Bees (Hymenoptera: Apidae) That Drink Human Tears

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ABSTRACT: Lisotrigona cacciae, L. furva and Pariotrigona klossi (Meliponini, Apidae) workers drank lachrymation (tears) from human eyes in more than 262 naturally-occurred cases at 10 sites in N and S Thailand during all months of the year. A few visits were also seen to eyes of zebu and dog, indicating a probable broad mammalian host range. On man the bees were relatively gentle visitors, mostly landing on the lower eyelashes from where they imbibed tears for 0.5–2.5 min, often singly but occasionally in congregations of 5–7 specimens per eye. Less typically, they also took sweat, a behavior found in 11 other species of anthropophilous meliponines which are not lachryphagous. Nine further meliponine species were not anthropophilous. Lachryphagy in bees is compared to lepidopterous tear drinking and related feeding strategies such as puddling by various insects, mostly for salt requirements but in other cases proteins are sought. We propose that L. cacciae, L. furva and P. klossi drink tears for their high content in proteins in addition to, or in lieu of pollen, rather than only for salts and water. Few reports of flower visitation, rare presence of only minor amounts of pollen on legs, reduced pilosity, absence of resin on body and legs, presence of a strongly extensible metasoma for fluid transport, are all interpreted as possible indications of an adaptation to lachryphagy for proteins. The potential hazard of pathogen transmission by eye-visiting bees is discussed.

KEY WORDS: Anthropophily, cattle, dog, Drosophilidae, lachryphagy, Lisotrigona, man, Pariotrigona, eye diseases, stingless bees.

Stingless bees (Meliponini: Apinae: Apidae) are a species-rich tribe of highly eusocial bees (Michener, 1974). Besides foraging for nectar and pollen, they also suck plant saps, honeydew, and collect nest-building material such as resin, soil and, at least in the neotropics, even feces and carrion (e.g., Schwarz, 1948; Roubik, 1982; Wille, 1983; Baumgartner and Roubik, 1989; Michener, 2000). Among carrion visitors, a few species of neotropical Trigona have developed obligate necrophy (Roubik, 1982; Baumgartner and Roubik, 1989; Camargo and Roubik, 1991; Noll et al., 1997; Serrão et al., 1997). However, species of African Cleptotrigona and neotropical Lestrimelitta are robber (cleptobiotic) bees (Portugal-Araújo, 1958; Sakagami et al., 1993) which, in complex raiding parties, steal food, wax and resin from other meliponines, generally without exterminating the victim. Finally, many meliponines are known to settle on the skin of man to suck perspiration (Schwarz, 1948; Barrows, 1974; Michener, 1974, 2000), a behavior also exhibited by sweat bees (Halictidae) and occasionally by other bees. It appears that there are no prior publications about bees seeking lachrymation (tears) from humans or other vertebrates.
Diurnal lachryphagy (tear drinking) by various insects, especially flies (Diptera) of the families Chloropidae, Cryptochetidae, Drosophilidae, and Muscidae, on cattle, horses and other mammals including man, is common knowledge. Less well-known is nocturnal lachryphagy exhibited pantropically by moths (e.g., de Joannis, 1911; Shannon, 1928; Reid, 1954; Guilbride et al., 1959; Büttiker and Whellan, 1966; Büttiker, 1973a, b; Bänziger, 1973, 1988). Some 100 species of six lepidopterous families have been found to be involved in imbibing tears from Ungulata, Proboscidea, and some Marsupialia; human eyes are occasionally visited by 23 species (Bänziger, 1992, 1995). Tear drinking is related to both the sucking of sweat (whether on hosts or from the vegetation where it has been smeared off) and to the ‘puddling’ behavior (‘filth’ visiting and ‘sodden earth’ sucking) by dipterans, hymenopterans and lepidopterans (e.g., Collenette, 1928; Bänziger, 1973, 1996; Arms et al., 1974; Adler, 1982; Roubik, 1989; Beck et al., 1999; Michener, 2000). Salt (NaCl) has been shown to be a main constituent sought by halictid bees (Barrows, 1974) and lepidopterans (Adler and Pearson, 1982; Pivnick and McNeil, 1987; Smedley and Eisner, 1995; Boggs and Dau, 2004; Bänziger, 2007). However, as pointed out by Bänziger (1973), tears are special in having a relatively high content of protein (as high as salt) and he proposed that at least some lepidopterans imbibe lachrymation because of its protein content. There is experimental evidence that amino acids are taken by some butterflies which visit puddles (Beck, 2007), suck nectar (Mevi-Schütz and Erhardt, 2005) or take pollen (Gilbert, 1972).

