Neosomes of tungid fleas on wild and domestic animals

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Abstract Tunga is the most specialized genus among the Siphonaptera because adult females penetrate into the skin of their hosts and, after mating and fertilization, undergo hypertrophy, forming an enlarged structure known as the neosome. In humans and other warm-blooded animals, neosomes cause tungiasis, which arises due to the action of opportunistic agents. Although its effects on humans and domestic animals are well described in the literature, little is known about the impact of tungiasis on wild animals. This review focuses on the morphology, taxonomy, geographical distribution, hosts, prevalence, sites of attachment, and impact of tungid neosomes on wild and domestic animals. Because neosomes are the most characteristic form of the genus Tunga and also the form most frequently found in hosts, they are here differentiated and illustrated to aid in the identification of the 13 currently known species. Perspectives for future studies regarding the possibility of discovering other sand flea species, adaptation to new hosts, and the transfer of tungids between hosts in natural and modified habitats are also presented.

Keywords Neosome · Tungid fleas · Sand fleas · Wild and domestic animals · Siphonaptera

Introduction

Adult fleas (Siphonaptera) are obligate hematophagous ectoparasites that infest humans and wild and domestic animals. There are approximately 3,000 species and subspecies of fleas included in 238 genera and 15 families worldwide (Lewis 1998). Tungidae is the most specialized family in that the females of the genera Tunga Jarocki (Tunginae) penetrate the skin of their hosts (Hopkins and Rothschild 1953; Linardi and Guimarães 2000), and after mating, the gravid females undergo hypertrophy, becoming neosomes (Audy et al. 1972) in spite of the genus Neotunga Smit of the family Pulicidae also presenting penetrating females. Another genus, Hectopsylla Frauenfeld (Hectopsyllinae), includes species that are also considered neosomatic, but the females are semipenetrating and only attach their mouthparts to the hosts.

According to Audy et al. (1972), neosomes are organisms that are altered by the formation of a new external morphological structure and the secretion of new cuticle, accompanied by significant enlargement during an active process of metamorphosis. Although neosomy exists in other Arthropoda, in fleas, the process occurs in approximately 90 sessile or semisessile species (Rothschild 1992), primarily in the families Vermipsyllidae and Tungidae. Neosomatic vermipsyllids, also called alakurt fleas, include two species—Dorcadia ioffi Smit and Vermipsylla alakurt Schimkewitsch—that parasitize ungulates, particularly domestic sheep, horses, and yaks in Central Asia, but their females do not burrow beneath the skin as do tungids, which are endoparasitic.

In tungids, neosomes are the most frequently observed form in hosts. Because neosomes involute with the death of the parasite after oviposition (Lavoipierre et al. 1979), specific identification can be difficult because certain characteristics cannot be observed in the most commonly dissected
specimens. Later, the neosomes can be absorbed or sloughed from the host epidermis by tissue repair mechanisms (Eisele et al. 2003; Lavoipierre et al. 1979).

Whereas Neotunga is composed of only one valid species, Neotunga euloidea Smit, which parasitizes African pangolins (Lewis 1998), the genus Tunga includes 13 species of sand fleas (De Avelar et al. 2013). Two Tunga species are found in China and Japan, and the other 11 occur in the New World tropics. One of these, Tunga penetrans (L., 1758), also occurs in Sub-Saharan Africa (Beaucournu et al. 2012b; De Avelar et al. 2012; Lewis 1998; Linardi and Guimarães 2000).

However, because there is little knowledge of this group, some misidentifications have been recorded, especially given that many specimens collected from parasitological investigations or veterinary surveys were named according to their hosts. This circumstance is compounded by the fact that, with the exception of De Avelar et al. (2012), taxonomic keys rarely contain data on neosomes.

Tungiasis causes serious ectoparasitosis, and harmful infections and their effects on humans are well documented, especially in Heukelbach (2005, 2006) and Karunamoorthi (2013). With respect to domestic animals, a review can be found in Pampiglione et al. (2009). However, little is known about the impact of tungiasis on wild animals. The present article provides a selective review of the morphology, taxonomy, geographical distribution, hosts, prevalence, preferred sites of attachment, and impact of neosomes on wild and domestic animals. The paper also presents perspectives for future research regarding the possibility of discovering other sand flea species, adaptation to new hosts, and the interchange of tungids between hosts from natural and modified habitats.

Morphology and taxonomy

Currently, the genus Tunga includes the following species: T. penetrans (L., 1758); Tunga caecuta (Enderlein, 1901); Tunga caecigena Jordan & Rothschild, 1921; Tunga travassosi Pinto & Dreyfus, 1927; Tunga bondari Wagner, 1932; Tunga terasma Jordan, 1937; Tunga callida Li & Chin, 1957; Tunga libis Smit, 1962; Tunga monositus Barnes & Radovsky, 1969; Tunga trimamillata Pampiglione et al., 2002; Tunga bossii De Avelar et al., 2012; Tunga bonneti Beaucournu & González-Acuña, 2012; and Tunga hexalobulata De Avelar et al., 2013. Tunga penetrans is the most well-known species, having been described in the eighteenth century and referred to in the literature as the sand flea, sandfloh, puce de sable, chigoe, jigger, chigger, chique, nigua, and bicho-de-pê, among other names. In Peru alone, when searching for the evidence of tungiasis in pre-Hispanic America, Maco et al. (2011) used 35 different local names for T. penetrans.

Eight of the 13 species of the genus Tunga have known males: T. penetrans, T. terasma, T. caecigena, T. callida, T. libis, T. monositus, T. trimamillata, and T. bonneti. Four species—T. travassosi, T. bondari, T. bossii, and T. hexalobulata—are known only by their neosomes. Only two species—T. penetrans and T. monositus—have immature forms that have been described. The species T. libis, T. bondari, T. bossi, and T. hexalobulata are known only through a small number of specimens.

Neosomes vary in form and size, but the enlargement of the abdomen generally occurs between abdominal segments II and III, as seen in T. caecigena (Jordan 1962), T. monositus (Barnes and Radovsky 1969), and T. penetrans (Eisele et al. 2003). The posterior part has the form of a caudal disk-like or conical prominence that bears respiratory, anal, and genital apertures and is exposed through an opening in the host’s skin (Audy et al. 1972). In the dorsal view, the caudal disk is sclerotized, resembling a crater. Data regarding the morphology of neosomes are presented in Table 1. For the first time, the neosome of T. bondari is illustrated, although a brief description was included in De Avelar (2010). Neosomes of T. travassosi have been described with the head and thorax evaginated in relation to the abdomen (Pinto and Dreyfus 1927). However, after the observation of specimens deposited in the scientific collection of the Museum of Zoology of the University of São Paulo, Brazil, and the Department of Parasitology of the Federal University of Minas Gerais, Brazil, it was verified that such structures are, in fact, invaginated, and they can be seen only after dissection of the neosomes.

