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Mammals, birds and reptiles as hosts of *Lisotrigona* bees, the tear drinkers with the broadest host range (Hymenoptera, Apidae)

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Eusocial *Lisotrigona cacciae* (Nurse) and *L. furva* Engel (Meliponini) presumably suck tears for their relatively high protein content as a supplement to pollen for rearing their young. Humans, dog and zebu (*Bos indicus*) have been reported as hosts in Thailand. In order to assess the likely broadest host range, open-air trials were carried out with a mammal (rabbit, *Oryctolagus cuniculus*), bird (rooster, *Gallus gallus*) and a reptile (yellow tortoise, *Indotestudo elongata*). They were tested singly for 1–2 hours at two sites where *L. cacciae* or *L. furva* occurred naturally and sucked regularly the authors' lachrymation. The animals were exposed in a wide-meshed cage, such that they were easily accessible to the bees and that the tear drinking activity could be exactly studied, and photographed. Up to six *L. furva* sucked tears simultaneously from the tortoise, but the rooster displayed the mildest or no reaction when a bee fed at its eye. Compared to other lachryphagous insects (flies, moths) the bees were the most gentle suckers at human eyes, except when up to ten specimens congregated at closed eyes, causing tickling. In Thailand, at least 45 mammal, 21 bird and 17 reptile species are potential hosts in *Lisotrigona*'s sylvatic and synanthropic habitats. Accession to this diverse pool of tear sources is facilitated by the sophisticated communication systems typical for eusocial bees.

Key words: Anthropophily, bees, birds, host range, lachryphagy, *Lisotrigona*, mammals, Meliponini, reptiles, Thailand.

INTRODUCTION

Until recently, insects known to trouble the eyes of man and animal belonged to the order of Diptera during the day and Lepidoptera (almost exclusively) at night. Among the most familiar eye visitors pestering man and animal are the bazaar fly (*Musca sorbens* Wiedemann) and the face fly (*M. autumnalis* (De Geer)) (Muscidae), respectively (e.g. Mullen & Durden 2002). Less well known are three other dipterous families. The eye gnats (e.g. *Hippelates* spp., *Liohippelates* spp., *Siphunculina* spp., Chloropidae) (Mullen & Durden 2002; Paganelli & Sabrosky 1993), *Cryptochetum* sp. (Cryptochetidae) (Merz, pers. comm.; H.B., pers. observ.), and the small fruit flies (Drosophilidae) (e.g. Chen *et al.* 2005; Otranto *et al.* 2005, 2008; Bächli, pers. comm.; Toda, pers. comm.). In Thailand alone, at least 31 drosophilid species of *Amiota*, *Apsiphortica*, *Paraleucophenga*, and *Phortica* were recently collected from human eyes; a cluster of three species was photographed while sipping tears (Bänziger *et al.* 2009, Fig. 4). Lachryphagy among Lepidoptera is found in tropical and some subtropical regions by moth adults of the Geometridae, Noctuidae, Notodontidae, Pyralidae, Thyatiridae and Sphingidae (e.g. de Joannis 1911; Shannon 1928; Reid 1954; Büttiker 1964, 1972; Büttiker & Bezuidenhout 1974; Büttiker & Gallagher 1980; Bänziger 1987, 1992, 1995).

Unexpectedly, recently an additional order of insects has been reported to exhibit the curious predilection for tears: Hymenoptera, namely the minute bees *Lisotrigona cacciae* (Nurse), *L. furva* Engel and *Pariotrigona klossi* (Schwarz) (Apidae: Meliponini). Biological, ecological, ethological, feeding and parasitological aspects of these stingless bees have already been described and discussed (Bänziger *et al.* 2009). Although infrequently collected (until recently), *L. furva* has been reported from N and C Thailand, *L. cacciae* also from elsewhere in SE Asia and India, and *P. klossi* from S Thailand and elsewhere in Sundaland (Sakagami 1975; Engel 2000; Michener 2000, 2002, 2007). We found them at well over a dozen sites in N and S Thailand, but extremely localized, viz. within a radius of about 100 m around their presumed nest. Their scattered distribution, diminutive size, surreptitious tear drinking behaviour, and people's confusion of them with drosophilids, largely explain why their tear feeding habits were so long overlooked. Nevertheless, the lachryphagous (and less pronounced sweat-sucking) habits were highly predictable and, with seasonal fluctuations, present throughout the year; at certain sites and periods, dozens of specimens may circle around one's head.

