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Bees that love tears: A review of *Lisotrigona* congregating at human and animal eyes (Hymenoptera: Apidae, Meliponini)

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Abstract. Stingless bees (Apinae: Meliponini) exhibit astonishing and unusual behaviours, including tear-drinking or lachryphagy. In this review, we summarize lachryphagy in stingless bees, providing updated insights into their taxonomy, foraging patterns, ecology, hosts, evolutionary origins, and potential for pathogen transmission. In Northern Thailand, marked workers of the minute stingless bees Lisotrigona cacciae (Nurse) and L. furva Engel repeatedly return to human eyes, harvesting tears in short bouts that can last for hours or even over multiple days. Behavioural evidence suggests the presence of specialized tear collectors within these species. Single, experienced individuals can harvest tears gently, going unnoticed by the host, though large congregations can become bothersome. Lachryphagy occurs year-round and appears to be driven by high protein content in tears, in addition to salt and water. While *Lisotrigona* also visit flowers for nectar and pollen, tear collection may supplement or even replace pollen protein when floral resources are scarce or absent in their restricted habitats. Confirmed hosts include humans, zebu, dogs, cats, rabbits, chickens, and yellow tortoises. Lachryphagy has also been reported in other species of *Lisotrigona* in India. Interestingly, the similarly minute and widespread Tetragonula fuscobalteata (Cameron) is not lachryphagous but sucks sweat, as do other stingless bees, including Lisotrigona, though all visit flowers. This review also examines the potential for pathogen transmission via tear-drinking, particularly concerning viruses entering through the ocular surface, and discusses the evolutionary origins of lachryphagy in stingless bees.

INTRODUCTION

Tears, present on the eyes of terrestrial vertebrates (except snakes and geckos), is a saline liquid with proteins and minor amounts of lipids and other components,

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with the main function to lubricate eye lid movements, wash off debris, protect against pathogens, and prevent desiccation (Millodot, 2009). Many insects visit human and animal eyes for their tears, especially flies of the families Chloropidae, Cryptochetidae, Drosophilidae, and Muscidae (e.g., Greenberg, 1973; Sabrosky, 1987; Moon, 2002; Otranto et al., 2006; Bänziger et al., 2009). The latter authors, besides mentioning that 172 specimens of 31 species of drosophilid flies sucked human tears in Thailand, and that many moths (Lepidoptera) are nocturnal lachryphages, for the first time also documented stingless bees (Apidae: Meliponini) as avid tear drinkers: the tiny Lisotrigona cacciae (Nurse), L. furva Engel (Fig. 1), and to a lesser degree Pariotrigona *klossi* (Schwarz). Unpublished observations on some minute meliponines occasionally pestering humans, including occasional flying to eyes, had already been locally known, but were interpreted as accidental during more normal sucking of moisture and salt from human skin. Attraction to human sweat by minute meliponines had been reported from afro- and neotropics (Michener, 1990a, b), but not from Asia (Michener, 2000). More recently in Thailand, pestiferous sweat suckers have not only been found among minute species, including to a degree the mentioned lachryphagous species, but also in medium-sized species such as Lepidotrigona terminata (Smith) and Tetragonula sirindhornae (Michener & Boongird) (Bänziger et al., 2009). Tear- and sweat-drinking species of Lisotrigona Moure have been recently observed also in India (Thangjam et al., 2021). According to a very brief study in SW China by Li et al. (2021) on Lisotrigona carpenteri Engel, now Ebaiotrigona carpenteri (Engel), it is not clear whether it is essentially a sweat sucker, more or less accidentally approaching the eye and imbibing tears that happened to be mixed with sweat in proximity of human eyes or, a rather weak tear drinker. Similar observations were made by Tuan Anh Truong (Engel et al., 2022) in N Vietnam. However, during a long-term study of the nesting biology of E. carpenteri from March to December, Chinh et al. (2005) did not mention any sweat- or tear-drinking behaviour by this species near at least 17 natural nests at Cuc Phuong, Ninh Binh Prov., N Vietnam. Also the first author in the present contribution (H.B., unpubl. data), did not note lachryphagy in this species at the same site in Vietnam, but observations were very brief (4 and 10 December, 2010). On the other hand, persistent attraction to, but no settling on, the upper parts of humans by L. cacciae and L. furva was observed in Cambodia and Laos, respectively (Lee et al., 2016), and similarly by L. cacciae in Sri Lanka (Karunaratne et al., 2017), without any teardrinking cases. Nonetheless, on 13 December, 2008, one L. furva drank tears from the eye of H.B. at Banteay Srei, near Angkor, Siem Reap, Cambodia (Bänziger & Bänziger, 2010). Interestingly, according to Engel et al. (2021), in the neotropics apparently there are no meliponines exhibiting the typical lachryphagous behaviour as described for Thailand, although minute species of Trigonisca Moure are vernacularly known as 'eye-lickers' in Latin America. Of course, whether a bee is successful in snatching tears from a human also depends on his willingness to let meliponines have free access to the eyes and, in the case of a researcher, on his patience to wait sufficiently long for them to locate him as a source.

