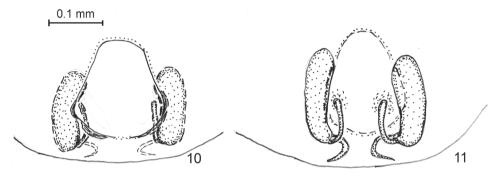
tal spines. Tibial apophysis long, reaching ca ½ of tibia length, wide, with parallel margins, bifid, with acute apices. Cymbium apical part shorter than tibial apophysis. Tegulum oval in plane, without conical apophyses. Embolus poorly chitinized, lying directly on apical surface of tegulum. Subtegulum not visible.

Female. Carapace length 1.05, 1.05, width 0.75, 0.75, ratio 1.4, 1.4. Body coloration as in male, but carapace being pale reddish brown. For leg measurements, see Table 3 (in all female measurements, the first one is for the paratype from Mardakyan, the second for that from the Botanical Garden).

Leg spination: F I d 1, pl 1, F II–IV d 1, Ti III–IV pl 1(ap), Mt III–IV v 1.2.

Leg/Article	F	Pt	Ti	Mt	Т
Ι	0.63, 0.70	0.35, 0.38	0.48, 0.55	0.40, 0.45	0.38, 0.43
II	0.60, 0.68	0.30, 0.38	0.48, 0.55	0.40, 0.45	0.38, 0.38
III	0.53, 0.58	0.30, 0.28	0.38, 0.43	0.38, 0.43	0.30, 0.40
IV	0.75, 0.75	0.33, 0.35	0.65, 0.68	0.60, 0.68	0.38, 0.40
Total	2.51, 2.71	1.28, 1.39	1.99, 2.21	1.78, 2.01	1.44, 1.61

Table 3. Leg measurements of female Arboricaria zonsteini sp. n.



Figures 10-11. Arboricaria zonsteini sp. n., female copulatory organs. 10 epigyne 11 vulva.

Abdomen length 1.55, 1.88, width 0.78, 1.00, ratio 1.88, 1.99.

Epigyne and vulva as in Figs 10–11. Epigynal groove subpyriform, as long as wide, with slightly convex edges; distance between its posterior edge and epigastric furrow being ¼ of groove length. Copulatory openings small (like in most *Arboricaria* and *Micaria*), lying at lateral edges of groove in its posterior one-third. Copulatory tubes thin, almost vertical and parallel to each other, about half the length of spermathecae. Spermathecae oblong-oval, parallel to each other, being 2/3–3/4 as long as epigynal groove.

Distribution. Northern Kyrgyzstan and Apsheron Peninsula (Azerbaijan).

Arboricaria cyrnea (Brignoli, 1983)

Micaria canestrinii: Wunderlich 1980: 292–293, figs 37a–d (♂). *Micaria cyrnea* Brignoli, 1983: 564 (*nomen novum*). *Arboricaria cyrnea*: Bosman and Blick 2000: 461–463, figs 24–31 (♂♀). Note. This is the type species of the genus.

Distribution (after Bosmans and Blick 2000). Greece: north Aegean Islands; Italy (continental); France: Corsica. The records from Russia are erroneous (see below under *A. sociabilis*).

Remark. The new name was proposed by Brignoli (1983) for *Micaria canestrinii* Roewer, 1951 as misidentified by Wunderlich (1980).

Arboricaria subopaca (Westring, 1861)

Fig. 3

Micaria subopaca Westring, 1861: 336.
= Micaria albostriata L. Koch, 1877.
= Micaria humilis Kulczyński, 1885.
Micaria subopaca: Wunderlich 1980: 290–291, figs 35a–e, 59 (♂♀).

Material. 1 \Diamond , 1 \bigcirc (ZMMU Ta-2119), Russia, Moscow Area, environs of Bolshevo, 55°56'N, 37°51'E, under pine bark, 28.02.1926 (leg. et det. V.I. Pereleshina); 1 \bigcirc (ZMMU), Belarus, Minsk Area, Myadel Distr., Lake Naroch, ca 54°49-53'N, 26°40-50'E, song thrush nest, 11.07.1967 (leg. A.S. Gembitsky, det. E.M. Zhukovets); 1 \bigcirc (ZMMU), Belarus, Minsk Area, Soligorsk Distr., Velichkovichi, ca 52°37'N, 27°14-15'E, 12.05.1982 (leg. Yu.M. Zhukovets, det. K.G. Mikhailov).

