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REVIEW ARTICLE

A review and illustrated description of *Musca crassirostris*, one of the most neglected haematophagous livestock flies

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Abstract. Tabanids, stomoxyine flies, hippoboscids and tsetse flies are the most well-known brachyceran biting flies of livestock. Only a few other higher Diptera have developed the unique mouthparts required for blood feeding. These neglected blood feeders can also have direct effects on hosts through blood loss, and are likely to contribute to the transmission of pathogens. *Musca crassirostris* (Diptera: Muscidae) is one of the most abundant of the muscid flies with this haematophagous lifestyle; it is widespread in the Palaearctic, Afrotropical and Oriental regions. The present study reviews and summarizes the biology and morphology of this species, and its potential for impact on animals and humans. The study also provides a fully illustrated description of the fly to facilitate its identification, and reviews information on abundance, with a focus on recent trapping surveys in Thailand. When sampled using traps designed for other biting flies, *M. crassirostris* appears to be four and 45 times more abundant than stomoxyines and tabanids, respectively. High numbers of *M. crassirostris* in the vicinity of livestock have also been associated with outbreaks of disease, such as that of a fatal plague in bovine farms in Egypt. This calls for a reconsideration of its potential impacts on livestock economics and health, and thus the development of suitable control methods.

Key words. Bloodsucking fly, cattle fly, illustration, identification, impact.

Introduction

Among the many flies annoying livestock, the most well known of the haematophagous brachyceran biting flies globally are tabanids, hippoboscids and stomoxyines, which are notably responsible for the mechanical transmission of trypanosomes such as *Trypanosoma vivax* and *Trypanosoma evansi* (Surra) (Kinetoplastida: Trypanosomatidae) (Baldacchino *et al.*, 2013, 2014); tsetse flies [*Glossina* (Diptera: Glossinidae)] are also well known in Africa because they transmit nagana and sleeping sickness (Bitome Essono *et al.*, 2015). Only a few other higher Diptera of the genus *Musca* have evolved the mouthparts required for blood feeding. These neglected blood feeders can also have direct effects on hosts through blood loss and through the mechanical transmission of pathogens (Skidmore, 1985).

The family Muscidae is divided into seven subfamilies and contains about 4500 species in 180 genera (de Carvalho *et al.*, 2005; Nihei & de Carvalho, 2007). The subfamily Muscinae contains two tribes of veterinary importance: the Stomoxyini, which consists of bloodsucking insects such as species within the genera *Stomoxys*, *Haematobia* and *Haematobosca*, and the Muscini, which contains non-biting insects such as those of

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the genera *Fannia*, *Hydrotaea*, *Morellia* and the most important *Musca* (Skidmore, 1985; Nevill, 1997; Nihei & de Carvalho, 2007). The genus *Musca* Linnaeus is cosmopolitan and includes roughly 60 species, at least one of which, *Musca domestica*, is found worldwide as a result of its close association with humans. The *Musca* spp. include both anthropophilic 'house flies' ('sponging flies', such as *M. domestica*, *Musca nebulo* and *Musca humilis*) and less well-known 'wild flies'. Several species are haematophagous (although in some of them this status has been subject to controversy), including *Musca ventrosa*, *Musca albomaculata*, *Musca spinohumera*, *Musca bezzii*, *Musca lineata*, *Musca inferior*, *Musca conducens*, *Musca planiceps* and *Musca crassirostris* (Patton, 1922). These species are typically referred to as 'bloodsucking flies' rather than 'biting flies'; in other words, they are not 'skin-piercing' flies.

All *Musca* spp. can feed on liquids containing organic matter from various substrates (such as organic wastes, excrements, carcasses, secretions from wounds and sores, and lacrimation fluids). They may also regurgitate to dampen substrates, or to dilute coarse or viscous fluids, in order to take up liquids through the pseudotracheae, or to partially digest materials before ingesting them (Nevill, 1997). Some flies, such as *Musca pattoni*, feed on blood that oozes from punctures made by true biting flies and are suspected to contribute to the mechanical transmission of blood pathogens, such as trypanosomes (Patton, 1922). A number of haematophagous species, such as *Musca autumnalis*, *Musca bezzii*, *Musca lusoria* and others, follow the pattern of true skin-piercing, blood-sucking flies (such as *Stomoxys* spp.), which causes them to withdraw the proboscis in order to suck up any blood or serum that commonly exudes from the bite (Patton, 1932); such flies may land next to a true biting fly and push it laterally to dislodge its proboscis from the skin in order to suck the blood that oozes immediately after proboscis removal (MD, personal observation, 2007–2017).

All *Musca* spp. have one or more circles of prestomal teeth; the first row of these prestomal teeth ranges in size and form, according to the species. A moderate development of these teeth can allow the fly to scratch the surface of a blood clot; in this way, they can 'refresh' wounds left at biting sites by true biting insects. This will drain more blood after the bite, as described for *Musca lineata* or *M. conducens* (Patton, 1922) (also called *Philaematomia lineata*), and for *M. lusoria* and *M. autumnalis* (Nevill, 1997); such behaviour makes them facultative haematophagous flies (Russel *et al*., 2013). The mentum and teeth are more strongly chitinized in true blood feeders such as *M. planiceps* (Patton & Senior-White, 1924). This type of proboscis reaches its highest evolution with a strongly chitinized mentum and fully developed prestomal teeth in *M. inferior* and *M. crassirostris*. These flies are able to abrade the skin of their hosts in order to feed on blood (Patton, 1923; Patton & Senior-White, 1924), to rasp scabs or wounds, and possibly to pierce soft skin by injuring epidermal and dermal tissues (James, 1969; Greenberg 1971, quoted by Skidmore, 1985). Some authors therefore consider them to be 'biting flies' (Mellor, 1978; Nevill & Sutherland, 1987). Others do not consider them to be 'true' biting flies as the proboscis does not penetrate the skin (Patton & Cragg, 1913; Patton & Senior-White, 1924; Muirhead Thomson, 1947; Crosskey, 1993). Finally, *M. crassirostris* belongs to a group of true obligate blood feeders (Hopla *et al*., 1994), together with *M. planiceps* and *M. inferior* (Patton & Senior-White, 1924), and thus it should be considered as an obligate parasite.

Musca crassirostris is present in the Palaearctic, Afrotropical and Oriental regions (Walker, 1994); it is found in Africa, from South Africa to the Mediterranean coast, through the Middle East and India to Asia, including Taiwan and Southeast Asia, and as far as Indonesia (James, 1947; Skidmore, 1985). It is also called the 'Indian fly' (Russel *et al*., 2013), and, as suggested by Patton (1922), it could as well be called the 'cattle fly' because it is very abundant around cattle. Most of the authors reporting this fly mention that it is very abundant on cattle (Patton & Patton, 1920).

Musca crassirostris Stein, 1903 was also designated *Philaematomyia insignis* Austen (Patton & Cragg, 1913), *Musca (Philaematomyia) crassirostris*, Stein (Patton, 1922), *Philaematomyia crassirostris* (Stein) and *Musca insignis* Austen (James, 1947); all these names are now considered synonymous. Following Austen, the subgenus *Philaematomia* was created (as a genus) because of the stout proboscis of *crassirostris* with its prestomal teeth. However, *M. inferior*, *Musca senior whitei* and a few other species, which are more or less similar in this characteristic, were not included in this genus (Van Emden, 1965). As has been clearly stated, and notably based on the structure of the proboscis, which is similar to that of *M. domestica*, there is no doubt that *crassirostris* belongs to the genus *Musca* (Patton, 1932).

The systematic position of *M. crassirostris* is: Order Diptera; suborder Brachycera; family Muscidae; subfamily Muscinae; tribe Muscini; genus *Musca*, and species *crassirostris* (Borror & White, 1970; Skidmore, 1985).

The present paper reviews and summarizes the biology and morphology of *M. crassirostris*, and its potential for impacts on animals and humans. It also provides a fully illustrated description of the fly in order to facilitate its identification, and reviews information on its abundance, with a focus on recent trapping surveys in Thailand.