Apidological research in Thailand has mainly focused on honeybees, but wild apines including meliponines have also been studied (Burgett and Sukumalanand, 2000; Burgett et al., 2005; Rajitparinya et al., 2001). Some 30 species of stingless bees have so far been found in Thailand (Boongird, unpubl. data), including the recently described *T. sirindhornae* (Michener and Boongird, 2004).

The present account details the tear drinking habits of the minute stingless bees *Lisotrigona cacciae* (Nurse), *L. furva* Engel and *Pariotrigona klossi* (Schwarz) (Apidae: Meliponini) at the human eye, the first time that lachryphagy is reported for Hymenoptera. Further, we compare the habit and its physiological significance to that of other anthropophilous habits (liking humans, in this case body fluids) in meliponines and other insects. Finally, we propose an explanation for this unexpected habit in hymenopterans, why it has remained so long unreported, and discuss its medical implications.

**Materials and Methods**

Lachryphagous bees were studied at the following sites. North Thailand: (A) in forest, 600 m a.s.l., (B) at water fall, Pha Lad forest temple, 300 m distant from (A), Doi Suthep, Chiang Mai Prov. (C) garden of former and (D) garden of new residence of H.B., 350 m a.s.l., SW and NW of Chiang Mai town. (E) near Ton Luang Temple, 760 m a.s.l., Chiang Dao, Chiang Mai Prov. (F) Pang Ma Pha village, 590 m a.s.l., (G) about 20 km W of latter, 720 m a.s.l., Mae Hong Son Prov. South Thailand: (H) Phato, 300 m a.s.l., Chumphon Prov. (I) and (J), two hills above Phang Nga, 10 km from each other at 410 and 240 m a.s.l., respectively, Phang Nga Prov. The habitats included mixed deciduous tropical forest on granitic (A, B) and limestone (E–G) soil, secondary tropical evergreen rain forest (H), primary evergreen tropical forest on limestone (I–J, 3 and 1 hr hiking distance from the nearest house, respectively), a semi-
wild garden (C) and an old fruit orchard (D) both near secondary mixed deciduous tropical forest. Tear drinking bees were not found in many, appropriate-looking sites not mentioned here. A total of 38 investigations of 2–8 hr each were carried out at sites A–J, December 2007–November 2008.

For ethological study, bees were given complete freedom of action in their behavior by not interfering in their approach, landing and sucking from one’s eyes, though it was often difficult not to involuntarily blink the lids when the landing was abrupt. To aid observation of the insects’ behavior at one’s own eye, a pocket mirror was used. For capture, a semi-transparent film canister was placed over one’s eye with the insect, which seemed little affected, if at all, in its eagerness to suck. Once it flew to the bottom of the canister, this was rapidly capped. Only insects which sucked at least 10 sec were considered lachryphagous. Except for Fig. 7 by Ms. K. Srimuang, all photographs are by H.B. who photographed himself. All tear drinkers shown were collected to verify identification.

Trials with following baits (one or several at the same time) were presented at sites (A), (E), (H), (I), (J): 1. steamed fish (sardine), 2. salted (smoked and non-smoked) fish, 3. smoked ham, 4. cheese (Gruyère), 5. fresh meat (pig), 6. smelly but not yet decomposed meat, 7. Ovaltine powder (Nestlé’s beverage). The bait trials were not systematic except on April 5, 2008 at (E) where types 1, 2, 4–6, were laid out in trays on the ground at 1–2 m distance from each other, interchanged every half hour, and watched for 4 hr. Use of baits did not interfere with tear-seeking bees because, as it turned out, they were not attracted to the baits, unlike other stingless bees.

Field observations were carried out by H.B., with frequent assistance by S. Bä. Identifications of meliponines were mainly by S.Bo. *Lisotrigona furva*, recently described by Engel (2000), is extremely similar to *L. cacciae* and the most accurate and practical method to differentiate them is by size (Michener, 2007). Our identifications are based on the latter’s analysis, viz. range of head width in *L. cacciae* 1.075–1.175 mm, in *L. furva* 1.250–1.350 mm. *Pariotrigona klossi* was identified with the aid of Schwarz (1939) and Michener (2000). The only other similarly minute species, the non-lachryphagous anthropophilous *Trigona fuscobalteata* Cameron, can be clearly distinguished by several characters (see Michener, 2000). The species *T. laeviceps* Smith and allies, and the bicolorous group around *T. sarawakensis* Schwarz, are somewhat problematic; our identifications are based on Sakagami (1978) and Sakagami and Inoue (1985), respectively.