Distribution. All Europe north to Norway. Russia east to Urals, with scattered records in Transbaikalia and Kamchatka.

Russia and adjacent countries (all as Micaria, exceptions are marked).

Russia. Karelia (Palmgren 1943). Leningrad Area (Charitonov 1928, as M. albostriata; Oliger 2010). Moscow Area (Pereleshina 1928, as M. albostriata; Mikhailov 1987). Ryazan Area (Mikhailov 1987). Kaluga Area (Esyunin et al. 1993). Lipetsk Area (Panteleeva 1982, as M. albostriata). Voronezh Area (Panteleeva 2007). Belgorod Area (Kulczyński 1913, as M. albostriata; Ponomarev and Polchaninova 2006, as Arboricaria). Ulyanovsk Area (Kuzmin and Alekseenko 2011). Samara Area (Krasnobaev and Ovtsharenko 1986; Krasnobaev and Matveev 1993; Krasnobaev 2004, 2007). Volgograd Area (Ponomarev and Khnykin 2013, as Arboricaria). Rostov Area (Ponomarev et al. 2006; Ponomarev and Lebedeva 2014, both as Arboricaria). Komi Republic: Pechoro-Ilychskiy Nature Reserve (Kazantsev 2013, as Arboricaria). Sverdlovsk Area (Tuneva 2007, as Arboricaria). Perm Area (Esyunin and Efimik 1995; Tuneva 2007, as Arboricaria). Chelyabinsk Area (Esyunin and Efimik 1996; Tuneva 2007, as Arboricaria). SE part of West Siberia (Romanenko 2007). Altai Province (Azarkina and Trilikauskas 2013). Krasnoyarsk Province: Stolby Nature Reserve (Tuneva 2007, as Arboricaria). Buryatia (Danilov 1993, 2008). Kamchatka (Kulczyński 1885, as M. humilis; 1926, as M. albostriata).

Estonia (Vilbaste 1987).

Lithuania (Pupiska 1939, as *M. albostriata*; Vilkas 1992; Biteniekytė and Rėlys 2011). Latvia (Šternbergs 1981, as *M. albostriata*).

Belarus: Minsk Area (Gembitsky et al. 1985).

Ukraine. Chernovtsy Area (Fedoriak and Rudenko 2007). Chernigov Area (Evtushenko 1992). Lugansk Area (Polchaninova and Prokopenko 2013). Donetsk Area (Polchaninova and Prokopenko 2008). Kherson Area (Talanov and Nazarenko 1989) [doubtful data; confirmation needed (Polchaninova and Prokopenko 2013)].

Moldova (Roșca 1941, as M. albostriata).

Arboricaria sociabilis Kulczyński, 1897

Figs 12-20

- *Micaria sociabilis* Kulczyński in Chyzer & Kulczyński, 1897: 254 & 255 (key), 258–259, Tab.X., figs 21 (♀) 25a–b (♂).
- *M. canestrinii* Roewer, 1951: 447 (replacement name for *M. aurata* Canestrini, 1868, praeocc.).
- *M. sociabilis*: Wunderlich 1980: 291–292, figs 36a–b (♂, doubtful, see note in the text below, incorrect drawings), 60a (♀).

Arboricaria koeni Bosmans in Bosmans & Blick, 2000: 465, figs 32–35 ($\Im Q$), **syn. n.** *Micaria sociabilis*: Pfliegler 2014: 145 (record), figs 3e, 4c ($\Im Q$).

Micaria sociabilis: Sentenská et al. 2015: figs 4, 6 (\mathcal{F}_{φ}).