Unlike the vulture bees, such as the neotropical *Trigona necrophaga* Camargo & Roubik, which, instead of pollen-eating are obligate necrophages (Roubik, 1982; Camargo & Roubik, 1991), and occasionally carnivores (Mateus & Noll, 2004), *Lisotrigona* also forage for pollen and nectar, probably their main foodstuff when available in the restricted habitat of the tiny bees, although data on this are still poor. *Lisotrigona furva* was collected from *Callistemon* sp. (Myrtaceae) and *Buddleia asiatica* Lour. (Buddlejaceae) (S. Boongird & C. Michener, in Engel, 2000), and from *Tetrastigma*

baenzigeri C. L. Li and *T. hookeri* (Lawson) (Vitaceae) (Bänziger *et al.*, 2009); *L. cacciae* and *L. furva* were observed harvesting nectar and pollen from lichi (*Litchi chinensis* Sonn.) (Fig. 2) and longan (*Dimocarpus longan* Lour.) (Sapindaceae), and carry pollen from *Leucaena leucocephala* Lam., *Senna siamea* (Lmk.) Irwin & Barn (Leguminosae) (and other flowers the pollen of which, however, could not be identified) (Bänziger, 2018).

Herein, we review the lachryphagous behaviour of minute stingless bees, providing updated information on their taxonomy, foraging behavior, ecology, hosts, evolutionary origin, and potential for pathogen transmission.

Taxonomic Notes on Lachryphagous Species

In a genus-level revision of *Lisotrigona* Moure, Engel *et al.* (2022) transferred *L. carpenteri* to the new genus *Ebaiotrigona* Engel & Nguyen on convincing morphological



Figures 1–2. Tear-drinking and flower visiting *Lisotrigona furva* Engel. **1.** A row of 18 worker bees sipping tears from the eye of H. Bänziger in self-portrait. **2.** Workers collecting pollen and nectar from flowers of lichi (*Litchi chinensis* Sonn.) (Sapindaceae). Scale bars 6 mm. Photos H. Bänziger.

evidence. Workers of *E. carpenteri* are easily distinguished from those of *Lisotrigona* and *Pariotrigona* by the yellow face maculation (among other characters, including the slightly larger size of *E. carpenteri*). This removal from *Lisotrigona* could also support the behavioural difference between species of the two genera, namely, that *E. carpenteri* is not truly lachryphagous, or at most only rather weakly or accidentally so.

The very similar *L. cacciae* and *L. furva* from Thailand are best identified by differences in body size, as shown by Michener (2007), and confirmed with further measurements by Bänziger & Bänziger (2010), viz. head width 1.05–1.23 mm in *L. cacciae* and 1.25–1.41 in *L. furva*, without overlap. The body length is not a reliable measurement because it is dependent on the crop fullness of the telescoping metasoma.

In India, besides the presence of *L. cacciae*, five new species of *Lisotrigona* were recently described, viz. *L. mohandasi* Jobirai & Narendran (Jobiraj & Narendran, 2004), *L. chandrai* Viraktamath & Sajan Jose, *L. revanai* Viraktamath & Sajan Jose (Viraktamath & Sajan Jose, 2017), *L. darbhaensis* Viraktamath, and *L. kosumtaraensis* Viraktamath & Jagruti (Viraktamath *et al.*, 2023). Whereas in the report by Thangjam *et al.* (2021) there is no doubt that several specimens of *Lisotrigona* drank tears in three separate cases in India, according to Viraktamath (pers. comm., 11 March, 2022), the identity of such species remains unknown. Also, there is some controversy regarding the actual number of good species of *Lisotrigona* in India (Rasmussen *et al.*, 2017; Viraktamath *et al.*, 2021).

Regarding *Pariotrigona klossi*, Schwarz (1939) described it as a variety of *P. pendleburyi* (Schwarz), then under *Trigona*, both from Peninsular Malaysia. But Michener (2002 [2001]) found intergrading characters in specimens from Borneo, Sumatra and Malaysia, and proposed *P. klossi* as a synonym of *P. pendleburyi*. This was followed by Rasmussen (2008), Rasmussen *et al.* (2017), and Engel *et al.* (2018, 2022). However, in lachryphagous specimens found by H.B. in S Thailand, the main characters consistently matched *P. klossi*, and Michener, whom H.B. had sent specimens for verification, did not question H.B.'s identification. Unfortunately, Michener died before we could redescribe *P. klossi* for validation. This is now in preparation, based on additional material.