The bees' main host were humans, but *L. cacciae* visited also dog (*Canis familiaris*) and *L. furva* zebu (*Bos indicus*). This is unusual when compared to tear drinking moths, the hosts of which are Ungulata, Proboscidea and occasionally humans, but never Carnivora (e.g. de Joannis 1911; Reid 1954; Büttiker 1964; Bänziger & Büttiker 1969; Bänziger 1995).

However, some unexpected hosts have also been noted among the Lepidoptera. In Brazil the butterfly *Dryas iulia* (Fabricius) (Nymphalidae) has repeatedly been reported to visit the eyes of the yellow-throated caiman (*Caiman latirostris*) and in Peru the yellow-spotted side-necked turtle (*Podocnemis unifilis*) (Turner *et al.* 1986). Hand (1991/1992) appears to be the first to have published a photograph (taken by Mr. Michael Fogden) of butterflies on the head of a reptile. Lamas (1986) mentioned that pierids also visit the heads of species of both reptile families. More exceptional were three cases where the noctuid *Hemiceratoides hieroglyphica* (Saalmüller) applied its proboscis to the eyes of the birds *Neewtonia brunneicauda* (Vangidae) and *Copsychus albospectularis* (Muscicapidae) in Madagascar (Hilgartner *et al.* 2007). Also exceptional was the documentation of the nymphalid *Salamis anteva* (Ward) (several specimens or several times the same individual, same site, same day) taking tears from a person, again in Madagascar (Duckworth *et al.* 2009).

Since study of the bees' host range (other than humans) has been preliminary, the aim of the present research was to assess the host spectrum in more detail, update data on *Lisotrigona*, as well as to provide a greater insight into the lachryphagy by insects.

MATERIAL AND METHODS

Because of the mentioned narrow localization of the bees, potential hosts were brought to two promising sites in Chiang Mai Province, N Thailand, where our eyes had been regularly visited by *Lisotrigona*. Main site (A) was at the foot of a limestone rock face near Chai Prakan, 700 m a.s.l., Fang District, where *L. furva* and to a very minor extent *L. cacciae* were present. Site (B), Ton Luang Temple, 760 m a.s.l., Chiang Dao District, was a synanthropic spot, surrounded by secondary forest,

where mainly *L. cacciae* but only occasionally *L. furva* visited human eyes. For more habitat details see Bänziger *et al.* (2009, 2011).

In order to assess the broadest potential host range, the hosts selected were as distantly related as possible, i.e. on a class or order level. For birds, a rooster (*Gallus gallus*), Phasianidae, var. 'Pradu Hangdam', 3 kg, was selected. For reptiles, the yellow tortoise (*Indotestudo elongata*), Testudinidae, 2.7 kg, carapace length 26.5 cm, was used. Since among mammals primates, ungulates and carnivores are already confirmed host orders, a lagomorph was chosen, viz. a rabbit, *Oryctolagus cuniculus*, Leporidae (Lagomorpha), var. 'Chinchilla', 2.6 kg. They were transported to and exposed at the study sites in a cage, 34x36x39 cm, bar spacing 3x5–7.5 cm, wide enough for the minute bees (body length 2.5–3.8 mm in *L. cacciae* and 3.3–4.4 mm in *L. furva*, depending on whether the metasoma was empty or full) to easily fly in and out unhampered. The wide-spaced bars also allowed photography between them, all by H.B.