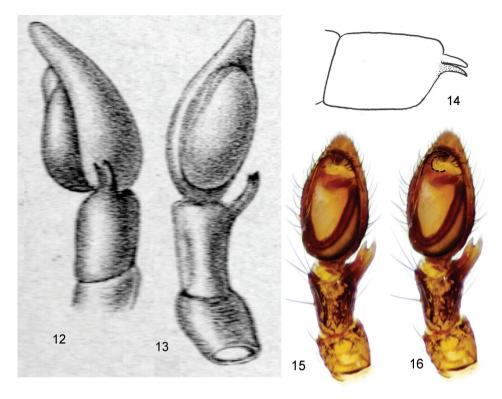
Not *M. sociabilis*: Wunderlich 1980: figs 60b–c (\mathcal{Q} , = *A. brignolii*, see below).

Material. 1 ♂ (IRSNB, holotype of *A. koeni*), Greece, Kreta, Chania, [in bark], 22.V.1994 (leg. Koen van Keer); 1 ♂ (IRSNB, paratype of *A. koeni*, left palp missing), Kreta, Chania, 22-5-1994; 1 ♂ (ZMMU; left palp and leg I only), Russia, Rostov-on-Don, 47°13'33"N, 39°41'59"E, window of living flat, 8.06.1978 (leg. et det. A.V. Ponomarev).

Taxonomic remarks. Originally, the male was matched with the female with some doubts (Chyzer and Kulczyński 1897), because they were taken from different, but not extremely distant localities of the former Austro-Hungarian Empire. Syntypes $(1 \ 3, 1 \ 9,$ "Ungarn" = "Hungary") are listed by Wunderlich (1980), but he only redescribed the female. Comparing the epigynes of *A. sociabilis* and *A. koeni* shows no essential difference between them; therefore, these names are to be synonymized. The position of the copulatory openings is a little variable; in the type of *A. sociabilis*, they are closer to the middle part of the epigynal groove, in the *A. koeni* type and the *A. sociabilis* material as depicted by Pfliegler (2014) closer to the posterior one-third.

A male syntype of *Micaria sociabilis* from Mukachevo is currently kept in the Zoological Museum in Warsaw, Poland, but both palps are missing (W. Wawer, pers. comm.). The tibial apophysis as redrawn by Wunderlich (1980: Fig. 36a, see also Fig. 14) from the original description (Chyzer and Kulczyński 1897: tab. X, fig. 25b, see also Fig. 12) is certainly incorrect. No deep bifurcation is visible in the original figure. Miller (1971) in his key to Czechoslovak spiders, pointed out: "Tibial apophysis apically [sic! – KM] forked with 2 teeth, lower tooth narrower and more pointed; it is laterally slightly bent, ventrally rounded outside and bent forward and it has the same width" (translated from Czech by A. Šestaková). Miller's specimen of *M. sociabilis* was never depicted and is currently missing among the other *Micaria* samples kept in the National Museum in Prague, Czech Republic (Kůrka 1994).

The picture of the *M. sociabilis* male palp as presented by Pfliegler (2014) certainly indicates the identity of this species with *Arboricaria koeni* (male types examined, see above in Material) and additionally confirms the synonymy of these names. To be ex-

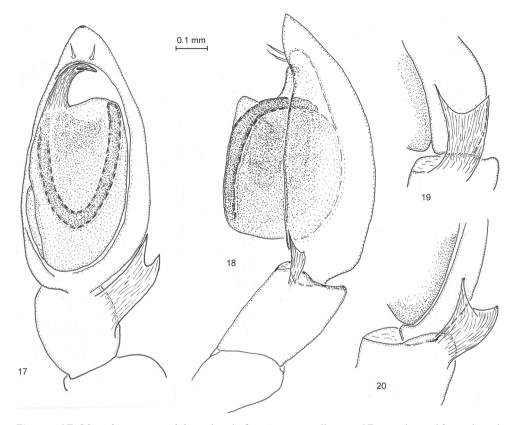


Figures 12–16. *Arboricaria sociabilis*, male palp, from different sources. **12**, **13** original drawings by Chyzer and Kulczynski (1897) **14** "improved" drawing by Wunderlich (1980) **15** original photo from Pfliegler (2014) paper **16** same photo with traced embolus. No scale. 12, 13, no copyright, 14, with permission of Joerg Wunderlich, 15, courtesy of W. Pfliegler (Debrecen, Hungary).

act, not enough details are visible in the publication, but a correct shape of the embolus is shown in the original photograph kindly sent to me by the author (cf. Figs 15 and 16 with traced embolus).