Figure 1 shows the shape of the gravid females of Tunga species found both in wild and domestic animals. Figure 11 is a dorsal view of T. bonneti, whereas in the other panels, the neosomes are shown in a lateral view. Figure 2 shows neosomes after dissection from their respective hosts. A neosome of the semisessile flea Hectopsylla pulex (Haller, 1880) is included for comparison.

Geographical distribution

Species of Tunga have been found from 34° 41’ N to 33° 29’ S and from 38° 30’ W to 135° 30’ E. According to Barnes and Radovsky (1969), the center of distribution and the apparent origin of the genus Tunga are in the Neotropical region. Indeed, of the 13 described species, nine are restricted to South America, and another, T. penetrans, exhibits a wide Neotropical distribution, as it is now permanently established in much of tropical Africa (Lewis 1998). In spite of occasional records of Tunga fleas on humans in the USA (Bell et al. 1979; Brothers and Heckmann 1975; Goldman 1976; Reiss 1966; Sanusi et al. 1989), Italy (Veraldi et al. 1996; Veraldi and Valsecchi 2007), and
New Zealand (Pilgrim 1993), sand fleas do not appear to have established themselves in these countries.

De Avelar (2010) described the presence of T. penetrans in the following countries: Argentina, Brazil, Colombia, Chile, Ecuador, Guyana, French Guiana, Paraguay, Peru, Suriname, Trinidad, Uruguay, Venezuela, and the Caribbean Islands in Latin America and South Africa, Angola, Botswana, Cameroon, Congo, Ivory Coast, Eritrea, Gabon, Ghana, Guinea, Liberia, Libya, Madagascar, Mali, Mauritania, Mozambique, Namibia, Niger, Nigeria, Kenya, Central African Republic, São Tomé, Senegal, Sierra Leone, Somalia, Sudan, Tanzania, Tunisia, Uganda, Zaire, Zambia, Zanzibar, and Zimbabwe in Sub-Saharan Africa. According to Pampiglione et al. (2009), tungiasis has been reported in approximately 70 nations.

Except for T. penetrans, Table 2 presents the geographical distribution by country and respective state or province where the species have been recorded as well as the ranges of distribution and altitude. Eight of the 13 species occur in Brazil, six of which are endemic in that country. Although the extent of the distribution depends upon the number of localities recorded for the species, and although T. bossii and T. hexalobulata have been found only in the localities in which they were described, the ranges of the distribution of each species, which vary from 494 to 5,465 km, may also indicate the level of dispersion of each species. Similarly, certain species, such as T. trimamillata, T. libis, and T. bonneti, which are found in the Andean regions, can also occur at high altitudes. Except for new Brazilian occurrences (Table 3), all of the records of other localities of capture were detailed and presented by Beaucournu et al. (2012b) along with their geographical coordinates.

### Hosts

Because the degree of specificity among flea/host species is variable, both fleas and hosts can be classified by the pattern of their relationships to separate natural and casual associations (Holland 1964; Krasnov 2008; Marshall 1981; Wenzell and Tipton 1966). In these circumstances, hosts can be considered as true, primary, accidental, or secondary for a given species of flea. True hosts, also called normal, essential, or primary hosts, are those that provide favorable conditions under which a flea species can reproduce indefinitely. Except for T. penetrans, Table 2 presents the geographical distribution by country and respective state or province where the species have been recorded as well as the ranges of distribution and altitude. Eight of the 13 species occur in Brazil, six of which are endemic in that country. Although the extent of the distribution depends upon the number of localities recorded for the species, and although T. bossii and T. hexalobulata have been found only in the localities in which they were described, the ranges of the distribution of each species, which vary from 494 to 5,465 km, may also indicate the level of dispersion of each species. Similarly, certain species, such as T. trimamillata, T. libis, and T. bonneti, which are found in the Andean regions, can also occur at high altitudes. Except for new Brazilian occurrences (Table 3), all of the records of other localities of capture were detailed and presented by Beaucournu et al. (2012b) along with their geographical coordinates.

### Table 1  Morphology and morphometry of the neosomes of Tunga species

| Tunga species | Neosomes | Measurements (mm) (length×width×height) | Head and thorax in relation to abdomen (lateral view) | Caudal disk (segments IV–X) |
|---------------|----------|----------------------------------------|-----------------------------------------------------|-----------------------------|
| **T. penetrans** | Globular without lobes | 6×5×4 | Evaginated | Flattened, wider than long |
| **T. caecata** | Globular without lobes | 7×6×6 | Invaginated | Conical, almost as wide as long |
| **T. travassosi** | Globular without lobes | 13×8×10 | Invaginated | Conical, as wide as long |
| **T. terasma** | Subcylindrical with four lateral prominent lobes | 10×9×13 | Evaginated | Cylindrical, longer than wide |
| **T. bondari** | Mushroom-shaped with a stem, as that generated by a nuclear explosion | 6×6×5 | Evaginated | Cylindrical, longer than wide |
| **T. caecigena** | Elliptical with four lobes: dorsal and ventral portions of similar dilatation | 7–10×5×6 | Not visible in profile | Cylindrical, longer than wide |
| **T. callida** | Spherical with four lobes: dorsal portion more swollen than the ventral portion | 4.5×4.5×4.5 | Not visible in profile | Cylindrical, as long as wide |
| **T. libis** | Vertically elliptical and without lobes | higher than long | Not visible in profile | – |
| **T. monositus** | Bell-shaped with 8 lobes, arranged as 4 large outer lobes and 4 small inner lobes located anteriorly | 6×5.4×4.5 | Evaginated but not visible in profile | Flattened, wider than long |
| **T. trimamillata** | Globular with 3 lobes | 12×5×5 | Evaginated but not visible in profile | Conical, wider than long |
| **T. bossii** | Globular without lobes | 9×8×7 | Invaginated | Flattened, wider than long |
| **T. bonneti** | Horizontally elliptical with rugby ball shape | 10×6 | Invaginated | – |
| **T. hexalobulata** | Spherical with six lobes located anteriorly, pearl-white colored, slightly compressed in anterior direction | 4×4×4 | Evaginated but not visible in profile | Conical, wider than long |
A secondary host is an intermediate category for those considered neither a true nor an accidental host. According to Holland (1964), this category is transitional for some animals because a secondary host may eventually become a true host.