Marking Experiments and Feeding Behaviour of the Bees

This was carried out in N Thailand, with wild populations of *Lisotrigona* in forest sites to make sure that the behaviour was not potentially influenced by artificial components (*e.g.*, bees from meliponaries, degraded environment). Two sites were visited at least once monthly, May 2013 to November 2014, another was visited daily, 31 May to 20 June, 2013; session time lasted 1.5–11 h depending on the bees' harvesting time (averaging more than 3 h), total session time 360 h (Bänziger, 2018). Bees were marked (Fig. 3) while they avidly sucked tears, H.B. being both lachrymation source and experimenter, by his applying a minuscule drop of waterproof paint to the mesosoma back with a finely trimmed brush, viewed in a concave mirror. Generally, during one day, only one or two bees were marked, the touching causing the bee to fly off. If she returned, the colour, shape and position of the mark, which differed in every bee, were photographically recorded for correct recognition among large assemblages over hours, and days. The marking, 34 *L. cacciae* and 23 *L. furva*, revealed that the very same bees can visit human eyes up to 78 and 144 times in one day, respectively. Depending on the bees' position at the eye and competition with other bees, sucking

lasted 0.4–6.2 min (average 2.2 min) in *L. cacciae*, 0.4–5.3 min (average 1.6 min) in *L. furva*. Intervals between consecutive visits were 1.5–7.5 min (average 3.3 min) and 2.0–8.0 min (average 3.8 min), respectively. In one day, the same bees may collect tears for up to 10.5 h (includes round trip time), average 3 h 15 min in *L. cacciae*, 2 h 14 min in *L. furva*; five workers of each returned on the following day for up to 78 and 44 harvesting bouts, respectively; one *L. furva* came on three consecutive and on the seventh day. Tear drinking occurred throughout the year (rainy, dry hot, and dry cold seasons), except during heavy rain and at temperatures below 22°C when no workers left the colony to forage. Lachryphagy was observed even during light rain and after a downpour. So water was not the principal component sought. The other well-known component is salt (NaCl) but, generally not appreciated, there is a third main component, viz. proteins, and they are on a par with that of salt, ca. 6.7 mg in 1 ml (Rauen, 1964), 200 times the proteins present in sweat.

Tear collecting is not a simple matter of imbibing moisture; it requires special behavioural adaptations because the source is not dead matter or a flower, but can be a highly mobile, sensitive and reactive vertebrate. Although single experienced tear collectors can be so surreptitious and gentle to occasionally avoid detection by the host, more often they tend to be avid and persistent to become pestiferous when in large groups. The most critical time for lachryphagy is during the bees' approach to the eyes - not while sucking there. Humans normally flip them away when circling near the face (in zig-zag flight in the horizontal plane, whereas the common lachryphagous drosophilid flies tend to zig-zag vertically). The bees are likely to return and, if they manage to avoid the flipping and are about to reach the eye, the eyelids may automatically blink repulsing the bee. Animals, especially large herbivores, are less sensitive but flip with their ears, chase them off by tail, paw, claws, or shake their head. But in their persistence the bees tend to return time and again – like face flies do. The host may walk away but, unless running, the bees tend to follow in pursuit. The most experienced tear collectors will fly in low and very gently land below near the cilia or at the inner corner of the eye (e.g., Fig. 3) (no eyelashes there), less often at the outer corner, and then advance to where their proboscis can reach the tears accumulating in the menisci and trench between lid and eyeball. They evidently crawl by using only the tarsal soft arolia pads but with the claws automatically in retracted position, as described for honey bees when crawling on vertical smooth surfaces (Federle et al., 2001). Once landed and feeding at the eye, often only a faint tickling is perceived, if at all (H.B. occasionally had to check by mirror if a bee was still sipping or had already departed). The bees' proboscis is very fine and soft (about 1mm long, a third of the bee's body length, and only 0.025 mm wide distally) so essentially it is not perceived on the conjunctiva and the eyeball, unlike the bees' tarsi and claws of inexperienced drinkers which may cause tickling to the host. When settled, the bees would not fly off if the host walks or even slowly runs away, but continue to feed until satiated.

Analysis of 117 photographs of *Lisotrigona* at human eyes revealed that none of the 302 bees present carried pollen loads, whether small or large (Fig. 4), in their corbiculae. From stereomicroscope checks of collection specimens from eyes, only a few had pollen remnants, presumed result of the age polyethism from previous pollen collecting, or from contacts with nest-inmates. Because, as detailed above, lachryphagy is not a simple imbibing of liquids, but requires specific and unusual behavioural adaptations, including additional features described below (*e.g.*, the consecutive bouts of tear drinking instead of switching to the much easier sucking of sweat), Bänziger (2018) proposed that *Lisotrigona* might have specialized tear collectors – a new division

of labour in meliponines *sensu* Michener (1974), who used it in a broad sense, which in *Lisotrigona* probably is a part-time division of labour.

