New species and new locality records of the nematode genus *Labiosimplex* (Strongylida: Chabertiidae) from macropodid marsupials in Western Australia

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**ABSTRACT** – *Labiosimplex mawsonae* sp. nov. is described from the stomach of *Macropus irma* (Jourdan) (type host) from north of Williams, Western Australia. The new species is distinguished from all congeners by a combination of characters including the proportions of the lateral lip, the form of the bursa and dorsal ray, the length of the spicules and the length of the vagina vera. *Labiosimplex camporum* sp. nov. from the stomach of *M. rufus* (Desmarest) (type host) and *M. robustus* Gould from the Karratha region, is distinguished from all congeners by a combination of characters including the shape of the submedian lips and the form and size of the oesophageo-intestinal diverticula and the length of the spicules. *Labiosimplex kungi* Mawson is reported from Western Australia for the first time and new locality records are reported for *L. irma* Smales, *L. occidentalis* Smales, *L. longispicularis* Smales and *L. thomaeae* Smales. The patterns of occurrence of species of *Labiosimplex* within species of *Macropus* suggest both colonization and co speciation may have occurred.


**INTRODUCTION**

The genus *Labiosimplex* Smales, 2002 (Labiostrongylina: Cloacininae: Chabertiidae) comprises large stomach worms, parasites of macropodid and potoroid marsupials that are found throughout Australia, Papuan Indonesia and Papua New Guinea. Of the 23 known species of *Labiosimplex* nine have been reported from the five species of *Macropus* that are found in Western Australia. Two of the hosts, *M. robustus* Gould, 1841 and *M. rufus* (Desmarest, 1822), are distributed across the continent, two *M. eugenii* (Desmarest, 1817), *M. fuliginosus* (Desmarest, 1817) are southern species and the fifth, *M. irma* (Jourdan, 1837) occurs only in Western Australia (Van Dyck and Strahan 2008). Three of the nine parasite species *L. irma* (Smales, 1995) from *M. irma*, *L. occidentalis* (Smales, 1995) from *M. fuliginosus* and *L. thomaeae* (Smales, 1995) from *M. eugenii* have been found only in Western Australia. A fourth species, *L. longispicularis* (Wood, 1929) was first reported in eastern Australia from *M. robustus* and *M. rufus* and subsequently from *M. robustus* in Western Australia (Wood 1929; Johnston and Mawson, 1938; Smales, 1995). The remaining five species, *L. aridus* (Smales, 1995) from *M. rufus* and *M. robustus*, *L. kungi* (Mawson, 1955), *L. major* (Smales, 1995) and *L. laterilabellosus* (Smales, 1995) from *M. fuliginosus* and *M. giganteus* and *L. robustus* (Smales, 1995) from *M. robustus*, are known only from eastern and central Australia (Smales 1995, 2006).

The nematode parasites of Western Australian macropodid species, however, have been studied to a much lesser extent than those of eastern Australia (Appin et al. 2004). Consequently much more work needs to be done to establish the full extent of the geographic range of those species presently reported only from eastern and central Australia and to determine the existence of any additional species occurring only in Western Australia.

In this paper the examination of recent collections from the five macropodine hosts found in Western Australia has provided further information on the geographic distribution of the genus *Labiosimplex* and two new species are described herein.

**METHODS**

Specimens dissected from the stomach of *M. rufus* by R. Martin in 1997 and from the stomachs of *M. eugenii, M. fuliginosus, M. irma, M. robustus* and *M. rufus* collected from Western Australia between 2001 and 2002 by I. Beveridge, R. Brazelle and S. Middleton and from 2004 to 2010 by I. Beveridge were fixed in Berland's fluid or 5% formalin and stored in 70%
ethanol prior to examination. Worms were examined microscopically after clearing in lactophenol. Spicule preparations were made using Berlese’s mountant. Drawings were prepared with the aid of a drawing tube attached to an Olympus BH microscope. Unless otherwise stated measurements, given in μm, are of 10 specimens presented as the range followed by the mean in parentheses. Classification follows Chilton et al. 1997 and Smales 2002. Some of this material had been registered in the Australian Helminthological Collection (AHC) of the South Australian Museum, Adelaide (SAMA) but had not been fully identified. Type specimens have been deposited in the Western Australian Museum (WAM) where required.