The rooster, tortoise and rabbit were investigated singly on 6 April, 2010 (1110–1250 h at (B) and 1530–1635 h at (A)), 3 May, 2010 (1130–1300 h at (B) and 1500–1630 h at (A)), and 20 March, 2010 (1215–1330 h at site (B) and 1530–1730 h at site (A)), respectively. Dogs and cats were freely resident at site (B), so at site (A) our dog Bruno (local breed, 16 kg), on a leash, was initiated to bee rendez-vous on 6 June, 2010 (1230–1400 h). When humans were studied as hosts, we simply allowed them free access to our eyes without flipping them off.

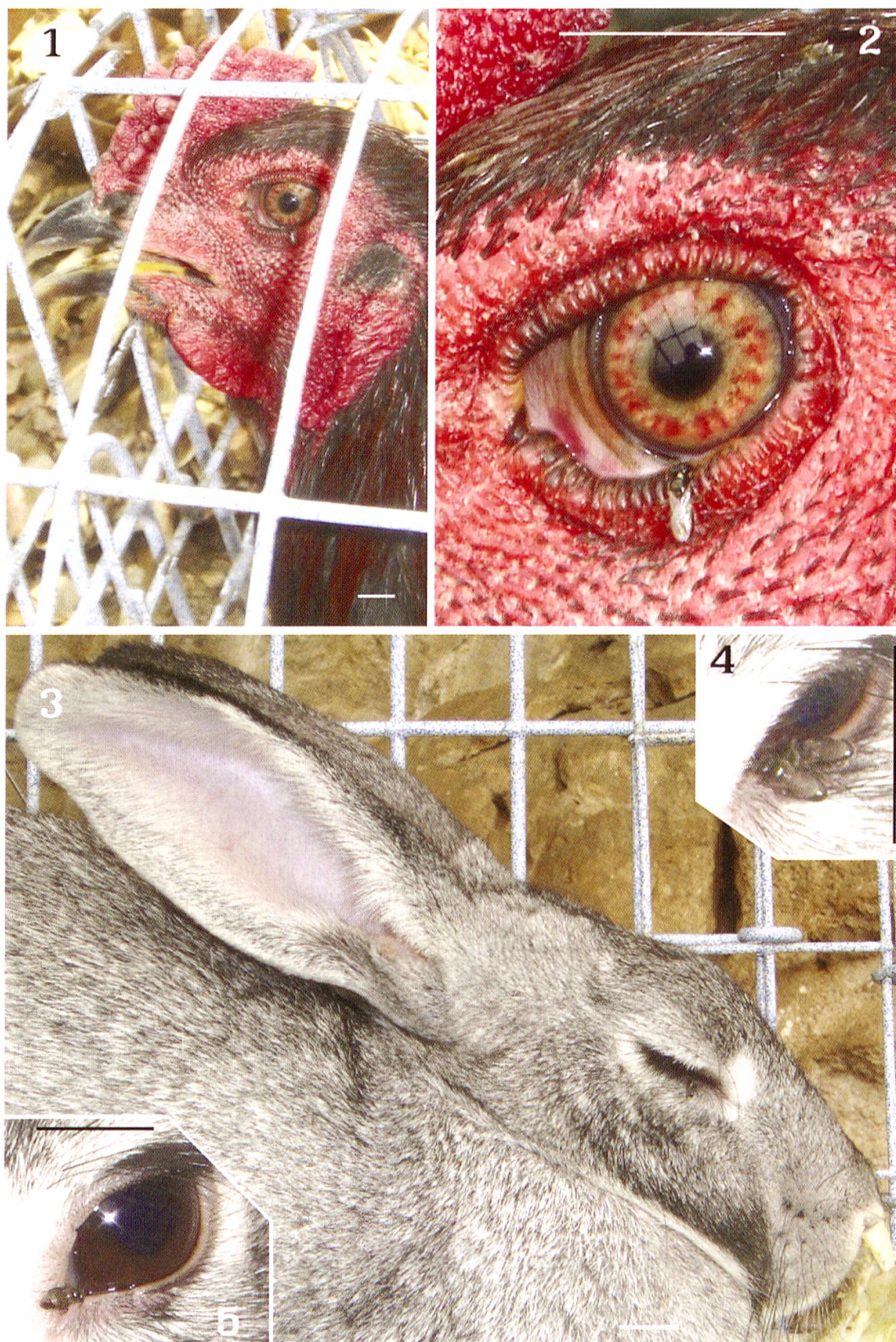
TAXONOMIC NOTES ON THE BEES

Lisotrigona cacciae and *L. furva* are extremely similar but they can be reliably distinguished by head size (Michener 2007). In the 23 *L. cacciae* and 25 *L. furva* available workers he analyzed, head widths varied around maxima at 1.13 mm and 1.30 mm, with a range of 1.08–1.18 mm and 1.25–1.35 mm, respectively. With hundreds of specimens of both species collected by H.B. in N and S Thailand in nearly three years, the range was, as expected, slightly broader, i.e. 1.05–1.23 mm for *L. cacciae* and 1.25–1.41 mm for *L. furva*, confirming Michener's findings. Specimens approaching intermediate sizes, e.g. large *L. cacciae* (1.23 mm) and small *L. furva* (1.25 mm) were rare. Further convincing data that two good species are involved, is their different nest entrance dimensions, round to slightly elliptic: in *L. cacciae* 1.5–4.5 mm across, where generally one or at most two bees (heads) were on guard, and in *L. furva* 4.0–7.0 mm (Fig. 10, Bänziger *et al.* 2011), where three or even four were on guard. Finally, the two species can be closely sympatric, in some cases with nests less than one meter distance from each other. Voucher specimens are deposited at the senior author's laboratory.

RESULTS

Observations under natural conditions (Fig. 8)

Since the last publication on hymenopteran lachryphagy (*loc. cit.*), but before the present study, the following new data were obtained: *Lisotrigona cacciae*, previously found from 240 to 760 m a.s.l., has now been confirmed up to 1200 m a.s.l.



Figs 1–5. Lachryphagous meliponine bees. — Fig. 1. *Lisotrigona cacciae* sucking tears from the eye of a rooster. Fig. 2. — Same by one *L. furva*. — Fig. 3. *L. furva* sipping tears from the closed eye of a rabbit. — Fig. 4. Two *L. furva* at the eye of a rabbit. — Fig. 5. *L. furva* imbibing tears from the eye corner of a rabbit. Bar length 1 cm.