Bee Scent Marking and Recruiting

Some *Lisotrigona* were also seen along the groove between the lids of closed eyes of a drowsy or sleeping animal host, *e.g.*, a dog. Presumably the bees can locate the eye when they have scent marked it during a previous visit, or when attracted by the odour of tear incrustations or tear seepings along where the lids meet. Scent marking is indeed likely to occur: a fully satiated bee with turgid crop would not directly fly away but often remain a second or so while moving her head, antennae and forelegs, and then causing a typical tickling sensation to the lid/cilia of H.B. as if forcibly grasping them for an instant on take-off. Such head movements have been noted in neotropical *Trigona hyalinata* (Lepeletier) for odour-marking by mandibular glands (Nieh *et al.*, 2003), and in *Melipona seminigra* Friese for tarsal 'footprint' marking (Hrncir *et al.*, 2004). Quite often H.B. felt a slight burning or itching sensation at the eyelid, continuing after the bee had left, which indicate probable cases of scent marking.

The observation that there tended to be an exponential increase in arrivals following the first tear collector, indicates that *Lisotrigona* employ some form of recruiting. No traillaying was observed. Possibly, an experienced collector piloted a recruit by sight and/ or by an aerial scent plume released by the guide. Occasionally, H.B. noted that when a *Lisotrigona* was squeezed between his fingers, a strong odour was perceived; such a volatile might be used as a guiding plume. This type of recruiting had been proposed by Lindauer & Kerr (1958) for neotropical meliponines. The information exchange and recruiting behavior in *Lisotrigona* supports the use of the term 'congregating' rather than 'aggregating' when describing lachryphagous *Lisotrigona*. The former suggests a directional approach towards a known assembling site, whereas the latter denotes arrivals from any direction, casually attracted by a local resource.

Tear Proteins as Nutrition

The repetitive ingestion of full-crop loads of tears in successive sucking bouts is possible only if the preceding load is either regurgitated or anally excreted. In the latter case, tears would have to go through the digestive system and, since the proteins are dissolved, we know of no mechanism how *Lisotrigona* could extract and separate the proteins from the tears to be selectively discarded by excretion, if proteins were indeed unwanted ballast. They would inevitably be digested and assimilated, making them a nutritional resource rather than waste.

More likely is regurgitation where there are two possibilities, viz. trophallaxis to receiver bees, or disgorging into containers (pollen and/or honey pots, and/or brood cells). Bänziger (2018) thought that trophallaxis would be the more probable procedure because the tear collectors can readily return to harvest more tears. In the nest, tears might be used to dilute highly concentrated honey for the brood. Or nurse bees may process the tears to produce brood food. In all these cases the tears' dissolved proteins end up, *volens nolens*, enriching the nourishment.

Although pollen is far richer in proteins and lipids (Winston, 1987), tears are superior in having dissolved, readily digestible proteins, not enclosed in indigestible

exine walls as in pollen. Also, 20–25% of the protein in human tears is lysozyme (*e.g.*, Millodot, 2009), an enzyme with bactericidal properties, which could help against spoilage of tears in pots, until itself consumed as nutrition. The basic main tear composition of proteins, salt and water is also present in other mammals, birds and reptiles though the concentration of total proteins is highest in humans and lowest in reptiles (Raposo *et al.*, 2020; Oriá *et al.*, 2020). Moreover, tears are energetically less costly in harvesting. Namely, no hovering for pollen transfer to corbiculae is required, crop filling is in a settled position, taking just 1–6 min, and crop transporting allows a larger load than corbiculae (Michener, 1974), hence fewer return trips are necessary than for pollen. Additionally, pollen production by a flower is not continuous and soon exhausted, whereas tears are not only secreted continuously (30–120 μ l/h in humans; Millodot, 2009), hence produced virtually in unlimited amounts for tiny *Lisotrigona* but, unlike seasonal flowering, are produced year-round.

Finally, under certain circumstances tears could be a crucial alternative to pollen protein because small bees typically have narrower flying ranges than larger species (*e.g.*, Araújo *et al.*, 2004). The much larger honey bee has a harvesting range of over 100 km² (Seeley, 1985), but *L. furva*'s is only a small fraction of that. Since a small area is more prone to scarce or temporary lack of flowering than a large one due to its lower biodiversity, tears could compensate or replace pollen protein.

