



# Neotropical *Melyroidea* group cockroaches reveal various degrees of (eu)sociality

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## Abstract

Eusociality in its various degrees represents an animal social system characterised by cooperative brood care, differentiation into castes and generational overlap. The fossil record indicates that eusociality is likely to have originated in hymenopterans and blattodeans during the Cretaceous. In this study, we present findings from surveys in Peruvian (Villa Carmen) and Ecuadorian (Rio Bigal, El Reventador) cloud forests revealing the first extant cockroach species living in complex, structured groups ( $n = 90$ –200 individuals,  $> 20$  adults). We observed and described behaviours that suggest the existence of cooperative care, nest guarding, nest chamber preparation within hardwood *Casearia* sp. (Salicaceae) and bamboo (Bambusoideae), multiple overlapping generations ('different stages of' instars), colony translocation, possibly a sole reproductive female (1.25 times larger white 'queen', but no potential 'king' observed), and morphologically diversified immature stages. In order to define the lineage where this type of sociality originated and occurs, the forms of *Melyroidea magnifica* Shelford, 1912, *M. ecuadoriana* sp. n., *M. mimetica* Shelford, 1912 and an undescribed species from Peru are also described in a separate section of this study. Blattoid morphological characteristics such as typical styli suggest categorisation within distinct Oulopterygidae (Rehn, 1951), outside Corydiidae Saussure 1864. Transitional advanced sociality or semisociality in related *Aclavoidea socialis* gen. et sp. n. is documented in a rotting stump ( $n = 80$  individuals, few adults). Close phylogenetic relation between the genera, conserved morphology of numerous characters and their diverse feeding strategies generally lacking specialisation suggests a rather recent origin of a social way of life in this group. Eusociality in invertebrates and vertebrates can thus originate in various phylogenetical and ecological trajectories including predation, parasitism, care for herbs and the new one, documented through diet shift from detritivory to fungivory and algaevory. Interdisciplinary approaches reveal the low degree of knowledge of rainforest ecosystems, with fundamental groups remaining still systematically and also behaviourally undescribed.

**Keywords** Eusocial · New species · New genus · UNESCO BR · Mountain rainforest

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## Introduction

Herein, we present new findings on population structure and behaviour of an enigmatic group of tropical cockroaches as well as delve into their taxonomy. Due to the broad range of material covered in this study, this study is split into two portions: a systematic portion and a behavioural portion. In a systematic section, we discuss the taxonomy of the *Melyroidea* group, including a definition of new taxa. In the behavioural section, we thoroughly describe and analyse their social structure.

## Behavioural and morphological observations

Eusociality or ‘full sociality’ is a social system characterised by cooperative brood care, differentiation into castes and a complete generational overlap (Michener 1969; Wilson 1971). It results into loss of individuality and so called superorganismal structure of animal units (Queller and Strassmann 2002). Eusociality is thought to have first originated in termites (Vršanský and Aristov 2014; Vršanský et al. 2017, 2019a), and has independently evolved in various groups of insects, including ants and paper wasps (Hines et al. 2007), parasitic encyrtids (Ivanova-Kasas 1972; Giron et al. 2007), bees (Batra 1966; Michener 1969), gall thrips (Crespi 1992), aphids (Aoki 1977), extinct socialids (Vršanský 2010), mastotermites (Watson et al. 1977; Nalepa and Lenz 2000), eutermites (Bartz 1979; Abe 1987), and one beetle (Kent and Simpson 1992). Coeval independent origin of eusociality within wasps and cockroaches at the 127 Ma Early Cretaceous diversification point is remarkable.

## Specimens and their taxonomy

Cockroaches belong to the same order as termites, Blattodea (Inward et al. 2007). However, eusociality in either its basal or derived forms have not yet been described in any extant cockroach species. Nonetheless, *Cryptocercus* (Scudder 1862), an extant and basal genus of cockroaches, contains species that are often regarded as primitive, showing transitional behaviours between gregariousness (more or less ordinary pooling) and sociality (with different structure of generations). The species of this genus are considered as semi-social rather than truly eusocial as despite showing an overlap of two generations they do not exhibit other characteristics of eusociality (Wilson 1971).

First described in 1912, the cockroach genus *Melyroidea* Shelford, 1912 has been rarely observed and remains poorly known. The discovery of an active nest of *Melyroidea* sp. in 2017 allowed us to conduct the first observational study of living individuals of the genus. In this study, we present the results of our observations. Our observations provide

evidence of eusocial behaviour in this enigmatic cockroach genus residing in cloud forests on the Eastern slopes of the Andes (in Peru, Ecuador and Brazil). A male of *M. magnifica* is described for the first time here along with two entirely new species.

## Material and methods

### Specimens

Although rare in museum collections, when present, the collections always contained numerous adults from the same locality, which suggested a possibility of social structure within the genus *Melyroidea* and among its relatives.

Immature stages and white adult of *M. magnifica* Shelford, 1912 photographed at Rio Bigal originate from Rio Bigal Biological Reserve Station, UNESCO BR Sumaco, Ecuador with GPS coordinates 0°25' 59.8" S, 77° 19' 58.4" W, 972 m a.s.l. Nymphs of *Melyroidea* sp. were examined also from photographs originating from the Teparo ridge at the Villa Carmen research station (12° 53' 43.1" S, 71° 24' 26.6" W) of the Amazon Conservation Association, Peru. The top of the ridge is at approximately 1100 m.

Specimens collected by early collectors are deposited at the Pontificia Universidad Católica del Ecuador, Quito, Ecuador (herein formalised types), Oxford Scientific collections (*M. mimetica* Shelford, 1912 and *M. magnifica* Shelford, 1912 types), NMNH Washington D.C. and BMNH London (*M. magnifica* additional material). During the present research, no individuals were collected or damaged.

## Behavioural and morphological observations

External morphological characters of dry cockroach specimens were observed using a Leica M205C stereomicroscope and photographed with an attached Digital Camera Leica DFC295 (Leica Microsystems GmbH). The specimens at Rio Bigal, UNESCO Biosphere Reserve Sumaco, Ecuador were photographed with a Panasonic Lumix DMC-FT4 (Panasonic Corporation) camera and edited in Adobe Photoshop CS8 (Adobe Inc.). Video documentation was made by a 3.9 mm AV handheld endoscope (Shenzhen Sheng Da Rong Hua Industrial Co., Ltd) and a Panasonic Lumix DMC-FT4 camera. Drawings were made with CorelDrawX7 (Corel Corporation).

An incidental encounter and photograph of an individual triggered a huge effort to find additional specimens and a nest. Nearly 20 years after the initial observation of a *Melyroidea* cockroach in the region, a complete active nest was discovered in 2017. T.G. constructed a permanent, cloud forest research station. We present results of direct observations of the nest and its structure non-invasively conducted in situ. An

abandoned nest at Rio Bigal was cut with a handsaw. The endoscope was inserted into nests in order to monitor the activity within. Additionally, the endoscope was mounted close to the entrance in order to observe individuals exiting from and entering into the nest. Specimens were consequently subjected to light sources of diverse intensity, strong airflow, slight physical disturbance, and were offered different food sources (i.e., fungi, wood, moss, fruit, and insect). Movement modes were quantified by measuring the duration ( $s^{-1}$ ), pause time between speed bursts ( $s^{-1}$ ), number of antennations per second and number of palp movements per second. Jeol 6610 with SEI detector and Environmental Chamber SEM Zeiss (20 kV; no coating) (JEOL Ltd.) were used for the scanning electron microscopy (acceleration voltage 2 kV; no coating).