**Fig. 1** Shape of gravid females of the species of *Tunga*: A *T. penetrans*; B *T. caecata*; C *T. caecigena*; D *T. travassosi*; E *T. terasma*; F *T. bondari*; G *T. callida*; H *T. libis*; I *T. monositus*; J *T. trimamillata*; K *T. bossii*; L *T. bonneti*; M *T. hexalobulata*

**Fig. 2** Neosomes of some species of *Tunga* after removal from their hosts: A *T. penetrans*; B *T. travassosi*; C *T. terasma*; D *T. bondari*; E *T. monositus* (after Lavoipierre et al. 1979); F *T. trimamillata*; G *T. hexalobulata*
| Species      | Countries: states or provinces                                                                 | Limits of distribution | References                                      |
|-------------|-----------------------------------------------------------------------------------------------|------------------------|-------------------------------------------------|
| T. caecata  | Brazil: Minas Gerais (MG), Paraná (PA), São Paulo (SP)                                        | Caratinga MG/Curitiba PA 965 533 to 1,141 | Linardi and Guimarães (2000)                     |
| T. travassosi | Brazil: SP, MG                                                                              | Sorocaba SP/Belo Vale MG 494 566 to 800  | Linardi and Guimarães (2000)                     |
| T. terasma  | Brazil: Goiás (GO), MG, SP, Espírito Santo (ES), Mato Grosso do Sul (MS)                      | Anápolis GO/São Paulo SP 965 98 to 1,141   | Linardi and Guimarães (2000); Antunes et al. (2006) |
| T. bondari  | Brazil: Bahia (BA), SP, MG                                                                    | Salvador BA/Brasília SP 1,268 0 to 1,141   | Hopkins and Rothschild (1953); Linardi and Guimarães (2000) |
| T. caecigena | China: Chekiang (CH), Fukien (FU), Kiangsu (KJ), Shanghai (SH), Szechuan (SZ), Soochow (SU) | Nishinomyia HY/Futsing FU 839 9 to 229     | Jordan (1962); Beaucournu et al. (2012b)         |
| T. callida  | China: Yunnan (YU)                                                                            | –                     | –                                               | Li and Chin (1957)                               |
| T. libis    | Ecuador: Chimborazo (CM)                                                                       | –                     | Riobamba CM/Reserva Nacional Las Chinchillas 3,418 0 to 2,200 | Smit (1962); Beaucournu et al. (2012b)         |
| T. monositus| Mexico: Baja California (BC), San Martin Island (SM), USA: Utah (UT)                          | –                     | Washington County UT/San Quintin Bay (BC) 841 0  | Barnes and Radosky (1969); Hastriter (1997)      |
| T. trimamillata | Ecuador: Azuai (AZ), Loja (LO), Santa Isabel, Cuenca, Machala Peru: Piura (PI)              | Sujo PI/Felixlandia MG 5,465 29 to 2,709   | Fioravanti et al. (2006); Ribeiro et al. (2007); Linardi et al. (2013); Lucchetti et al. (2005a) |
| T. bossii   | Brazil: Rio de Janeiro (RJ)                                                                   | –                     | Itataia National Park RJ 2,359                  | De Avelar et al. (2012)                         |
| T. bomneti  | Chile: Atacama (AT), Santiago (SA), Limari (LI), Huasco (HU), Antofagasta (AN), El Loa (EL) | Quebrada de Inca EL/Dunas Las Cruces SA 1,405 0 to 3,794 | Beaucournu et al. (2012a)                       |
| T. hexalobulata  | Brazil: MG                                                                                  | Funilândia MG – 692  | De Avelar et al. (2013)                         |
host. According to Marshall (1981), from the ectoparasitological viewpoint and depending upon the species number of their true hosts, fleas can be regarded as one of the following: monoxenous (only one host), oligoxenous (two or more host species in the same genus), pleoxenous (two or more host genera in the same family), or polyxenous (several hosts in multiple families).

Among the 13 known species of Tunga, T. penetrans is the most promiscuous, having been found on hosts belonging to eight different orders of mammals, including Cingulata, Pilosa, Artiodactyla, Perissodactyla, Carnivora, Rodentia, Primates, and Proboscidea; in total, T. penetrans has been found on 27 genera of wild and domestic animals (De Avelar 2010) in addition to two occurrences that have only recently been recorded (Frank et al. 2012; Widmer et al. 2013). However, in spite of the broad spectrum and category of hosts, the pig is considered the most important animal reservoir for T. penetrans (Pampiglione et al. 1998; Ugboroiko et al. 2008). Humans and dogs might be considered secondary hosts or even true or essential hosts undergoing the process of adaptation. The parasitism of T. penetrans on elephants (Ruthe 1961), gorillas (Ewing and Fox 1943), and monkeys (Fitzsimmons 1966) should be seen as accidental. However, because the identification of this species is not always performed by experts and is sometimes based on the sole criterion of “penetrating fleas,” some misidentifications may have occurred. In fact, records of T. penetrans on bats (Blanchard 1890) may be attributed to the sessile flea H. pulic. Similarly, the infestation of this species on Gallas gallus cited by Macchiavello (1948) might have been confused with the stick-tight flea Echidnophaga gallinacea (Westwood, 1875), and the parasitism on the passerine Volatinia jacarina reported in Lima and Hathaway (1946), if not accidental, must be attributed to Hectopsylla psittaci Frauenfeld, 1860. Similarly, the occurrence of T. bondari on Cariama cristata, cited by Hopkins and Rothschild (1953), is likely an accidental finding.

Concerning domestic animals, until now, only three species of sand fleas have been found as ectoparasites: T. penetrans on the pig, cow, dog, cat, and horse; T. trimamillata on the cow, goat, sheep, and pig; and T. hexalobulata, which was recently found on cattle. Only T. penetrans and T. trimamillata parasitize humans. The other 10 species exclusively infest wild animals, regardless of the number of host species. These species are listed in Table 4 and are based on Beaucournu et al. (2012b), Cunha (1914), Hopkins and Rothschild (1953), Johnson (1957), Lima and Hathaway (1946), Linardi and Guimarães (2000), Pinto (1930), and several studies included in De Avelar (2010). Host nomenclature follows Wilson and Reeder (2005).

Another category of host is experimental animals, such as Mus musculus (Lavoipierre et al. 1979) and Wistar rats (an albino strain of Rattus norvegicus), which are used to establish the life cycle of T. penetrans in the laboratory (Feldmeier et al. 2007; Nagy et al. 2007), or dogs, which are used to test the efficacy of drugs against tungiasis (Klimpel et al. 2005).