The Significance of Salt in Tears

No doubt the tears' salt (NaCl) plays a role. In a review of publications on animals searching for salt, Bänziger (2021) listed seven mammal and three bird families with species visiting salt licks, and various insects imbibing sweat, tears or visiting saltcontaining puddles, including seven families of lachryphagous moths (Lepidoptera). Interestingly, many of these zoophilous moths are unable to digest proteins in the adult stage, including, unexpectedly, the vampire moths (8 species of *Calyptra* Ochsenheimer, Erebidae) which sequester salt as the main substance from blood. In Thailand, the following non-lachryphagous stingless bees are known to settle on human skin to imbibe sweat: Tetragonula fuscobalteata (Cameron) (Fig. 5), T. hirashimai (Sakagami), T. pagdeni (Schwarz), T. pagdeniformis (Sakagami), T. sirindhornae (Michener & Boongird), T. testaceitarsis (Cameron), Lepidotrigona doipaensis (Schwarz), L. flavibasis (Cockerell), L. satun Attasopa & Bänziger, and L. terminata (Smith) (Bänziger et al., 2009; H.B., unpubl. data). At present it is not known whether they search for salt, water, or more probably either of them depending on circumstantial requirements. However, considering the above-mentioned wide-spread want for salt, generally this is the main resource sought. Similarly, those *Lisotrigona* that imbibe perspiration are probably after the salt but, significantly, all marked tear collectors consistently harvested only tears, in dry and humid weather. Hence, despite the importance of salt across the mentioned animal world, these harvesters prefer tears, although sweat is available over a much wider body area, and does not require special eye-landing dexterity. Since tears are 200-times richer in proteins than sweat, this component is a likely reason for their predilection. Presumably salt is not required in such large amounts as harvested by long-term tearsucking Lisotrigona but the surplus can be easily excreted via the Malpighian tubes (Wigglesworth, 1973).



Figures 3–5. Tear and sweat-drinking stingless bees. **3.** Seven workers of *Lisotrigona cacciae* (Nurse) imbibing tears from the eye of H. Bänziger in self-portrait. The orange-marked bee (arrow) is on the 21st of her 74 visits of her second day of lachryphagy. **4.** Pinned specimen of *L. furva* Engel with large corbicular pollen loads. **5.** *Tetragonula fuscobalteata* (Cameron) (left) and *L. furva* (right) sucking sweat on wrist of H. Bänziger. Note slightly larger *T. fuscobalteata* with whitish bands on mesosoma (lacking in *L. furva*), and yellowish-brown metasoma (blackish in *L. furva*). Scale bar 2 mm, except 3 mm in Fig. 3. Photos H. Bänziger.

The Significance of Water in Tears

The tears' water is likely important in honey dilution and moisture replenishment during dry hot periods. March to early May tend to have the highest temperature and lowest humidity at the study sites (T: min-max 26–35.7 °C, averages 27–33 °C; RH: min-max 25–67%, averages 35–54%). Dozens of the mentioned sweat sucking meliponines may crawl at the same time all over one's skin to avidly lick perspiration, often in mixed-species assemblages (*e.g.*, Fig. 5) and annoying persistence. Under such conditions, water appears to be the more important resource, presumably

also for *Lisotrigona* which come in greater numbers, whether sweat-drinking or tear-harvesting. Despite the abundance and accessibility of sweat, all marked tear-collecting *Lisotrigona* kept undeterred their regular bouts in drinking, leaving and returning to the eyes, throughout their hour-long tear harvesting. The persistent focus of *Lisotrigona* on collecting tears, rather than switching to sweat for salt or moisture, strongly suggest a division of labour within the species. One would expect the marked *Lisotrigona* to switch to sweat if it were not for their specific role in harvesting tears, further emphasizing their specialized task.

Lisotrigona were never seen at water basins placed at the study sites, nor observed to drink water from natural pool sides or at wet sand at streams where other meliponines, honey bees, and other hymenopterans gathered. Possibly, guttation from plants or atmospheric water condensation early in the morning may be sufficient sources for these tiny bees. Dew formation in the tree canopy and on ground vegetation is often very profuse in N Thailand due to marked overnight cooling between December and March (Bänziger, 2021: p 183).