Voucher specimens of stingless bees are or will be deposited in the Department of Entomology, Faculty of Agriculture, Chiang Mai University (DEFACU), the National Parks, Wildlife and Plant Conservation Department, Bangkok (DNP), and the Entomology Division, Natural History Museum, University of Kansas, Lawrence, Kansas, USA.

**Results**

We collected a total of (lachryphagous and non-lachryphagous) 205 *Lisotrigona cacciae*, 89 *L. furva*, and 22 *Pariotrigona klossi*. *Lisotrigona cacciae* was found at sites A, B, E, I, J; *L. furva* at A, B, C, D, G, H, I (twice also at E and once at F); whereas *P. klossi* was present only at I. Hence at I all three species and at A, B both species of *Lisotrigona* were present. Both *Lisotrigona* were found in N and S Thailand, in seasonally dry and in everwet climates, in primary and secondary forests, and in
Figs. 5–7. Meliponine workers sucking human tears. 5. Seven *L. cacciae* at eye (one airborne, one on top of another); feeding at the eye corner and at the upper lid is less common. 6. *L. furva* feeds while settled on the ciliae; note proboscis (lower end of line) and distended metasoma. Self-portraits by Hans Bänziger. 7. A tickling assemblage of about 50 meliponine workers sucking sweat from arms and hands of H.B. Most are *Trigona terminata*, but *T. laeviceps* and *T. pagdeniformis* are also present. Photograph by Ms. Kanokorn Srimuang. (Printed with permission).
more or less synanthropic habitats. *Pariotrigona klossi* was found only in primary evergreen forests on limestone in S Thailand. So far, both genera were only found at elevations lower than 800 m a.s.l., although habitats appeared suitable up to well over 1000 m a.s.l. The bees visited human eyes during all months of the study period.

Lachryphagy was most conspicuous during hot days of the dry season, when 35% RH and 36°C were registered (site E, 5 April 2008), but occurred during the same period also near streams and puddles (site B) which were frequented by various bees but not *Lisotrigna*. Tear sucking continued throughout the rainy season, when 90% RH and 27°C were measured (site G, 3 September 2008).

The lachryphagous habits of bees were first noted during pollination studies in tree canopies by H.B. *Lisotrigona cacciae* and *L. furva* landed at his eyes but not on any of several species of flowers under observation, although other meliponines, viz. *Trigona collina* Smith and *T. apicalis* Smith, did visit such flowers. Both *Lisotrigna* were later found to be just as commonly lachryphagous also at ground level. Throughout the study period, *L. furva* was found only twice on flowers, viz. one individual on the liana *Tetrastigma baenzigerii* C. L. Li and another on *T. hookeri* (Lawson) Planchon (Vitaceae), although the main pollinators of both were actually *Pachyhalictus burmanus* Blüthgen (Halictidae) (Bänziger, unpubl.). *Lisotrigna cacciae* and *P. klossi* have not yet been seen on flowers. Also, at site B where both *Lisotrigna* species imbibed tears, neither was ever seen visiting *Wedelia trilobata* (L.) Hitch. (Compositae) which flowered near by, despite it being frequented by stingless bees (*T. laeviceps*) and many other insects. Lachryphagous bees were not attracted to any of the 7 baits offered.