According to Smit (1962), the genus Tunga comprises two species groups that are separated by morphological characteristics and host affinities: caecata and penetrans. In the caecata group, which is considered the most primitive, the following species are currently included, all of which exclusively parasitize rodents: T. caecata, T. caecigena, T. caecigena, T. libis, T. monositus, T. bossii, and T. bonneti. The finding of T. caecigena on Suncus murinus (Insectivora) might be accidental. The penetrans group is the evolutionarily advanced, as it is composed of T. travassosi, T. bondari, T. terasma, T. trimamillata, T. hexalobulata, and obviously T. penetrans, with the first three species associated primarily with edentates.
Table 4 Hosts species for *Tunga* species

| Species of *Tunga* | Type: number of true hosts | Species of mammal hosts |
|--------------------|---------------------------|-------------------------|
| *T. penetrans*     | Polyxenous                | Artiodactyla: *Bos taurus*, *Sus scrofa*, *Capra hircus*, *Ovis aries*, *Pecari tajacu*, *Lama glama*, *Vicugna vicugna*, *Potamochoerus porcus*<br>Carnivora: *Canis familiaris*, *Felis catus*, *Panthera onca*<br>Cingulata: *Dasypus novemcinctus*, *D. hybridus*, *Chaetophractus villosus*<br>Perissodactyla: *Tapirus terrestris*, *Equus caballus*, *Equus sp.*<br>Pilosa: *Tamandua tetradactyla*, *Myrmecophaga tridactyla*<br>Primates: *Homo sapiens*, *Gorilla gorilla*, *Papio sp.*<br>Proboscidea: *Loxodonta africana*<br>Rodentia: *Cuniculus paca*, *Dasyprocta punctata*, *Mus musculus*, *M. musculoides*, *Rattus rattus*, *R. norvegicus*, *Cavia porcellus*, *Cavia aperea*, *Myoprocta acouchy*, *Hystrix sp.*<br> | |
| *T. caecata*       | Polyxenous                | Rodentia: *M. musculus*, *R. rattus*, *R. norvegicus*, *Akodon cursor*, *Necromys pixuna*, *Nectomys squamipes*, *Oligoryzomys nigripes*, *Oxymycterus sp.*, *Rhipidomyus mastacalis*<br> | |
| *T. travassosi*    | Monoxenous                | Cingulata: *Dasypus novemcinctus*<br> | |
| *T. terasma*       | Pleioxenous               | Cingulata: *Cabassous unicinctus*, *Dasypus novemcinctus*, *Euphractus sexcinctus*, *Priodontes maximus*<br> | |
| *T. bondari*       | Monoxenous                | Pilosa: *Tamandua tetradactyla*<br> | |
| *T. caecigena*     | Polyxenous                | Rodentia: *R. rattus*, *R. norvegicus*, *M. musculus*, *M. bactrianus*, *Eothenomys castos*<br>Insectivora: *Suncus murinus*<br> | |
| *T. callida*       | Pleioxenous               | Rodentia: *Rattus sp.*, *R. rattus*, *R. norvegicus*, *Apodemus chevrieri*, *M. bactrianus*, *Eothenomys castos*<br> | |
| *T. libis*         | Pleioxenous               | Rodentia: *Akodon mullis*, *Phyllotis andium*, *Phyllotis darwini*<br> | |
| *T. monositus*     | Pleioxenous               | Rodentia: *Peromyscus maniculatus*, *P. eremicus*, *P. crinitus*, *Neotoma lepida*, *Neotoma sp.*<br> | |
| *T. trimamillata*  | Polyxenous                | Artiodactyla: *Bos taurus*, *Sus scrofa*, *Capra hircus*, *Ovis aries*<br>Primates: *Homo sapiens*<br>Rodentia: *Hydrochoerus hydrochoerus*<br> | |
| *T. bossii*        | Monoxenous                | Rodentia: *Delomys dorsalis*<br> | |
| *T. bonneti*       | Oligoxenous               | Rodentia: *Phyllotis darwini*, *P. xanthopygus*<br> | |
| *T. hexalobulata*  | Monoxenous                | Artiodactyla: *Bos indicus*<br> | |
| *Tunga sp.* (caecata group) – | – | Rodentia: *Akodon montensis*, *Delomys sublineatus*, *Oligoryzomys nigripes*<br>Didelphimorphia: *Monodelphis americana*<br> | |

However, regardless of Smit’s proposal and according to Traub (1980), fleas generally parasitize the hosts with which they evolved. Thus, primitive hosts tend to have primitive fleas, whereas the most advanced mammals are associated with the most evolutionarily recent fleas. Thus, the primitive hosts of sand fleas might have been animals such as the Edentata, which are devoid of means to remove the neosomes (incisor teeth, nails) inserted in the infested sites (feet, belly, skin of abdomen). It is also assumed that tungids and their primitive edentate hosts occurred in Pangaea, and later, with the fragmentation of the continental blocks, both were isolated in South America, with the fleas then undergoing adaptive radiation and infesting new hosts (Traub 1985). After the disappearance of the primitive hosts in certain regions, such as the Nearctic and Palearctic, rodents became the primary reservoirs (Mascarenhas 2002).

A recent study based on the molecular phylogeny of fleas indicated that the basal position in the cladogram and the association of several species of the *penetrans* group with basal mammals (sloths and armadillos) suggest that the origin and diversification of Siphonaptera coincide with the diversification of basal mammals (Whiting et al. 2008). Possibly, mammals such as sloths (Pilosa) and armadillos (Cingulata) are the primary hosts, with other mammals (pigs, dogs, cats, rats, etc.) corresponding to secondary associations (Whiting et al. 2008).

Wild pigs are also speculated to have been the primitive hosts, despite the meager records thus far reported.

It is known that domestic animals came to Brazil soon after its colonization by Europeans. At that time, wild animals such as the wild pig and the capybara had already been domesticated by indigenous natives. Thus, the extent to which wild and domestic pigs in the same areas and locations might have interchanged their ectoparasites is still unknown. In fact, in Angola, *T. penetrans* was found infesting the wild suid *Potamochoerus porcus* (Ribeiro 1974).
Infestation

Flea infestations on hosts are usually defined by their mean abundance and prevalence. From an epidemiological point of view, mean abundance and prevalence have different meanings. Abundance, formerly known as the rate of infestation (or infection) or the index of parasitism (Marshall 1981), is a parameter that has been little used, mainly because the parasite load and intensity of infestation have been considered, incorrectly, to be synonymous by some ectoparasitologists. Mean abundance, however, is a parameter that can be employed as an indicator of the state of health of the host. Thus, high abundance might be related to the inability of the host to oppose the action of the parasite by means of its immune system and/or its behavior (for example, by grooming), as suggested by Stanko et al. (2002). In this respect, the effect of the age and sex of the host on parasite abundance requires further investigation because the defensive capacity of mammals may well increase or decrease over time and ectoparasite grooming might be more prevalent in one of the sexes. Multiple infestations of a single host by ectoparasites of different taxonomic groups may also influence the mean abundance of fleas, as these infestations are mediated by several types of ecological associations (intra- and interspecific competition, predation, mutualism, etc.). Furthermore, an increase in the mean abundance of fleas might reflect the increasing mortality of a host following infection by a pathogen.