While water could have a cooling function to prevent overheating of the nest by evaporation of collected water, as found in honey bees (Lindauer, 1954), this ability is thought to be lacking in meliponines (Roubik, 2006). However, neotropical *Melipona colimana* Ayala, and *Scaptotrigona depilis* (Moure), have recently been found to regurgitate water and fan their wings to cool down (Macías-Macías *et al.*, 2011; Vollet-Neto *et al.*, 2015). It is not excluded that *Lisotrigona* may be able to use tears for cooling, but in the forest habitat temperatures were mostly below 33 °C during the hottest months and reached a maximum of 35.7 °C only once. This is below the maximum brood chamber temperature of 36.2 °C recorded in neotropical *Trigona spinipes* (F.) (Zucchi & Sakagami, 1972) and is well below 38.5°C and 40°C when 0% and 50% mortality, respectively, occurred in *S. postica* (Latreille) (Macieira & Proni, 2004). For comparison, optimal brood temperatures for honey bees range between 34 and 36 °C (Seeley, 1985). Given these relative low temperatures, cooling via tear collection would likely not be necessary for *Lisotrigona*.

Hosts

Apart from humans, L. cacciae imbibed tears from cat, dog, chicken (Fig. 6), and the elongated tortoise [or yellow tortoise, Indotestudo elongata (Blyh)] (Fig. 7), but settling attempts on rabbit [Oryctolagus cuniculus (Linnaeus)] were repulsed by eye blinking. Lisotrigona furva also imbibed tears from rabbit and zebu (Bos indicus Linnaeus) (Bänziger et al., 2009; Bänziger & Bänziger, 2010), with photographic documentation of lachryphagy of all except from cat and zebu. In Packer (2023), there is a photograph by K. Kulkarni of a group of *Lisotrigona* sp. at the eyes of a changeable hawk-eagle [Nisaetus cirrhatus (Gmelin)] in the wild in Madhya Pradesh, India, and H.B. has noted in a documentary film where incidentally tiny meliponines were attacking the eye of a harpy eagle [Harpia harpyja (Linnaeus)] in South America, and in another where a minute meliponine was molesting a goliath frog [Conraua goliath (Boulenger)] on its eye in Cameroon, W Africa. The latter case would be the first where an amphibian eye was visited by a stingless bee, but there is need of further observations to confirm that it was not an anecdotal, abnormal case. Interestingly, contrary to what one would intuitively expect in birds as sensitive animals, the chicken was the least reactive against the bees sucking from its eyes. Also, the nictitating membrane of the eye did not affect the bees, they just continued sucking, at most briefly retracting their proboscis.

It is important to point out that all these animals (not considering the nonreconfirmed case of the frog) lack sweat, showing that perspiration plays no role in attracting *Lisotrigona*, and that lachryphagy is not an accidental feeding upon sweat. Rather, that *Lisotrigona* have developed specialized capabilities to locate and recognize variously shaped eyes of different vertebrates, probably both by vision and olfaction, to harvest their lachrymation. In humans, though, perspiration could play a role in attracting tear collectors from a distance.

A problem of bees sucking tears compared with visiting flowers is that animals can be highly mobile. Hence, while the bees avidly imbibe tears, the host may move beyond the homing range of *Lisotrigona* which could risk being unable to find her way back. Because of this, there was motivation to assess a bee's returning range while on lachryphagous duty. This required novel experimental methods, different from conventional ones. One method was to obtain the distance covered by a gently running host (H.B.) while a marked *L. furva* sucked his tears, from the starting point where she had landed on the waiting host to where she flew off once satiated. The distance run by the host was considered her returning capability, if the same marked bee later came back to the host at the original starting point (where she had been eye visiting for some time already) for another tear-drinking bout. This was repeated with the same marked bee on the host running in the opposite direction. This was required because the nest's exact position was not known, but must have been somewhere between the two direction ends. The most conservative assumption was a position halfway between the opposite extremes (205 m and 650 m), *i.e.*, 425 m – the distance could not have been less than this. However, on subsequent surveys (Bänziger, unpubl. data) the nest was found 30 m distance from the waiting place, on a limestone rock face 2.2 m above ground, a fissure with a tiny tubelet entrance of 4.5x6 mm. Hence the maximum returning distance must have been up to at least 680 m. The results are preliminary, the data too limited (9 *L. furva* examined) for statistical analysis. The distance is very high for such a minute bee, possibly an adaptation to feeding from mobile vertebrates.

Are there enough acceptable hosts for *Lisotrigona* to harvest significant amounts of tear proteins? As suitable potential hosts (*i.e.*, cat-size and larger), Bänziger & Bänziger (2010) mentioned that in Thailand there are, conservatively, some 45 medium- to large-sized terrestrial mammal species (Lekagul & McNeely, 1977; Francis, 2001; Parr, 2003), 21 phasianid-sized bird species (Lekagul & Cronin, 1974), and 24 turtle- to crocodile-sized reptilian species (Das, 2010). Several of the hosts are common domestic animals, and *Lisotrigona* occasionally nest in house poles or garden trees. Further, animals are not necessarily on the move all the time but can be site-bound for as long as a plant in flower when rearing their nestlings for weeks. Ruminants lay down chewing for hours. Whereas most modern urban people are unlikely to allow tear snatching, people engaged in hard rural work are less sensitive, and tropical forest natives are so accustomed to mosquito and other scourges that they will tolerate *Lisotrigona* as a minor nuisance.