Biology of *M. crassirostris*

Both adult males and females of *M. crassirostris* are haematophagous; males suck blood as voraciously as females (Patton & Cragg, 1913). Some authors do not consider this fly to be an obligatory parasite, stating that it can survive on various animal secretions, and, indeed, adult *M. crassirostris* have also been observed sucking some organic fluids at the surface of fresh cattle dung (Patton & Cragg, 1913). However, the species is especially attracted by wounds and blood for feeding (Taylor *et al*., 2007). To feed on blood, *M. crassirostris* flies can either make their own lesions by rasping the skin with the labella, or can act as secondary blood feeders, either by refreshing a biting site by rasping the clot resulting from the feeding of a true biting fly (tabanid or stomoxyine), or by lapping liquid blood from around wounds or punctures made by true bloodsucking flies. For these reasons, some authors consider these flies as true blood feeders and even qualify them as 'biting flies' (Patton & Senior-White, 1924; Hopla *et al*., 1994); however, the proboscis of this species does not penetrate the skin (Patton & Senior-White, 1924).

This species, although not a stomoxyine, is very similar to *Haematobia* species (Diptera: Muscidae) in its general biology (Lane & Crosskey, 1993). Gravid females have been observed on the fresh dung of cows and buffaloes, and sometimes in horse dung (Patton & Cragg, 1913). However, in a study carried out in Egypt, eggs were found only in bovine dung and not in the dung of equines, camels, sheep, goats, poultry, pigs, rabbits or humans (Hafez & Gamal-Eddin, 1966).

The female is oviparous; before laying eggs, it looks for a crack or crevice in fresh dung into which to insert its ovipositor. Within 6–10 min, a female can lay 40–60 large eggs (2.0–2.2 mm in length, 0.4 mm in breadth) into freshly dropped cattle or horse dung, or some rotting organic material (Patton & Cragg, 1913; West, 1951). Greenberg, quoted by Skidmore (1985), refers to the species as a symbovine that is hemi-synanthropic in some areas. In 1951, Zimin [quoted by Skidmore (1985)] reported up to seven females laying simultaneously on one cowpat, covering it with masses of large eggs. This gregariousness was also observed and carefully described by Patton & Cragg (1913), who reported up to 36 females laying 560 eggs in one spot; such gregarious behaviour is unique among muscids. Gregarious behaviour was also described in males, which have been observed to swarm in their hundreds in India (Van Emden, 1965).

These large eggs suggest some early development inside the uterus (Patton, 1922). Indeed, the eggs of this species hatch very quickly after being laid, in 8–9 h or less (Patton & Cragg, 1913); this time is so short, compared with that for other *Musca* spp. (on average 20 h), that some authors even consider *M. crassirostris* as taking a step towards larviparous behaviour (Patton, 1932), or even as demonstrating ‘facultative viviparity’ as the brief period between oviposition and larval hatching suggests that all eggs in a batch are retained for some time in the uterus of the female (Meier *et al*., 1999). Finally, *M. crassirostris* is the only muscid species to cumulate haemophagocity and facultative viviparity. However, its viviparity is not advanced (James, 1969), and is nothing to compare with that of *M. planiceps*, which deposits its larvae one at a time in fresh cow dung in the early third stage, after retaining them *in utero* during two moults (Patton, 1932).

The larvae are saprophagous and can be reared to maturity on dung alone. First-instar larvae stay together and feed in the dung for 24 h and then move deeper into the dung or deeper into the earth under litter to continue development. Larvae (maggots) are a deep lemon-yellow colour, and are segmented and cylindrical. The three larval stages feed on decomposing organic material and mature within 3–7 days under suitable conditions. Mature larvae move deeper into the damp soil below cattle dung, or to drier areas around the larval habitat to pupariate (Mellor, 1978). In laboratory rearing in Egypt at 25 °C and 32 °C, respectively, development took 11 h and 7 h (eggs), 6.5 days and 3.2 days (larvae) and 6.7 days and 4.0 days (pupae) (Hafez & Gamal-Eddin, 1966). Complete development took 14 days and 8 days at 25 °C and 32 °C, respectively.

Puparia measure 5–10 mm in length and are of a mahogany colour (Patton & Cragg, 1913). Adult flies have been observed to emerge between 3 and 26 days later, depending on the temperature (Taylor *et al*., 2007). Thus, under optimal conditions, complete larval development can occur in as short a period as 1 week and the species may produce several generations per year in temperate climates; in tropical areas, breeding may be continuous.

A study of temperature limits in adults indicated that the lowest temperatures at which movement of adult flies was noted averaged 10.4 °C; heat paralysis began at 44.9 °C and was complete at 46.3 °C (West, 1951). Studies in Egypt have shown that flies are scarce when the temperature is below 21 °C or above 35 °C, but are very abundant at temperatures between 21 °C and 30 °C (Hafez & Gamal-Eddin, 1966). Like other haematophagous flies, adults of *M. crassirostris* have been shown to be significantly attracted by carbon dioxide (Bernier *et al*., 2008).

Musca crassirostris may be parasitized by nematodes such as *Heterotylenchus crassirostris* (Tylenchida: Allantonematidae), which affects the ovaries of females and could potentially be used for biological control (Yatham & Rao, 1981). However, because of the specific affinity of this fly for fresh dung, especially cattle dung, a simple management technique for fly control in stables involves the rapid and regular removal of dung. This will limit the habitat suitable for egg laying and larval development, but is not practical in the context of free-ranging livestock.

Impact of *M. crassirostris* on animals and humans

Reducing the direct impacts of this fly on livestock is a priority of livestock owners in some areas; for example, cattle deaths at high abundances have been reported in Egypt (Hafez & Gamal-Eddin, 1966). However, indirect impacts linked with pathogen transmission should not be neglected.

Direct pathogenic effects

Musca crassirostris was considered as one of the most important pests of cattle in India (Patton, 1922). Earlier research recorded huge numbers of these flies on cattle, especially on the legs, which required the cattle to spend a lot of time and energy fending off these insects, and concluded that their feeding behaviour and incredible numbers must significantly reduce milk production (Patton, 1922). In Oman, average numbers of five to 200 flies have been observed on cattle at one time, with numbers sometimes exceeding 500 (Mellor, 1978). The animal stress resulting from visual, aural and tactile harassment must be substantial, even without considering the impacts of all other insects annoying livestock. *Musca crassirostris* most often feeds on the legs and belly; cattle typically lie down on their legs to protect themselves from attacks (Patton, 1922). This extreme behaviour has also been seen in French Guyana, where cattle try to escape very high tabanid pressure (Desquesnes, 2004). Because of their nuisance effects, flies distract and essentially limit the time available for normal feeding activity. The resulting reduction in food intake, combined with the stress and the energy spent on dislodging flies, is the most important effect of *M. crassirostris* on livestock in pasture. This leads to reduced weight gain in beef cattle, reduced milk production in dairy cattle, and reduced manure production (Patton, 1922). However, the specific impact of *M. crassirostris* on livestock has yet to be measured independently of the impacts of other flies, including biting flies.

Musca crassirostris attacks mainly cattle, causing severe irritation and sometimes weakening the animal so much that death may result (Hafez & Gamal-Eddin, 1966; Harwood & James, 1979).

Musca crassirostris can attack horses and donkeys, although the species is more usually found on bovines (cattle and buffaloes), and it may occasionally attack humans and dogs (Patton & Cragg, 1913; Lane & Crosskey, 1993; Chin *et al*., 2010). It has also been found on camels (Dia, 1997), and on tigers and deer, as observed in a natural park in India (Veer *et al*., 2002). Animals in poor condition have more flies than others, which may relate to the exhaustion of these animals, which are no longer able to fend off the insects (Mellor, 1978).

When using the prestomal teeth to rasp the skin, at either a wound or any altered part of the skin, *M. crassirostris* is responsible for a painful bite that generates stress that contributes to immunosuppression in animals; subsequently, when feeding, the fly is responsible for the depletion of blood, which also impacts animal production.

The sizes of the bloodmeals taken by a number of haematophagous flies were established by Gooding (1972). Based on his estimates, and the size of the insect, the bloodmeal of *M. crassirostris* amounts to about 10–40 mg per fly [the closest size is *Stomoxys calcitrans*, which takes a bloodmeal of 7–25 mg (Gooding, 1972)]. In a situation in which more than 500 *M. crassirostris* may attack one cow (Mellor, 1978), the blood depletion of cattle may be high and the medical impact quite substantial.

