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Three new species of fleas belonging to the genus *Macrostylophora* from the three-striped ground squirrel, *Lariscus insignis*, in Java

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Abstract. Three new species of fleas belonging to the genus *Macrostylophora* (Siphonaptera, Ceratophyllidae) are described from the three-striped ground squirrel, *Lariscus insignis*, from Tjibodas, West Java (Jawa Barat), Indonesia at an elevation of 1500 m. *Macrostylophora larisci* sp. n. is described from three male specimens, *Macrostylophora debilitata* sp. n. is described from one male and *Macrostylophora wilsoni* sp. n. is described from one female. Non-genital morphological characters of the female specimen, including ctenidial spine shapes and lengths, show that it is not the corresponding female for either *M. larisci* sp. n. or *M. debilitata* sp. n. It is unusual for three different species of congeneric fleas to parasitize the same host species in the same geographical location. These three new species represent the first known records of *Macrostylophora* from Java and they could be enzootic vectors between rodents of flea-borne zoonotic pathogens such as *Rickettsia typhi* and *Yersinia pestis*, both of which are established on Java. A list is provided of the 43 known species and 12 subspecies of *Macrostylophora* together with their known geographical distributions and hosts. A map depicting the distributions of known Indonesian (and Bornean) species of *Macrostylophora* is also included.

Key words. *Macrostylophora debilitata* sp. n, *Macrostylophora larisci* sp. n, *Macrostylophora wilsoni* sp. n, Ceratophyllidae, fleas, Indonesia, Java, Siphonaptera.

Introduction

The flea genus *Macrostylophora* Ewing, 1929 is primarily Oriental and secondarily Palaearctic in distribution (Traub *et al.*, 1983). Members of this genus are mainly associated with tree squirrels (family Sciuridae) (Li, 1981; Traub *et al.*, 1983) although some species have been collected from ground squirrels (e.g., *M. gansuensis* Zhang & Ma, 1982), murid rodents (e.g., *M. theresae* Durden & Beaucournu, 2006) (Durden & Beaucournu, 2006), or Scandentia (tree-shrews, family Tupaiidae) (e.g., *M. kinabaluae* Beaucournu & Wells, 2009) (Beaucournu & Wells, 2009). Several groups have been proposed within the genus *Macrostylophora*; two that are often cited are the '*hastata*' group and the '*euteles*' group. Males of species assigned to the '*hastata*' group are characterized by the presence of a sclerotized process in the form of a 'stylet' (also referred to as a 'stylophore,' 'style' or 'medial marginal process arising between the bases of the antepygidial bristles') located on the posterior margin of tergite VII between the antesensilial bristles. Males of species assigned to the '*euteles*' group lack this character. Also, Li & Traub (1998) erected the subgenus *Songshupsylla* to accomodate 11 Chinese species (now accomodating 13 species, one of which has been divided into two subspecies, and including some taxa from Indonesia) based on a suite of shared characters, with the remaining species in the genus belonging to the nominate subgenus. It is not possible to review the entire genus *Macrostylophora* at the present time because type specimens of several species are unavailable for

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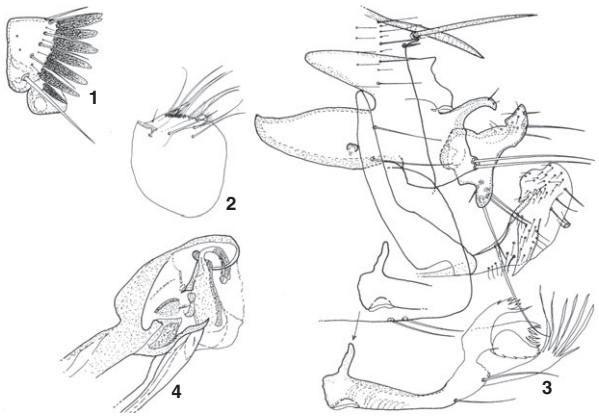
taxonomic study and because only one sex is known for some species.

During the examination of a large number of specimens of *Macrostylophora* received on loan from the Robert Traub Flea Collection in the Carnegie Museum of Natural History (CMNH) in Pittsburgh, USA, three new species were found in material collected in Java, Indonesia in 1965 by our late colleague, Nixon Wilson (1930–2011) (three specimens) and by J. M. Stusak (two specimens). These three new species are described in this paper. Following the descriptions and brief discussion, we provide a taxonomic list of all known species of *Macrostylophora* together with their known geographical distributions and host associations. We also include a map of Indonesia (including non-Indonesian parts of Borneo) to show the distribution of known species of *Macrostylophora* in this region. Mammal nomenclature used in this paper follows relevant chapters in Wilson & Reeder (2005).



Figs. 1-4. *Macrostylophora larisci* sp. n., Holotype male: 1, Prothorax; 2, Tergite VIII and anal valves; 3, Segment VII, segment IX and sternite VIII; 4, apex of phallosome.

Macrostylophora larisci Durden & Beaucournu, sp. n.

Type material. Holotype male ex *Lariscus insignis* (F. Cuvier, 1821) ('three-striped ground squirrel') (Rodentia: Sciuridae: Callosciurinae), Indonesia, West Java (Jawa Barat), Tjibodas (7°23′S, 107°31′E), elevation 1500 m, 3 October 1965, Coll.: Nixon Wilson. Collected during Bernice P. Bishop Museum Expedition (Accession No. BBM ISA 85357); Traub Flea Collection Accession No. B83332-1. One Paratype male A, same collection data as Holotype (except Traub Flea Collection Accession No. B83332-2 and on different slide); Holotype and this Paratype collected from the same host individual. Another Paratype male B, same locality and host species but collected, 2 August 1965 by J. M. Stusak (Traub Flea Collection Accession No. B78350-2; No BBM Accession No. on slide); this Paratype is on a separate slide.