## Results

### Systematics

**Blattaria Latreille, 1810**

Blattoidea Latreille, 1810

Oulopterygidae Rehn, 1951

Melyroidea Shelford, 1912

Zoobank code: 78BBFB74-2144-4F2E-B1B5-D128456B13C0

### New species of social cockroach described

**Melyroidea ecuadoriana** Vidlička et Vršanský, sp. n.  
(Fig. 1g, h)

Zoobank code: FDA9315C-0D54-4433-B57D-DABEADEC78D

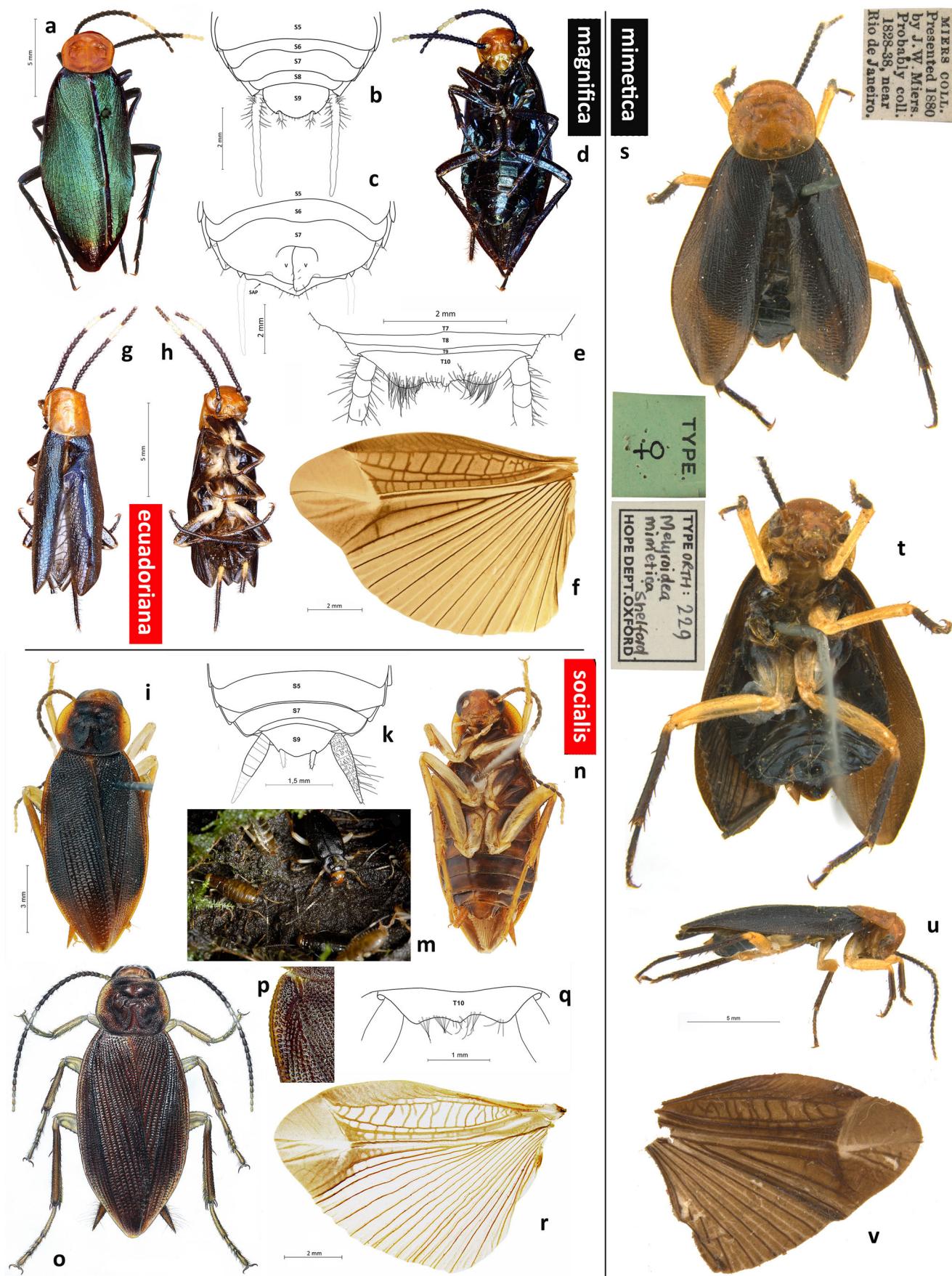
**Holotype** One ♀, Ecuador, Pastaza, Puyo, 938 m, 77°59' W 01° 28' S, 23.VI.2001, leg. P. Portero, coll. Deposited at the Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

**Differential diagnosis** The body is markedly smaller than *E. magnifica*, a blue colour compared with green of *M. magnifica*, an adult coloured white from below like immatures of *M. magnifica*.

**Description** The head is large, spherical, yellow and orange coloured. Small eyes are located near antennal sockets, and are probably black because on the type of the specimen the left eye is black, and the right one is pale, but a black macula is evident. Maxillary palps are five-segmented, with very short first and second segments, yellow in colour. The third segment is three times as long as the second one, narrow and brown; the fourth segment is as half as long as the third, narrow, distally enlarged and brown. The fifth

segment is elliptical and broad with the tip widely oval and fuscous. Labial palps are three-segmented; first and second segments are narrow, yellowish-brown. The third segment is flat and elongated, distal end broad and widely truncated, piceous with yellow hairs. Antennae are short, reaching approximately to the hind femora. Scape, pedicel and third segments are longer than wide and slightly spinous on distal end, fuscous. The following are 21 spherical segments, gradually elongated and spinous. Proximal part of segments has longer spines; first 16 segments following them are black, and the following three segments are white and last five are black. The total number of segments is indeterminate, but likely less than 30. The pronotum is quadrate, moderately longer than broad, with straight margins. The hind margin is rounded with widely rounded angles and discrete tubercles present on the disc of pronotum; the colour of pronotum is bright, yellowish-orange. Sclerotised tegmina are with distinct venation, veins raised (elevated), with numerous cross-veins, cells between veins filled with dots. The clavus is observable; the left tegmen is largely metallic blue, and only the tip is transparently dark brown; the right tegmen is similar, but the surface is overlapping with the left tegmen, dark brown with blue shine. Hind wings possess an appendiculate apical field that is longitudinally doubled and tightly rolled at rest. The anal field is folded and fan-like; the entire wing surface is pale brown with a dark-brown venation. The legs are slender, and the dorsoventral margin of front femur has a row of innumerable (12) short and thin spinules, terminating in one short genicular spine (type C1). The plantulae (on under side of the tarsal segments) are missing or are indistinct, and the first tarsomere is long. The following are 3 short tarsomeres, and a terminal, long tarsomeres are with symmetrical claws. The broad basal half of the claws is with an abruptly tapering distal portion. The arolium (between claws) is absent, distal end of coxae; the proximal third of the femur, genicular joint and proximal quarter (at fore and middle legs) or proximal sixth (at hind legs) of the tibiae is white in colour, and the rest of the legs are brown. Thoracic and abdominal sternites are dark brown with pale-brown central parts. Abdominal tergites are dark brown to black. Cerci are very long and narrow, with the segments difficult to distinguish (12–13 segments), lateral and underside with conspicuous hairs, proximal quarter is white while the rest is brown. The supraanal plate is symmetrical, moderately protruding in the central part and coloured black. The subgenital plate has obviously slightly asymmetrical valves. Valves are equally long, but the left lobe partially overlaps the right one.

**Measurements** ♂ (mm): body length (with tegmina), 11.0 mm; length of tegmina, 8.8 mm; largest width of tegmina, 1.8 mm; pronotum (length × width), 2.3 × 2.2 mm.



◀ **Fig. 1** New species and new male *Melyroidea* a–r: ownership of authors, s–v: originals, in ownership of Oxford University Museum of Natural History) a–f: *Melyroidea magnifica*, a, b, d: dorsal, ventral views and male terminalia, c, f: subgenital plate and a hindwing of a female; g–h, e: *Melyroidea ecuadoriana* sp.n. female holotype in dorsal and ventral views and supraanal plate; i–r: *Aclavoidea socialis* sp.n. male holotype, i: dorsal view on, k: terminalia, m: individuals in the wild of UNESCO Biosphere Reserve Sumaco, Ecuador, n: ventral view on holotype, o: illustration of the restored holotype, p: detail on elytra lacking clavus, q: supragenital plate, r: hindwing; s–v: *Melyroidea mimetica* female holotype in dorsal, ventral, lateral views and a hindwing

### Male of the known cockroach *M. magnifica* (unknown to be fully social) described

*Melyroidea magnifica* Shelford, 1912 redescription and male description (Fig. 1a–f, 2m–q).

**Studied material** One♂, Ecuador, Napo, El Reventador, 6.VIII.1996, 760 m, leg. C. carpio, Coll.: PUCE, Quito, Ecuador 1♀, Ecuador, Pastaza, Puyo, 820 m, 19.XI.1984, leg. Lilian Real, coll.: PUCE, Quito, Ecuador

One♀, Ecuador, Pastaza, Puyo, 11.II.1976, leg. Spangler et al., Coll.: USNMNH 2039895

**Additional known material** One♀, Peru, Chanchamayo, Dept. Junin, 1200 m, 6.V.1948, Leg. J.M. Schunke, Coll.: USNM specimens identified by A.B. Gurney, 1949. Unique identifier USNMENT1455026. Compilations of records were completed by Julia Snyder, 03.05.2018.

Nine adults (sex not determined), 1 nymph, Ecuador, Pastaza, Puyo, 11.II.1976, Leg. Spangler et al., Coll.: USNM (same collection as one loan female, which was studied). Additional data: Unique identifier USNMENT1455026–1455029, 1455031–1455034, 1455036, 1455038, 1455045. Label in unit tray says ex. giant bamboo, roaches active during daylight. Compilations of records were completed by Julia Snyder, 03.05.2018

Three photos and 2 videos—Del Rio Bigal Reserva Biológica (Bigal River Biological Reserve), Orellana, Ecuador (1 photo—27.04.2010; 2 photos and 2 videos from 16.04.2018)

One photo—Teparo ridge at the Villa Carmen research station of the Amazon Conservation Association in Peru (April 2018)—near the town of Pilcopata (Dept. Cusco)