The saliva of *M. crassirostris* has significant anticoagulant activity (Lane & Crosskey, 1993); it is greater in females than males, and greater in flies that have taken a bloodmeal than in newly emerged insects [Cornwall and Patton, 1914, quoted by Gooding (1972)]. Anticoagulant activity is likely to increase the total loss of blood in animals on which this fly feeds (Van Emden, 1965).

In addition to its effects as an adult fly, *M. crassirostris* is responsible for some accidental intestinal myiases, in humans notably. Intestinal pseudoparasitism has been described after the oral absorption of eggs and larval development in the human digestive tract. This pseudoparasitism is rare and of little consequence. Patton attributed cases of intestinal myiases observed in India to a ritual practice involving the consumption of five products of a cow, including fresh cattle dung [Patton, quoted by James (1947)]. Another circumstance occurs in cases of extreme poverty when people try to find undigested barley grains in horse dung [Onorato, 1922, quoted by West (1951)]. A similar case was reported from Italy (Hall & Smith, 1993).

Musca crassirostris *as a vector of pathogens*

Similarly to non-biting flies, *M. crassirostris* is considered to be a mechanical carrier of pathogens, especially bacteria such as *Escherichia coli* (Enterobacteriales: Enterobacteriaceae), *Moraxella bovis* (Pseudomonadales: Moraxellaceae) (pinkeye) and *Staphylococcus aureus* (Bacillales: Staphylococcaceae) (Walker, 1994). More importantly, like biting flies, *M. crassirostris* is considered as a mechanical vector of some pathogens; many years ago it was shown to transmit surra and haemorrhagic septicaemia (Du Toit & Nieschlutz, 1933; Gill, 1977). High numbers of pathogens can be transmitted by insects acting as mechanical vectors (Taylor *et al*., 2007) and those that may be transmitted by *M. crassirostris* are unlikely to differ from those recently reviewed for stomoxyines and tabanids (Baldacchino *et al*., 2013, 2014). Some examples are viruses such as equine infectious anaemia virus and lumpy skin disease virus, bacteria such as *Bacillus anthracis* (Bacillales: Bacillaceae) and *Anaplasma marginale* (Rickettsiales: Anaplasmataceae) and protozoa such as *Besnoitia besnoiti* (Eucoccidiorida: Sarcocystidae) and *Trypanosoma* spp. (notably *T. evansi* and *T. vivax*).

In addition, a number of nematodes are suspected or proven to be biologically transmitted by *M. crassirostris*. All scratching *Musca* (such as *M. senior-whitei*, *Musca fletcheri*, *M. planiceps*, *M. inferior* and *M. crassirostris*) are potential transmitters of pathogenic organisms, and *M. crassirostris* has been considered as a probable transmitter of *Habronema* spp. (Spirurida: Habronematidae) in India as these nematodes were found to develop in it (Patton, 1932). According to Nevill, (1975), theoretically *M. crassirostris*, as well as *Haematobia* spp. and *M. conducens*, would all be ideal transmitters of *Parafilaria bovicola* (Spirurida: Filariidae) because they are able to lap up infected blood and later infect animals through the wounds they cause by their own feeding; however, experimental evidence is lacking.

Thelazia (Spirurida: Thelaziidae) are eyeworms. Adult worms and first-instar larvae live in the eye annexes of animals and humans; *Thelazia rhodesi* is found in bovines. This nematode occurs on the surface of the cornea, under the nictitating membrane, in the conjunctival sac and lacrimal duct. The worms are viviparous and first-stage larvae are passed by females into lacrimal secretions, where they are ingested by non-biting Diptera (Naem, 2007). First instars, free in the lacrimal secretion, are absorbed by secretophagous flies in which they implement their development until they achieve the status of third-stage larvae and migrate to the labium from which they emerge and are released in the eye of a host (Otranto & Traversa, 2005). The lateral serration of the *Thelazia* cuticle is responsible for mechanical damage to the conjunctival and corneal epithelium, which results in ocular discharge and increases worm transmission as flies feed on lacrimal secretions containing first larval stages. Adult and larval stages of *Thelazia* are thus responsible for eye disease, the symptoms of which vary in severity and include lacrimation, ocular discharge, epiphora, conjunctivitis, keratitis, corneal opacity and ulcers. *Musca crassirostris* is a known vector of *T. rhodesia* (Otranto & Traversa, 2005). In India, *Thelazia* larvae were found in the thoraces of 1.6% of 4364 *M. crassirostris*, collected in January 1977 from cattle grazing in villages in the vicinity of Hyderabad; this was the first report of this fly species as an intermediate host of *Thelazia* in southern India (Reddy & Rao, 1982).

A synergistic action of *Thelazia*, biologically transmitted, and *Mox. bovis* (pinkeye), mechanically carried by *M. crassirostris*, may occur. Indeed, *Thelazia* infection may create suitable conditions for *Mox. bovis* development; the symptoms of bacterial bovine keratitis caused by *Mox. bovis* are similar to those of thelaziosis, and both diseases occur when secretophagous flies are present. The incidence of pinkeye increases proportionally to the density of the fly population (flies carry *Mox. bovis*) and pinkeye most probably develops on traumatic lesions caused by *Thelazia* spp. (Otranto & Traversa, 2005).

Morphology and illustrated description of *M. crassirostris*

Amongst its other aims, this review is intended to make the identification of adult *M. crassirostris* easier in order to help field technicians to recognize and consider its potential impact.

Morphology of larval stages of M. crassirostris

The egg, larva and puparium are typical of *Musca* spp. (Crosskey, 1993). The eggs are large, measuring about 2.0–2.2 mm, of the form usual for *M. domestica*, cream in colour, and smooth with a slightly concave dorsal surface marked by a pair of parallel ribs (Muirhead Thomson, 1947). The first-stage larva cannot be distinguished from that of *M. inferior*, and there is nothing distinctive about the form of the buccopharyngeal skeleton (Muirhead Thomson, 1947). The mature larva (third instar) is on average 10.5 mm in length; it is of a deep lemon-yellow colour that, according to Patton & Cragg (1913), distinguishes it from the larvae of other species of Muscidae (although in the present authors' observations, *Stomoxys* larvae can also be yellow). The buccopharyngeal skeleton of the third instar is fairly similar to that of *M. bezzii*, but the left lateral hook is slightly smaller than the right hook, and the anterior spiracles possess seven or eight finger-like processes (James, 1947). The posterior spiracles are densely sclerotized, brownish, with a blackish peritreme, and present as a kidney shape included in a D shape; they are separated by a distance of less than their width (Van Emden, 1965); each of them has three well-separated, paler, strongly sinuous slits representing spiracular openings (Muirhead Thomson, 1947); the middle (outer) slits of the posterior spiracles are in approximately vertical positions (Van Emden, 1965) and exhibit four curves; the others are in approximately horizontal positions; the lower slit exhibits six curves, and the upper slit has four curves, the latter two of which flatten towards the median part.

Description of the adult stages of M. crassirostris

Adult flies trapped in the field should first be identified to the genus; however, for the purposes of identifying species within the genus *Musca*, the reader is referred to a recent and complete identification key. A total of 67 species in this genus have been described, distributed in the Afrotropical, Andean, Australasian, Nearctic, Neotropical, Oriental and Palaearctic regions (Nihei & de Carvalho, 2009).

For species identification, a number of keys are available (Patton & Patton, 1920; Patton, 1923; Patton & Senior-White, 1924; Tumrasvin & Shinonaga, 1977; Couri *et al*., 2012). These are based on the following limited number of morphological criteria: medium size, grey colour; the presence of four dark longitudinal stripes (vitae) on the thorax (better marked in males); the grey–olive colour of the abdomen; eyes bare (widely separated in females); light orange palpi; a bare proepisternum and suprasquamal ridge; a large, shiny, boat-shaped proboscis; fully developed prestomal teeth, and a mid-tibia with a strong anteroventral seta on the middle third.