Deposition of types. Holotype and both Paratypes deposited in the Robert Traub Flea Collection, CMNH.

Etymology. The specific epithet is derived from the generic name of the host.

Description. Macrostylophora larisci n. sp. is a stylate species and therefore belongs to the '*hastata*' group. Segment IX is well characterized in the males and unlike that of any other Indonesian species.

Head capsule morphology characteristic for genus. Labial palp long but not reaching apex of coxa I.

Thorax: pronotal ctenidium with 18 spines (Fig. 1). Prothorax with eight thin setae, the most dorsal being semi-erect. Mesothorax with eight long, thin, semi-erect setae inserted midway along segment and two fairly long pseudosetae. Metathorax with eight long, thin setae inserted along posterior margin.

Abdomen (non-genital segments): dorsal spinules on anterior tergites as follows: 2 2 1 2 0 0 for Holotype, 3 3 2 2 1 0 for Paratype A, 2 3 2 1 0 0 for Paratype B. On each tergite after segment II, a row of seven long, slender setae, the last slightly below the spiracle. Spiracles circular, with the exception of spiracle on metepimeron which is shaped somewhat like a 'nightcap.'

Ventral sternites as follows: on segment II, one fairly long, thin, submarginal seta; on segments III–VII, 1–2 setae including 2–5 small ventral setae and a field of vertically inserted setae on the posterior portion of segment consisting of 3–5 small setae and 4–7 long, thin setae. On sternite II, a fine *striarium* appearing somewhat like a 'fingerprint' occupies the major part of the segment.

Abdomen (genital segments): tergite VII (Fig. 3) with long, sclerotized 'style,' antesensilial seta distinct and flanked by a short, thick seta; tergite of segment VIII (Fig. 2) subcircular and with six long, thin marginal setae plus three identical setae inserted in upper quarter; at the level of the first four setae, a small spinose area is present on the internal surface of this tergite; the sternite (Fig. 3) is thin with two narrow, marginal setae and a leaf-like membranous extension. Segment IX (Fig. 3): apodeme and manubrium of tergite forming an acute angle; manubrium large (for *Macrostylophora*). *Processus basimerus* narrow and arched with two acetabular setae. *Processus telomeris* triangular, internal surface apically with one fairly long seta, following very marked concavity and on infero-posterior angle, always on inner surface, two identical setae equal in length to apex, and then one very long, thin, apical seta. Sternite with proximal arm subrectangular and distal arm gently curved, distinctly widened at apex which is adorned with micro-setae and short, fine setae along the posterior border. Segment IX (anal segment) with two membranous valves covered with slender setae, the ventral valve with a rounded apex.

Phallosome (Fig. 4) with quadrangular *ductus ejaculatorius*, almost four times as long as wide at apex. There is no Wagner's gland.

Dimensions (slide-mounted specimens). Holotype male, 2.3 mm; Paratype males, 2.3 mm and 2.4 mm.

Macrostylophora debilitata Beaucournu & Durden, sp. n.

This unique specimen is a member of the '*euteles*-group.' It can be separated from *Macrostylophora larisci* sp. n. by a variety of characters, in addition to those of the genitalia: including morphology of the maxillary palps, leg setation and chaetotaxy of the abdominal segments. However, this specimen has suffered various forms of damage. During the late pupal phase, mechanical compression, evidently due to partial desiccation of the future exuvium, is apparent on the dorsal surface of this insect and has caused some malformations (hence the name *debilitata*) in the insertion of setae and spinules *sensu lato,* pseudo-setae and 'spinelets,' and from the occipital zone to tergite IV. Laterally and ventrally, no deformities are present. The collection of this specimen on a host and not in leaf litter or in a host nest demonstrates that it was perfectly functional. Moreover, buccal morphology (e.g., maxillary palps, labial palps and epipharynx), legs and genitalia are normal. In addition, before this specimen was slide-mounted, it was over-cleared (in potassium hydroxide) and partially crushed. Nevertheless, parallelism and symmetrical genitalia morphology between left and right, allow us to describe this flea as a new species.

Type material. Holotype male ex *Lariscus insignis* (F. Cuvier, 1821) ('three-striped ground squirrel') (Rodentia: Sciuridae: Callosciurinae), Indonesia, West Java (Jawa Barat), Tjibodas (7°23′S, 107°31′E), elevation 1500 m, 2 August 1965, Coll.: J. M. Stusak. Collected during Bernice P. Bishop Museum Expedition (No. BBM number on slide – only 'BBM-ISA' is written there); Traub Flea Collection Accession No. B78350-2.

Deposition of type. Holotype male deposited in the Robert Traub Flea Collection, CMNH.

Etymology. Specific epithet based on the teratological characters exhibited in this specimen.