**Description** A medium-sized cockroach is similar to female, with a large spherical and orange-coloured head. Small eyes are located at the back of the head, near the antennal sockets (the eyes are only slightly larger than the antennal socket). Maxillary palps are five-segmented, very short first and second segments; the third segment is four times longer than the second, uniformly narrow; the fourth segment is twice as long as the second, distally enlarged; the fifth segment same length

as third with a widely oval tip; all segments are dark. Labial palps are three-segmented. The short antennae is reaching approximately to the hind femora; the scape is twice as long than wide, and the pedicel and third segment is moderately longer than wide, slightly spinous, shiny, dark blue green; following are 14 spherical segments, gradually elongated, opaque, grey brown and spinous. Longer spines present on proximal part of segments; following are three segments in form very similar as previous, slightly elongated, but dully white coloured; next (minimal four) are segments grey brown, more elongated than the previous, total number of segments indeterminate; the bright orange-red pronotum is quadrate, slightly broader anteriorly than posteriorly with straight margins and widely rounded angles. Four weak tubercles present on the disc of pronotum, two anteriorly and two laterally. Tegmina are strongly sclerotised with distinct venation, with raised (elevated) veins and numerous cross-veins. The cells between veins are filled with dots, with the clavus observable; the left tegmen is nearly completely bright metallic green with a transparently dark-brown tip; the right tegmen is similar, but the surface overlapped by the left tegmen is glossy dark blue. Hind wings with an appendiculate apical field are longitudinally doubled and tightly rolled when at rest; the anal field is fan-like folded; the whole wing surface is pale yellowish-brown with dark-brown venation. Legs are slender, dark with blue-green shine. The dorsoventral margin of the front femur is with a row of innumerable short spinules, terminating in one short genicular spine (type C1); an indistinct plantulae (on underside of the tarsal segments), first tarsomere long, is followed by 3 short tarsomeres. The last tarsomere is long with simple symmetrical claws, and the arolium (between claws) is absent. Thoracic and abdominal sternites are dark with green-blue metallic shine. Abdominal tergites are metallic green. Cerci are very long and narrow with indistinct segments (7–10 segments); lateral and below sides with long hairs; auric-brown to blue. The supraanal plate is moderately protruding, central part sinuous, but in the middle with small projection. Lateral lobes are with very long yellowish hairs. The subgenital plate is symmetrical, with two equal styli. Tergal glands are absent.

**Measurements** ♂ (mm): body length (with tegmina), 14.6 mm; length of tegmina, 12.9 mm; largest width of tegmina, 3.9 mm; pronotum (length × wide), 2.2 × 3.2 mm.

### Female diagnosis is extended on hindwing characters, which were never examined before

Hind wings have similar shape and venation as *Melyroidea mimetica* documented by Shelford (1912) and *Oulopteryx meliponarum* Rehn, 1951 (Rehn 1951). The apical third of the anterior margin are evenly arcuate within the area between the radius and media that is relatively large and divided into

numerous large cells. Only one false dividing vein among CuP and A1 (plical—see Comstock and Needham 1898) vein is present. The anal area is well developed and contains 13 axillary veins. The subgenital plate (S7) in the centre is with a visible suture and two slightly asymmetrical valves projecting. The left valve is longer than the right valve and is partially overlapping it.

### Description of a new genus and species of partially social cockroach

*Aclavoidea* Vidlička et Vršanský, gen. n.

Zoobank code: 4002213F-CE6B-41C1-B6AF-6075A3DB2BBE

**Type species** *Aclavoidea socialis* Vidlička et Vršanský, sp. n. described below and by monotypy.

**Differential diagnosis** Differing from all other cockroach genera with tegmina lacking a visible clavus, the entire visible surface of the tegmina is densely covered with rows of very distinct, large and deep pits. The longitudinal rows of pits overlap the main veins. Tegmina resemble ancient cupedoid archostematan beetle elytra. The lifestyle is similar to that of *Melyroidea*, differing mainly in occupation of rotting wood as opposed to living wood which *Melyroidea* occupies. General habitus, colouration of head and antenna, structure of hindwing, cerci and styli, and structure of tegmina, except the reduced clavus, resemble the closely related *Melyroidea* and *Oulopteryx*.

**Male** Medium-sized cockroaches (about 10-mm length) are with a relatively large head and a markedly overlapping pronotum. Tegmina are very hard, covered with rows of pits. Hind wings possess an appendiculate apical field; the anal field is fan-like folded. The abdomen is without tergal glands, the legs have poor armament, and the anteroventral margin of the front femur is of D1 type, a detailed description as for species.

**Derivation of name** The generic name is combined from the prefix ‘aclavo-’ in the sense ‘without clavus’ which is not visible on tegmen, and the suffix ‘-idea’, which refers to its close relationship with *Melyroidea*.

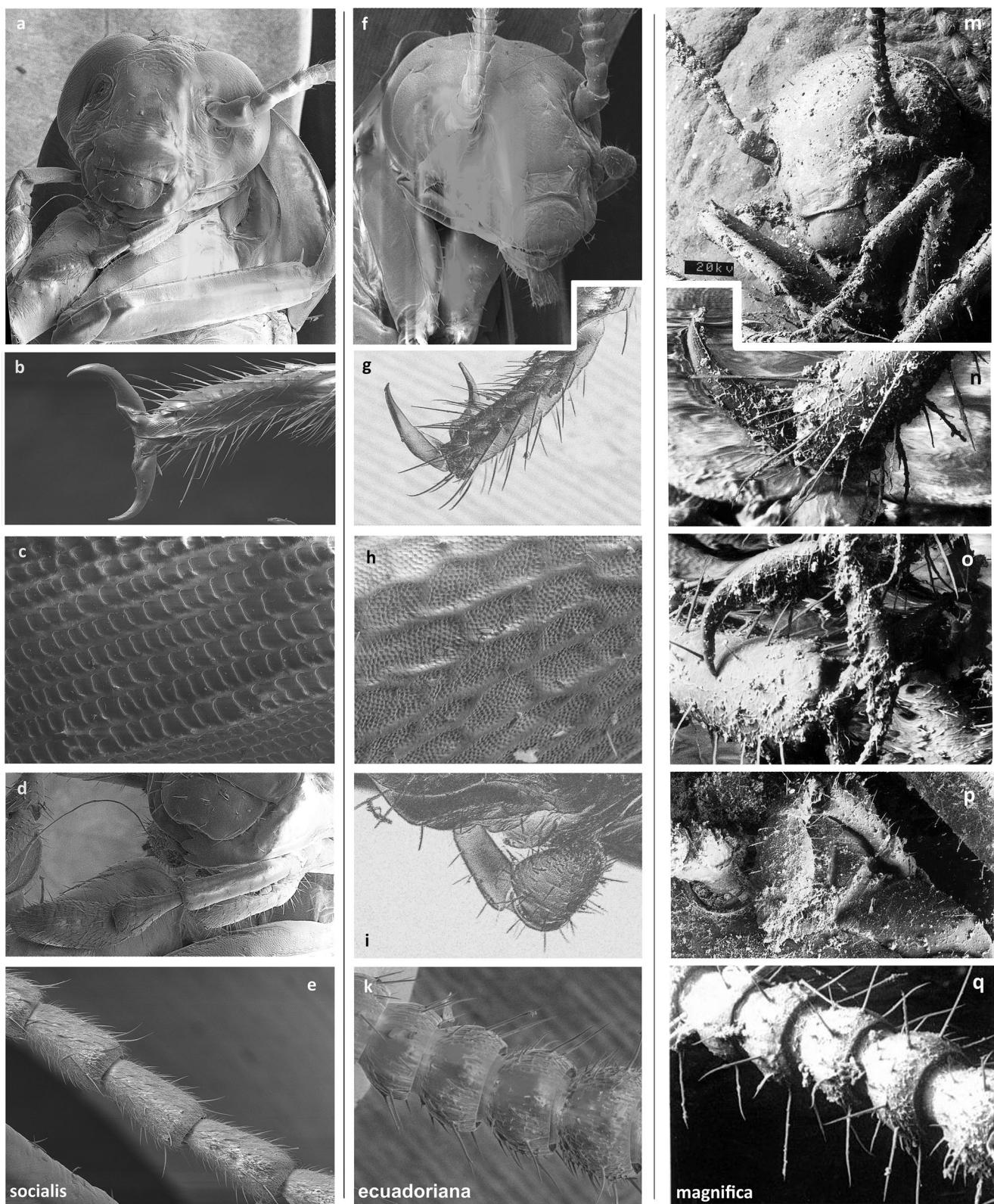
*Aclavoidea socialis* Vidlička et Vršanský, sp. n. (Figs. 1i–r, 2a–e; SI2)

Zoobank code: BCB1D4B3-5A84-4C80-B405-E12D3888E71D

**Holotype** One♂, Ecuador East, Francisco de Orellana distr., 250 m, Estación Científica Yasuni, 22.III.2008, leg. J. Jácome, coll. PUCE, Quito, Ecuador.