When seeking tears, *Lisotrigna* first circled around one’s head, then zig-zagged in front of the eyes, occasionally the ear or the neck, then generally back again to the eyes. After a few seconds it flew toward the eye, landed on the lower eyelashes and, grasping the ciliae, crawled toward the eye where it plunged the extended proboscis into the gutter-like trough between lid and eye ball to suck lachrymal fluid (Figs. 1–3, 5–6). In many cases the landing on ciliae was so close to the eye that the proboscis could reach the trough without crawling. During sucking, all legs either continued to clutch the ciliae (Fig. 6), or the fore legs were placed on the lid or conjunctiva (Fig. 1, 3), while the middle and hind legs continued to grip the ciliae. In rare cases a foreleg was placed onto the eye ball, and in one case the bee even climbed onto it with all legs. Landing at the corner of the eye, on the upper eyelashes (Fig. 5), or on the skin below the lower eyelashes, was infrequent. In this case the bee pushed itself through the gaps between the ciliae, or climbed them to reach the eye. On landing, automatic blinking with the eye often prevented the bee from getting a firm hold, causing it to fall off the eyelashes. If so, the bee persistently tried again and again until it was successful, or finally gave up and flew off. In a very few cases the approach was so gentle that the host (H.B.) did not realize he had a *Lisotrigna* attached to his lid, imbibing his tears. After landing and whilst sucking tears, H.B. often could barely feel the presence of a bee; indeed, checking by mirror was then required to make sure whether it was still there or had left. However, when several bees were involved, the experience was rather unpleasant, causing strong tear flow. Once a bee had settled and more were approaching, these tended to settle near each other in a row. Closing the eye did not necessarily dislodge bees but some continued to suck at the slit. They were even able to find and settle at closed eyes (experiment with a small swarm which was waived away after some specimens had taken tears). Landing on front, temple,
cheek, nose and, less frequently on hair, ear, hand, arms, to suck sweat also occurred, especially on very hot days, when one perspired more profusely, or when mass assemblages occurred. Nevertheless, it was evident that the primary aim of the vast majority of *Lisotrigona* were the eyes to obtain lachrymation.

Feeding time was 0.5 up to 2.5 min, in most cases 0.8–1.5 min. The metasoma became fully distended to reach 1.8 mm in length (about double its unfilled length) and much widened, exposing the translucent membranes between tergal and sternal plates of each segment. In this turgid state, clear (lachrymal) fluid was evident behind the membranes, i.e., in the crop. In Figs. 2, 6 the distention had not yet reached its maximum.

At any particular study site, visits to eyes occurred within an area 50–200 m wide. If one walked off the spot where *Lisotrigona* were circling around one’s head, the bees could follow for a 100–200 m. Visits were single (site F) or sporadic events (sites B, C, D), or occurred in a succession of single landings over a period of many minutes to several hours (sites A, G, I, J), or could be in aggregations of up to 20–30 bees swarming around the head, resulting in up to seven bees sucking at the same time at one eye and five at the other (site E, 13 January and 5 April 2008)(Fig. 5). At sites A, B *Lisotrigona* regularly did not start arriving until ¼ to 1 ½ hours after the observer had arrived, whereas at sites E, G they started circling 5–10 min after one arrived.

At site G, 21 June 2008, *Lisotrigona furva* were seen circling, landing and sucking from the eyes of a ruminating zebu (*Bos taurus indicus* L. (Bovidae)) which was molested at the same time by many face flies. The zebu regularly flipped its ears to get rid of the flies, thereby chasing off the bees as well, but flies and bees just as quickly returned to suck. After less than five minutes of observation, bees but not flies started to settle at our own eyes, 5–10 m from the zebu. Some *L. furva* continued to arrive and suck from our eyes after the zebu had walked off, presumably with some *L. furva* and flies at its eyes or in pursuit. At site E, 23 August 2008, after our eyes had been visited by several *L. cacciae* for half an hour, a dog (*Canis familiaris* (Canidae)) came. A few minutes later, up to three bees tried to get at the eyes of the dog which attempted to chase them away. They always returned and two managed to suck tears undisturbed once they settled at its eye; however, we continued to be the main attraction even in presence of the dog, and for a good hour after it had left.

An overall total of 159 specimens of *Lisotrigona cacciae* and 60 of *L. furva* were collected whilst sucking from the eyes of H.B., 27 and 16, respectively, from assistants. However, many bees avoided capture, were involuntarily flipped off, or were not successful in landing. During mass aggregations not all drinking bees were collected.

Behavior of the much rarer *Pariotrigona klossi* was similar but it exhibited a rather weaker lachryphagy and sucked sweat more often than *Lisotrigona*. We managed to capture only two *P. klossi* from the eye (H.B.) (Fig. 3) but several more were present. At the only site where we found this species, there was a nest 40 m distant on the other side of a cliff. Workers were seen entering and leaving their coral-like nest, a system of interconnected tubes, each with a tiny entrance ornamented with crystal-like wax formations. At least a few *P. klossi* returning to their nest had hind legs fully loaded with pollen; no lachryphagous or anthropophilous behaviour occurred on H.B. at the nest, but observation was possible only for 0.5 hr one late afternoon. No nest of *Lisotrigona* was found at the study sites despite repeated searches.