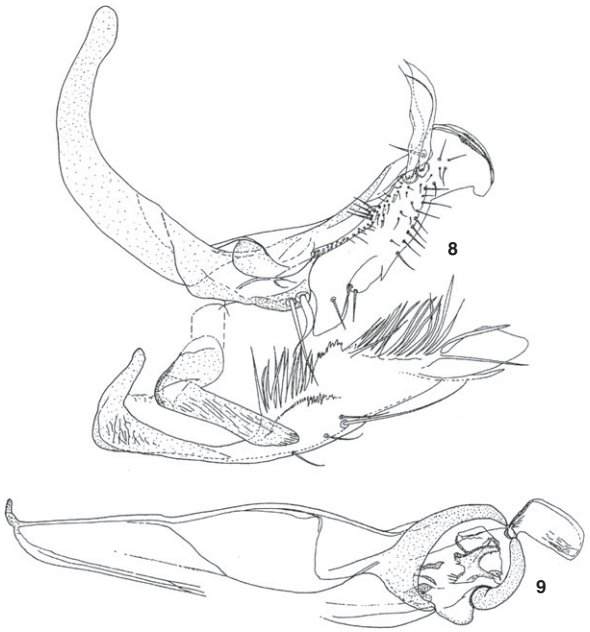
Description. Macrostylophora debilitata sp. n. belongs to the non-stylate *Macrostylophora* group and to the '*euteles*' group which also includes *M. theresae* Durden & Beaucournu, 2006 described from North Sulawesi, Indonesia. Although there is some superficial resemblance between the genitalia of these species, it does not stand up to detailed examination.

Head capsule: frontal tubercle situated in lower third of frontal curvature: maxillary and labial palps much shorter than coxa I (extending two thirds along this structure); the four articles of the maxillary palp are subequal , the last however is a little longer than the preceding articles; last article of labial palp almost as long as the three preceding articles combined. Cephalic chaetotaxy uncertain because of compression but two pre-ocular setae and the absence of post-ocular setae are apparent.

Thorax: prothoracic ctenidium in this specimen abnormal for two of the eight spines, the dorsal section being naked which is teratological; the row of ctenidial bristles is curved at a right angle towards the anterior region as is also the case for the analagous rows of 8–10 setae on the meso- and metathorax. Notable on the mesothorax are two long *pseudo-setae* situated towards the dorsal part of the collar. Metepimeron with six slender setae; spiracle almost circular, although a slight indentation evokes the shape of a classic 'nightcap.' Pleural arch poorly developed. Femoral guard bristles lacking distinctive characters. Tibiae with all stout and somewhat pointed setae; dorsal surface of tibia III (Fig. 5) with eight notches each with thick setae, but most relatively short and slightly pointed apically; the setal ratio of these notches is, from base to apex, 2 (including a long seta), 1, 2, 4 (including a long seta and a slender seta); longest apical tibial seta not extending to apex of tarsus I; longest apical seta of tarsus I extending to apex of tarsus II; longest apical seta of tarsus II extending to apex of tarsus III.

Figs. 5-7. *Macrostylophora debilitata* sp. n., Holotype male: 5, Tibia III; 6, Tergite VIII; 7, Tergite IX.

Abdomen (non-genital segments): tergites I–IV deformed by compression as mentioned above. Two spinules on tergite I; 4–5 contiguous spinules on tergites II–IV; no spinules on the following tergites. An interesting observation concerns tergite III where, on each side, four spinules are preceded or surmounted by two long and equally stout *pseudo-setae*: this indicates for this segment a normal row of six 'spines' because it is assumed that *pseudo-setae*, ctenidial spines and spinules have the same origin (Smit, 1972). For tergites II–IV, these 'spines' and spinules are relatively long: as long as the distance between the areola of the setal insertion and the border of the segment; they are only half this length in *M. larisci*, *M. wilsoni* or *M. theresae.* This is similar to the vestigial or pseudo-ctenidia seen in *Hystrichopsylla, Ctenoparia* (Hystrichopsyllidae), *Stenoponia* (Ctenophthalmidae) or *Afrostivalius* (Pygiopsyllidae), etc. This appears to be a novel character for *Macrostylophora.* Rows of tergal setae with nine setae on all tergites; on tergites I and II, the lower is below the spiracle; on the following tergites, the lowest



Figs. 8-9. *Macrostylophora debilitata* sp. n., Holotype male: 8, Sternites VIII and IX; 9, Phallosome.

seta is at the level of the spiracle. All spiracles round from tergites I to VII. A single antesensilial seta is present but it lacks a micro-seta at its base. Sternites: on sternite II, two setae on the ventral margin; on sternite III, 5–7 small marginal and ventral setae; on sternite IV, three setae in a marginal row; on sternites V and VI, four setae in a marginal row and 2–3 ventral setae; on sternite VII, five long marginal setae.

Abdomen (genital segments): Tergite VIII (Fig. 6) subcircular with two large fields of dorsal and ventral setae, the ventral field almost as setose as the dorsal field which is very unusual. Tergite IX (Fig. 7) with a long apodeme; *processus basimeris dorsalis* with a single short apical seta; apex appearing curved and acuminate but in fact it is connected by a thin membrane to the *processus acetabularis*. It bears two long classical setae. Ventrally, there is an oval lobe entirely adorned with fine spicules alligned in parallel lines. *Processus telomeris* triangular: pre-apically, with an angular projection on its anterior border; 10 equally short setae and two long setae apically; at the postero-ventral angle, four setae of which three are thick and sclerotized at the acuminate apex. Sternite IX (Fig. 8) structurally complex, with a flat apex and ventrally rounded, but mainly characterized by two stout, palmate setae, lanceolate and hyaline, which are unusual characters for *Macrostylophora*. Ventrally, there is a sclerotized, oblong structure which is classically associated with sternite IX, but which, here, seems to be equally associated with sternites IX and VIII; in other species in which this structure is present, it is either hyaline or membranous, but not sclerotized. Sternite VIII (Fig. 8) mainly consists of a large hyaline area divided into thin strips, as is typical for the genus *Macrostylophora*.