Although most adult fleas spend a part of their time in the nest and certain species are almost exclusively nest inhabitants as adults, mammal fleas are commonly found on their hosts’ bodies, often in considerable numbers. In neosomatic fleas, the largest abundance recorded on a single individual was 7,000 alakurt Dorcadia from a sheep (Ioff 1950 in Marshall 1981). In tungids, 31 T. caecigena were counted on a Rattus species (Jordan 1962). In T. travassosi, tens of neosomes can be found in the belly of its host, Dasypus novemcinctus. Regarding T. penetrans, approximately 80 lesions were found on dogs, 50 on cats, 16 on rats, and 199 on humans from Fortaleza, Brazil (Heukelbach et al. 2004a), whereas in a community in rural Nigeria, Ugboroikoa et al. (2008) observed the following maximum numbers of lesions: 184 on pigs, 21 on dogs, and 13 on Rattus rattus. In a study of flea infestations of Panthera onca, Widmer and Azevedo (2012) recorded more than 20 lesions on a young female. Prevalence is also related to the propagation of ectoparasites on their respective hosts. Thus, a high prevalence might be the result of a microenvironmental overlap among hosts that, when associated with environmental factors, would favor the development of immature stages. In this context, prevalence would be related to spatial factors, including the territoriality and dispersion of the host.
Tungid fleas show consistent preferences for attachment sites. The semipenetrating flea *H. pulex* prefers bats’ heads, especially body regions with sparse hairs, such as the ears (Esbérard 2001), although these fleas are also found on the tragus, shoulder blade and tibia, anus, wings, axilla, mouth, and dactylopatagium (Luz et al. 2009). On pangolins, the pulicid *N. euloidea* is usually attached to the soft skin of the ventral region.

### Sites of Attachment

Table 5 Prevalence of infestation by *T. penetrans* on hosts in different locations

| Location, state, country          | Hosts | Species | Examined (no.) | Infested (no.) | Prevalence (%) | References                  |
|-----------------------------------|-------|---------|----------------|----------------|----------------|-----------------------------|
| Coqueiros do Sul, RS, Brazil      | Pigs  | *T. penetrans* | 72             | 64             | 88.9           | Pedroso-de-Paiva et al. (1997) |
| São Tomé Island, Africa           |       |         | 100            | 28             | 28.0           | Pampiglione et al. (1998)   |
| Araruama, RJ, Brazil              |       |         | 12             | 2              | 16.6           | Carvalho et al. (2003)      |
| Rural zone, Nigeria               |       |         | 31             | 17             | 54.8           | Ugbomoiko et al. (2008)     |
| Curitiba, PR, Brazil              | Dogs  |         | 7.811          | 58             | 0.7            | Vernalha et al. (1984)      |
| Araruama, RJ, Brazil              |       |         | 123            | 75             | 60.9           | Carvalho et al. (2003)      |
| Fortaleza, CE, Brazil             |       |         | 150            | 76             | 50.7           | Heukelbach et al. (2004a)   |
| Rural zone, Nigeria               |       |         | 11             | 5              | 45.5           | Ugbomoiko et al. (2008)     |
| Juiz de Fora, MG, Brazil          |       |         | 101            | 2              | 2.0            | Rodrigues et al. (2008)     |
| Manaus, AM, Brazil                |       |         | 42             | 20             | 47.6           | Corrêa et al. (2012)        |
| Araruama, RJ, Brazil              | Cats  |         | 24             | 2              | 8.3            | Carvalho et al. (2003)      |
| Fortaleza, CE, Brazil             |       |         | 158            | 72             | 45.6           | Heukelbach et al. (2004a)   |
| Fortaleza, CE, Brazil             |       |         | 34             | 14             | 41.2           | Heukelbach et al. (2004a)   |
| Rural zone, Nigeria               | *R. rattus* |       | 17             | 5              | 29.4           | Ugbomoiko et al. (2008)     |
| Rural zone, Nigeria               | *M. minutoides* |      | 13             | 2              | 15.4           | Ugbomoiko et al. (2008)     |
| Buenos Aires, BA, Argentina       | *C. villosus* |       | 4              | 1              | 25.0           | Ezquiaga et al. (2008)      |
| Buenos Aires, BA, Argentina       | *D. hybridus* |     | 13             | 1              | 7.7            | Ezquiaga et al. (2008)      |
| Uberlândia, MG, Brazil            | *M. tridactyla* | 3    | 2              | 66.7           | Frank et al. (2012)        |
| Pantanal region, MS, Brazil       | *P. onca* |      | 12             | 12             | 100            | Widmer and Azevedo (2012)   |

### Table 6 Prevalence of infestation by some sand fleas on the respective hosts

| Tunga species | Hosts     | Species | Collected (no.) | Infested (no.) | Prevalence (%) | Location                       | References                  |
|---------------|-----------|---------|-----------------|----------------|----------------|-------------------------------|-----------------------------|
| *T. caecata*  | *R. norvegicus* | 824    | 82              | 9.9            | São Paulo, SP, Brazil | Meira (1934)                 |
|               | *R. rattus*      | 445    | 13              | 2.9            |                |                               |                             |
|               | *M. musculus*    | 135    | 2               | 1.5            |                |                               |                             |
| *T. caecigena*| *R. rattus*      | 250    | 68              | 27.2           | Soochow, China  | Wu (1930) in Jordan (1962)   |
|               | *R. norvegicus*  |        |                 |                |                |                               |                             |
| *T. terasma*  | *D. novemcinctus* | 34     | 4               | 11.7           | Alegre, ES, Brazil | Antunes et al. (2006)        |
|               | *E. sexcinctus*  | 31     | 1               | 3.2            | Pantanal da Nhecolândia, MS, Brazil | Medri (2008) |
| *T. monositus*| *P. eremicus*    |        |                 |                |                |                               |                             |
|               | *P. crinitis*    | 21     | 6               | 28.6           | Washington County, UT, USA | Hastriter (1997)            |
|               | *N. lepida*      |         |                 |                |                |                               |                             |
| *T. trimamillata* | *Bos taurus* | 170    | 130             | 76.4           | Felixlândia, MG, Brazil | Ribeiro et al. (2007)        |
| *T. trimamillata or T. penetrans* | *Bos taurus* | 550    | 375             | 68.2           | Jataí, GO, Brazil | Da Silva et al. (2001)       |
Among sand fleas, *T. penetrans* occurs commonly between the toes and periungual regions when parasitizing humans (Eisele et al. 2003), justifying the vernacular name bicho-de-pé in Brazil (Cunha 1914; Linardi and Guimarães 2000). This species also can be found on other sites, such as the hands, soles, elbows, neck, anus, gluteal area, genital region, buttocks, heels, groin, face, etc. (Bezerra 1994; Heukelbach et al. 2002). Some authors (Cardoso 1981; Clyti et al. 2003) have also reported multiple sites spread over a large part of the body on a single person.