Of the 262 *Lisotrigona* collected from human eyes, none had a full load of pollen, two *L. cacciae* carried very little pollen and 18 only very few single grains, one *L. furva* had a fair amount and three had very little or just single grains, the remaining
Lisotrigona carried no pollen. The two *P. klossi* from the eyes had little pollen or only few grains. The pollen was carried mainly on hind tibiae, dispersed on venter, or sometimes on basitarsi. Also, no *Lisotrigona* and *Pariotrigona* collected from eyes carried any resin or other material. They were not ‘sticky’ like most other meliponines but glossy, dry, clean.

No unpleasant perception at eyes persisted after one or a few bees visited. But the mentioned hours-long tear drinking orgy caused a slight reddening of the eye and conjunctiva in H.B. and S.Bä., and a sensation of irritability and itching which persisted for 36 hr.

The other anthropophilic meliponines were non-lachryphagous, and only took sweat from man. In most cases such species settled as single specimens on bare skin of hand and arms of the observers, more rarely on the head or clothes. However, occasionally some species would congregate in fairly large numbers to become a nuisance. For instance, while studying orchid pollination in the tree canopy, 20–30 workers of *Trigona flavibasis* Cockerell, which were not attracted to the orchids, sucked sweat from arms and hands of H.B. (Doi Inthanon, 22 February 1993). Rather more obnoxious were mixed congregations of up to 60–100 *T. terminata* Smith, *T. laeviceps* Smith and *T. pagdenformis* Sakagami crawling and sucking sweat over all exposed parts of the skin of H.B. (Fig. 7), and as many on his assistant 50 m away, in persistent day-long tickling scourges (Hills beyond Umphang, 14–16 May 2008). (Insect repellents could not be used because of ongoing pollination research.) *Lisotrigona* were absent from both sites. The worst thing to do was to crush one of them, because this released even more of the assembling pheromone (clearly perceivable even to the human nose) and attracted increasing numbers of them. Most non-lachryphagous sweat sucking bees had pollen, resin and/or other materials on their hind tibiae.

Table 1 summarizes the feeding habits of lachryphagous and non-lachryphagous anthropophilic stingless bees.

The non-anthropophilic species, *T. collina* Smith and *T. doipaensis* Schwarz, exhibited ‘puddling’ behavior, the drinking of moisture from the sand of a pool ‘contaminated’ with decomposing organic matter and minerals (presumably NaCl). Nearby fresh water from a stream was not visited. Settling on fish, meat and cheese baits involved no evident biting off of chunks of these resources. Instead, meliponines were seen sucking liquid exudates from these which, besides salts, must have contained more or less decomposed proteins, amino acids, lipids, and minor constituents.

Species so far not found to be anthropophilous are *Trigona apicalis* Smith, *Trigona canifrons* Smith, *Trigona collina* Smith, *Trigona doipaensis* Schwarz, *Trigona fimbriata* Smith, *Trigona hirashimai* Sakagami, *Trigona melanoleuca* Cockerell, *Trigona thoracica* Smith, *Trigona* sp. 2 aff. *flavibasis* Cockerell. Only a very few specimens of *T. doipaensis*, *T. hirashimai* and *T. sp. 2 aff. *flavibasis* were found and observations on larger populations may well show them to suck perspiration.

Discussion

No information on foraging from flowers is available for *Lisotrigona cacciae* and *Pariotrigona klossi*. *Lisotrigona furva* had been collected from flowers of *Callistemon* sp. (Myrtaceae) and *Buddleja asiatica* Lour. (Buddlejaceae) in N and NE Thailand by S. Boongird and C. Michener (Engel, 2000). Here we add the flowers of two *Tetrastigma* species (Vitaceae), visited by a mere two *L. furva*. 