Phallosome (Fig. 9): This structure is fairly standard for the genus *Macrostylophora*, but its apex is unusual; we can not explain this, or the shape of the apical lobe, or its function. There is no Wagner's gland.

Dimensions (slide-mounted specimen): Holotype male, 3.1 mm. This size has undoubtedly been augmented as a result of the sub-standard slide preparation.

Macrostylophora wilsoni Durden & Beaucournu sp., n.

The only specimen of this new species is a female which was collected with males of the two other new species described in this paper. Several non-genital morphological features including the length and shape of the ctenidial spines and the number of dorsal spinules on the anterior abdominal tergites show that this female is not the unknown female for either *Macrostylophora larisci* sp. n. or *Macrostylophora debilitata* sp. n.

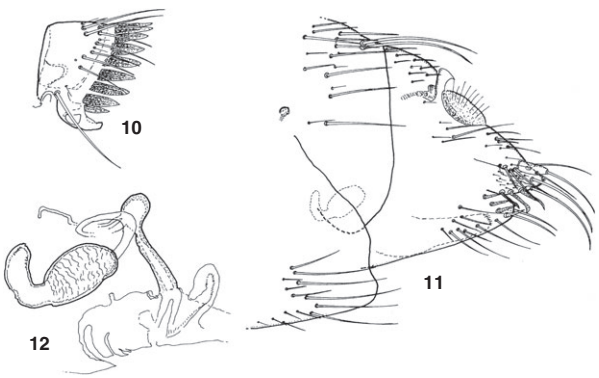
Type material. Holotype female ex *Lariscus insignis* (F. Cuvier, 1821) ('three-striped ground squirrel') (Rodentia: Sciuridae: Callosciurinae), Indonesia, West Java (Jawa Barat), Tjibodas (7°23′S, 107°31′E), elevation 1500 m, 3 October 1965, Coll.: Nixon Wilson. Collected during Bernice P. Bishop Museum Expedition (Accession No. BBM ISA 85357); Traub Flea Collection Accession No. B83332-2. (same data as for Paratype A of *Macrostylophora larisci* n. sp. and on the same slide as that specimen).

Deposition of type. Holotype female deposited in the Robert Traub Flea Collection, CMNH.

Etymology. This species is named in honor of Nixon Wilson in recognition of his many contributions to the taxonomy and host associations of ectoparasites, and because he collected the only known specimen (the Holotype).

Description. Head capsule morphology characteristic for genus. Labial palp long but not reaching apex of coxa I.

Thorax: pronotal ctenidium with 20 spines (Fig. 10). Spines relatively wide, short and poorly pigmented. Prothorax with



Figs. 10-12. *Macrostylophora wilsoni* sp. n., Holotype female: 10, Prothorax; 11, Segments VII,VIII and anal segment; 12, Spermatheca and *ducti*.

eight thin setae, the most dorsal being semi-erect. Mesothorax with eight long, thin, semi-erect setae positioned midway along segment, two fairly long pseudosetae. Metathorax with eight long, thin setae inserted along posterior margin.

Abdomen (non-genital segments): dorsal spinules on anterior tergites 2 3 2 0 0 0. On each tergite after segment II, a row of eight setae, then a gap, then one seta below the spiracle. Spiracles circular, with the exception of spiracle on metepimeron which is shaped somewhat like a 'nightcap.'

Ventral sternites as follows: on segment II, six small setae and one fairly long, thin, submarginal seta; on segments III–VII, 2–5 small ventral setae and a field of vertically inserted setae on posterior portion of segment consisting of 3–5 small setae and a range of 4–7 long, thin setae (Fig. 11). On sternite II, a fine *striarium* appearing somewhat like a 'fingerprint' occupies the major part of the segment.

Abdomen (genital segments) (Fig. 11): Segment VII: at level of tergite, the two antesensilial setae are positioned, as is characteristic for this genus, some distance from posterior border; they are equal in size, contiguous, relatively short and thin and without small adjacent setae; sternite with weak concavity along posterior margin bearing several small, ventral setae, then two rows of perpendicular setae on ventral border, the first row with four short setae, the second, some distance from posterior margin, with six long, thin setae. Segment VIII: on tergite, a dozen small setae anterior to and above spiracle, then several setae below sensilium; postero-ventral margin, below segment IX, with four short, spiniform setae, and on internal surface two relatively long setae, then an area of nine setae of various lengths, none of them located on or near ventral margin: sternite VIII 4–5 times longer than wide, lacking distinct characters. Segment IX: anal stylet about four times longer than wide, with one apical seta almost three times as long as stylet; ventrally, at level of spiniform setae of tergite VIII, this segment has two stout, slightly twisted setae.

Spermatheca (Fig. 12): *bulga* with convex borders, *area cribiformis* apical but slightly offset towards upper surface; *hilla* curved with very small apical *papilla*. *Ductus bursae* almost straight, slightly longer than spermatheca; *ductus obturatus* inconspicuous but quite short.