This section presents a fully illustrated description of the male and female adult *M. crassirostris*, including the main criteria used for their identification in the various keys available. The species *M. crassirostris* is described below, based on reports in the literature (Patton & Cragg, 1913; Patton & Patton, 1920; Patton, 1923; Patton & Senior-White, 1924; James, 1947; Skidmore, 1985; Taylor *et al*., 2007) and completed by the authors' observations of over 100 flies trapped in Vavoua and Nzi traps (Laveissiere & Grebaut, 1990; Mihok, 2002) in various locations in Southeast Asian countries (Table 1). Thirty-three of these latter specimens were kept as vouchers at the Department of Entomology, Faculty of Agriculture, Kasetsart University (Kamphaeng Saen, Nakhon Pathom Province, Thailand). These included: two males and three females trapped on 5 December 2011 in Changmai, Thailand; three males and two females trapped on 22 November 2013 in Ipoh, Malaysia; five males and five females trapped on 17 December 2014 in Nakhon Pathom, Thailand; four males and six females trapped on 7 October 2015 in Nabong, Lao People's Democratic Republic, and two males and one female trapped on 18 January 2018 in Muñoz, Philippines.

Body. Adult *M. crassirostris* are of medium size; males and females are approximately the same size, about 5.5–7.5 mm in length, and may vary in colour from light to dark grey, with typical olive–green tones (Fig. 1). This makes them relatively easy to distinguish from other *Musca* (which are mostly black or yellow in colour) when separating insects harvested using insect traps in the field.

Eyes. In living and fresh flies, the eyes are a brown–red colour (burnt sienna, reddish brown) (Figs 1A and 2A, D), but the colour fades to dull brown when the insect is dead and dries (Figs 1B and 2B, E). The eyes are bare (thus differing from the hairy eyes of *Musca lasiophthalma*, and males of *Musca convexifrons*, *Musca interrupta*, *M. bezzii* and *Musca formosana*) (Tumrasvin & Shinonaga, 1977; Couri *et al*., 2012). The frons is very large in females (Fig. 2D) and very narrow in males (Fig. 2A). The present authors observed that the frontal index [calculated as the ratio of the smallest space between the eyes to the greatest length of the eye (Duvallet *et al*., 2017)] is 0.59–0.72 in females and 0.10–0.15 in males. Viewed from the side of the head, the border of the eye is straight (Fig. 2C), whereas in other *Musca* it is curved and convex (Fig. 2F).

Table 1. Locations, dates and specimens of *Musca crassirostris* captured by the present authors in Southeast Asia, and vouchers conserved.

Location	Date	Observed specimens	Voucher specimens∗
Buriram, Thailand	14/01/2010	Males, females	
Surin, Thailand	16/11/2010	Males, females	
Surat Thani, Thailand	15/06/2011	Males, females	
Ratchaburi, Thailand	28/09/2011	Males, females	
Military camp, Chiang Mai, Thailand	05/12/2011	Males, females	2 males, 3 females
Tha Wang Pha, Nan, Thailand	23/03/2013	Males, females	
Nakhon Sawan, Thailand	01/05/2013	Males, females	
Nakhon Si Thammarat, Thailand	26/06/2013	Males, females	
Ipoh, Malaysia	22/11/2013	Males, females	3 males, 2 females
Yogyakrta, Indonesia	21/05/2014	Males, females	
Bogor, Indonesia	26/05/2014	Males, females	
Hanoi, Vietnam	28/11/2014	Males, females	
Nakhon Pathom, Thailand	17/12/2014	Males, females	5 males, 5 females
Nabong, Lao	07/10/2015	Males, females	4 males, 6 females
Kamphaeng Saen, Nakhon Pathom, Thailand	19/09/2016	Males, females	
Muñoz, Philippines	18/01/2018	Males, females	2 males, 1 female
Mindanao, Philippines	10/03/2018	Males, females	3 males, 3 females

∗Vouchers kept at the Department of Entomology, Kasetsart University, Kamphaeng Saen Campus, Nakhon Pathom, Thailand.

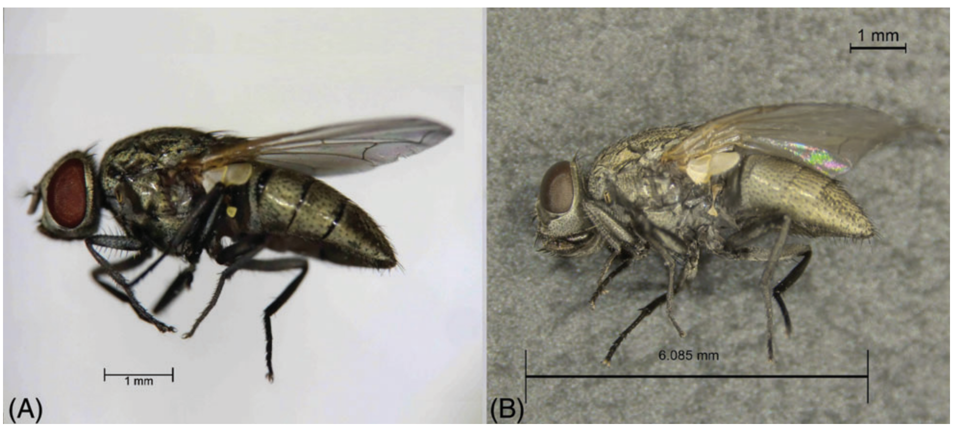

Fig. 1. Lateral views of (A) fresh and (B) dry specimens of *Musca crassirostris*.

Antenna. The antenna is of a typical cyclorrhaphan type and the arista has seven to 10 bristles on the dorsal side and five on the ventral side (Fig. 3).

Mouthparts. In terms of their physiological position, the mouthparts are folded up under the head; in a ventral view of the head, the labella are then usually visible, but the teeth are not visible as they are hidden inside (Fig. 4A). In some cases, the labella are everted and the prestomal teeth are visible (Fig. 4B, C); however, in most specimens, it is necessary to pull the mouthparts out to properly see the rostrum, palps and proboscis. When pulled out, the mouthparts show a very characteristic stout, bulbous proboscis with a boat-shaped, black, shiny mass of chitin: the mentum (also called the ‘haustellum’) (Fig. 4C, D). This bears 6–8 long bristles, and 20–28 short bristles (Fig. 4A–C). The labella harbours rasping prestomal teeth greatly increased in size and strength compared with those in other *Musca* spp. (Fig. 4C, E, F). This is characteristic of *M. crassirostris*: four large lateral teeth and four medium-sized (two dorsal and two ventral) teeth can be seen (Fig. 4F).

Maxillary palps are attached to the rostrum; they are characteristically yellow–orange in colour (Fig. 4C, E, F) [most of the *Musca* spp. other than *M. conducens*, *M. planiceps*, *M. inferior* and *M. crassirostris* have black palps (Patton & Senior-White, 1924)]. The maxillary palps are cylindrical in shape and narrow towards their bases (Patton & Cragg, 1913; Walker, 1994) (Fig. 4F).

Thorax. The thorax varies in colour from smoke grey to a slightly yellowish grey, especially in females, and exhibits four distinct dark longitudinal stripes (vitae), which are broad and well marked in males (Fig. 5A), and narrow and more lightly marked in females (Fig. 5B). The inner stripes are interrupted before they reach the scutellum (around the middle of the second thoracic segment). The propleuron is bare (Fig. 5C, white arrow), and the postalar ridge is without setulae.