on Doi Suthep, Chiang Mai, reaching well into tropical evergreen hill forest. The distribution of *L. furva*, collected from the eyes of H.B. at Angkor Vat, Siem Reap Province, is now extended to Cambodia. The previously unknown nests of *L. cacciae* and *L. furva* were discovered. This made it possible to observe workers entering their nests with large pollen loads on their hind tibiae, proving that they do in fact collect pollen, so lachryphagy is indeed facultative. They had rarely been collected from flowers and since workers sucking tears never carried full loads of pollen or only rarely minor amounts of it, evidence for a pollen diet remained elusive. Interestingly, lachryphagy did not occur in the direct vicinity of the workers' own nest (but can occur near the nest of other colonies of the same species). During the cool season, when at the elevation of the research sites the temperature in January can fall well below 15° C in the morning, *Lisotrigona* did not leave their nests until around midday when the outside air temperature approached 19–21° C. Before that time only their heads were evident at the entrance.

Lisotrigona regularly pestered dogs, and occasionally a cat, at site B. They lay around in the area, never fleeing the tiny bees, at most walking to another spot 10–20 m distant, with the bees in pursuit. When annoyed, they snapped the bees, shook their heads or scratched them off with a paw. But, possibly because the dogs were used to them and because the bees generally were gentle suckers (confirmed by personal experience of H.B., who at times had to check by mirror whether or not a bee was present at his eyes), they mostly tolerated them. When the hosts were drowsy or asleep the bees landed undisturbed near the eye and crawled to the lids where they found tear incrustations or minor amounts of tears leaking out between the lids — a droplet can feed several of the tiny bees. In trials with H.B. at a particularly pestilential site for *L. cacciae* on Doi Suthep, the bees were able to find his closed eyes, at least after bees had already visited his open eyes (the bees were then dislodged, but probably not before they presumably had scent-marked the spot). As soon as one bee landed at the closed eye, more followed in a crescendo, probably additionally guided by the sight of already present bees, finally resulting in an orgy of up to 10 closely settled suckers (Fig. 8). Such assemblages could also form on the forehead, arm or hand when the bees were persistently prevented from landing at eyes. They evidently were content in sucking sweat, the protein concentration of which must have increased due to evaporation.