On the other hand, with well over 262 cases of drinking human tears by *Lisotrigona cacciae*, *L. furva* and a few by *Pariotrigona klossi*, at 10 localities in N and S Thailand, all months of the year, it is evident that lachryphagy must be a normal, though not exclusive, feeding habit of these species. During our study, we learned that local bee keepers at a site in SE Thailand occasionally were molested by tiny bees flying into their faces; also, Dr. P. Schwendinger and Prof. Dr. K. Fiedler got tiny meliponines into their eyes in N Thailand and Malaysia, respectively, but the matter was not further pursued. Since we also saw *L. cacciae* and *L. furva* at the eyes of zebu and dog, it can be expected that tear sucking from various mammals is common. (Mammals other than man have been given scant attention as potential hosts so far.) However, unlike lachryphagous lepidopterans and dipterans which do not take care of their progeny but are unrestricted in their dispersal, in eusocial bees the habit is limited to the foraging range around their nests. The small (3.2–4.0 mm long) *Trigona minangkabau* Sakagami and Inoue has an estimated range of 84–434 m (Inoue et al., 1985), the slightly larger *T. iridipennis* Smith (4.5–5 mm) flew up to 120 m from the nest (Lindauer, 1957), the much larger *Melipona fasciata* Latreille, 2.1 km (Roubik and Aluja, 1983), thus the minute *Lisotrigona* may fly only 100–200 m from their nests, since size of wing and body are predictive for flight distances in bees (Araújo et al., 2004). The very localized occurrence of visits to us corroborates this view. This narrow localization may be one explanation why lachryphagy in bees remained so long unreported. Another explanation is that people flip away such intruders, precluding the chances to identify them. Moreover, small bees are easily confused with ‘similar’ flies attracted to eyes, e.g., eye-gnats (Diptera: Chloropidae), Cryptochetidae, and especially certain fruit flies (Drosophilidae). Some drosophilids are widespread and common tear drinkers in China and Japan (Wang et al., 2002; Chen et al., 2005; Toda, pers. comm.) and are occasionally

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<thead>
<tr>
<th>Tear drinkers</th>
<th>Human tears</th>
<th>Human sweat</th>
<th>Salted, smoked fish</th>
<th>Gruyère cheese</th>
<th>Fresh meat</th>
<th>Ovaltine powder (wet)</th>
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<tbody>
<tr>
<td><em>L. cacciae</em> (Nurse)<em>1</em></td>
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<td><em>L. furva</em> Engel<em>1</em></td>
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<td><em>P. klossi</em> (Schwarz)</td>
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<td>Sweat suckers</td>
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| *T. flavibasis* Cockerell | | | | | | +
| *T. fuscobalteata* Cameron | + | + | + | | |
| *T. itama* Cockerell | + | | | | | |
| *T. laeviceps* Smith | + | | | | | |
| *T. minangkabau* Sakagami & Inoue | + | + | | | |
| *T. pagdeni* Schwarz | + | | + | | |
| *T. pagdeniformis* Sakagami | + | + | | + | |
| *T. sp. 3 aff. sarawakensis* Schwarz | + | | | | | |
| *T. sirindhornae* Michener & Boongird | + | + | + | | |
| *T. sp. 1 aff. sirindhornae* | + | + | | | | |
| *T. terminata* Smith | + | | | | | |

1 *T. cacciae* and *T. furva* also settled at the eyes of dog and zebu, respectively.
annoying in Europe (Otranto et al., 2006; Bächli, pers. comm.; Merz, pers. comm.). At sites A, E and F, fruit flies occasionally visited the eyes of H.B. but they were much more common at higher elevations and in more shady habitats (Fig. 4). Among 172 specimens of drosophilids caught while sucking from the eyes of H.B. (Bänziger, unpubl.), there were at least 31 species of Amiota, Apsiphortica, Paraleucophenga, and Phortica (more than half new to science) (Prof. Dr. M. J. Toda, pers. comm.). Such flies cannot be distinguished reliably from Lisotrigona while they circle around one’s head (too near to focus on), which most people will try to prevent anyway. Similar also were the sucking times (viz. 20 sec to 2.7 min in fruitflies), and the fact that they are a nuisance throughout the year in Thailand. Nevertheless, drosophilids tended to approach the eye by dancing in the vertical plane, often repeatedly bumping against one’s eye before landing on the eyelashes in more or less direct contact with the conjunctiva, whereas Lisotrigona zig-zagged in the horizontal plane and landed more gently.