Interestingly, in diversity of host spectrum, spanning three vertebrate classes, *Lisotrigona* beat their moth (Lepidoptera) homologues whose lachryphagy is, essentially, restricted to mammals as the only class. This dearth is not due to lack of data, because tear-drinking moths are comparatively well-researched, discovered already a century ago (*e.g.*, de Joannis, 1911; Büttiker & Whellan, 1966; Bänziger & Büttiker, 1969; Bänziger, 1988, 1995) and counting more than 100 species in seven families (Bänziger, 2021: p 67, 191). An important difference to *Lisotrigona* is that being nocturnal reduces visual detection by their hosts and, due to drowsiness, the

hosts' alertness and tactile sensitivity. This allows far larger sizes in these moths (up to 84 mm wingspan in notodontid *Tarsolepis remicauda* Butler), and more aggressive behaviour. Some species can cause pain to eyes due, not to their proboscis, which apically is relatively soft but, as photographically documented, mainly by clawing of the eyelid (Figs. 8, 9). In drepanid *Chaeopsestis ludovicae* Le Cerf, wingspan 45 mm, the foretarsi alone of 4.4 mm length is much longer than the entire body length of *L. furva* (2.7–3.3 mm; in Fig. 8 the foretarsi may appear shorter but this is due to their inclined position).



Figures 6–9. Tear-drinking stingless bees and moths. **6.** *Lisotrigona furva* Engel drinking tears from the eye of a chicken. **7.** *Lisotrigona furva* imbibing flowed-down tears from the eye of an elongated tortoise [*Indotestudo elongata* (Blyh)]. **8, 9.** Drepanid moth *Chaeopsestis ludovicae* Le Cerf imbing tears from the eye of H. Bänziger in self-portrait. Note the moth's foretarsi clawing the eyelid (arrows in photo 8, lines in drawing 9). Modified from H. Bänziger (1992). Scale bars 6 mm. Photos H. Bänziger.

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Medical and Veterinary Significance

The feeding from such a wide host spectrum in three vertebrate classes, some as domestic animals in close vicinity to humans, can have medical and veterinary implications. Previously, stingless bees most likely to pose a health danger were necrophagous and filth visiting species in Peru (Baumgartner & Roubik, 1989), but these bees were considered of only minimal danger as vectors of pathogens because their species richness and abundance was highest in asynanthropic areas (lacking human settlements), and they did not settle on humans to feed. Lisotrigona are both synanthropic and asynanthropic. Not only can they settle on humans in numbers, but tend to do so repeatedly and, significantly, at a very exposed site for pathogen entrance (see below), viz. the ocular surface with the conjunctiva of the lids. Transmission could occur via contact of the bees' foretarsi and proboscis applied to the lid's conjunctiva, the proboscis also reaching into the trough between the conjunctiva and eye ball and, occasionally, brief direct contact with the eye ball. The antennae also touch from time to time the ocular surfaces. Importantly, L. furva and L. cacciae exhibited readiness to use multiple hosts, viz. zebu-man and man-dog, respectively (Bänziger et al., 2009: p 141).

Potentially, *Lisotrigona* could pose a danger similar to eye gnats (Chloropidae), suspected vectors of the bacterium *Haemophilus influenzae* biogroup *aegyptius* (Hae), which causes conjunctivitis in human and, in virulent forms, Brazilian Purpuric Fever, which is highly lethal to young children (*e.g.*, Paganelli & Sabrosky, 1993). More recently, Miner *et al.* (2016) found the Zika virus to cause eye inflammation and shedding of the virus in mice tears.

Of particular significance is ophthalmologist Coroneo (2021) who reviewed the evidence that ocular and periocular tissue in human may be uniquely placed as an entry portal for viral invasion and primary site of virus replication. Also, he drew attention that Dr. Li Wenliang, the whistle-blower who warned about the outbreak of COVID-19 in late 2019 and subsequently died from it, was an ophthalmologist who probably got infected by SARS-CoV-2 via the eyes in Wuhan, China. In retrospect, although H.B. (2018) assessed the risk of pathogen transmission by lachryphagous *Lisotrigona* as remote, his decision to be sole experimenter during his field study, was, after all, appropriate.