Outdoor experiments with confined hosts

Rabbit (Figs 3–5)

There was little activity of *L. cacciae* around the head of the rabbit; one specimen attempted to settle at the eye but was not successful, but 41 *L. furva* managed, although some only briefly. Approach was often slow, as very long ciliae protected somewhat the eye. In many cases the bees landed somewhat below the eye and crawled up to settle around the middle of the lower lid, though the inner angle of the eye was also used. To get rid of the bees the rabbit shook its head or dislodged them by scratching with the paw. However, after some time the rabbit seemed to be resigned. It tended to keep the eyes closed to reduce annoyance but from its mild reaction the nuisance did not seem to be strong. At any rate, the bees were not deterred and were able to get to the lids, or sneak in between them since they were not firmly closed (Fig. 3). At times 3–4 bees were at one eye and 2–3 at the other.

Rooster (Figs 1–2)

Some 32 *L. cacciae* (up to two at the same time) and 12 *L. furva* settled at its eye, respectively. The bees often approached the eye directly, without much zig-zagging as with other hosts. A couple of times the rooster used its feet to scratch off a bee, at other times it shook its head. Unexpectedly, however, of all hosts the bird showed the least reaction to bees imbibing its tears, mostly letting them drink unopposed. The nictitating membrane had no effect on the bees, they just continued sucking lachrymation.

Tortoise (Fig. 6)

Fewer *L. cacciae* were active than on previous occasions. Only 7 specimens attempted to reach the eyes, one or two managing to briefly settle but were dislodged by the tortoise's eye blinking. At times, up to a dozen *L. furva* swarmed around the head of the tortoise and about 45 settled, usually somewhat below the eye, only occasionally at the eye corner or above the eye. A maximum of 6 bees were seen imbibing lachrymation at the same time from the area below the eye, which was visibly wet with tears. Also, whenever the bees touched the edge of the lower eye lid, they were dislodged by blinking. Reasons for these feeding positions are discussed below. Apart from blinking, the tortoise moved its head to one side and pressed the foreleg against it to remove the intruders, or it retracted the head into the carapace to squeeze them off, occasionally killing a specimen.

Dog (Fig. 7)

The main data are as mentioned in the chapter with observations under unconfined conditions. Unlike the resident dogs at site B, Bruno was rather restless at site A. Nevertheless, 12 *L. furva* settled to take tears, in two cases two bees were present at the same time.

Discussion

Are our experiments reliable proof for *Lisotrigona*'s host range spanning three vertebrate classes? The bees were attracted to the animals, were able to locate, approach, settle and suck from their eyes at the sites where the bees occurred in the wild or naturally in a synanthropic habitat. They were free to enter and leave the cages without impediment. For the tiny *Lisotrigona*, flying through the wide-spaced cage bars must have been little different from approaching a flower in tall grass or a bush thicket. Hence the caged animals are evidently true hosts of the bees. However, it may be argued that, even though the hosts had ample possibility to prevent the bees from landing or to dislodge them, the hosts were precluded from fleeing the intruders, so that the experiments were not fully adequate substitutes of what may occur in the wild. Obviously this does not apply to tortoises whose speed is proverbial. *Lisotrigona* will persistently circle around the head and attempt to settle at the eyes of a human, even when he is walking and, once landed and firmly gripping ciliae and lid, will continue to drink tears, even if he runs or moves his head vigorously (*loc. cit.*). As to the rooster, its very mild or lack of reaction to *Lisotrigona* sucking its tears lets one surmise that in most cases it will not flee the bees in nature. The rabbit's reaction under natural conditions can be expected to be comparable to the dog's and tolerate the bees, at least while resting, dozing or asleep in