Dimensions (slide-mounted specimen).. Holotype female, 2.9 mm.

Discussion

The three new species described in this paper represent the first of the genus *Macrostylophora* Ewing, 1929, to be described from Java.One of these species was noted previously but without details, and without a species-name by Durden & Traub (1990). The type host genus, *Lariscus*, is not endemic to this island, and neither is the type host species, *L. insignis*. Collectively, the four described species of *Lariscus* are widely distributed in peninsular and mainland southeast Asia and *Lariscus insignis* is found in Thailand, peninsular Malaysia, Borneo, Sumatra, Java and adjacent small islands (Thorington & Hoffmann, 2005). It is interesting and somewhat unusual that the three species of congeneric fleas described in this paper were collected from the same host species at the same locality. Two or more different species of *Macrostylophora* have been recorded from a single squirrel species in China (Table 1) but typically each of these species occurs in a different geographical region.

No other species of *Macrostylophora* from the Indonesian region have morphological characters similar to those of *Macrostylophora larisci* which belongs to the '*hastata*' group because males are 'stylate.' The most closely related species, based solely on morphology rather than on geographical distribution, is *M. theresae* Durden & Beaucournu, 2006, which is known from North Sulawesi (Sulawesi Utara), Indonesia (Table 1, Fig. 13). However, *M. theresae* is a non-stylate species. With respect to other geographical regions, additional species with some morphological affinities with *M. larisci* include the 'non-stylate' species *M. euteles* (Jordan & Rothschild, 1911), *M. cuii* Liu, Wu & Yu, 1964 and *M. abazhouensis* Liu, Liu & Zhai, 1981, and the 'stylate' species *M. bispiniforma bispiniforma* Li, Hsieh & Yang, 1976, all taxa known only from China (Liu *et al.*, 1986). This clearly shows, in our opinion, the lack of phylogenetic value of the criteria 'stylate' versus 'non-stylate' species, especially since no morphological characters of females allow them to be placed in either group in the absence of accompanying males (Jordan, 1939). Moreover, certain species have extremely reduced 'styles' as noted by Li & Traub (1998); the last species described from this 'group' was *M. durdeni* Beaucournu & Wells, 2009 from Sabah (Borneo). Traub *et al.* (1983) stated, '*Macrostylophora* .....may be a heterogeneous group,' and Li & Traub (1998) created the sub-genus *Songshupsylla* for (Chinese) taxa lacking a 'style.' In our opinion, and that of Jordan (1939), although the 'style/stylophore' character could perhaps be useful for placing males in a dichotomous key, the '*hastata*' and '*euteles*' groups are artificial, as is *Songshupsylla*, and they describe a particular morphological character of interest but apparently without phylogenetic value.

Another enigmatic structure is Wagner's gland which is present in a number of ceratophyllid fleas. It is situated in the abdomen of males on each side, near the base of sternite VIII. Some *Macrostylophora* species have a distinct Wagner's gland but others do not. For example, Wagner's gland is visible in *M. levis* (Jordan & Rothschild, 1922), *M. kinabaluae* Beaucournu & Wells, 2005 and *M. durdeni* Beaucournu & Wells, 2009 all from, presumably, the '*hastata* group.' However, this structure does not exist in *M. theresae* Durden & Beaucournu or in *M. larisci* sp. n. Unfortunately, this organ is not clearly designated in most *Macrostylophora* species and its presence does not correlate with the presence or absence of a 'stylophore.' Therefore, the presence or absence of Wagner's gland can not be used as an additional character to separate stylate versus non-stylate groups of *Macrostylophora*.

With respect to *Macrostylophora debilitata* sp. n., it is always risky to describe a species from a unique specimen when it shows teratological aspects. However, one of us (JCB) has studied many cases of 'monstrous' Siphonaptera (six publications on this topic from 1969 to 2001) (e.g., Beaucournu, 1969; Beaucournu *et al.*, 1999) and we believe we can distinguish what is abnormal from what is genetic in this specimen. In fact, even in this specimen the unprecedented characters observed

Table 1. Known species and subspecies of *Macrostylophora* including their documented geographical distributions and hosts (listed alphabetically by flea species/subspecies).