RESULTS

NEW LOCALITY RECORDS

The geographic range of the following species has been extended to include localities in Western Australia:

**Labiosimplex kungi** (Mawson, 1955) from 7 *M. fuliginosus* from Kalgoorlie (30°45'S, 121°27'E), AHC 32263, AHC 32265, AHC 32266, AHC 32270, Waroona (32°50’S, 115°52’E), AHC 33248, AHC 32264 and 105k N Williams (32°11’S, 116°52’E), AHC 33010.

**Labiosimplex longispicularis** (Wood, 1929) from 2 *M. robustus* from Yalgoo (28°20’S, 116°41’E), AHC 32258; from 10 *M. rufus* from Menzies (29°41’S, 121°02’E), AHC 45443, AHC 45445, AHC 45447, AHC 45449, AHC 45453, AHC 45454, Kalgoorlie (30°45’S, 121°27’E), AHC 32259, AHC 32267, AHC32268, AHC 32269, AHC and Yalgoo (28°20’S, 116°41’E), AHC 32262.

The localities of the following Western Australian species have been extended:

**Labiosimplex irma** (Smales, 1995) from 6 *M. irma* from between York and Perth (31°53’S, 116°30’E), AHC 30068, Collie (33°21’S, 116°09’E), AHC 32959, 80 k N Williams (32°21’S, 116°52’E), AHC 45778, 95 k N Williams (32°14’S, 116°52’E), AHC 33013 and Mt Trio (34°20’S, 118°06’E), AHC 33021, 33022.

**Labiosimplex thomasae** (Smales, 1995) from *M. eugenii* from the Perup River (34°24’S, 116°25’E), AHC 32908.

**Labiosimplex occidentalis** (Smales, 1995) from 3 *L. fuliginosus* from Manjimup (34°14’S, 116°08’E), AHC 30088 and 80 k N Williams (32°21’S, 116°52’E), AHC 45645, AHC 45646.

Phylum Nematoda

**Family Chabertiidae** (Popova, 1952)

Lichtenfels, 1980

**Genus Labiosimplex** Smales, 2002


TYPE SPECIES

**Labiostrongylus australis** Kung, 1948, by original designation.

**Labiosimplex mawsonae** sp. nov.

Figures 1-17

MATERIAL EXAMINED

Holotype

**Australia: Western Australia:** ♀, 80 km N. of Williams (32°21’S, 116°52’E), 11 December 2008, I. Beveridge (WAM V7711). Host: *Macropus irma* (Jourdan, 1837) (Marsupialia: Macropodidae); localisation: stomach.

Allotype

**Australia: Western Australia:** ♀, same data as holotype (WAM V7712).

Paratypes

**Australia: Western Australia:** 40 ♀, 38 ♀, same data as holotype (SAMA AHC 45790, WAM V7713).

Additional material studied

**Australia: Western Australia:** 1 ♀, Talbot (32°01’S, 116°39’E), 15 July 1961, W.H. Butler (WAM 18-81 (1)). Host: *Macropus irma* (Jourdan, 1837) (Marsupialia: Macropodidae); localisation: leg muscle.

Prevalence: present in one of six hosts examined between 1994 and 2008.

DIAGNOSIS

Large robust nematodes; mouth opening surrounded by 6 prominent fleshy lips with distinct pulp cavities; 2 lateral lips, simple, bearing amphids, as long as submedian lips: 4 submedian lips, broader at base, bearing cephalic papillae on mid region; oesophagus long clavate; oesophago-intestinal diverticula large; bursa large, lobes clearly delineated; dorsal trunk branching at 1/2 its length, bifurcating at 2/3 its length; spicules long, alate, with curved tips; female tail tapering, conical; vulva immediately anterior to anus; vagina vera long, sinuous; parasites of macropodid marsupials.