On pigs, *T. penetrans* occurs particularly on the feet, snout, and scrotum (Cooper 1976) but also on the mammary glands (Pedroso-de-Paiva et al. 1997) and in the calcaneal region (Pampiglione et al. 2009). On both dogs and cats, neosomes can be seen around the claws, on the pads and, especially, on the muzzle (Heukelbach et al. 2004a). Female dogs can also exhibit lesions in the nipples (Klimpel et al. 2005). On Brazilian wild mammals, Frank et al. (2012) reported lesions on the feet of the giant anteater *Myrmecophaga tridactyla*, and on the jaguar (*P. onca*), Widmer and Azevedo (2012) observed neosomes confined to the animals’ paws.

When infesting bovines, goats, and sheep, neosomes of the species *T. trimamillata* are found along the coronary band, in the coronary and digital cushions, and sometimes on the sole of the hoof (Pampiglione et al. 2009). In cattle, this species can also be observed on the edge of the nail wall development, that is, at the level of the perioptic tafe, as well as on the perianal area, on the udder of cows and prepuce of bulls (Vaz and Rocha 1946). On pigs, neosomes of this species also tend to be localized on the calcaneal region and scrotum in males and the udder in females (Pampiglione et al. 2009).

Other species of *Tunga* exhibit the following preferential attachment sites on their respective hosts: *T. caecata*, upper surface of rat ears (Jordan 1962); *T. travassosi*, dermis of the ventral abdominal region of edentates (Lima 1943; Pinto 1930); *T. tarsamia*, ventral abdomen and toes of edentates (Antunes et al. 2006); *T. bondari*, ventral abdomen of edentates (Wagner 1932); *T. caeciogena*, at the edge of the pinna but also on the dorsal surface of rat ears and, in one case (only on a specimen of *R. rattus*), at the base of the tail (Jordan 1962; Yang 1955); *T. callida*, rear end of the body, especially around the anus of rats (Li and Chin 1957); *T. libis*, ears of rodents (Beaucournu et al. 2012a); *T. monositis*, basal portion of the upper surface of the pinna of rodents (Barnes and Radovsky 1969); *T. bossii*, base of the tail of wild rodents (De Avelar et al. 2012); *T. bonneti*, parallel to the great axis of the tail of rodents (Beaucournu et al. 2012a); and *T. hexalobulata*, coronary band of cattle (De Avelar et al. 2013). Figure 3 shows sites of attachment for neosomes of some tungids on their hosts, including *H. pulex*.

Considering the data recorded thus far, the most frequent attachment sites are the feet, ventral abdominal, ears, and tails of hosts. The choice of these respective sites depends upon the following factors: (i) regions that regularly contact the soil, such as the feet in humans and domestic and wild animals or the ventral abdominal region in both domestic and wild mammals; (ii) areas from which the hosts have the greatest difficulty dislodging the parasites by grooming or eating, such as the ears and tail in rats or the ventral abdominal region in edentates, which are devoid of incisor teeth and nails; and (iii) the structure of the hair and thickness of the coat related to microclimates such as temperature and skin structure, as in bats and pangolins (Marshall 1981). According to Nagy et al. (2007), older cats and dogs have fewer neosomes than young individuals because of the thicker skin on their paws. Because species of *Tunga* have a reduced pleural arch (Traub 1972) and, consequently, are unable to jump very high, the lesions produced by *T. penetrans* are more concentrated or confined to the feet of animals, as reported by Klimpel et al. (2005).

**Impact on the hosts**

The impact of tungid fleas depends on the sites of attachment on their hosts. The effects of parasitism are well known for *T. penetrans*, as it is the best known and disseminated species in the genus, infesting humans and domestic and wild animals.

In humans, the symptoms, direct impact, and complications have been well documented. Briefly, intense pain and itching are perceived to be the most irritating symptoms (Feldmeier et al. 2004), with most infestations occurring on the feet and provoking deformation of the digits and the loss of toenails. In some cases, severe inflammation and deep skin fissures prevent individuals from walking normally (Ariza et al. 2007; Heukelbach et al. 2007; Hoeppli 1963; Matias 1989). In the Kasulu district, western Tanzania, Mazigo et al. (2012) observed the following symptoms in individuals examined for *T. penetrans*: difficulty walking (22.1 %), and loss of toenails (21.3 %).

Superinfected lesions, primarily caused by *Staphylococcus aureus* and Gram-negative bacteria, lead to the formation of pustules, suppuration, and ulcers that may also be a port of entry for *Clostridium tetani* (Greco et al. 2001; Obengui 1989; Soria and Capri 1953; Tonge 1989). Other pathogenic microorganisms isolated from superinfected lesions include *Streptococcus pyogenes*, *Enterobacteriaceae*, *Bacillus* spp., *Enterococcus faecalis*, *Pseudomonas* spp., and various other anaerobic bacteria (Feldmeier et al. 2002; Heukelbach et al. 2007). Symptoms and signs used to determine the severity of acute tungiasis have been reported by Kehr et al. (2007).

Other complications include cases of gangrene, lymphangitis, lymphadenitis, and sepsis (Veraldi and Schianchi 1999). Brumpt (1949) reported a strain of *Yersinia pestis* isolated from *T. penetrans* in the Congo. Using molecular techniques, Wolbachia was also identified in a neosomic female *T. penetrans* from Ghana (Fischer 2002).
et al. 2002), Brazil (Heukelbach et al. 2004b) as well as in swine from localities in Ecuador and in humans from different localities in Burundi, Kenya, and Zaire (Luchetti et al. 2004; 2005b).

Despite the effects of tungiasis in humans, very little is known of its parasitism on animals, especially wild mammals. In pigs, the infestation causes walking difficulties due to the presence of the parasite in the hoofs. When the lesions are located in the teats, they can cause agalactia and mastitis in lactating sows due to obstruction of the galactophorous channel, blocking milk production and subsequent involution of the mammary glands and causing starvation of the piglets (Pedroso-de-Paiva et al. 1997; Verhulst 1976).