**Description** Male, medium-sized cockroaches with a head that is large, spherical, broad, and orange coloured; the eyes are brown, comparatively large, interocular space narrower than the space between antennal sockets. Ocelli are absent. Maxillary palps are yellowish-white, five-segmented; first and second segments are very short. Third to fifth segments are long and narrow; the fourth segment is distally enlarged, and the fifth segment is elliptical and broad. Labial palps are yellowish-white, three-segmented. Antennae are many-coloured and not very long; scape is longer than wide, pedicel is short, both yellow. The following 13 segments are spherical, gradually elongated, spinous and brown. The following are three white segments, then six fuscous segments, two tawny, and the last four yellow ones. Other segments are not preserved. The pronotum is rectangular, moderately broader than long with lateral and hind margins weakly convex and angles broadly rounded. The anterior margin is nearly straight, truncate, not covering the vertex of the head; the disc of pronotum with slight elevation and depression; brown, lateral parts of pronotum yellowish-brown. The whole surface with the exception of disc elevations is densely covered by impressed dots. Tegmina are dark brown, outer margins and apex are pale brown, fully developed, reaching over the body, strongly sclerotised (on right tegmen only partially visible, left tegmen overlapped largely by right one). Venation is not visible, and the whole surface is covered by longitudinal rows of pits. The pronotum and tegmina are very sparsely distributed hairs. Hind wings possess a large appendiculate apical field that in repose is longitudinally doubled and tightly rolled. The anal field is fan-like and folded with numerous (17) veins; The whole wing surface pale yellow, almost transparent, with a yellowish-brown venation. Legs are slender, coxae long, distal part brown, proximal part yellowish-white. Femurs are yellowish-white, only inner surfaces are pale brown; the dorsoventral margin of the front femur is without visible spinules, terminating in one short genicular spine (type D1). The tibiae and tarsi are yellowish-brown, with very weak armament; the plantulae (on tarsal segments) and arolium (between claws) are absent; claws are simple and symmetrical. Abdominal tergites are brown, sternites are pale brown. Cerci are orange brown, short, 11-segmented, conical, distal part broad, proximal part narrow and underside with long hairs. The supraanal plate is moderately protruding, central part sinuous, but in the middle with small projection, lateral and central lobes with long hairs are glued with secretion (possibly containing pheromone, phagostimulants and uricose as nuptial gifts—Roth and Willis 1952; Nojima et al. 1999; Mullins and Keil 1980; Schal and Bell 1982). The subgenital plate is nearly symmetrical with two equal, short, narrow pale styles on the convex central part.

**Lifestyle** This species was observed (June 2019, Rio Bigal Reserva Biológica, Orellana Prov., Ecuador) in the group



**Fig. 2** Scanning electron microscope representations of *Aclavoidea socialis* sp.n. (a, b, c, d, e); *Melyroidea ecuadoriana* sp.n. (f, g, h, i, j, k); *M. magnifica* (m, n, o, p, q) a, f, m: general view on head; b, g, n, o

tarsal claws; c, h elytra details; d, i, p maxillary palp and e, k, q antenna.  
Ownership of authors

setting with at least 80 specimens (4 different nymphal instar stages and two adults) foraging algae or fungi on the rotten tree trunk.

**Measurements ♂ (mm):** body length, 10.4 (total length with tegmina, 12.0); length of tegmina, 9.3; largest width of tegmina, 2.7; pronotum (length × width), 2.8 × 3.2.

### Systematic position of the group

The phylogenetic position of *Melyroidea* was unclear. Shelford (1912) described *M. magnifica* from Ecuador and *M. mimetica* from female specimens collected in the surroundings of Rio de Janeiro, Brazil. Nevertheless, the latter falls outside the distribution of the lineage and most likely represents a specimen transferred to the city by the timber trade. The males were unknown until now. Rehn (1951) established Oulopterygidae, based on the distinctively formed apical portion of the hind wings—i.e., apical field without venation, coiled in a spiral in repose and assigned *Oulopteryx* Hebard 1921 and possibly *Melyroidea*, therein without examining *Melyroidea* specimens. Gurney (1948) studied one adult female of *M. magnifica* but lacked specimens of *M. mimetica*. He confirmed their placement and presumed that these two species clearly represent distinct genera and maybe different families. He designated *M. magnifica* Shelford, 1912 as the type species of the genus *Melyroidea* and assumed that *M. mimetica* possibly belongs to *Oulopteryx*. Despite the magnificent and unusual metallic green tegmina and body, *M. magnifica* was not the subject of any studies until now. Thus, the classification of the *Melyroidea* genus was obscure. Oulopterygidae was divided into Areolariinae which included *Areolaria* Brunner von Wattenwyl 1865, *Anareolaria* Shelford, 1909, *Prosoplecta* Saussure 1864 (Asian genera) and *Euhypnorna* Hebard 1921 (Central America genus), and Oulopteryginae Rehn 1951 with *Oulopteryx* and *Melyroidea* (South American genera) (Princis 1965; previously, the genus *Prosoplecta* was also placed within Oulopteryginae Princis 1960). Roth (1991) placed *Areolaria* within Blattellidae and later *Prosoplecta* within Pseudophyllodromiinae (Roth 1994). The genus *Melyroidea* was originally classified in the subfamily Blattinae (=Periplanetinae; Shelford 1912), which corresponds with current Blattidae (for origin of Blattidae see Šmídová 2020; Šmídová and Lei 2017; Sendi and Azar 2017; Vršanský et al. 2019c). Rehn (1951) considered Oulopterigidae as a relative of Blattidae. Gurney (1948) confirmed their placement to the family Oulopterigidae. Brues et al. (1954) classified Oulopterigidae within Blattoidea, as well as Princis (1960, 1965). Princis divided the family into Areolarinae Princis 1960 and Oulopteriginae Princis 1965 (with *Melyroidea*). Bonfils (1975) noticed species *Oulopteryx dasilloides* Hebard, 1921 from French Guyana among Blattellidae,

Anaplectinae. Originally, *Oulopteryx* was assigned to Corydiinae Saussure 1864 (=Corydiidae; Hebard 1921, 1926). Roth (1991, 1994) made changes within Areolarinae (genus *Areolaria* classified in the Blattellidae and genus *Prosoplecta* in the Pseudophyllodromiinae Brunner von Wattenwyl 1865), but did not mention Oulopteriginae. Roth (2003) classified *Oulopteryx* within Blaberoidea Saussure 1864, Polyphagidae (=Corydiidae) and *Melyroidea* within Blaberoidea, Blattellidae (Karny, 1908), currently Ectobiidae Brunner von Wattenwyl 1865, Pseudophyllodromiinae. *Melyroidea* is currently classified within Corydioidea (Saussure 1864), Corydiidae (Saussure 1864) (Beccaloni 2014). Recent classification also indicates relations within Ectobiidae (Pellens and Grandcolas 2008). Molecular analysis has not been conducted due to contamination of old samples with fungi, prohibiting DNA analyses. Nevertheless, typical blattid terminalia with distinct symmetrical styli and valval rudiments suggest position close to Blattidae (Latreille 1810), out of Corydiidae. Thus, the original proposition of Rehn on the familiar rank of this group as Oulopterygidae seems most likely.

### Behaviour

The natural history of *Melyroidea* was unknown until we examined 10 adults and 1 nymph of *Melyroidea magnifica* in an organised group (NMNH collection, Washington D.C., USA, presented herein), collected at the same time from a single bamboo plant (Spangler, 11.02.1976, Puyo, Ecuador) as they were diurnally active together. At another locality at Rio Bigal Reserve, Ecuador, *M. magnifica* was confirmed living inside bamboo culms (T.G., April 26, 2010; T.G., June 19, 2019, presented herein). Additional evidence (T.G., 3 photos and 2 videos; 2017, T.G., presented herein) from Rio Bigal, at a site c.a., 120 km NE from Puyo, confirms heterogeneous groups containing at least 10 adult individuals and numerous immature cockroaches of overlapping generations. Furthermore, South at Villa Carmen, near Pilcopata in Peru, an agglomerate of 35 nymphs of various sizes belonging to an unknown *Melyroidea* species was observed (A.T., presented herein at Fig. 3a). *Melyroidea* from Peru were first reported by Gurney (1948), as *M. magnifica*. Adult females are superficially indiscernible from the Ecuadorian species, while immatures differ in appearance (see Fig. 3a). One Peruvian female is recorded from locality Chanchamayo, dept. Junín, 470 km NW from Pillcopata.

Predation on *Melyroidea magnifica* was never observed in Bigal, despite common encounters with ants, but contact was followed with alarm reactions from ants. One individual of *M. magnifica* exhibited signs of former injury, perhaps due to a depredation attempt (Fig. 4o, ‘Predation’). Older nymphs are metallic blue green, having a white colouration on the underside of the body, like adults of *M. ecuadoriana* (all legs;