Figs. 6–7. Lachryphagous meliponine bees. — Fig. 6. Five *Lisotrigona furva* sucking flowed-down tears below the eye of a yellow tortoise. — Fig. 7. *L. furva* at the eye of a dog. Bar length 1 cm.

open-air enclosures of farms (wild rabbits, sleeping in burrows, would not be accessible to the bees since they avoid dark recesses, except their nests; besides there are no indigenous rabbit species in Thailand). The country's only autochthonous lagomorph, the Siamese hare (*Lepus peguensis*), is mainly crepuscular-nocturnal (Parr 2003), so that the strictly diurnal *Lisotrigona* will encounter it dozing or asleep in its nest ('form') on the ground in thickets. Incidentally, a wild hare inadvertently disturbed by us was seen running for cover less than 100 m from the spot where we exposed the rooster to bee attacks on 6 April, 2010. The closest wild relatives of the dog in Thailand are the golden jackal (*Canis aureus*) and the red dog (dhole) (*Cuon alpinus*). As to the rooster, the local, and in fact all domestic chicken breeds worldwide, descended from the jungle fowl (*G. gallus*), native to SE Asia. The yellow tortoise is also widespread from India to Indochina.

Regarding the intensity of the reaction to sucking bees, the zebu's were, besides the rooster's, the mildest, if there was any. Its flipping the ears from time to time was clearly to dislodge the rather annoying face flies from its eyes, thereby removing also *L. furva*, but they all readily returned (*loc. cit.*). It has already been mentioned that it is thanks to *Lisotrigona*'s sneaky approach, gentle tear drinking manners and diminutive size that occasionally they can snatch tears from unwitting man. The finding that *L. cacciae* can congregate at closed eyes (Fig. 8) means that they could have unopposed access to lachrymation if he is taking a siesta in the open.

Lisotrigona furva's assembling somewhat below the eye of the tortoise is understandable on two counts. The nasal duct is absent in tortoises (Mihalkovics 1898, mentioned in Witmer 1995), which in mammals and birds drains tears and prevents their spilling over. Superfluous tears overflow the lower eye lid of tortoises, dry up there (Schmitz, pers. comm.) or run down the cheek to some extent. Secondly, the eye lid appears to be quite sensitive in tortoises, hence their consistent blinking when bees are present. Consequently they have to settle somewhat below the lower eye lid which incidentally is the part which moves upwards to close the eye. The upper eye lid moves little and is protected by a row of scales. Bees were able to settle there unchallenged. However, due to their minuteness their proboscis is short, reaching less than 1 mm beyond their front, and so it cannot extend sufficiently to reach the tear-rich area. This must be the reason why *Lisotrigona* overwhelmingly, and in all hosts, imbibe tears from below rather than above the eyes. In the average-sized lachryphagous moth *Lobocraspis griseifusa* Hampson (Noctuidae) the proboscis is 13 mm long and it successfully obtains tears from above the eye.

The third tear drinking bee species, *Pariotrigona klossi*, being absent in the present study area, could not yet be tested for its host range. Although it exhibited a somewhat less pronounced lachryphagy in man, we do not expect it to have a significantly different host spectrum from that of *Lisotrigona*.

Because of the very long field research periods carried out on lachryphagous moths, they are the best studied tear drinkers, including their hosts. Their range is: Ungulata (Bovidae, Camelidae, Cervidae, Giraffidae, Hippopotamidae, Suidae, Equidae, Rhinocerotidae, Tapiridae), Proboscidea (Elephantidae), Marsupialia (Macropodidae) and Primata (Hominidae) (de Joannis 1911; Shannon 1928; Reid 1954; Büttiker 1964; Büttiker & Gallagher 1980; Bänziger 1987, 1995; Bänziger &



Fig. 8. *Lisotrigona cacciae* at the closed eye of H.B. who photographed himself. A packed congregation of 9 workers are snatching tears from the inner corner of the eye, one from the outer corner, yet another is on the eyebrow. Bar length 1 cm.