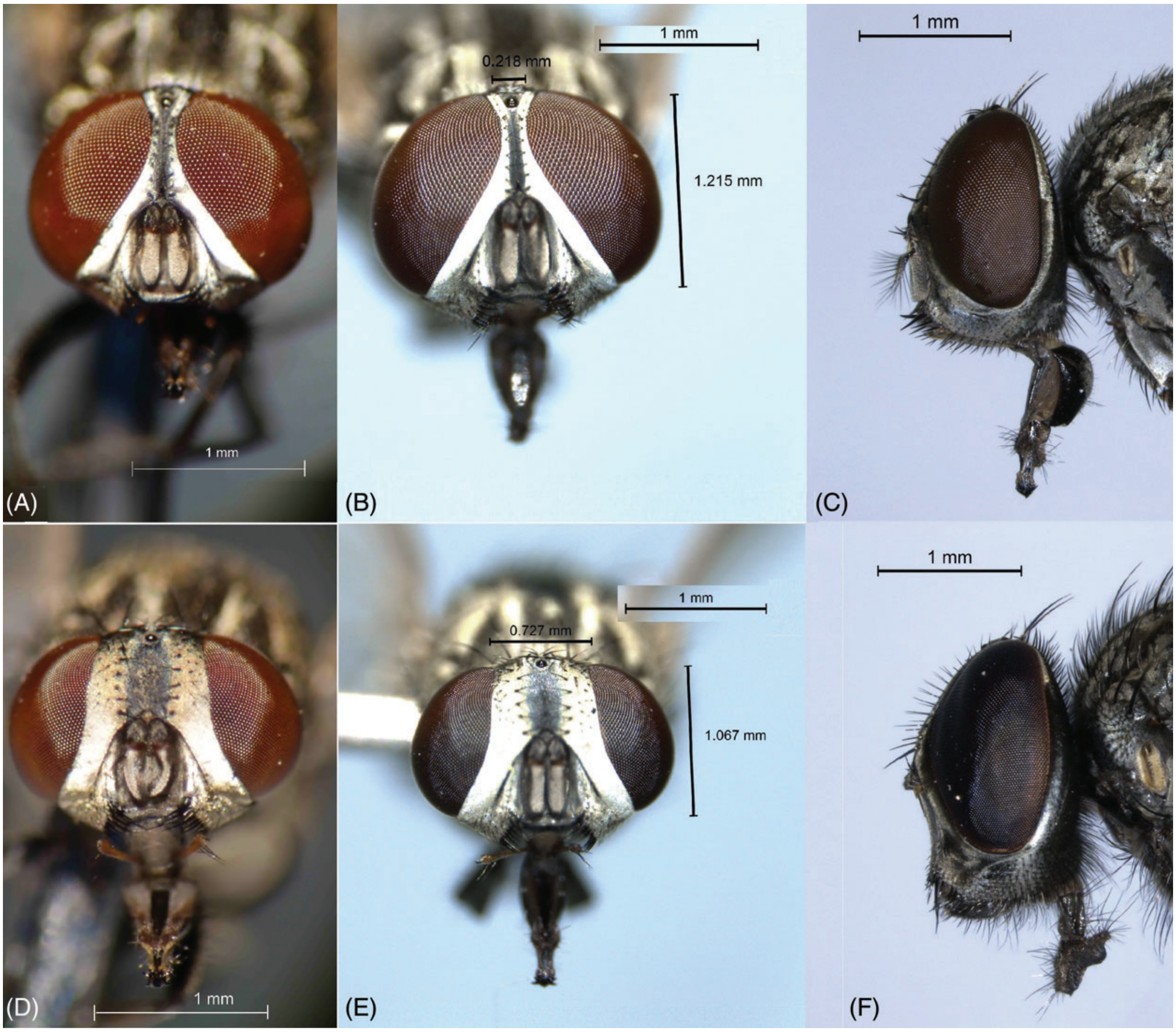

Fig. 2. Frontal view of the head in *Musca crassirostris*, in (A) fresh male, (B) dry male, (D) fresh female and (E) dry female specimens. Lateral views of the head in (C) *M. crassirostris* and (F) *Musca domestica*.

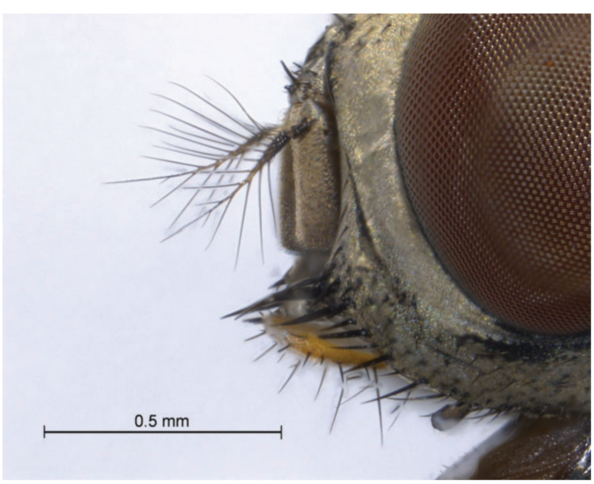

Fig. 3. *Musca crassirostris*: lateral view of the antenna and arista.

The anterior spiracle is light brown to beige (Fig. 5C, grey arrow). It has been described as 'dark brown' in specimens from Namibia (Couri *et al*., 2012); however, in the present specimens from Thailand, Malaysia, Indonesia, Philippines, Vietnam and Lao, no such colour was observed and only light brown colouring was seen. Similarly, in five specimens caught in 1993 in the northern semi-desert area of Ngurunit, Kenya (Mihok *et al*., 1995), the anterior spiracle was of a light brown colour (Steve Mihok, personal communication, 2017). The suprasquamal ridge is bare (Fig. 5D, black arrow); two anterior sternopleural bristles are present. The thoracic chaetotaxy (macrochaetae) was completely described by Patton & Cragg (1913); there are three sternopleural bristles, arranged in a '1 : 2' pattern (see sternopleural bristle 1 : 2 in Fig. 6A).

Wings. The wings are pale grey and yellowish at the anterior edges; they harbour some black bristles at the base of the costa

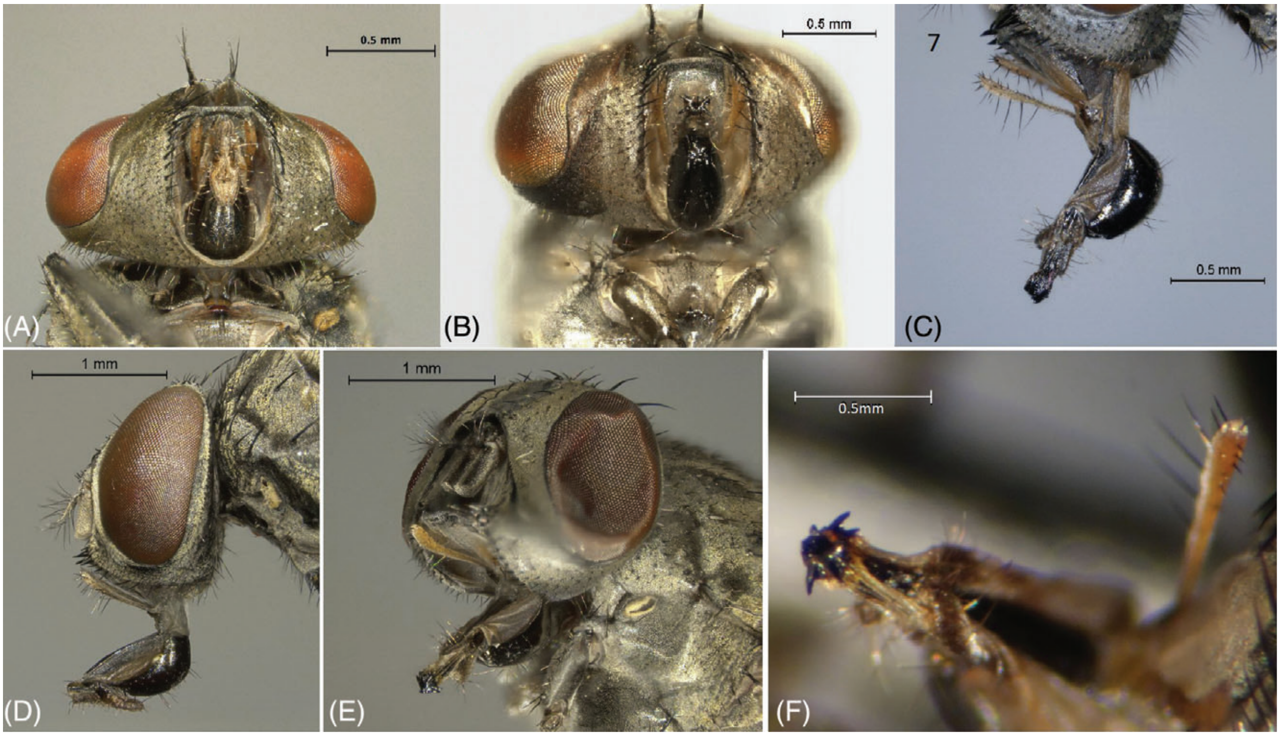

Fig. 4. *Musca crassirostris*. Ventral views of the head with (A) labella visible, teeth not visible and (B) labella everted, teeth visible. (C) Side view of the proboscis showing detail of the mentum and prestomal teeth (labella everted). Lateral views of the head, with (D) the proboscis pulled out and (E) the prestomal teeth visible. (F) Detail of the prestomal teeth.