M. abazhouensis Liu, Liu & Zhai, 1981
Distribution: China (Sichuan Province)
Host: *Marmota himalayana* (Hodgson, 1841) (Sciuridae)
M. aeretesites Li, Chen & Wei, 1974
Distribution: China (Sichuan and Gansu Provinces)
Hosts: *Tamiops swinhoei* (Milne-Edwards, 1874) (Sciuridae), *Aeretes melanopterus* (Milne-Edwards, 1867) (Sciuridae), *Apodemus sylvaticus* (Linnaeus, 1758) (Muridae)
M. angustihamulus Li, Zhang & Zeng, 1988
Distribution: China (Gansu Province)
Host: *Trogopterus xanthipes* (Milne-Edwards, 1867) (Sciuridae)
M. bispiniforma bispiniforma Li, Hsieh & Yang, 1976
Distribution: China (Yunnan Province)
Hosts: *Tamiops swinhoei* (Sciuridae), *Callosciurus erythraeus* (Pallas, 1779) (Sciuridae)
M. bispiniforma gongshanensis Gong & Xie, 1990
Distribution: China (Yunnan Province)
Hosts: *Tamiops swinhoei* (Sciuridae), *Dremomys lokriah* (Hodgson, 1836) (Sciuridae), *Niviventer eha* (Wroughton, 1916) (Muridae)
M. borneensis (Jordan, 1926)
Distribution: Borneo (Sabah and Sarawak)
Host: *Sundasciurus jentinki* (Thomas, 1887) (Sciuridae)
M. congjiangensis Li & Huang, 1979
Distribution: China (Guizhou Province)
Hosts: *Tamiops swinhoei* (Sciuridae), *Petaurista petaurista* (Pallas, 1766) (Sciuridae)
M. cuii Liu, Wu & Yu, 1964
Distribution: China (Zhejiang and Fukien Provinces)
Hosts: *Tamiops swinhoei* (Sciuridae), *Hylopetes alboniger* (Hodgson, 1836) (Sciuridae)
M. debilitata Beaucournu and Durden (present paper)
Distribution: Indonesia (Java)
Host: *Lariscus insignis* (F. Cuvier, 1821) (Sciuridae)
M. durdeni Beaucournu & Wells, 2009
Distribution: Borneo (Sabah)
Host: *Dremomys everetti* (Thomas, 1890) (Sciuridae), *Tupaia montana* Thomas, 1892 (Tupaiidae)
M. euteles (Jordan & Rothschild, 1911)
Distribution: China (Yunnan and Sichuan Provinces), Thailand.
Hosts: *Callosciurus erythraeus* (Sciuridae), *Dremomys pernyi* (Milne-Edwards, 1867) (Sciuridae), *Dremomys rufigenis* (Sciuridae), *Dremomys* sp. (Sciuridae), *Sciurotamias davidianus* (Sciuridae), *Tamiops swinhoei* (Sciuridae), *Petaurista petaurista* (Sciuridae), *Belomys* sp. (Sciuridae) – *B. pearsonii* (Gray, 1842) is the only species currently recognized in this genus (Thorington & Hoffmann, 2005), *Rattus* spp. (Muridae)
M. exilia Li, Wang & Hsieh, 1964
Distribution: China (Chekiang Province)
Host: 'squirrel' (Sciuridae)
M. fimbriata (Jordan & Rothschild, 1921)
Distribution: Himalayas: Pakistan, Kashmir, India (Punjab and Uttar Pradesh States)
Hosts: *Eoglaucomys fimbriatus* (Gray, 1837) (Sciuridae) – originally listed as *Petaurista fimbriatus, Petaurista petaurista* (Sciuridae)
M. fulini Hou & Liu, 2003
Distribution: China (Xizang Province)
Hosts: *Dremomys lokriah* (Sciuridae), *Niviventer andersoni* (Thomas, 1911) (Muridae)

Table 1. Continued.

M. furcata Shi, Liu & Wu, 1985
Distribution: China (Hebei Province)
Host: *Dremomys rufigenis* (Sciuridae)
M. gansuensis Zhang & Ma, 1982
Distribution: China (Gansu Province)
Host: *Tamias sibiricus* (Laxmann, 1769) (Sciuridae)
M. hastata hastata (Jordan & Rothschild, 1921)
Distribution: Myanmar
Host: *Callosciurus pygerythrus* (I. Geoffroy Saint Hilaire, 1833) (Sciuridae), *Dremomys rufigenis* (Blanford, 1878) (Sciuridae), *Paradoxurus hermaproditus* (Pallas, 1777) (Viverridae)
M. hastata hainanensis Liu & Pan, 1986
Distribution: China (Guangdong Province: Hainan Island)
Host: *Tamiops maritimus* (Bonhote, 1900) (Sciuridae) – originally reported as *Tamiops swinhoei hainanensis* which is listed as a junior synonym of *T. maritimus* by Thorington & Hoffmann (2005).
M. hastata malayensis Traub, 1950
Distribution: Malaysia (West Malaysia)
Host: *Callosciurus erythraeus* (Sciuridae), 'tree squirrel nest'
M. hastata menghaiensis Li, Wang & Hsieh, 1964 (synonym: *M. hastata yunnanica* Liu, 1965)
Distribution: China (Yunnan Province)
Hosts: *Dremomys rufgenis* (Sciuridae), *Tamiops swinhoei* (Sciuridae), *Tupaia glis* (Diard, 1820) (Tupaiidae), *Rattus tanezumi* Temminck, 1844 (Muridae) – originally reported as *Rattus flavipectus* which is listed as a junior synonym of *R. tanezumi* by Musser & Carleton (2005).
M. hastata nepali Traub, 1950
Distribution: Nepal
Host: *Callosciurus* sp. (Sciuridae)
M. hastata sikkimensis (Jordan & Rothschild, 1922)
Distribution: Sikkim
Host: *Callosciurus pygerythrus* (Sciuridae)
M. hebeiensis hebeiensis Liu, Wu & Chiang, 1979
Distribution: China (Hebei Province)
Host: *Trogopterus xanthipes* (Sciuridae)
M. hebeiensis shennongjjiaensis Liu & Ma, 1999
Distribution: China (Hebei Province)
Host: *Trogopterus xanthipes* (Sciuridae)
M. heinrichi Jordan, 1939
Distribution: Myanmar
Hosts: *Tamiops* sp. (Sciuridae), *Callosciurus pygerythrus* (Sciuridae), *Callosciurus* sp. (Sciuridae)
M. heishuiensis Li, 1996
Distribution: China (Sichuan Province)
Host: *Apodemus* sp. (Muridae)
M. idonea (Rothschild, 1919)
Distribution: Indonesia (Sumatra)
Hosts: *Sundasciurus tenuis* (Horsfield, 1824) (Sciuridae), *Maxomys fulvescens fraternus* (Muridae)
M. jiangkouensis Li and Huang, 1979 - treated as a subspecies, *M. cuii jiangkouensis*, by some authors but assigned full species status by Li & Traub (1998), Durden & Beaucournu (2006) and Hastriter & Bush (2010)
Distribution: China (Guizhou Province)
Hosts: *Tamiops macclellandi* (Sciuridae), *Tamiops swinhoei* (Sciuridae)
M. jingdongensis Li, 1996
Distribution: China (Yunnan Province)
Host: *Dremomys rufigenis* (Sciuridae)

Table 1. Continued.