Characteristically, a male specimen from Rostov-on-Don was initially identified by A.V. Ponomarev as *Micaria sociabilis*, only later re-labeled as *Arboricaria koeni*.

Distribution. Ukraine: Transcarpathia: Mukachevo (= Munkácz in Chyzer & Kulczyński [1897]). NE-Hungary (two other localities from the original description; Debrecen [Pfliegler 2014]); Spain, continental France, together with Corsica, Italy, Croatia, Macedonia, continental Greece, together with Crete, Bulgaria, Romania, Czech Republic, Slovakia (Helsdingen 2014, for *M. sociabilis* and *M. koeni*). Russia: Rostov Area (Ponomarev and Tsvetkov 2006a, as *A. cyrnea*; Ponomarev 2008; Ponomarev and Dvadnenko 2013), Krasnodar Province: Kushchevskaya (Ponomarev and Tsvetkov 2006b, as *A. brignolii*; Ponomarev 2008). Azerbaijan (Caucasus Major: Huseynov, Alieva, 2010, as *A. koeni*, Apsheron Peninsula: Huseynov 2002, as *A. koeni*), all for *M.* (or *Arboricaria*) *koeni*. The records of *A. cyrnea* from the Rostov Area,



Figures 17–20. *Arboricaria sociabilis*, male palp from ZMMU collection. **17** ventral view **18** retrolateral view **19**, **20** tibial apophysis, different projections.

as well as those of *A. brignolii* from the Rostov Area and Krasnodar Province belong to *A. sociabilis* (A.V. Ponomarev, pers. comm., as *A. koeni*). **Biology** See Sontenglé and Balér (2013). Sontenglé et al. (2015)

Biology. See Sentenská and Pekár (2013), Sentenská et al. (2015).

Arboricaria brignolii Bosmans & Blick, 2000

Micaria ? sociabilis: Wunderlich, 1980: Fig. 60b, c. *Arboricaria brignolii* Bosmans & Blick, 2000: 463–465, figs 28–31 ($\stackrel{\circ}{\land} \bigcirc$).

Distribution (after Bosmans and Blick 2000). Portugal, France: Dept. Var: Le Lavandon (new). Records from Russia are erroneous (see above, under *A. sociabilis*).

Remark. As it was already pointed out by Bosmans and Blick (2000), with some doubts, the record of *M. sociabilis* from France by Wunderlich (1980: 291) is referred to *Arboricaria brignolii*. I support this reference.

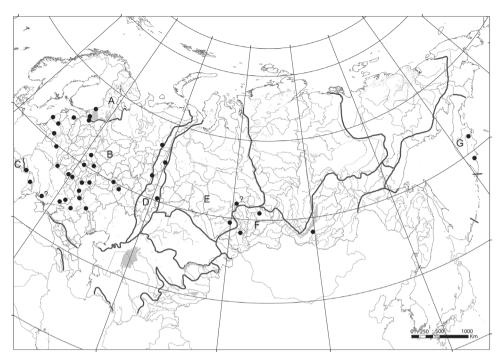


Figure 21. Localities of *Arboricaria subopaca* in Russia and other post-Soviet republics. Main physiographical areas accepted in Mikhailov (1997, 2013) are indicated: **A** Fennoscandia **B** Russian Plain **C** Carpathians **D** Urals **E** West Siberia **F** mountains of South Siberia **G** Kamchatka.

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References

Azarkina GN, Trilikauskas LA (2013) Spider fauna (Aranei) of the Russian Altai, part II: families Gnaphosidae, Hahniidae, Linyphiidae, Liocranidae and Lycosidae. Euroasian Entomological Journal 12(1): 51–67.