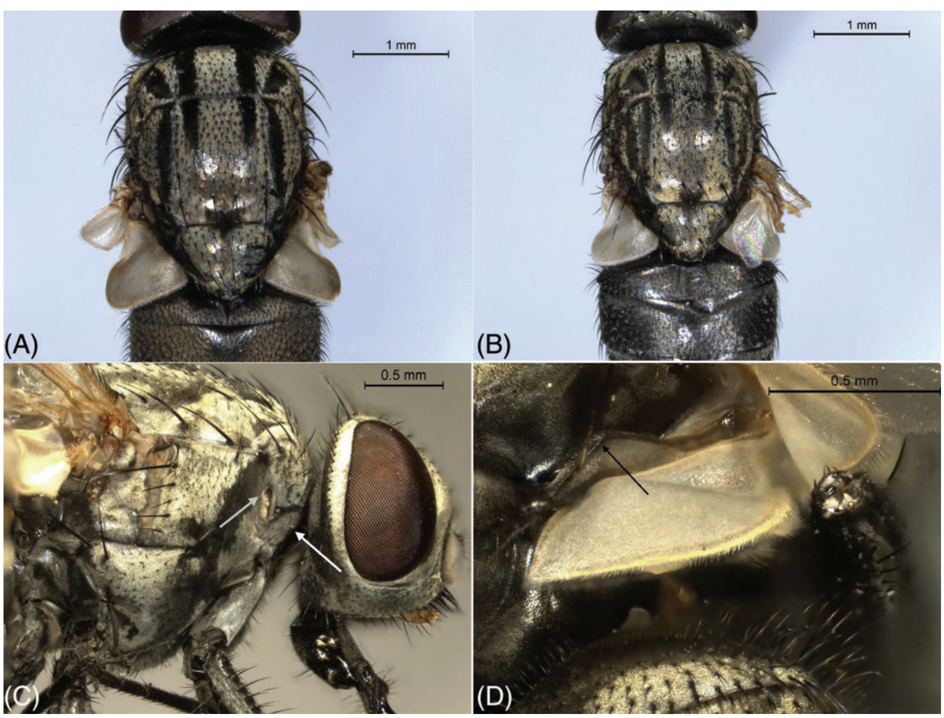

Fig. 5. *Musca crassirostris*. Dorsal views of the thorax (wings removed) in (A) male and (B) female specimens. (C) Lateral view of the thorax and head (white arrow: propleuron; grey arrow: spiracle). (D) Detailed view of calypters (the black arrow points to the bare suprasquamal ridge).

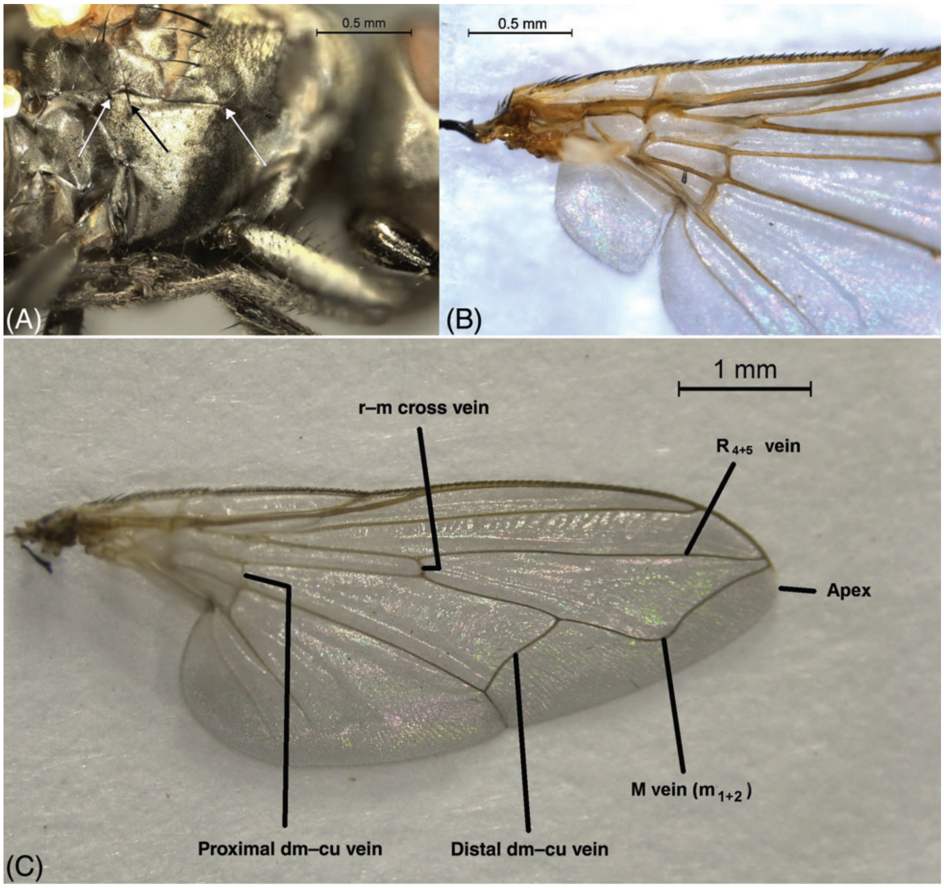

Fig. 6. *Musca crassirostris*. (A) Lateral view of the thorax (the black arrows point to one anterior and two posterior sternopleural bristles). (B) Basal part of the wing, showing black bristles at the base and black hair along the costa. (C) Annotated image of the wing.

and several rows of black hair along them (Fig. 6B). Their venation is similar to that in most other *Musca*, but the M vein (fourth longitudinal vein, or m_{1+2}) bends up at a sharper angle (almost a right angle) to reach the costa anteriorly to the apex, very close to the third longitudinal vein (R_{4+5}), at a distance below the length of the r–m cross vein; vein r_1 is bare, and the anal vein does not reach the wing margin (James, 1947). The discal cell is delimited anteriorly by a proximal dm–cu vein (Fig. 6C).

Abdomen. The abdomen shows four segments which may or not alternate in black and light markings (Taylor *et al.*, 2007). Indeed, the abdomen may appear to be mostly greyish when the insect is unfed (Figs 7 and 8A), but when it is distended by the bloodmeal, very dark and shiny anterior parts of the sternites and tergites (2–4) appear between the abdominal segments, giving the abdomen a transversally striped appearance (Fig. 8B). In both sexes, on the dorsal abdomen, darker areas can be seen on the lateral sides of segments 2 and 3, whereas segment 4 appears mostly darker; the median area is different in males and females.

In males, the abdomen is grey, of a heart shape, with a width : length ratio close to 1 (Fig. 7C, D). Segment 1 has a dark, almost black, transverse patch extending to the sides but not reaching the hind margins; segment 2 has a triangular brown–black longitudinal stripe pointing backwards but not reaching the lower edge; segment 3 has a dark longitudinal median band, extending almost the whole length of the segment, and segment 4 has a faint dark, longitudinal median band, extending the whole length of the segment (Fig. 7C) (Patton & Cragg, 1913).

In females, the abdomen is olive or greyish-yellow to green, and is longer than it is wide with a width : length ratio of around 0.7; it has black bristles that are regularly spread all over the mesopleuron and sternopleuron, but are absent from the hypopleuron (different from calliphorid flies). The middle line of segment 1 has no mark or a small darker area anteriorly; segment 2 has a narrow longitudinal band; segment 3 has an incomplete band, and segment 4 has no band (Fig. 7A) (Patton & Cragg, 1913). The ovipositor is slender with two dark cerci at the extremity (Fig. 8C). The cerci are well developed, and are either sub-cylindrical with an inner surface that is sclerotized and haired on the apical half, or compressed with an inner surface that is membranous and without hairs (Huckett & Vockeroth, 1987).