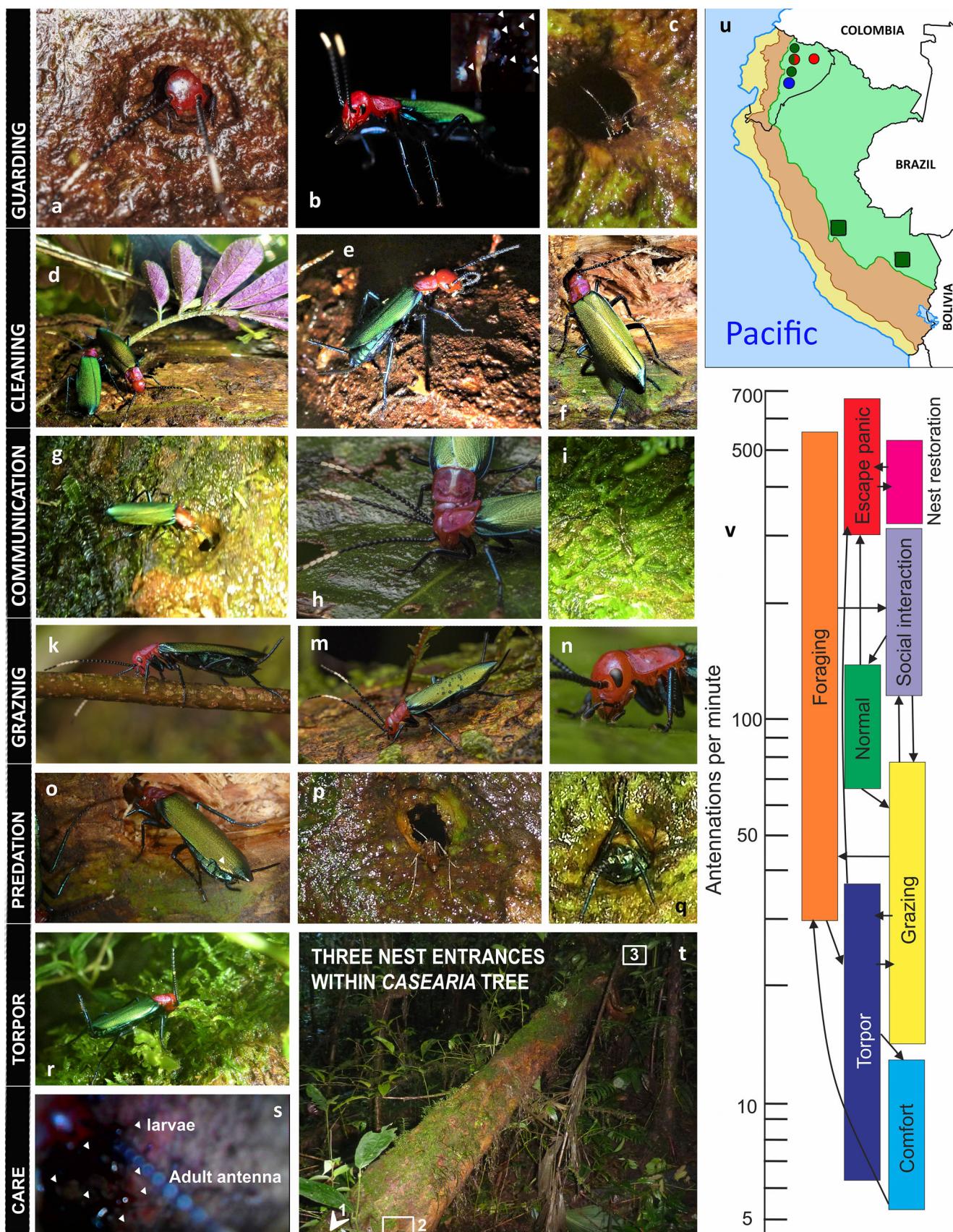
**Fig. 3** The only eusocial and only herbivorous cockroaches *Melyroidea* aff. *Magnifica* and *M. magnifica* in *Casearia* tree in Villa Carmen, Peru (a); and Rio Bigal, UNESCO Biosphere Reserve Sumaco, Ecuador (b, c, d, e, f, g, h). a Colony translocation consisting of 4 stages without a documented adult; b clustering of adults and metallic last immature

stages near main nest entrance; c, d, e first three, morphologically differentiated instars; f adult ‘worker’, metallic last instar and a non-sclerotized wing ‘queen’ 1.25 times bigger than other adults; g adult ‘worker’ with metallic last instar; h adult ‘worker’ detail. Ownership of authors

Fig. 1g, h). In addition, the cerci on the second morph of the youngest instar are long and crossed, and with visible styli. The youngest instars are also morphologically distinct.

Our observations conducted in 2017–2019 indicate a colony of cockroaches *M. magnifica* occupying cavities inside of a rare tree *Casearia* sp. (Salicaceae). At Rio Bigal, the specimens occupied a fallen but still living hardwood tree, about 15 m long and 1 m wide at the widest portion. Two openings with a diameter of 4.0 mm could be seen, and the distance between them was ~4 m. One of the holes was examined and

determined to lead to a small cavity, without any connecting or visible galleries, where the presence of two adults guarding and provisioning numerous immatures was confirmed (Video at SI4). The interior of the second entrance higher along the tree trunk is still unsurveyed due to efforts for preservation of the rare nest. The previously inhabited hole at the lower tip of the tree was abandoned by the cockroaches and opened using a saw during the cleaning of a trail which led to the discovery of the nest (April 2017, first documentation February 2018; Fig. 5a, c). The interior chamber was oval in shape



**Fig. 4** The only documented eusocial and only herbivorous cockroach *Melyroidea magnifica* behavioural displays and nest location in *Casearia* tree in Rio Bigal, UNESCO Biosphere Reserve Sumaco, Ecuador (a, b, c, d, e, f, g, h, i, j, k, l, m, n, o, p, q, r, s, t). Arrows show parasitic/commensal springtails (b guards), forewing damage (o predation) and immature individuals (s care); u localisation of social cockroaches in Ecuador and Peru (green is for rainforest, brown are for Andes, sandbrown is for a coastal environment; *M. magnifica* green dot, *M. magnifica* complex green rectangle, *M. ecuadoriana* blue dot, *Aclavoidea socialis* red dot); s dependance of behavioural displays on antennation frequency and transitions among behavioural traits. Ownership of authors

(approximately 5.5 cm × > 7.5 cm) with height 25–37 mm. It was not connected with any additional chambers or galleries, and no eggs or food deposits were observed. The surface of the tree was covered by extensive layers of moss, sparsely distributed microfungi and a thin layer of green algae.

Neither adults nor nymphs were observed to frequently wander far from this nest. Individuals were observed moving from the second to third entrance hole and back (entrances were documented in Figs. 4t and 5c). Several individuals left the lower hole and foraged for a short time during which their behaviour was characterised by short movements in various directions before stopping foraging and quickly moving directly up the length of the tree until reaching and entering the second hole.

Colony structure was complex. The observation of *Melyroidea* sp. from Villa Carmen in Peru reveals at least two different nymphal stages—a larger metallic green-coloured stage with fully developed wing pads (16 individuals) and a smaller pale brown-coloured stage without wing pads (19 individuals). It also seems that this group already contained at least four different instars (Fig. 3a). The colour variability of instars was much higher than of any other known cockroach.

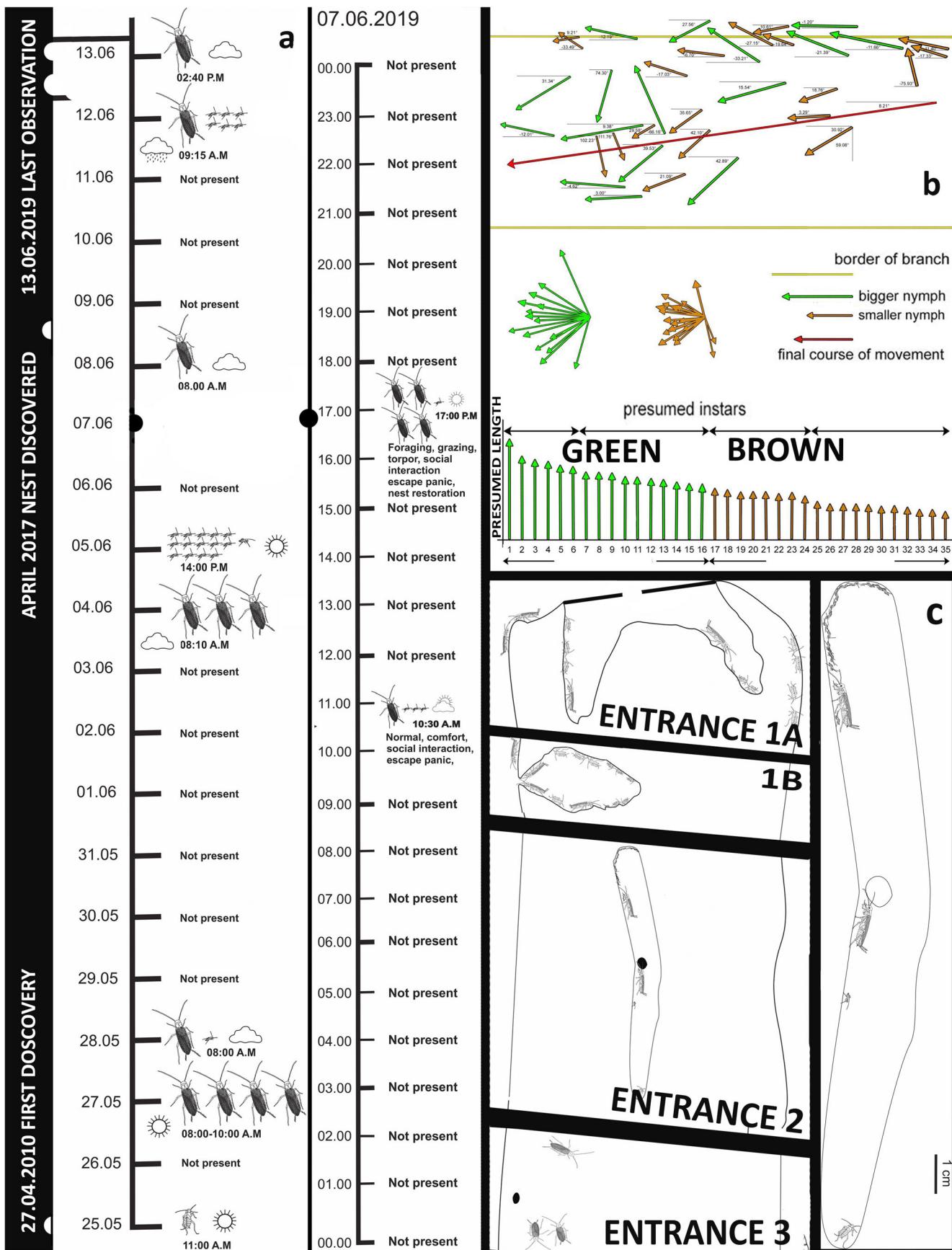
The colony of *M. magnifica* observed at Rio Bigal was very different, changing over time and in the most recent observation consisting of partially melanised 1st stage nymphs ~ 3 mm in length (15 individuals seen at the same time, i.e., 2019-06-05, observed clustered in a circle and immediately dispersing upon stimulation; Fig. 3c), 2nd stage individuals characterized by being entirely melanised and entirely black, solitary at surface (one individual observed at the same time 2019-06-05; Fig. 3d). The 3rd stage characterized by fully melanised cockroaches with partially yellow-coloured pronotum and a partially red-coloured head (one individual observed at the same time 2019-06-05; Fig. 3e) differing from the same stage in the Peruvian species, in which the head and pronotum are entirely red and the abdomen is striped, while the adults were superficially identical. The 4th stage, with metallic structural colours, was not observed in this group but was documented by 5 individuals in April 2018. These specimens apparently transformed into the next, the fully metallic 5th stage with developed wing pads, and in 2019 present in at least 6 individuals