- Biteniekytė M, Rėlys V (2011) The checklist of Lithuanian spiders (Arachnida: Araneae). Biologija 57(4): 148–158. doi: 10.6001/biologija.v57i4.1926
- Bosmans R, Blick T (2000) Contribution to the knowledge of the genus *Micaria* in the west-palaearctic region, with description of the new genus *Arboricaria* and three new species (Araneae Gnaphosidae). Memorie delle Società Entomologica Italiana 78 (for 1999) (2): 443–476.
- Brignoli PM (1983) Ragni d'Italia XXXIV. Le specie descritte da G. Canestrini (Araneae). In: Atti XIII Congresso Nazionale Italiano di Entomologia. Sestriere-Torino, 561–567.
- Charitonov DE (1928) Materials to the fauna of Araneina of the Leningrad Gouvernement. Izvestiya Biologicheskogo nauchno-issledovatelskogo instituta pri Permskom universitete 6(1): 1–8. [In Russian, with German summary]
- Chyzer C, Kulczynski W (1897) Araneae Hungariae. Editio Academiae Scientiarum Hungariae, Budapest. T.2. Pars 2. Zodarioidae, Agelenoidae, Drassoidae, Zoropseoidae, Dysderoidae, Filistatoidae, Calommatoidae, Theraphosoidae. [I]–[II], 147–366, Tab.VI–X.
- Danilov SN (1993) Spiders of the genus *Micaria* (Araneae, Gnaphosidae) from Siberia. Annalen des Naturhistorischen Museum in Wien 94/95B: 427–431.
- Danilov SN (2008) Catalogue of spiders (Arachnida, Aranei) of Transbaikalia. Buryatskiy Nauchnyi Tsentr Sibirskogo otdeleniya, RAN Publ., Ulan-Ude, 108 pp. [In Russian]
- Esyunin SL, Efimik VE (1995) Remarks on the Ural spider fauna, 4. New records of spider species (excluding Linyphiidae) from the Urals (Arachnida Aranei). Arthropoda Selecta 4(1): 71–91.
- Esyunin SL, Efimik VE (1996) Catalogue of the spiders (Arachnida, Aranei) of the Urals. KMK Sci. Press Ltd., Moscow, 229 pp.
- Esyunin SL, Golovatch SI, Penev LD (1993) The fauna and zoogeography of spiders inhabiting oak forests of the East European Plain (Arachnida: Araneae). Berichte der naturwissenschaftliche-medizinische. Verein, Innsbruck 80: 175–249.
- Evtushenko KV (1992) Ecofaunistical studies of spiders of the Chernigovskoe Polesye. In: Fauna i ekologiya paukov, skorpionov i lozhnoskorpionov SSSR. Trudy Zoologicheskogo Instituta AN SSSR, Leningrad, 226 (for 1990): 113–115. [In Russian]
- Fedoryak MM, Rudenko SS (2007) Communities of spiders (Aranei) of Chernivtsi City Horse Chestnuts. In: Materials of III All-Polish Young Science Conference "Young scientists – to agricultural practice" (24-26 April 2007, University of Rzeszow). Rzeszowski Universytet, Rzeszow, 119–123.
- Gembitsky AS, Efremova GA, Zhukovets EM (1985) Spiders (Aranei) from the bird nests in Byelorussia. Vestsi AN ByalSSR. Ser. Biyal. nauk (1): 81–87. [In Byelorussian, with Russian and English summaries]
- Helsdingen PJ, van (2014) Araneae. Fauna Europaea. http://www.european-arachnology.org/ reports/fauna.shtml [accessed 29.05.2015]
- Huseynov EF (2002) Spider (Arachnida: Araneae) species new to the fauna of the Caucasus. In: Chetvertaya Mezhdunarodnaya konferentsiya "Biologicheskoe raznoobrazie Kavkaza", posvyashchennaya 60-letiyu so dnya rozhdeniya prof. Abdurakhmanova G.M. Makhachkala, 291–293. [In Russian]
- Huseynov EF, Alieva TV (2010) Review of fauna of gnaphosid spiders (Araneae: Gnaphosidae) of Azerbaijan. Proceedings of the Azerbaijan Society of Zoologists 2: 304–310. [In Russian, with English summary]