Infested dogs change their position constantly, lick their pads, and are reluctant to stand up (Heukelbach et al. 2004a). In severe cases, dogs are unable to walk and may even die (Wolffhügel 1910), presumably due to the superinfection of lesions, leading to septicemia. Loss of digits can also be observed in rat tungiasis with severe inflammation (Heukelbach et al. 2004a).

Infestation on the feet of giant anteaters provokes inflammation that prevents the animals from breaking up termitaria with their forefeet, thus preventing them from accessing their main food. According to Frank et al. (2012), tungiasis most likely prevents or at least hinders this natural behavior, and as a consequence, the anteaters avoid common food sources in preference for those that are less suitable but more accessible.

*T. trimamillata* is the second species for which the effects on its hosts are known. In humans, local inhabitants of the Andean regions that have been co-infested by *T. penetrans* and *T. trimamillata* report that the infestation caused by the latter is more painful (Pampiglione et al. 2009). In bovines, infestation causes deformation of the nails. Some animals become completely crippled, refusing to walk or even unable to stand. When such injuries occur in a breeding animal, its inability to sustain its own weight can be compounded by pregnancy. The process is often complicated by secondary infection with ulceration on the upper edge of the nails as a consequence of the rupture of the neosomes caused by excoriation. In some cases, flies deposit their eggs in the ulcers that are so formed, increasing the destruction of the living tissue (Vaz and Rocha 1946). *Wolbachia* was also found in samples of *T. trimamillata* collected from goats and cattle in Santa Isabel, Ecuador, and identified through PCR amplification and sequencing of the bacterial ribosomal 16S and *ftsZ* genes, with prevalences of 40 and 11 %, respectively (Luchetti et al. 2004, 2005b).
Little is known about the impact of other species of *Tunga* on wild animals. In contrast to *T. penetrans*, in which both males and females are blood feeding (Geigy and Herbig 1949; Witt et al. 2004), the larvae and adult males of *T. monositus* do not feed (Lavoipierre et al. 1979). According to these authors, after becoming attached to rodent skin, adult females of *T. monositus* feed principally off of fluid exudate and, for a few days, off of neutrophils, fibroblasts, collagen, and macrophages. Blood feeding commences from the 14th day.

Neosomes of sand fleas can reach a diameter of 1 cm or more (Table 1). *T. penetrans* may remain attached to the host for a period of more than 5 weeks (Eisele et al. 2003), whereas *T. monositus* lies embedded in the skin of the ear pinna for 2 or 3 months (Lavoipierre et al. 1979). As in other ectoparasitoses, the lesions may affect weight gain and milk production, and as in humans and domestic animals, the lesions might also become infected and be a port of entry for various pathogens. Considering the abundance of neosomes, their attachment sites and affected organs, as well as the lifespan of the embedded sand fleas, what is the real impact of these infestations on wild animals? Armadillos are insectivores that use the toes of the forefoot for digging into galleries to feed chiefly on ants, termites, and other small invertebrates. They have also been observed to roll about on ant hills to dislodge and consume the resident ants. How do we evaluate the action of tens of neosomes of *T. travassosi* on the toes or the 30 cm ventral surface of armadillos? Or similarly, more than 30 neosomes of *T. caecigena* over the ears or the tail of a rat that measure, respectively, 24 and 180 mm? It is important to stress that in rats, the pinna can be rotated to catch the slightest sound from almost any direction. This ability is useful for an animal whose activity is primarily confined to darkness. Rats also control their body temperature through their tails by dilating or constricting their tail blood vessels and use their tails for balance (Yulong et al. 1995). In the same manner, to what extent will the presence of neosomes of *H. pulex* on the ears of bats inhibit their ability to navigate, considering that the ears act as biosonar-receiving antennas?

**Perspectives**

Among the 13 species currently included in the genus *Tunga*, more than 30 % have been described in the last 12 years; thus, the chances of discovering new species are high. Some samples of *T. penetrans* have displayed slight variations when collected from different hosts in Fortaleza, Brazil, which may indicate the existence of different strains or races or the beginning of such a formation (Nagy et al. 2007). Recently, De Avelar and Linardi (2010) showed that the multiple displacement amplification (MDA) technique enables the amplification of the genomic DNA of siphonapterids that have been preserved for long periods, with the successful amplification of one neosome of *T. bondari* that was collected in 1909. This technique may be a valuable tool for molecular studies involving samples of sand fleas that are preserved in scientific collections.

The Neotropical region stands out as the most promising region in which new taxa might be found, as it contains a diversity of biomes and at least 40 dispersion centers, 13 of which are located in Brazil (Müller 1972). Furthermore, Brazil is considered a hotspot of global biodiversity (Mittermeier et al. 1998; Myers et al. 2000), as it occupies a vast area and contains approximately 13 % of the world’s mammal fauna (Reis et al. 2006) that are recognized as valid species (Wilson and Reeder 2005). Rodents, representing approximately 36 % of the Brazilian mammals, deserve particular attention because in this country, rodents host five different *Tunga* species that are included in the *caecata* group. Additionally, considering that three species of *Tunga* that belong to the *penetrans* group are primarily associated with edentates (Hopkins and Rothschild 1953; Lima and Hathaway 1946; Linardi and Guimarães 2000) and that only seven of the 14 species of Brazilian Myrmecophagidae (Pilosa) and Dasyypodidae (Cingulata) (Reis et al. 2006) have been recorded as hosts for these sand fleas, both armadillos and anteaters are taxa that should be further examined for occurrences of tungids because they exhibit a large geographical distribution and range throughout various biomes (Da Fonseca et al. 1996), which, according to Krasnov et al. (2003), are among the most promising factors for the discovery of a new species of flea. In fact, a new species of *Tunga* and located in the carapace of *Zaedyus pichiy* and perforating the osteoderms is being now described by Ezquiaga et al. (unpublished work) from Argentina. Additionally, it is important to verify whether, in fact, Artiodactyla species represent true hosts for *Tunga* species because Rodrigues and Daemon (unpublished work) also found *T. trimamillata* on the capybara *H. hydrochaeris* in Brazil. In contrast, thus far, only *M. americana* of the 54 Brazilian species of Didelphimorphia (Reis et al. 2006) has been found to be infested with neosomes (Bossi 2003).