M. kinabaluae Beaucournu & Wells, 2005
Distribution: Borneo (Sabah)
Host: *Callosciurus prevostii* (Desmarest, 1822) (Sciuridae)
M. larisci Durden & Beaucournu (present paper)
Distribution: Indonesia (Java)
Host: *Lariscus insignis* (F. Cuvier, 1821) (Sciuridae)
M. levis (Jordan & Rothschild, 1922)
Distribution: Malaysia (Peninsular Malaysia), Indonesia (Sumatra)
Host: *Dremomys rufigenis* (Sciuridae), *Sundasciurus tenuis* (Sciuridae)
M. liae Wang, 1957
Distribution: China (Fukien Province), Taiwan, Vietnam
Hosts: *Callosciurus erythraeus* (Sciuridae), *Callosciurus* sp. (Siuridae), *Dremomys rufigenis* (Sciuridae), *Dremomys* sp. (Sciuridae), *Tamiops mcclellandii* (Horsfield, 1840) (Sciuridae), *Tamiops swinhoei* (Sciuridae)
M. luchunensis Huang, 1980
Distribution: China (Yunnan Province)
Host: *Ratufa bicolor* (Sparrmann, 1878) (Sciuridae)
M. lupata lupata (Jordan & Rothschild, 1921)
Distribution: India (Manipur State), Nepal, Sikkim
Hosts: *Callosciurus caniceps* (Gray, 1842) (Sciuridae), *Callosciurus erythraeus* (Sciuridae), *Callosciurus pygerythrus* (Sciuridae), *Dremomys lokriah* (Sciuridae), *Rattus nitidus* (Hodgson, 1845) (Muridae)
M. lupata bamana Jordan, 1939
Distribution: Myanmar
Host: Probably *Callosciurus erythraeus* (Sciuridae) - Traub *et al.* (1983) listed the host as 'probably *Callosciurus griseimanus*' which is treated as a subspecies of *C. erythraeus* by Thorington & Hoffmann (2005).
M. microcopa Li, Chen & Wei, 1974
Distribution: China (Sichuan Province)
Hosts: *Tamiops swinhoei* (Sciuridae), *Apodemus agrarius* (Pallas, 1771) (Muridae), *Apodemus sylvaticus* (Muridae)
M. muyuensis Liu & Wang, 1994
Distribution: China (Hebei & Guizhou Provinces)
Host: *Sciurotamias davidianus* (Sciuridae)
M. nandanensis Li, Zeng & Zeng, 1987
Distribution: China (Guangxi Province)
Hosts: *Petaurista petaurista* (Sciuridae), 'squirrel' (Sciuridae), *Sorex* sp. (Soricidae) – listed as *Sorex araneus* Linnaeus, 1758 in the original description but the range of this shrew species does not extend as far east as the type locality for this flea (Hutterer, 2005).
M. paoshanensis Li & Yan, 1980
Distribution: China (Yunnan Province)
Host: *Sciurotamias davidianus* (Milne-Edwards, 1867) (Sciuridae)
M. perplexa Beaucournu & Sountsov, 1999
Distribution: Vietnam
Hosts: *Dremomys rufigenis* (Sciuridae), *Menetes berdmorei* (Blyth, 1849) (Sciuridae)
M. phillipsi (Jordan, 1925)
Distribution: Sri Lanka
Hosts: *Funambulus layardi* (Blyth, 1849) (Sciuridae), *Funambulus sublineatus* (Waterhouse, 1838) (Sciuridae)
M. pilata (Jordan & Rothschild, 1922)
Distribution: Vietnam
Hosts: *Dremomys rufigenis* (Sciuridae), *Tamiops maritimus* (Sciuridae)
M. probata (Jordan & Rothschild, 1922)
Distribution: Laos, Vietnam
Hosts: *Callosciurus* sp. (Sciuridae), *Dremomys* sp. (Sciuridae), *Tamiops* sp. (Sciuridae), *Tupaia* sp. (Tupaiidae)

Table 1. Continued.