(all stages were documented in Fig. 3f, g, one individual observed at the same time 2019-05-25). The 7th stage was represented by adults, differing in possessing fully developed forewings (and covered hindwings). Following the nest damage during the trail cleaning, 3 adults were seen simultaneously, and only 5 were determined to be present in total. The last form was observed in April 2018 and was represented with a fully melanised female with a red pronotum and coloured legs, with white wings lacking melanisation (Fig. 3f). This specimen was nearly 1.25 times larger than the other observed adults who were all uniformly sized. The fully functional wings suggest this was probably a reproducing female, ‘queen’. It was always observed surrounded by cockroaches at other stages, and it disappeared after 3 days (dispersed, or eaten; it can easily be discerned from moulting individuals or colourless mutants which might be similarly light coloured by its larger size; endoscopic examination revealed it had not retreated into the nest).

The activity of early nymphs of *M. magnifica* in Rio Bigal was nearly entirely restricted to within the nests. They were observed on the surface only once ( $n = 15$ ; 2019-06-05 14:00 PM) clustered together. Inside the nest, they spent most of their time hidden under an adult’s body (Fig. 4s). The attending adult was largely inactive, and the slow antennation rate of 1 antennal movement  $s^{-1}$  was probably related to the sound we produced during monitoring. Immature cockroaches (Video at SI3) were active, moving underneath the adult’s body and one individual apparently received provision from one of the two adults present in the nest during the observation time (2019-06-07-17:15 PM; Video at SI4). Other interactions at the surface are less frequent, and rare appearances of immature nymphs at the surface were always accompanied by frequent antennations (Video at SI5). Communication between adults and other immature stages are rare at the surface and are mostly restricted to cavities. Adults and other older stages were frequently (from every 3 to 6 days) observed outside the nest, at the surface and revealed clumping/agglomerating behaviour.

Temporal activity within the Bigal nest (Fig. 5a). Both the adults and juveniles exit the nest infrequently. There were entire weeks when no roaches were seen foraging outside the nest, then several days where a solitary individual foraged alone for several hours and finally days where up to 7 individuals left the nest and foraged simultaneously. Monthly activity in May–June 2019 is provided in Fig. 5a. The longest activity period was observed on 07/06/2019 (J.H.).

Nest repair behaviour in Rio Bigal. Two days after blockage of the second upper entrance to the nest by wood debris, antennae were seen probing through the small crack. In the subsequent days, individuals from both outside and inside were seen antennating at high frequencies (11 antennal movements per  $s^{-1}$ ) and consequently manipulating, clearing the entrance with rapid mandible motions (Video SI6).



**Fig. 5** Activity graphs. **a** Diurnal and annual activity of the nest; **b** movement analysis of photograph from Peru (Fig. 3a). Course of movement and angle declination from straight course; movement courses of bigger and smaller nymphs; relative size of bigger and smaller nymphs and presumed instars; **c** nest structure. Ownership of authors

Comfort behaviour was observed in the form of cleaning the antenna, and consisted (lasting no more than 3 s) of a peculiar round pulling motion combined with swift movements of maxillary palps (4 movements per  $s^{-1}$ ). Two different types of motion occurred, one typical for cockroaches which involved quick movements with short pauses and another, slow movement with a search-type pattern. Very often, the cockroaches stopped and exhibited motionless torpor (Fig. 1r), which lasted for up to 10 min. It is interesting that during the torpor antennae and cerci are upright, differing from their position during all other types of behaviour. Escape behaviour (territorial and defence behaviour was absent) was characterised with higher activity, 300–600 antennation strikes  $min^{-1}$ . Normal (orientation) behaviour was characterised by antennation strikes of 67–132  $min^{-1}$ .

An ant trying to enter the nest was denied (Fig. 4p). After stimulation by a small twig, the guard cockroaches left the cavity opening. Initially, individuals were hesitant to leave, but when resolved to leave the cavity, they ran very quickly. Young instars were rarely at the surface, but when they were, they were permanently in contact, communicating and antennating at a rate of 4 antennations  $s^{-1}$ . At the entrance into the first nest (lower one) usually, one or two individuals or guards were present with antennae often slightly protruding outside. Guards covered (probably protected) the nest entrance with their head (Fig. 1a). Adult guards were almost always present during fair and sunny weather and sheltered inside during rain. Upon outer stimulation or indication of danger, the individual cockroaches outside the nest quickly dispersed or entered the nest by diving into the hole.

## Discussion

### Behavioural and morphological observations

The behaviour of cockroaches in their natural environments is understudied and remains virtually unknown; thus, as in any in situ ethological research, the observation of new ethological patterns was expected. Nevertheless, the discovered sociality is significant and surprising in its extent.

In addition to the distinct metallic habitus, *Melyroidea* species are one of the morphologically most distinct cockroaches. Their large red head might serve as a signal or as a cover of the entrance to the nest (Fig. 4a). The relatively small eyes suggest weak vision related to life within a nest and are possibly

indicative of facultative diurnal surface activities. There is evidence that this species might be chemically defended or mimics a defended species. The bright and conspicuous colouration, its slow movement, the fact that it shows diurnal activities in the open outside of the nest and the avoidance reactions of ants when encountering this species all indicate some level of chemical protection. The morphologically distinct youngest instar is an unusual trait (developmental differentiation) in cockroaches but is notably also present in the wood-eating semi-social cockroaches *Cryptocercus* Scudder 1862 and the termite *Mastotermes darwiniensis* Froggatt, (Froggatt 1897).

The direct path individuals passed among separate nest entrances several meters away indicates an awareness of both openings, willingness to use them in close temporal periods, and suggests free mixing between the occupants of the two separate nest cavities. Whether cockroaches manage the cavity in the tree trunk or whether they utilise cavities created by other organisms is still unknown. However, a specialised closed ‘offspring chamber’ of suitable size may suggest they create these cavity networks or have very specific requirements. They were never observed moving on the ground, which combined with their nest location inside a fallen tree suggests they are a largely arboreal species.

The variability of early instars does not seem to reflect the distinct colouration of the adults, which is in contrast to the earliest stages, metallic and uniform, with two forms at most, among individuals. Nymphs were observed moving on a branch together in a single direction (Fig. 5b). No adult was observed during this documentation, so the colony was either moving without an adult or potentially following the trail of an adult located nearby.

The observation of a ‘queen’ is the weakest evidence for eusociality, and future investigation such as measures of egg production, ovarian development and parentage analyses are needed to demonstrate that this one hymenopteran ‘queen’-analogue with white wings indeed monopolizes reproduction within the colony.

Our observations confirm overlapping generations, a key trait of eusociality. However, neither a soldier caste nor antagonistic behaviour was observed; although one morphotype with different, more opaque green colour could represent a worker caste. A slightly contrasting colour is clearly not enough to support the existence of a worker caste, and, by comparison, workers in termites are defined following developmental, morphological and behavioural features, which are more distinct differences than a slight difference in colour which can likely be explained by intraspecific variability.

Guards are mainly adults but there is some evidence of immature individuals exhibiting guarding behaviour as well (Fig. 4c ‘Guarding’). The prolonged period of transition through the immature stages through April 2018, and June 2019 suggests an extremely slow, annual lifecycle.

Further evidence of eusociality, in addition to complete generational overlap, was supported with another fundamental premise of eusociality, the cooperative care of offspring including transmission of provisions. One immature individual is captured on video feeding from an adult, but the specification of transferred food was not possible (Video SI4). Strangely, no faeces were observed. We hypothesise that on the surface immatures feed on viscous indistinct adult faeces transferring endosymbionts as it is common in other cockroaches (Troyer 1984; Ewald 1987; Nalepa 1991).