However, in spite of these possibilities, certain challenges exist for obtaining neosomes: (i) the extraction of the ectoparasites of mammals without killing the host in studies that do not allow the death of the host; (ii) incomplete inspection of the entire body of the animal by the collector, with the primary sites of attachment such as the belly, paws, ears, and tails not being examined; (iii) misdiagnosis, with the lesions being confused with larvae of *Cuterebra*, cicationratia of animals’ bites (Beaucomnu et al. 2012b) or abscesses, mycosis, larva migrans, and other symptoms; and (iv) misidentifications with other species of *Tunga* because the taxonomic identifications are not always performed by experts. In fact, some occurrences attributed to *T. penetrans* on certain hosts are likely incorrect (Linardi et al. 2013).
In fleas, only adults are ectoparasitic, whereas the immature stages develop in the soil, inside or close to the nests of the respective hosts and, consequently, are susceptible to predation or environmental modifications. The prevalence and mean abundance of these ectoparasites could thus assist nature conservation studies because they can serve as indicators of eventual alterations when compared temporally in a single locality. For *T. penetrans*, the natural habitat is primarily the sandy and warm soil of deserts and beaches (Veraldi and Schianchi 1999), thus justifying the vernacular names sand flea, sandflöh, and puce de sable, as cited by Beaucournu et al. (2012b) and Cunha (1914). Granular soils, which are considered favorable for *T. penetrans* by the majority of authors, are also favorable for other congeneric species (Beaucournu et al. 2012a). However, both adults and immature young of other species of *Tunga* must be searched for in the nests and burrows of their respective hosts, especially those of edentates and rodents. On tropical beaches, the dispersion of *T. penetrans* is ensured by infested dogs. Additionally, horse manure used to fertilize soils aids in sand flea dissemination because both *T. penetrans* and *T. trimamillata* also live in stables and stock farms as well as in the soil and dust close to farms. Other fecal matter such as bat guano supports the development of *H. pulex* (Hasitrier and Méndez 2000; Tipton and Méndez 1966).

It seems that the soil temperature, air temperature, and air humidity do not markedly affect the presence of *T. penetrans* in soil samples, as observed by Linardi et al. (2010) in three geographical regions of Brazil: Fortaleza (Ceará State), Barra do Garças (Mato Grosso State), and Alto Alegre (Roraima State). Larvae of this species were found in the sand in a depth of 2–5 cm (Nagy et al. 2007). Certain species are univoltine, as they are collected only during one season, including *T. caecigena* during the cold season and *T. callida* during winter months in China (Jordan 1962); *T. monostitus* in Utah from October through April (Hasitrier 1997); *T. libis* in June (Smit 1962), October, and November in Chile (Smit 1968); *T. bonneti* from July to December in Chile (Beaucournu et al. 2012a); and *T. hexalobulata* during the dry-cool season from April to September in Brazil (De Avelar et al. 2013). Similarly, both *T. penetrans* and *T. trimamillata* develop better in the dry season (Pampiglione et al. 2009), thus confirming the findings of Hoepli (1963), who reported for *T. penetrans* in Africa that “the number of sand fleas greatly decreases during the rainy season.” With respect to the species of *Tunga* found on edentates, data included as material deposited in the Rothschild collection of fleas of the British Museum (Hopkins and Rothschild 1953) indicate November as the month in which *T. travassosi*, *T. terasma*, and *T. bondari* were collected, which corresponds to the rainy season in Brazil. For *T. caecata*, Meira (1934) observed neosomes on a rat’s ear in the months of December, February, and April, with only the latter included in the dry-cool season in São Paulo, Brazil.

Concerning other geographical factors, only the latitude, with respect to its influence on temperature, would play a role in distribution because the same species can be collected at different altitudes (Beaucournu et al. 2012a). In Chile, *T. bonneti* occurs more frequently from July to December, decreasing in January and February (Beaucournu et al. 2012a).

Although the treatment and prophylaxis of tungiasis are not within the scope of this review, it is interesting to note that these actions have only been performed in humans and domestic animals when parasitized. Treatment consists of local excision or sterile curettage. Parasitized dogs can be treated with a subcutaneous application of ivermectin and healing ointments and repellent (Corrêa et al. 2012).

In humans, prophylactic measures include the wearing of shoes, improving hygiene, use of gloves for handling manure, sweeping floors, and the restriction of free movement of people and infested animals among households. According to Matias (1989), in some municipalities of Rio Grande do Sul State, Brazil, trucks carrying sand and sheaves of grass used for construction of houses can also act in the dissemination of this species.

Tetanus vaccination is recommended to prevent secondary infection. Both within and around the residences in two municipalities of Rio Grande do Sul State, Brazil, the pyrethroids cypermethrin and deltamethrin were used as a measure of environmental control (Matias 1991). Given the diversity of habitats, Linardi (1998) claimed that integrated actions were required for the control of tungiasis, involving clinicians, veterinarians, biologists, public health specialists, and technicians and companies responsible for vector control. An overview of human tungiasis and including risk factors, treatment, repellents, prevention, control, and healthcare stakeholders has been presented by Karunamoorthi (2013).

Until recently, tungiasis provoked by *T. penetrans* had been reported in approximately 70 nations, especially in Latin America and Sub-Saharan Africa, most commonly affecting poor populations (Pampiglione et al. 2009). The number of cases has been increasing, as reported in several publications worldwide. Now, tungiasis is endemic or potentially endemic to 89 countries with varying degrees of incidence and prevalence, which vary in relation to the area and population studied. It has been estimated that the prevalence of tungiasis may reach more than 50 % of the population in some of the hyperendemic zones, with often recurrent and sometimes massive parasitic infestations that are responsible for superinfections (Karunamoorthi 2013).

In Brazil alone, more than 10⁶ individuals are at risk for severe tungiasis (Heukelbach et al. 2001). In the villages of Tanzania, jigger parasitization is locally referred as inzyogo, which means “the disease of the dirty people” (Mazigo et al. 2012). The treatment involves surgical extraction of the sand flea under sterile conditions, but due to the low socioeconomic
status of some villages in Tanzania and Kenya, pins and other unsterilized equipment are being shared for jigger removal, leading to the possible further spread of HIV and AIDS and other diseases and increased opportunity for bacterial infection through the new open wounds that are often left uncovered (Wachirara 2012).

In recent decades, ecotourism in forest areas, caves, and mountains has become another cause of the increase in the chances of human infestation by sand fleas, which usually parasitize other animals. Additionally, as a result of the expansion of urban areas into wild environments, the opportunities for contact between domestic and wild animals have increased, thus facilitating the exchange of ectoparasites. For this reason, it is possible that sand fleas parasitizing wild mammals may be found on domestic mammals and vice versa. In fact, this situation may be the case for T. penetrans and T. trimamillata, as pasturelands for cattle are now found in cerrado areas occupied by rodents and edentates.

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