Legs. The legs are mostly of a dark greyish colour, with strong bristles on the ventral and dorsal parts of the fore femur (L1)

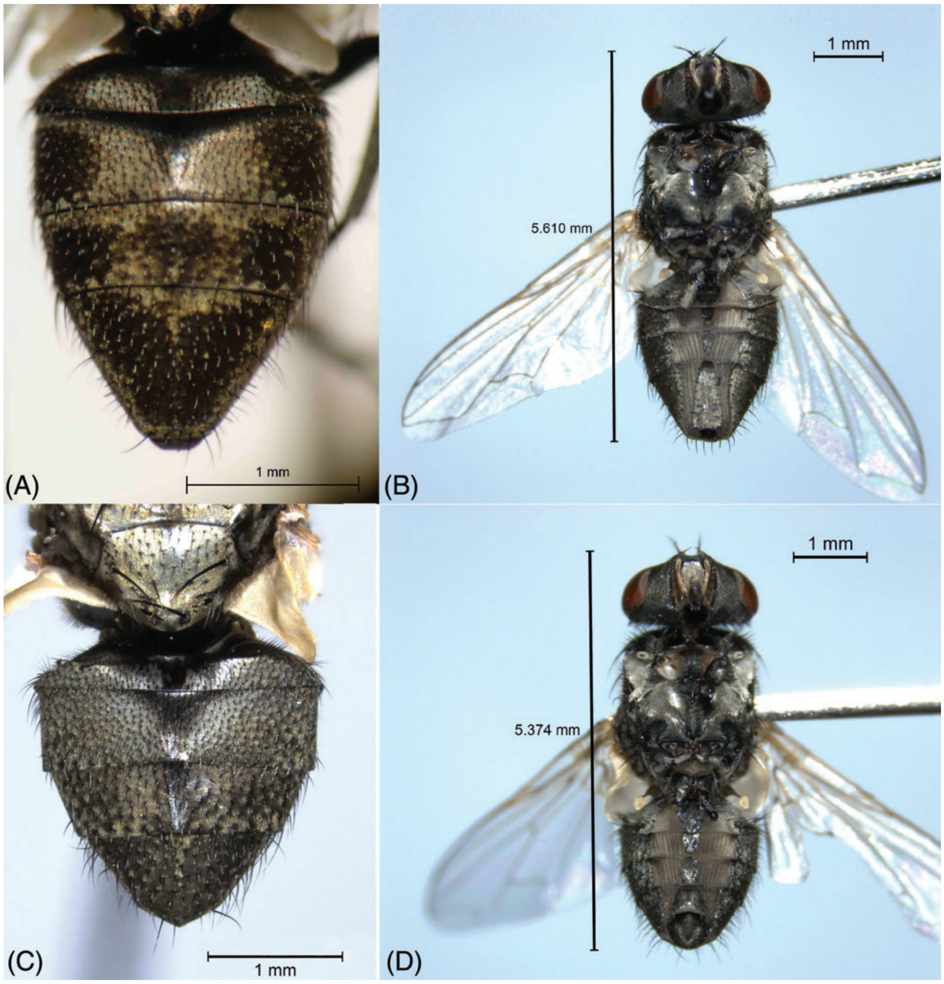

Fig. 7. *Musca crassirostris*. Dorsal views of the abdomen in (A) female and (C) male specimens. Ventral views of (B) female and (D) male specimens.

(Fig. 1A) and the dorsal part of the hind femur only (L3); the fore tibia are without ventral setae in the apical half; the mid tibia (L2) has a characteristic strong bristle (like a spur) pointing medially and located about two-thirds of the distance towards the distal end of the tibia (Fig. 8D, black arrow), as well as two medial and one external spur at its distal extremity (Fig. 8D).

Reports and surveys of *M. crassirostris*

Reports

Musca crassirostris is widely distributed from Africa through the Middle East, to Southeast Asia (James, 1947). A more detailed geographical distribution is difficult to establish because there are numerous but most often anecdotal reports of *M. crassirostris*. A non-exhaustive list of reports found in the literature is presented in Table 2, with reference to the authors (Patton & Patton, 1920; Patton, 1922, 1923; Du Toit & Nieschlutz, 1933; James, 1947; Muirhead Thomson, 1947; Mellor, 1978; Sucharit & Tumrasvin, 1981; Kigaye & Giffar, 1991; Shinonaga & Singh, 1994; Dia, 1997; Veer *et al*., 2002; Tyagi & Baqri, 2005; Huang *et al*., 2007; Dorrah, 2009; Chin *et al*., 2010; ElMahi, 2011; Al-Saffar *et al*., 2012; Couri *et al*., 2012; Moradi *et al*., 2013).

Musca crassirostris was recently captured in traps by the present authors in Thailand, Malaysia, Lao, Vietnam, Indonesia and the Philippines (Table 1).

Surveys of M. crassirostris *in Thailand*

Trapping studies using Nzi and Vavoua traps were conducted recently in Thailand, Malaysia, Indonesia, Lao, Vietnam and Philippines under the auspices of an informal consortium of researchers in Southeast Asia [the GREASE (Gestion des Risques Epidémiologiques Emergents en Asie du Sud Est) network and the BioZoonoSEA platform]. These have reported very high numbers of *M. crassirostris* in various workshops [http://www.grease-network.org/content/download/4694/35193/version/1/file/REPORT_BIVT_Workshop_Malaysia2013.pdf, http://umr-intertryp.cirad.fr/content/download/4379/32694/version/1/file/25+-+29th+

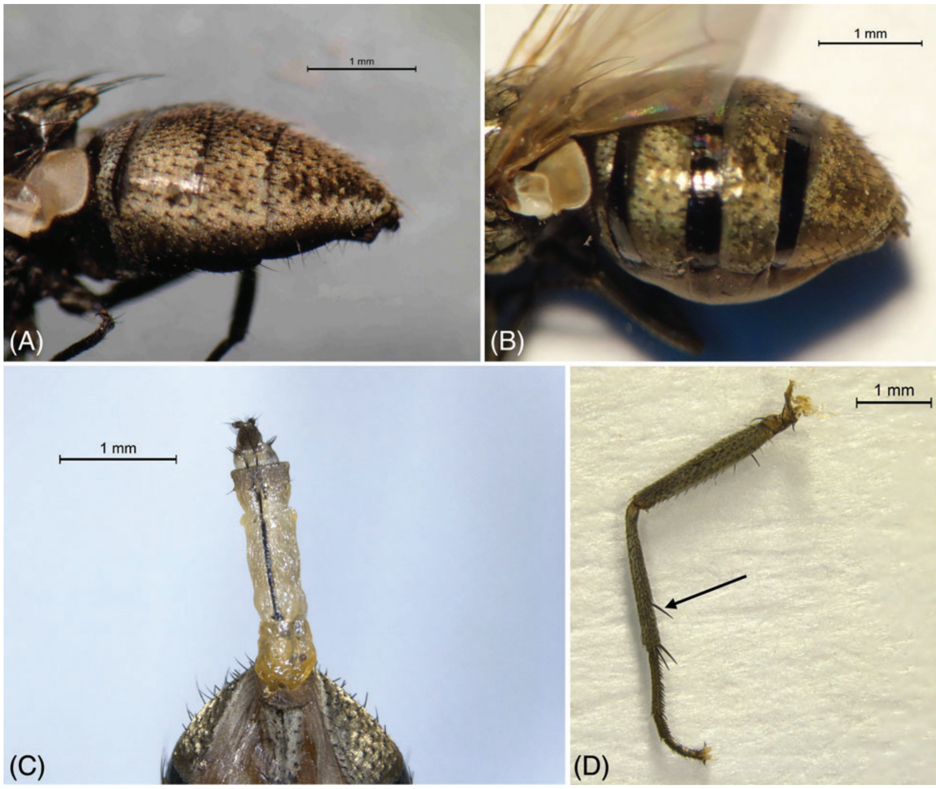

Fig. 8. *Musca crassirostris*. Side views of the abdomen in (A) unfed and (B) blood-fed specimens. (C) Female ovipository (externalized). (D) Mid-leg, showing a bristle two-thirds along the distal tibia (black arrow).

novembre+2014+Vietnam.pdf, http://umr-intertryp.cirad.fr/content/download/4410/32978/version/1/file/FINAL+PROGRAM+Workshop+LAO.pdf, https://www.grease-network.org/content/download/5562/41475/version/1/file/FINAL+REPORT+OW%26TW+at+PCC050218.pdf, https://www.grease-network.org/meetings-workshops2/workshops-meetings/2018/diagnosis-and-control-of-trypanosomes-and-their-vectors-in-animals-and-humans-in-sea (all accessed on 3 May 2017)]. In around a fifth of cases, the dissection of freshly captured *M. crassirostris* showed the presence of fresh blood in the guts, confirming the haematophagous character of the species. In a study carried out in Nigeria, 100% of specimens caught on lions and hyenas were blood-fed (Dipeolu, 1976); however, the trapping method (insects were caught in the cages of the animals) differs from the trapping techniques used in the present studies (field surveys). The high abundance, haematophagous character, and high bovine affinity of *M. crassirostris* strongly suggest that its impacts on livestock should be reconsidered. It should not be considered merely as 'another sponging fly', with little presumed impact.