M. sodalis (Rothschild, 1919)
Distribution: Indonesia (Sumatra)
Host: *Callosciurus nigrovittatus* (Horsfield, 1823) (Sciuridae)
M. theresae Durden & Beaucournu, 2006
Distribution: Indonesia (Sulawesi)
Hosts: *Bunomys fratrorum* (Thomas, 1896) (Muridae), *Paruromys dominator* (Thomas, 1921) (Muridae), *Rattus xanthurus* (Gray, 1867) (Muridae)
M. tonkinensis Jordan, 1939 (described as *M. hastata tonkinensis*; elevated to full species status by Beaucournu & Sountsov (1999).
Distribution: Vietnam, Myanmar
Hosts: *Tamiops* sp. (Sciuridae), 'rat' (Muridae?)
M. traubi Beaucournu & Wells, 2005
Distribution: Borneo (Sabah)
Host: *Dremomys everetti* (Sciuridae), *Dremomys* sp. (Sciuridae), *Tupaia montana* (Tupaiidae)
M. trispinosa (Liu, 1939)
Distribution: China (Chekiang Province)
Host: '*Sciurus* sp.' (Sciuridae) – presumably *Callosciurus* sp.
M. uncinalis Jordan, 1939
Distribution: Myanmar
Hosts: *Callosciurus pygerythrus* (Sciuridae), *Rattus* sp. (Muridae)
M. wilsoni Durden & Beaucournu (present paper)
Distribution: Indonesia (Java)
Host: *Lariscus insignis* (F. Cuvier, 1821) (Sciuridae)

in *Macrostylophora debilitata* suggest to us that it represents a new sub-genus. Nevertheless, because the systematics of the genus *Macrostylophora* is sufficiently complex, we do not wish to add another case to the discussion. Therefore, until additional material becomes available, *Macrostylophora debilitata* sp. n. should be considered to be a particularly unique member of the '*euteles*' group. Among the morphological characters that distinguish *Macrostylophora debilitata* sp. n. from other known species of *Macrostylophora* (from both the '*hastata*' and '*euteles*' groups) are the following: the chaetotaxy of femur III, the thoracic pseudo-ctenidia, the structure of the ventral lobe of tergite IX, the palmate setae on sternite IX, the sclerotization of the intermediary lobule between sternites VIII and IX, and the unique structure of the apex of the phallosome. Undoubtedly, *Macrostylophora deilitata* sp. n. represents a unique species, distinct from *Macrostylophora wilsoni* sp. n. even though a single male and a single female specimen, respectively, are known for each of these two taxa.

Some ceratophyllid fleas are vectors of zoonotic pathogens such as *Rickettsia typhi*, which causes murine (=endemic or flea-borne) typhus and/or *Yersinia pestis*, which causes plague (Traub *et al.*, 1983). Foci for both of these diseases exist in Java (Baltazard & Bahmanyar, 1960; Gasem *et al.*, 2009). While it is unlikely that any of the new species of *Macrostylophora* described in this paper would bite humans, they could serve as enzootic vectors of these pathogens between ground squirrels (and perhaps also between murid rodents). Bridge vectors that can feed on these rodents and also on humans would be required to subsequently transmit these pathogens to humans.

Fig. 13. Map of Indonesia (including non-Indonesian parts of Borneo and all of Timor) showing distributions of known Indonesian (and Bornean) species of *Macrostylophora* (b = *M. borneensis*, d = *M. debilitata*, e = *M. durdeni*, i = *M. idonea*, k = *M. kinabaluae*, l = *M. larisci*, m = *M. levis*, s = *M. sodalis*, t = *M. theresae*, u = *M. traubi*, w = *M. wilsoni*). Note: small Indonesian islands are not shown on this map and there are no records of *Macrostylophora* from them.

Table 1 lists the 43 currently known species and 12 subspecies of *Macrostylophora* together with their authors, year of description, geographical distribution and known hosts (and host family in parentheses). Traub *et al.* (1983) provide distribution maps and synopses of the taxonomy and hosts for the species of *Macrostylophora* that had been described up to 1974. Lewis & Lewis (1985) provide taxonomic, geographical and host data for species described between 1972 and 1983, and Lewis (1993) provides the same data for species described between 1984 and 1990. Lewis (2009) lists 37 species and 14 subspecies of *Macrostylophora* described through 2006 (note: *M. cuii jiangkouensis* has since been elevated to full species status and therefore *M. cuii cuii* no longer needs to be listed as a subspecies – these actions have reduced the current number of recognized subspecies in the genus to 12). Other papers that address multiple species of *Macrostylophora* include Traub (1972), Li (1981), Liu *et al.* (1986), Li & Traub (1998), Chin & Li (1991), Beaucournu & Sountsov (1999) and Beaucournu *et al.* (2000). As evidenced from Table 1, more than half (22) of the described species of *Macrostylophora* are only known from China, and although descriptions for some of these species are fairly widely available, some others are not. For this reason, we believe Table 1 provides useful information for flea researchers and vector biologists.

We include an outline map of Indonesia (plus non-Indonesian parts of Borneo) showing known distributions of *Macrostylophora* species in this region (Fig. 13). It is evident from this map that no species of *Macrostylophora* have been recorded any further east than Sulawesi in the Indo-Australian region. This is likely because *Macrostylophora* spp. fleas primarily parasitize squirrels (family Sciuridae) and, although native squirrel species are well represented on Sulawesi (by 10 endemic species) (Musser *et al.*, 2010), there are no native squirrels in this region to the east of Sulawesi (Durden & Traub, 1990; Thorington & Hoffmann, 2005). Interestingly, however, a few species of *Macrostylophora* have apparently adapted to non-squirrel hosts including *M. theresae* Durden & Beaucournu, 2006, the single species of this genus currently known from Sulawesi, which has only been collected from endemic murid rodents on that island. Perhaps undescribed species of squirrel-associated *Macrostylophora* await discovery on Sulawesi.

In the future, if type material and both sexes become available for most of the described species of *Macrostylophora*, a taxonomic review of the entire genus is recommended.

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