Büttiker 1969). A special case, requiring confirmation, is whether birds are regular (not just accidental) hosts of the noctuid *Hemiceratoides hieroglyphica* (Hilgartner *et al.* 2007), because that particular association is the most unexpected, and its study was beset with problems, as discussed by Bänziger (2007) and Duckworth *et al.* (2009). The case of man as a host to the butterfly *Salamis anteva* in Madagascar is possibly accidental (Duckworth *et al.* 2009). On the other hand, butterflies such as *Dryas iulia* and species of several pierid genera, have been repeatedly seen settling at eyes of caimans and turtles, at various locations in Brazil and Peru (Turner *et al.* 1986; Lamas 1986). Thus, whereas lachryphagous Lepidoptera (some 100 species worldwide) as a whole may have as wide a host range as the tear drinking Hymenoptera (three species so far), no single lepidopteran species spans three classes as both *Lisotrigona* species do.

Assessment of the host range is not only interesting in comparison with other tear drinkers but important also for evaluating their medical and veterinary implications, and for understanding the significance behind lachryphagy for the bees.

Their potential for pathogen transmission has already been discussed (Bänziger *et al.* 2009) and the finding of their wide host range can only increase the implications. But why do *Lisotrigona* and *Pariotrigona* take tears instead of the more accessible sweat (which they do to a very minor extent only), unlike those meliponines which are anthropophilous but not lachryphagous (11 species out of 20 so far observed by the authors in Thailand)? We proposed that they imbibe tears for their content of proteins which is more than 200 times that found in sweat, instead of only for its content of salt and water (*loc. cit.*). We suggested that they use the proteins (albumin and globulin) to feed their young, e.g. as a supplement to pollen when this is in short supply (*loc. cit.*). But the question is whether the bees would be able to find and access hosts frequently enough to obtain suitable amounts of lachrymation. The established broad host range lets us surmise, in Thailand, a potential host supply of about 45 large to medium-sized terrestrial mammal species (18 Ungulata, 15 Carnivora (not counting Viverridae and Mustelidae), 12 Primata, 1 Proboscidea, but not counting the Pholidota, Dermoptera and Rodentia (Lekagul & McNeely 1977; Francis 2001; Parr 2003)), 21 bird species (only Phasianidae counted (Lekagul & Cronin 1974) although there would be dozens of medium-sized birds of other families), and 17 reptilian species (3 Crocodilia, 14 Testudines (Cox *et al.* 1998)). Furthermore, since *Lisotrigona* can also occur synanthropically, domestic animals such as dogs, zebu, water buffalo (*Bubalus bubalis*), chicken, pig (*Sus scrofa*), are likely to play a significant role as hosts since they are ubiquitous in rural villages. In summary, despite the limited foraging flight range of *Lisotrigona*, there seems to be a potentially sufficient supply of hosts for the bees to obtain tears opportunistically. Humans appear to be the most attractive ones (though perhaps not the most successfully exploited ones), possibly because they are the only species secreting sweat (with partial exception of hippopotamuses whose 'sweat' is not quite the same). Perspiration must produce a more intense odour plume than lachrymation and thus could initially guide the bees from long distance. At close range, the odour of tears will be the leading attractant, besides visualization of the host's eye and bees already present there, if any. However, size also plays a role, humans being far larger than the test animals. Lachryphagous moths frequent large mammals (elephant, water buffalo) far more than barking deer (*Muntiacus muntjak*) or goat, and the mouse deer (*Tragulus* spp.) is not visited. Finally, what must significantly improve *Lisotrigona*'s ability to obtain tears is that as eusocial insects, their communication and recruiting system is highly sophisticated: in fact on a par with that of honey bees. Depending on the species, Meliponini can communicate by various 'dances', sound pulses, odour trails and food marking scents (e.g. Lindauer & Kerr 1958; Esch *et al.* 1965; Nieh & Roubik 1998; Nieh 2004). It is likely that the observed crescendo of *Lisotrigona* arrivals at a host eye is due to one or a combination of such communication strategies.

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