Possible Origin and Evolution of Lachryphagy in Stingless Bees

It has been proposed that tear collecting in stingless bees may have originated in connection with humans (Bänziger, 2018) because, unique among vertebrates (except amphibians and hippopotamuses) in producing significant amounts of perspiration, they are visited by sweat-sucking meliponines, at times in large and diverse assemblages. Among these, the minute-sized species were preadapted to develop tear collectors, thanks to their reduced visibility, weaker mechanical impact, and gentler feeding act, such that some of the tiniest species have evolved behaviours to snatch lachrymation without much disturbance. Moreover, a feature may have facilitated bee-human contact: meliponine nests in limestone hollows entered through fissures in rock faces (Bänziger & Bänziger, 2010; Bänziger *et al.* 2011). The many types of meliponine nests are otherwise well-known (*e.g.*, Wille & Michener, 1973; Camargo & Pedro, 2003; Rasmussen & Camargo, 2008; Roubik, 2006) overwhelmingly from the neotropics, but some also from Thailand (Inson, 2006; Khamyotchai, 2014), not so

nests in limestone fissures. But in some natural habitats of W and N Thailand, H.B. has found more stingless bee nests in limestone faces than in tree trunks - at least 12 meliponine species, from the smallest to the largest. Early humans frequented or lived in limestone caves for generations already 10^5 – 10^6 years ago when, thanks to this close vicinity, lachryphagy may have originated in *Lisotrigona* or her ancestors. An alternative to this two step (first sweat, then tears) hypothesis might be an earlier, 30–70 million years ago (mya), direct attraction to eyes of birds or mammals as a source of moisture during geologically periods of drier climate. Whether due to periodical water or salt constraints, in the course of time tear-drinking could have evolved into a yearround feeding habit, thanks to the tears' reliable content of ready-to-digest dissolved proteins as nutrition. Roubik (2023) expanded on this and conjectured a yet earlier possible lachryphagy when meliponines might have recruited nestmates to dinosaur eyes in late Cretaceous times (90 mya). Stingless bees have been detected in amber dating back 95–70 mya (Michener & Grimaldi, 1988) and were therefore contemporary with the late dinosaurs. Perhaps, because in those early times flowering plants were still uncommon – notwithstanding the then already presence of gymnosperms which produce pollen, though theirs is mostly wind-dispersed – primitive meliponines' diet may have consisted substantially of animal-derived proteins, including tears. Yet, all three proposals could be correct. Lachryphagy may have been developed, lost and redeveloped more than once by Lisotrigona and her ancestors, not necessarily phylogenetically related, during the 90 mya years since the appearance of stingless bees. For comparison, cleptoparasitism originated at least four times in Apidae (Cardinal et al., 2010). Interestingly, whereas minuteness appears to be a sine qua non condition for developing lachryphagy, not all minute meliponines exhibit tear-drinking habits. The smallest exponent of the widespread and species-rich genus Tetragonula Moure is the tiny T. fuscobalteata, head width 1.39–1.46 mm (Sakagami, 1978), hence only slightly larger than L. furva. It is one of six species of Tetragonula frequently found to suck sweat from H.B. (Fig. 5), but never his tears, nor are we aware of any report of an eye visitation from anywhere, although it is common and wide-spread, from mainland SE Asia to Sumatra, Borneo, the Philippines, and Sulawesi (Schwarz, 1939; Sakagami, 1978; Rasmussen, 2008; Lee et al., 2016). This is interpreted as a further indication that lachryphagy is not a simple uptake of fluid, but a result of special behavioural adaptations developed only by a select group of stingless bees for harvesting tears under the very eyes of their victims.

Future Studies

Our study focused on wild *Lisotrigona* populations in forest habitat to avoid potential non-typical behaviours (*e.g.*, meliponinary bees, degraded environment). Results suggest that tear drinking in *Lisotrigona* is neither accidental nor for individual bees' needs, but for colony requirements, by specialized tear collectors with an indication of a part-time division of labour. However, new questions arose and, since now lachryphagy is no more in doubt, future investigations should include experiments with bees inside and in close connection with nests/hives, with possible invasive techniques and use of artificial tears to avoid pathogen transmission.

Main questions are: Do *Lisotrigona* regurgitate their tear harvest to receiver bees as proposed above, rather than into honey or pollen pots, or brood cells? Are tear proteins eaten and assimilated by *Lisotrigona*'s brood? Do *Lisotrigona* disgorge tears onto nest surfaces and fan with their wings to cool the nest during very hot, lifethreatening temperatures, but not during the 'normal' forest temperatures we found? Do only some of the workers exhibit lachryphagy, or can it occur in all workers, and is it exhibited at a late age? When settled on human skin, do *Lisotrigona* imbibe sweat to cover their individual needs, or do they repeatedly return for additional harvesting for colony requirements, and if so, where do they regurgitate it: to adult nest inmates, into pots, brood cells, or nest surfaces?

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