- International Code of Zoological Nomenclature (ICZN) (1999) 4th Edition. http://www.nhm. ac.uk/hosted-sites/iczn/code/ [accessed 15.05.2015]
- Kazantsev DV (2013) Classification of groupings of herpetobiont spiders (Aranei) in plain and piedmont landscape regions of Pechoro-Ilychskiy Reserve. In: Problemy izucheniya i okrany zhivotnogo mira na Severe. Vtoraya Vserossiyskaya konferentsiya s mezhdunarodnym uchastiem. Materialy dokladov. 8–12 apr. 2013 g. Syktyvkar, Respublika Komi, Rossiya. Syktyvkar, 93–95. [In Russian]
- Krasnobaev YP (2004) Catalogue of spiders (Aranei) of Middle Povolzhye. Zhugulevskiy gosudarstvennyi prirodnyi zapovednik im. I.I. Sprygina, Samara, 213 pp. [In Russian]
- Krasnobaev YP (2007) Class Arachnida (Arachnids). Order Aranei (Spiders). In: Rosenberg GS (Ed.) Kadastr bespoznovochnykh zhivotnykh Samarskoi Luki. Samara, 79–93. [In Russian]
- Krasnobaev YP, Matveev VA (1993) Catalogue of spiders of Middle Povolzhye. Samarskaya Luka Publ., Samara, 74 pp. [In Russian]
- Krasnobaev YP, Ovtsharenko VI (1986) To the problem of the spider fauna (Aranei) of the Kuybyshev Area. In: Ekologicheskie issledovaniya v Srednem Povolzhie. Kuybyshev University, Kuybyshev, 89–98. [In Russian]
- Kulczyński W (1885) Araneae in Camtschadalia a Dre B. Dybowski collectae. Pamietnik Akademji umiejetnosci w Kraków, wydzial matematyczno-przyrodnyczy 11: [1]–[60], [1]–[6], Tab.IX–XI.
- Kulczyński W (1913) Arachnoidea. V. Velitchkovsky. In: Faune de district de Walouyki du gouvernement de Woronège (Russie). Cracovie (10): 1–30.
- Kulczyński W (1926) Arachnoidea camtschadalica. Annuaire du Musée zoologique de l'Académie des sciences de l'Union des Républiques soviétiques socialistes 27(1): 29–72, Tab. II–III.
- Kůrka A (1994) A survey of spiders (Araneida) in Prof. F. Miller's collection (Department of Zoology, Museum of Natural History – National Museum), part I. Journal of the National Museum (Prague), Natural History Series 163(1–4): 43–54.
- Kuzmin EA, Alekseenko YG (2011) Additions to the list of spiders (Arachnida: Aranei) of Ulyanovsk Area. In: Volodina YK et al. (Eds) Priroda Simbirskogo Povolzhya. Vyp.12. Ulyanovsk, 169–178. [In Russian]
- Miller F (1971) Araneida. In: Klíč zvířeny ČSSR, Praha, 4: 51–306.
- Mikhailov KG (1987) Contribution to the spider fauna of the genus *Micaria* Westring, 1851 of the USSR. I (Aranei, Gnaphosidae). Spixiana 10(3): 319–334.
- Mikhailov KG (1997) Catalogue of the spiders of the territories of the former Soviet Union (Arachnida, Aranei). Archives of the Zoological Museum of the Moscow State University 37: 1–416.
- Mikhailov KG (2012) Bibliographia Araneologica Rossica 1770–2011 (Bibliography on spiders of Russia and post-Soviet republics, 1770–2011). Proceedings of the Russian Entomological Society 83(2): 1–229. [In Russian, with English summary]
- Mikhailov KG (2013) The spiders (Arachnida: Aranei) of Russia and adjacent countries: a nonannotated checklist. Arthropoda Selecta. Supplement 3, 262 pp.
- Oliger TI (2010) Spiders of south-eastern Priladozhye. Trudy Sankt-Peterburgskogo obshchestva estestvoispytatelei. Saint-Petersburg. Ser.4. 89: 1–340. [In Russian]
- Murphy JA (2007) Gnaphosid genera of the World. British Arachnological Society, Vol. 1, 92 pp.