No interactions with parasites were observed on any individuals, although springtails, which are potentially commensal, were frequently documented in the nest (Fig. 4b arrows, Video at SI3). Other arthropods recorded in the vicinity of the nest were unidentified species of millipede, scorpion, spider and flies. Observations reveal that ants which come into contact with the cockroaches quickly reacted to avoid them, a possible reaction to chemical deterrents. Although, in one instance, an ant interacted closely with a cockroach, no antagonistic response from either side was observed. The ants avoided the youngest instars (2 documented encounters; no documentation exists for older instars), which superficially resemble myrmecomorphs (see Vršanský et al. 2018).

Temporal activity suggests that the cockroaches do not leave the nest every day and might emerge en masse to feed during good conditions. The first *Melyroidea* cockroach at Rio Bigal was spotted on April 26, 2010, but no others were seen for 7 years until a nest was discovered (and partially destroyed) in 2017. In 2018 (Fig. 3b), the nest was investigated, revealing about 100 individuals. The large white individual, potentially a hymenopteran ‘queen’-analogue, was seen for 3 days in 2018. The activity within a day with highest activity day was divided into escape, panic, torpor, foraging, social interaction and grazing. One individual was observed restoring the nest together with another individual inside the nest (Video SI6).

Mandibles were not seen functioning in other purposes than during the nest repair (they are inactive during feeding) so nest repair and maintenance might be their only function.

Communication between cockroaches at the Rio Bigal nest was classified herein as a social behaviour which was most commonly seen as antennation between an individual outside and one inside the nest. The individuals frequently communicated with each other, often immediately before entering the nest.

*M. magnifica* was herein observed as a strict herbivore (more precisely algaevore; hundreds of individuals observed, all stages, all years) analogically to wood-eating *Cryptocercus* and termites, and as opposed to majority of eusocial hymenopterans. This supports the hypothesis that a shift to herbivorous diet in cockroaches leads to socialisation, while in hymenopterans this shift is associated with different feeding strategies. The specimens observed during May 15–June 15,

2019 were exhibiting a moderate reaction to light and a lack of interest towards offered caloric or nitrogenous food. During the surface active time, adults and the last immature instar stage fed on algal film (Trebouxiophyceae on leaves, trunks, bark), while feeding of earliest immature instars appears to be confined to inside the nest. No predation or detritus feeding was observed. Communal feeding with specimens tightly clustered to each other and individual cockroaches slowly chewing or scraping the surface where green algae was frequent was observed (Figs. 3b, g and 4 k, m, n).

Specimens at Bigal and Villa Carmen inhabit tree cavities like termites and some eusocial Hymenopterans, but inhabited trees are much harder and still living—the occupation of a living tree is perhaps a response to the rapid decay of dead wood and organic matter in the tropics. Analogous mountainous range with lower decay time (Fig. 4u) along Andean slopes is thus logical and distinct. Due to the post Palaeocene origin of cosmopolitan living cockroach assemblages, the lack of SE Asian analogues supports an origin of the group in Neotropics. Semi-social precursors indicated here by *Aclavoidea socialis* are also restricted to this biome. The key difference between the two genera is in the choice of wood, while *Aclavoidea* uses rotting wood, *Melyroidea* uses living or nearly non-decaying wood. Transitional behaviour might appear in *M. mimetica*, which also has transitional characters such as wide cerci, but its lifestyle is entirely unknown (only a holotype collected in 1880; Fig. 1s–v).

## Specimens and their taxonomy

The newly discovered social structure within a single species, *M. magnifica*, warrants an exploration of its taxonomic placement in order to understand whether its high degree of sociality is a result of a highly specialized lifestyle or is maintained within the whole group. Our inspection in major entomological collections worldwide and in local collections from Ecuador reveal a new species, *M. ecuadoriana* (Fig. 1g, h), and provide evidence of the sociality of several related species within the genus. There appears to be at least one additional species, but it has only been documented photographically so far (Fig. 3a). None of these recorded species or their behaviour contradict the hypothesis that sociality within this group resulted from a dietary shift to algaevory. Based on the close relationship to Oulopterygidae, we examined all known world records within this group. Unfortunately, no ecological context of the group exists—no species has been ethologically studied. Perhaps of greater importance is a discovery of the distinct, morphologically unique new genus *Aclavoidea*, which reveals evidence for a diversity of feeding strategies within the group. This was confirmed by the discovery of a whole nest of *A. socialis* in Rio Bigal (Fig. 1m). This species appears to feed on fungi, perhaps not exclusively so, but does not appear to feed on algae. Its sociality is not developed to the extent of

*Melyroidea magnifica*. It is clear that further etho-ecological observations of more Oulopterigidae are necessary in order to get a clearer picture of the role of diet in transition to sociality. However, the observations presented here are strong evidence of the presence of diverse degrees of sociality and diverse feeding strategies within the lineage and thus its contemporaneous origin.

The discovery of two new and spectacular species described here, along with an aquatic cockroach species reported previously from the same site (Vršanský et al. 2019b), exemplify the currently poor level of understanding of blattodean natural history with little ecological data existing for the majority of species. Approximately 200 cockroach species live in this single location, indicating the existence of numerous undescribed species in neotropical forests, and thus highlighting the importance for protection of this biodiversity hotspot and continued examination of under investigated blattodean lineages. The newly discovered genus further exemplifies the lack of serious taxonomic data for species in the region. Our observations sharply contrast with the previously expected largely solitary way of life within this group, which was suggested on the basis of isolated records of most of taxa.

Our study exemplifies the importance of integrated systematical, taxonomical, phylogenetic and behavioural approaches to study organisms in their natural, critically endangered habitats.

## Conclusions

Our behavioural observations of cockroaches in the *Melyroidea* group (including a new genus *Aclavoidea*), reveal previously unknown social and group living behaviours in large family or social groups among cockroaches, representing an evolutionary intermediate in blattodean sociality and a transitional state falling between solitary living as found in many species of cockroaches and the complex social structure of fully eusocial termites. The social groups of these wood-dwelling cockroaches increase our understanding of the conditions and lifestyle of blattodeans that led to the evolution of complex eusociality involving huge networks of individuals in termites. However, to completely understand to what level these cockroaches are eusocial, further research is required to determine whether the large white *M. magnifica* was indeed a ‘queen’ and whether she represents the sole breeding individual within the colony, continued study is required to determine whether there is a male ‘king’ in the social structure and about the details of egg deposition and care among the cockroaches. A separate systematic study indicates the occurrence of various degrees of sociality in a wider spectrum of lineages of these cockroaches, which were undescribed until now. Integrated approaches to study these cockroaches highlight how much is left to learn both about

diversity and social evolution among insects as well as the need to protect their habitat as Neotropical cloud forest is one of the most imperilled ecosystems under threat from development, agriculture and climate change.

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**Author contributions** J.H. performed most of the direct observations of the nest and wrote the paper; P.V. (PI) designed research, discovered social structure, performed SEM and wrote the paper; T.G. discovered the observed nest; P.B., A.T., G.G. provided observation and logistics and conservation in Ecuador and Peru; P.B. additionally discovered nest of *A. socialis*; I.K. illustrated new genus; L.V. formalized new species, analysed species from Peru and wrote the paper. A.S. documented nests and co-wrote paper. Š.N. with L.V. performed SEM.

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## Compliance with ethical standards

**Conflict of interest** Multiple affiliations of P.V. are within one research body (Slovak Academy of Sciences); secondary affiliation of J.H. is in unpaid position. All the other authors declare that they have no conflict of interest.

**Ethical approval** This is an observational study. The Research Ethics Committee of Bioscience center of Slovak Academy of Sciences has confirmed that no ethical approval is required. Systematical material originated from old collections.

## References

- Abe T (1987) Evolution of life types in termites. In: Kawano S, Connell JH, Hidaka T (eds) Evolution and coadaptation in biotic communities. University of Tokyo Press, Tokyo, pp 125–148
- Aoki S (1977) *Colophina clematis* (Homoptera, Pemphigidae), an aphid species with “soldiers”. Kontyú 45:276–282
- Bartz SH (1979) Evolution of eusociality in termites. Proc Natl Acad Sci U S A 76:5764–5768. <https://doi.org/10.1073/pnas.76.11.5764>
- Batra SWT (1966) Nests and social behavior of halictine bees of India (Hymenoptera: Halictidae). Indian J Entomol 28:375–393
- Beccaloni GW (2014) Cockroach species file online. Version 5.0/5.0. World Wide Web electronic publication <http://Cockroach.SpeciesFile.org> Accessed 25 June 2019
- Bonfils J (1975) Blattopera (Orthopteroidea) récoltés en Guyane Française par la mission du Muséum national d’Histoire naturelle. Ann Soc Entomol Fr 11:29–63