Do meliponines suck tears for their content of water, salts or proteins? Whereas tear drinking was more conspicuous during hot dry weather, it occurred also where water was naturally available (e.g., nearby pools, streams), and during the rainy season when 90% RH was registered; hence water is not the only substance sought. NaCl salt has been mentioned to be one or the main constituent sought in sweat, as well as in such related sources as lachrymation, puddles, sodden earth mixed with animal body fluids, and ‘filth’ such as feces and carrion, by a variety of insects (references below). But there is strong indication that proteinaceous nutrients are also sought by certain species. To better understand this complex of related feeding habits, it should be noted that in most insect groups only the males are involved, although in a few groups only the females and in yet others both sexes visit such sources. For instance, virtually only males in puddling butterflies and moths (e.g., Arms et al., 1974; Adler, 1982; Beck et al., 1999; Bänziger, unpubl.); also males only in the vast majority of lachryphagous moths (viz. Geometridae, Pyralidae, Notodontidae, Thyatiridae, Sphingidae) including, significantly, the skin-piercing blood-sucking Calyptera moths (Noctuidae) (Bänziger, 1988, 1989, 1992); and again only males in the vast majority of tear drinking drosophilids (e.g., Otranto et al., 2006; M. J. Toda, pers. comm.; Bänziger, unpubl.). Notable exceptions with both genders involved were at least 19 species of sweat sucking hoverflies (Syrphidae) (Bänziger, 1996, Table 2; 2002, and unpubl.), and 10 species of tear drinking noctuid moths (Reid, 1954; Büttiker, 1973a; Bänziger, 2007). Intriguing are 8 species of sweat sucking blowflies of the genus Isomyia (Calliphoridae) where only females are involved (Bänziger, unpubl.), whereas in related blowflies Chrysomya and Lucilia neither sex is commonly attracted to human skin in Thailand. Only female bees of puddling Augochlora pura (Say) (Halictidae) are attracted (Barrows, 1974). With L. cacciae, L. furva and P. klossi we now have a special new case where the worker caste is actively involved in tear drinking.

The specific uptake of sodium from such sources has been proved to occur in male butterflies and moths and shown to be transferred to the females as ‘nuptial gifts’ during mating to replenish losses incurred during egg development (Adler and Pearson, 1982; Pivnick and McNeil, 1987) but may also be used by the males themselves for neuromuscular activity (Molleman et al., 2005). However, in certain cases there are indications that proteins (Beck et al., 1999) and/or amino acids (Gilbert, 1972; Arms et al., 1974; Mevi-Schütz and Erhard, 2005; Beck, 2007) play an additional role for males and females.
We propose that *Lisotrigona* and *P. klossi* primarily seek proteins from tears of humans and animals. Bänziger (1973, 2007) stressed that tears are special in having a high protein content, viz. more than two hundred times higher than perspiration: 670 mg protein (water soluble albumin and globulin) per 100 ml, whereas sweat has only 2.8 mg (Rauen, 1964). Tear drinking noctuid moths *Lobocraspis griseifusa* Hmps. and *Arcyophora* (three species), males and females, and a number of lachryphagous geometrids, pyralids and thyatirids (males only), were the first adult lepidopterans proved to have proteases capable of digesting proteins (Bänziger, 1973, 2007). Previously, adult Lepidoptera were thought to lack this ability (Wigglesworth, 1973). The resulting amino acids are assumed to be required by females for egg development, whereas in males, perhaps along with the salt, they may play a role as ‘male dowries’ for transfer to females during mating. However, they may also be used by the males themselves for neuromuscular activity, as possible ‘aphrodisiacs’, or as longevity factors.