- Palmgren P (1943) Die Spinnenfauna Finnlands. II. Pisauridae, Oxyopidae, Salticidae, Clubionidae, Anyphaenidae, Sparassidae, Ctenidae, Drassidae. Acta Zoologica Fennica 36: 1–112.
- Panteleeva NY (1982) To the study of spiders of the "Galichya Gora" Reserve. In: Issledovaniya rastitelnogo i zhivotnogo mira zapovednika Galichya Gora. Voronezh University Publishers, Voronezh, 89–92. [In Russian]
- Panteleeva NY (2007) To the study of spider fauna of Usmansky Bor. Trudy Voronezhskogo gosudarstvennogo zapovednika, Voronezh, (25): 266–279. [In Russian]
- Pereleshina VI (1928) Spider fauna of the environs of the Bolshevo Biostation. Zapiski biostantsii v Bolsheve (2): 1–74, 1 plate. [In Russian, with English summary]
- Pfliegler WP (2014) Records of some rare and interesting spider (Araneae) species from anthropogenic habitats in Debrecen, Hungary. e-Acta Naturalia Pannonica 7: 143–156.
- Platnick NI (2014) The World Spider Catalog, Version 15. American Museum of Natural History. doi: 10.5531/db.iz.0001
- Polchaninova NY, Prokopenko EV (2008) A checklist of the spider fauna (Araneae) of the "Svyati Gory" National Natural Park (Ukraine, Donetsk Region). Arthropoda Selecta 16 (for 2007) (3): 177–189.
- Polchaninova NY, Prokopenko EV (2013) Catalogue of the spiders (Arachnida, Aranei) of Left-Bank Ukraine. Arthropoda Selecta, Suppl. No. 2, 268 pp.
- Ponomarev AV (2008) Additions to the fauna of spiders (Aranei) of the south of Russia and Western Kazakhstan: new taxa and findings. Caucasian Entomological Bulletin 4(1): 49– 61. [In Russian, with English summary]
- Ponomarev AV, Dvadnenko KV (2013) Notes on the fauna of spiders (Aranei) of the southeast of Russian Plain and the Caucasus with the description of a new species of the genus *Hap-lodrassus* Chamberlin, 1922 (Gnaphosidae). Vestnik Yuzhnogo Nauchnogo Tsentra RAN 9(2): 46–56. [In Russian, with English summary]
- Ponomarev AV, Khachikov EA, Tsvetkov AS (2006) [Additional data of the spider (Aranei) fauna of the territory of M.A. Sholokhov Museum-Reserve]. In: "Muzie-zapovednik: ekologiya i kultura". Materaily Vtoroi nauchno-prakticheskoi konferentsii (stanitsa Veshenskaya, 13–16 sent. 2006 g.). Veshenskaya, 244–245. [In Russian]
- Ponomarev AV, Khnykin AS (2013) Spiders (Aranei) of Volgograd and its environs. Yugh Rossii: ekologiya, razvitie (4): 109–136. [In Russian, with English summary]
- Ponomarev AV, Lebedeva NV (2014) Spiders (Aranei) and some of their coenotic connection in gully forests of the Lower Don River // Aridnye Ekosystemy 20(2/59): 75–87. [In Russian, with English summary] [English translation in: Arid Ecosystems, 2014, 4 (2): 107–118.]
- Ponomarev AV, Polchaninova NY (2006) Materials on the spider (Aranei) fauna of Belgorod Area. Caucasian Entomological Bulletin 2(2): 143–164. [In Russian, with English summary]
- Ponomarev AV, Tsvetkov AS (2006a) Distribution of spiders of the family Gnaphosidae (Aranei) in the southeast of European part of the former USSR. In: Arzanov YG et al. (Eds) Rol' osobo okranyaemykh prirodnykh territoriy v sokhranenii bioraznoobraziya: Materialy mezhdunarodnoi nauchno-prakticheskoi konferentsii, posvyashchennoi 10-letiyu Gosudarstvennogo prirodnogo zapovednika "Rostovskiy", 26–28 apr. 2006 g., pos. Orlovskiy, Rostovskaya oblast'. Postov-na-Donu, 315–318. [In Russian]