- Brues CT, Melander AL, Carpenter FM (1954) Classification of insects. Keys to the living and extinct families of insects, and to the living families of other terrestrial arthropods. Bull Mus Comp Zool 108:1–917
- Brunner von Wattenwyl K (1865) Nouveau Système des Blattaires. G. Braumüller, Vienne
- Comstock JH, Needham JG (1898) The wings of insects. Am Nat 33: 117–126
- Crespi BJ (1992) Eusociality in Australian gall thrips. Nature 359:724–726. <https://doi.org/10.1038/359724a0>
- Ewald PW (1987) Transmission modes and evolution of the parasitism-mutualism continuum. Ann N Y Acad Sci 503:295–306. <https://doi.org/10.1111/j.1749-6632.1987.tb40616.x>
- Froggatt WW (1897) Australian termitidae. Part II. Proc Linnean Soc NSW 21:510–552
- Giron D, Ross KG, Strand MR (2007) Presence of soldier larvae determines the outcome of competition in a polyembryonic wasp. J Evol Biol 20:165–172. <https://doi.org/10.1111/j.1420-9101.2006.01212.x>
- Gurney AB (1948) The taxonomy and distribution of the Grylloblattidae (Orthoptera). Proc Ent Soc Wash 50:86–102
- Hebard M (1921) South American Blattidae from the Muséum National d'Histoire Naturelle, Paris, France. Proc Acad Natl Sci Phila 73: 193–304
- Hebard M (1926) The Blattidae of French Guiana. Proc Acad Natl Sci Phila 78:135–244
- Hines HM, Hunt JH, O'Connor TK, Gillespie JJ, Cameron SA (2007) Multigene phylogeny reveals eusociality evolved twice in vespid wasps. Proc Natl Acad Sci U S A 104:3295–3299. <https://doi.org/10.1073/pnas.0610140104>
- Inward D, Beccaloni G, Eggleton P (2007) Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. Biol Lett 3:331–335. <https://doi.org/10.1098/rsbl.2007.0102>
- Ivanova-Kasas OM (1972) Polyembryony in insects. In: Counce SJ, Waddington CH (eds) Developmental systems: insects, vol 1. Academic, New York, pp 153–186
- Kent DS, Simpson JA (1992) Eusociality in the beetle *Austroplatypus incomptus* (Coleoptera: Curculionidae). Naturwissenschaften 79: 86–87. <https://doi.org/10.1007/BF01131810>
- Latrelle PA (1810) Considérations générales sur l'ordre naturel des animaux composant les classes des crustacés, des arachnides, et des insectes, avec un tableau méthodique de leurs genres, disposés en familles. Chez F. Schoell, Paris
- Michener CD (1969) Comparative social behavior of bees. Annu Rev Entomol 14:299–342. <https://doi.org/10.1146/annurev.en.14.010169.001503>
- Mullins DE, Keil CB (1980) Paternal investment of urates in cockroaches. Nature 283:567–569
- Nalepa CA (1991) Ancestral transfer of symbionts between cockroaches and termites: an unlikely scenario. Proc R Soc Lond B 246:185–189. <https://doi.org/10.1098/rspb.1991.0143>
- Nalepa CA, Lenz M (2000) The ootheca of *Mastotermes darwiniensis* Froggatt (Isoptera: Mastotermitidae): homology with cockroach oothecae. Proc Biol Sci 267:1809–1813. <https://doi.org/10.1098/rspb.2000.1214>
- Nojima S, Sakuma M, Nishida R, Kuwahara Y (1999) A glandular gift in the German cockroach, *Blattella germanica* (L.) (Dictyoptera: Blattellidae): the courtship feeding of a female on secretions from male tergal glands. J Insect Behav 12:627–640. <https://doi.org/10.1023/A:1020975619618>
- Pellens R, Grandcolas P (2008) Catalogue of Blattaria (Insecta) from Brazil. Zootaxa 1709:1–109
- Princis K (1960) Zur systematik der Blattarien. EOS Rev Esp Entomol 36:427–449
- Princis K (1965) Blattariae: Subordo Blaberoidea: fam.: Oxyhaloidea, Panesthiidae, Cryptocercidae, Chorisoneuridae, Oulopterigidae, Diplopteridae, Anaplectidae, Archiblattidae, Nothoblattidae. In: Beier M (ed) Orthopterorum catalogus pars 7. Dr. W. Junk, 's-Gravenhage, pp 283–400
- Queller DC, Strassmann JE (2002) The many selves of social insects. Science 296:311–313. <https://doi.org/10.1126/science.1070671>
- Rehn JWH (1951) Classification of the Blattaria as indicated by their wings (Orthoptera). Mem Am Entomol Soc 14:1–134
- Roth LM (1991) The cockroach genera *Sigarella* Hebard and *Scalida* Hebard (Dictyoptera: Blattaria: Blattellidae). Entomol Scand 22:1–30
- Roth LM (1994) The beetle-mimicking cockroach genera *Prosoplecta* and *Areolaria*, with a description of *Tomeisneria furthi* gen. n., sp. n. (Blattellidae: Pseudophyllodromiinae). Entomol Scand 25:419–426
- Roth LM (2003) Systematics and phylogeny of cockroaches (Dictyoptera: Blattaria). Orient Insects 37:1–186. <https://doi.org/10.1080/00305316.2003.10417344>
- Roth LM, Willis ER (1952) A study of cockroach behavior. Am Midl Nat 47:66–129
- Saussure H (1864) Mémoires de la Société de physique et d'histoire naturelle de Genève. Société de physique et d'histoire naturelle de Genève 18:230
- Schal C, Bell WJ (1982) Ecological correlates of paternal investment of urates in a tropical cockroach. Science 218:170–173. <https://doi.org/10.1126/science.218.4568.170>
- Scudder SH (1862) Materials for a monograph of the North American Orthoptera. Bost J Nat Hist 7:409–480. <https://doi.org/10.5962/bhl.title.20701>
- Sendi H, Azar D (2017) New aposematic and presumably repellent bark cockroach from Lebanese amber. Cretac Res 72:13–17. <https://doi.org/10.1016/j.cretres.2016.11.013>
- Shelford RWC (1912) Mimicry amongst the Blattidae; with a revision of the genus *Prosoplecta* Sauss., and the description of a new genus. Proc Zool Soc London 82:358–376. <https://doi.org/10.1111/j.1469-7998.1912.tb07022.x>
- Šmídová L (2020) Cryptic bark cockroach (Blattinae: *Bubosa poinari* gen. et sp. nov.) from mid-Cretaceous amber of northern Myanmar. Cretac Res 109:104383. <https://doi.org/10.1016/j.cretres.2020.104383>
- Šmídová L, Lei X (2017) The earliest amber-recorded type cockroach family was aposematic (Blattaria: Blattidae). Cretac Res 72:189–199. <https://doi.org/10.1016/j.cretres.2017.01.008>
- Troyer K (1984) Microbes, herbivory and the evolution of social behavior. J Theor Biol 106:157–169. [https://doi.org/10.1016/0022-5193\(84\)90016-X](https://doi.org/10.1016/0022-5193(84)90016-X)
- Vršanský P (2010) Cockroach as the earliest eusocial animal. Acta Geol Sin 84:793–808. <https://doi.org/10.1111/j.1755-6724.2010.00261.x>
- Vršanský P, Aristov D (2014) Termites (Isoptera) from the Jurassic/Cretaceous boundary: evidence for the longevity of their earliest genera. Eur J Entomol 111:137–141. <https://doi.org/10.14411/eje.2014.014>
- Vršanský P, Oružinský R, Aristov D, Wei DD, Vidlička L, Ren D (2017) Temporary deleterious mass mutations relate to origins of cockroach families. Biologia 72:886–912. <https://doi.org/10.1515/biolog-2017-0096>
- Vršanský P, Bechly G, Zhang Q, Jarzemowski EA, Mlynšký T, Šmídová L, Barna P, Kúdela M, Aristov D, Bigalk S, Krogmann L, Li L, Zhang Q, Zhang H, Ellenberger S, Müller P, Gröhn C, Xia F, Ueda K, Vďačný P, Valaška D, Vršanská L, Wang B (2018) Batesian insect-insect mimicry-related explosive radiation of ancient alienopterid cockroaches. Biologia 73:987–1006. <https://doi.org/10.2478/s11756-018-0117-3>
- Vršanský P, Koubová I, Vršanská L, Hinkelmann J, Kúdela M, Kúdelová T, Liang J-H, Xia F, Lei XJ, Ren XY, Vidlička L, Bao T,

- Ellenberger S, Šmídová L, Barclay M (2019a) Early wood-boring ‘mole roach’ reveals eusociality “missing ring”. AMBA Projekty 9: 1–28
- Vršanský P, Sendi H, Aristov D, Bechly G, Müller P, Ellenberger S, Azar D, Ueda K, Barna P, Garcia T (2019b) Ancient roaches further exemplify ‘no land return’ in aquatic insects. *Gondwana Res* 68: 22–33. <https://doi.org/10.1016/j.gr.2018.10.020>
- Vršanský P, Šmídová L, Sendi H, Barna P, Müller P, Ellenberger S, Wu H, Ren X, Lei X, Azar D, Šurka J, Su T, Deng W, Shen X, Jun L, Bao T, Bechly G (2019c) Parasitic cockroaches indicate complex states of earliest proved ants. *Biologia* 74:65–89. <https://doi.org/10.2478/s11756-018-0146-y>
- Watson JAL, Metcalf EC, Sewell JJ (1977) A re-examination of the development of castes in *Mastotermes darwiniensis* Froggatt (Isoptera). *Aust J Zool* 25:25–42. <https://doi.org/10.1071/ZO9770025>
- Wilson EO (1971) The insect societies. Harvard University Press, Cambridge

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