In a recent study, carried out in five dairy farms in Saraburi Province, Thailand, using non-baited Malaise traps for 1 day per month, from June 2008 to October 2009, 100 403 flies were trapped; the relative abundances of flies, by increasing numbers, were: tabanids 0.2%; *Haematobia* spp. 0.4%; *M. domestica* 2.0%; *Stomoxys* spp. 24.4%, and *M. crassirostris* 73.0% (Phasuk *et al*., 2010, 2013). Hence, *M. crassirostris* was three and 348 times more abundant than *Stomoxys* spp. and tabanids, respectively; this study also suggested that Malaise traps are highly effective in catching *Haematobia* and *M. crassirostris*.

The authors of the present paper also carried out an original study at the Kamphaeng Saen Campus of Kasetsart University, Nakhon Pathom Province, using one unbaited Vavoua trap and one Nzi trap set up 1 day per week, during April–June 2016, in the vicinity of a beef cattle stable with six feeder cattle. Traps were set up at 20 m from the stable, 100 m apart and were set at 06.00 hours and removed at 19.00 hours (cages were changed every 2 h) to record the daily activity pattern of the flies (to be reported elsewhere). Over 3 months, 12 946 flies were trapped; on average, the relative abundances of the flies, by increasing numbers, were: tabanids 0.7%; *Stomoxys* spp. 7.8%; *M. crassirostris* 33.0%, and *M. domestica* 58.4%. Hence, *M. crassirostris* was four and 45 times more abundant than *Stomoxys* spp. and tabanids, respectively. Detailed results of these studies are presented in Table 3. During this study, direct observations of fly annoyance were made on the six feeder cattle kept inside the stable. During tail flick records (made to evaluate global insect annoyance; to be reported elsewhere), for 3 min on each cow in the morning and evening, *Stomoxys* spp. and *M. crassirostris* were observed mostly on the legs of the cattle. *Musca crassirostris* appeared to be at least three times more abundant than *Stomoxys* spp., and the defensive movements of the animals were clearly linked to the flies' landing and blood feeding. Meanwhile, *M. crassirostris* was also regularly

Table 2. Reports of occurrences of *Musca crassirostris*: regions, countries, areas and references.

Region	Country or area	References
East Asia	China	Sucharit & Tumrasvin (1981)
	Shantung (China)	James (1947)
	Taiwan	Huang *et al*. (2007)
	Japan	Huang *et al*. (2007)
Southeast Asia	All	James (1947)
	Burma	Sucharit & Tumrasvin (1981)
	Thailand	Sucharit & Tumrasvin (1981); present paper
	Lao	present paper
	Vietnam	James (1947); present paper
	Malaysia	Chin *et al*. (2010); present paper
	Indonesia, Borneo, Java, Sumatra, Lombok	Huang *et al*. (2007)
	Java (Indonesia)	Present paper
	Philippines	Patton (1923); James (1947); present paper
South Asia	India	Patton (1922)
	Assam (India)	Thomson (1947)
	Orissa (India)	Veer *et al*. (2002)
	Thar Desert (India)	Tyagi & Baqri (2005)
	Nepal	Shinonaga & Singh (1994)
	Sri Lanka	Huang *et al*. (2007); Sucharit & Tumrasvin (1981)
	Pakistan	Patton (1922)
	Iran	Moradi *et al*. (2013)
Middle East	All	James (1947)
	Caucasian Russian republics	Sucharit & Tumrasvin (1981)
	Georgia, Armenia, Azerbaidjan	Sucharit & Tumrasvin (1981)
	Turkey	Patton & Patton (1920)
	Cyprus	James (1947)
	Lebanon, Palestine, Israel	Patton (1922)
	Syria	Patton (1922)
	Iraq	Al-Saffar *et al*. (2012)
	Jordan, Mesopotamia	Patton & Patton (1920)
	Arabian peninsula	James (1947)
	Oman, including Dhorfar	Mellor (1978); ElMahi (2011)
	Socotra island (Yemen)	Al-Saffar *et al*. (2012)
North Africa	All	Dia (1997)
	Egypt	Dorrah (2009)
	Sinai peninsula (Egypt)	James (1947)
	Libya	Dorrah (2009)
	Mauritania, Cape Verde	Dia (1997)
West Africa	Senegal	Dia (1997)
	Ghana	Dorrah (2009)
East Africa	Ethiopia, Sudan	Kigaye & Giffar (1991)
Central Africa	Congo	Kigaye & Giffar (1991)
South of Africa	Zambia, Zimbabwe, Namibia	Couri *et al*. (2012)
	South Africa	Du Toit & Nieschlutz (1933)
Europe	Dodecanese Islands (Greece)	Patton & Patton (1920); James (1947)

reported to attempt to feed on the technicians making the observations, although not on intact skin and only on previously wounded skin areas at which blood was visible (either due to scratches or previous *Stomoxys* bites); *M. crassirostris* was obviously attracted by the blood in these observations.

In a study carried out in India, *M. crassirostris* represented 17% of the haematophagous insects trapped (Veer *et al*., 2002); in another study conducted in South Africa, the relative abundance of *M. crassirostris* was 20% vs. 11 other *Musca* spp. (Nevill, 1997). Although made in various locations, seasons and using various trapping methods, all these observations show very high relative abundances of *M. crassirostris* in comparison with other haematophagous flies, especially in bovine farms, and thus emphasize the need for further evaluation of this species' potential annoyance and direct impact on livestock.

Conclusions

This review and description of *M. crassirostris* highlights a rather neglected but very much present fly, especially on bovine farms. Seasonally in phase with the true biting flies, *M. crassirostris* is an obligate and true haematophagous fly, even if it may rely on the activities of true biting flies to successfully obtain most of its bloodmeals. Although very little attention has so far been paid to this fly, it is highly recommended that *M. crassirostris* be identified and distinguished from the true

Table 3. Detailed results of trapping surveys carried out in two provinces in Thailand.

	Saraburi, Saraburi Province, 2008–2009, Malaise traps∗	Kamphaeng Saen, Nakhon Pathom Province, 2016, Vavoua and Nzi traps†
Total pest insects trapped, *n*	100 403	12 946
Tabanids, *n*	215	96
Stomoxys spp., *n*	24 969	1012
Haematobia ssp., *n*	410	2
Musca crassirostris, *n*	74 809	4277
Musca spp. other than *M. crassirostris*, *n*	2051	7561
Ratio of *M. crassirostris* : tabanids	348	45
Ratio of *M. crassirostris* : *Stomoxys* spp.	3	4

∗Phasuk *et al*., 2010, 2013.
†This study.

sponging flies that are considered to be of lower impact as a result of their facultative blood feeding and lack of rasping mouthparts. The fly can be rapidly identified based on the shape and colour of its abdomen and the peculiar shape of its brilliant, stout proboscis; this readily distinguishes it from non-rasping, sponging flies. The identification and counts of this fly in regular trapping of livestock pests are strongly recommended to evaluate its potential impact. Through these activities, it may become apparent that *M. crassirostris* should be controlled together with tabanids and *Stomoxys* spp. Adapted tools currently under development for the control of *Stomoxys* spp. and tabanids [the Flyscreen project/French National Research Agency (ANR)] should then be jointly considered for the control of biting flies and *M. crassirostris*.

Acknowledgements

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