- Ponomarev AV, Tsvetkov AS (2006b) New and rare spider species of the family Gnaphosidae from the southeast of Europe. Caucasian Entomological Bulletin 2(1): 5–13. [In Russian, with English summary]
- Pupiska F (1939) Clubionidae, Drassidae i Dysderidae (Arachn.) okolic Wilna. Prace Towarzystwa przyjaciól nauk w Wilnie 13(45): 1–33.
- Roewer CF (1951) Neue Namen einiger Araneen-Arten. Abhandlungen des Naturwissenschaftlichen Vereins zu Bremen 32: 437–456.
- Romanenko VN (2007) Fauna of spiders (Arachnida, Aranei) of natural biocenoses in southern taiga of West Siberia. Proceedings of the Russian Entomological Society 78(1): 107–116. [In Russian, with English summary]
- Roşca A (1941) Araignées de Bessarabie. Analele Academiei Române. Memoriile Secțiunii ştiințifice. Ser. 3. 15 (for 1939–1940): 389–406.
- Sentenská L, Pekár S (2013) Mate with the young, kill the old: reversed sexual cannibalism and male mate choice in the spider *Micaria sociabilis* (Araneae: Gnaphosidae). Behavioral Ecology and Sociobiology 67(7): 1131–1139. doi: 10.1007/s00265-013-1538-1
- Sentenská L, Pekár S, Lipke E, Michalik P, Uhl G (2015) Female control of mate plugging in a female cannibalistic spider (*Micaria sociabilis*). BMC Evolutionary Biology 15(18): 1–12. doi: 10.1186/s12862-014-0278-9
- Šternbergs MT (1981) Materiāli par Latvijas zirnekļu faunu. V. Dzimta Clubionidae [Materials on the spider fauna of Latvia. V. Family Clubionidae]. Latvijas Entomologs. Zinatne, Riga, 24: 56–59. [In Latvian, with English summary]
- Talanov VP, Nazarenko SV (1989) To the spider fauna of the Lower Dnieper. In: Vsesoyuznoe soveshchanie po probleme kadastra i ucheta zhivotnogo mira. Tezisy dokladov. Chast 4. Opyt kadastrovoi kharakteristiki, materialy k kadastru po bespozvonochnym zhivotnym. Bashkirskoe knizhnoe izdatelstvo, Ufa, 262–264. [In Russian]
- Tuneva TK (2007) Review of the family Gnaphosidae in the Ural fauna (Aranei). 5. Genera Micaria Westring, 1851 and Arboricaria Bosmans, 2000. Arthropoda Selecta 15 (for 2006) (3): 229–250.
- Vilbaste A (1987) Eesti ämblikud (Aranei) Annoteeritud nimestik [Estonian spiders. An annotated checklist]. Valgus, Tallinn, 178 pp. [In Estonian, with Russian and English summaries]
- Vilkas A (1992) The check-list of spiders (Arachnida, Araneae) of Lithuania. In: New and rare for Lithuania insect species. Records and descriptions of 1992. Inst. of Ecology, Vilnius, 112 pp.
- Westring N (1861) Araneae svecieae. Göteborgs Kungliga Vetenskaps och Vitterhets Samhälles Handlingar 7: 1–615.
- World Spider Catalog (2015) World Spider Catalog. Version 16. Natural History Museum Bern. http://wsc.nmbe.ch [accessed on 15.05.2015]
- Wunderlich J (1980) Revision der europäischen Arten der Gattung *Micaria* Westring 1851, mit Anmerkungen zu den übrigen paläarktischen Arten (Arachnida: Araneida: Gnaphosidae). Zoologische Beiträge (Neue Folge) 25 (für 1979) (2): 233–340.