While engorging themselves with tears, workers of *Lisotrigona* and *P. klossi* evidently store the fluid in the crop, which completely fills the very distensible metasoma. Once back in their nests they presumably disgorge it into storage pots or to receiver bees to be processed as protein-rich food for their progeny and themselves in lieu of, or in addition to, pollen. The findings that tear drinkers rarely carried pollen and at most only in minor quantity, and that they were seldomly or never found on flowers, seem to support the importance of tears as protein sources. This scenario is comparable to the habit described for neotropical necrophagous *Trigona* species (Roubik, 1982; Baumgartner and Roubik, 1989; Camargo and Roubik, 1991; Noll *et al.*, 1997; Serrão *et al.*, 1997). Carrion feeding has become obligatory in these species and is correlated with morphological reduction of the pollen-carrying devices and improved biting capacity by additional mandibular teeth. They masticate cadaver flesh and partly predigest it before it is ingested as a slurry and carried in the crop to the nest (Roubik, 1982). Mandibles are not required for sucking tears, hence one would expect, if at all, a reduction rather than their development. The two mandibular teeth are about normal in *L. furva*, but less prominent and less sharp in *L. cacciae*, whereas in *P. klossi* only a tiny basal tooth remains and the second is barely discernible by a minute fissure. Since *P. klossi* exhibits the weakest lachryphagy, the reduction is possibly a case of preadaptation. In our tear drinking bees we did not find evident morphological reductions of the corbiculae, although the lack of feathery hairs on the hind tibiae and the absence or reduction of hairs around the middle of the outer surface of the hind tibiae could be interpreted as a reduction in pollen-carrying capacity. However, there are other features which may be connected to their tear feeding habits. They have a large crop filling an extensible metasoma that can expand by about 5 times its normal (unfed) volume for tear transport. Lack of resin on legs and body (often present in similarly minute *T. fuscobalteata* and other non-lachryphagous meliponines) presumably reduces the danger of becoming entangled by eyelashes, of getting stuck to eyelids, or of chemically irritating the conjunctiva of the host’s eye. All these traits may well represent evolutionary adaptations to lachryphagy in our bees. On the other hand, tear drinking bees have to be more evolved than necrophages in some other respects because, unlike scavenging upon cadavers, snatching tears requires sophistication in finding, approaching, settling and imbibing fluid from watchful and sensitive eyes of live mammals without being detected. The high percentage (91%) of specimens
without pollen and the complete lack of resin among bees visiting eyes might suggest a division of labor, viz. specialized tear foragers. Our bees may be both facultative tear drinkers and opportunistic pollen collectors, depending on what is available.

Meliponines variously mark food sources or lay odorous trails using assemblage pheromones (e.g., Lindauer and Kerr, 1958; Michener, 1974; Nieh et al., 2003). Odor trail laying (pheromone placed every few meters) may not be efficient for utilizing highly mobile mammalian sources, but release of assemblage pheromones (detectable even by human nose) must have triggered the observed aggregations of sweat sucking Trigona spp., and probably also the swarms of Lisotrigona around us. It is likely that lachryphagous bees also mark the visited ciliae and lids. This is the best explanation for several observations, e.g., for how the bees were able to find closed eyes (after some bees had already sucked there but were then chased away), for the crescendo in numbers of bees settling at eyes, and for the unpleasant irritation felt for 36 hr on our eyes following tear drinking bee orgies.

The danger posed by necrophagous and other ‘filth’ visiting meliponines as carriers of pathogens deleterious to humans, has been assessed as being minimal in the neotropics (Baumgartner and Roubik, 1989). Those bees are essentially asynanthropic (not living in human habitats), and their glandular secretions and nest building materials have antimicrobial properties (Roubik, 1989). However, at least 13 species are anthropophilic in Thailand and several, including Lisotrigona, are partly synanthropic. Lisotrigona species are comparable to other eye visitors, e.g., lachryphagous drosophilids Phortica variegata Fallén, an intermediate host of the ‘oriental eyeworm’ Thelazia callipaeda Railliet and Henry (Spirurida: Thelaziidae) in E Russia and Italy (Kozlov, 1962; Otranto et al., 2005, 2006), as is P. okadai (Máca) in China (Wang et al., 2002). The nematode causes ocular thelazioses in man, dogs, foxes, cats, rabbits in China, Japan, Thailand, Russia, C and S Europe (e.g., Kozlov, 1962; Bhaibulaya et al., 1970; Otranto et al., 2005; Shen et al., 2006; Schaffner, 2008). Eye gnats (Chloropidae) are suspected vectors of the bacterium Haemophilus influenzae biogroup aegyptius (Hae) which causes conjunctivitis in man, and in virulent forms, Brazilian Purpuric Fever, which is highly lethal to young children (e.g., Paganelli and Sabrosky, 1993). Bacilli, cocci, spirochaetes and mycoplasmas have been found in the midgut and/or proboscis of lachryphagous moths (Guilbride et al., 1959; Bänziger, 1973; Nicolet and Büttiker, 1975; Gouws et al., 1995) which have been suspected in spreading eye diseases of cattle. Noteworthy in Lisotrigona is their readiness to share hosts (zebu-man, man-dog); hence a potential rôle in communicating eye diseases should not be dismissed.

It is interesting to note that despite the meliponines’ far higher diversity in species and feeding habits in the neotropics, they did not develop lachryphagy there so far as known. As in the afrotropics, they do not lack minute species. The next research phase should investigate if and what rôle tear proteins actually play in the life of the bees, and focus on non-human hosts.

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