DESCRIPTION

Robust nematodes, cuticle with fine transverse striations, cephalic extremity with 6 fleshy well developed lips with pulp cavities, 4 submedian lips ridged, broader at base than distal end, bearing cephalic papillae on mid region, lateral lips simple, slender, about same length as submedians, bearing amphids. Oral opening circular, buccal capsule thick walled,
FIGURES 1–17  *Labiosimplex mawsonae* sp. nov. from *Macropus irma*: 1, anterior end, male, lateral view; 2, cephalic extremity, female, optical section, ventral view; 3, cephalic extremity, female, lateral view; 4, spicule, proximal end; 5, lateral lip; 6, cephalic extremity, apical view; 7, spicules, distal tips; 8, oesophago-intestinal diverticula; 9, excretory pore; 10, deirid; 11, gubernaculum, ventral view; 12, bursa, apical view; 13, ovejector, dissected from body of female; 14, dorsal rays, showing extra branchlets; 15, tail tips, female, showing variations; 16, genital cone, dorsal view; 17, posterior end, female, lateral view. Scale bars: 200 μm (Figures 1, 8, 13, 17); 50 μm (Figures 2-6, 14-16); 25 μm (Figures 7, 9-11); 100 μm (Figure 12).
cylindrical, wider than deep. Oesophagus long, clavate about 1/5 to 1/5.5 body length. Deirids long, fine, thread like, anterior to nerve ring which encircles oesophagus at about 1/4 its length. Excretory pore posterior to nerve ring. Oesophago-intestinal diverticula large, longer than width of oesophagus.

**Male**

Length 22-27 (23.9) mm, width 630 -885 (765). Buccal capsule 107-148 (131) wide by 100 -127 (110) deep. Nerve ring 940-1155 (1053), deirids 535-705 (592), excretory pore 1325-1935 (1500) from base of lips. Oesophagus 3875-4860 (4520) long. Bursa large, ventral lobes separate, dorsal, lateral and ventral lobes about same length. Ventro-ventral and latero-ventral rays apposed, same length, reaching margin of bursa; externo-lateral ray short, not reaching margin of bursa, medio-lateral and postero-lateral rays apposed, reaching margin of bursa; externo-dorsal arising close to lateral trunk, longer than externo-lateral, not reaching margin of bursa; dorsal trunk stout, giving off pair of branches at about 1/2 its length, bifurcating at 2/3 its length, branches reaching margins of bursa. Some specimens with additional single or paired branchlets given off the dorsal trunk. Spicules 7820-9350 (8390) about 1/3 body length, proximal ends irregularly knobbed, distal tips curved, alae striated extending to tips. Gubernaculum cordate. Genital cone about 1/2 length bursa, anterior lip larger, conical, posterior lip smaller, reniform with paired bifid appendages.

**Female**

Length 27-33 (30.3) mm, width 815-1120 (995). Buccal capsule 148-181 (160.5) wide by 114-141 (127.5) deep. Nerve ring 1140-1350 (1233), deirids 555-870 (776), excretory pore 1305-1880 (1717) from base of lips. Oesophagus 3706-5780 (5238) long. Body narrows at level of vulva, tail 1020-1275 (1277) long, tapering to blunt tip. Vulva close to anus 1955-2450 (2370) from tail tip. Ovejector with vestibule longest, about 280, infundibula, about 250, sphincters shortest, about 200. Vagina vera slightly sinuous 2380-3060 (2839) long. No eggs were found in specimens observed.

**REMARKS**

All the specimens examined conformed to the diagnosis of the genus *Labiosimplex* given by Smales (2002). Using the key of Smales (1995) they fell into a group of two species, *L. clelandi* (Johnston & Mawson, 1939) and *L. bancrofti* (Johnston & Mawson, 1939), with lateral lips as long as the submedian lips and the lobes of the bursa separate. *Labiosimplex mawsonae* sp. nov. differs from both *L. bancrofti* and *L. clelandi* in the length of the spicules, 8390 compared with 5695 and 6060 respectively, the shape of the gubernaculum, being neither subcordate with edges extending proximally nor subtriangular, and the shape of the female tail tip, having neither an irregular pointed nor knobbed tip (Smales 1995). *Labiosimplex mawsonae* further differs from *L. bancrofti* in the shape of the bursa, the dorsal lobe being longer than the lateral lobes in *L. bancrofti* and the form of the dorsal ray, bifurcating close to branching in *L. mawsonae* and proximal to branching in *L. bancrofti*. Female *L. mawsonae* have a longer vagina vera (2839 compared to 2200) than for *L. bancrofti*, and the proportions of the ovejector differ, the sphincters being the shortest element in *L. mawsonae* rather than the longest as in *L. bancrofti* (see Smales 1995). *Labiosimplex mawsonae* further differs from *L. clelandi* in the form of the dorsal ray, the distance between lateral branching and bifurcation being longer in *L. clelandi*, the longer vagina vera (2839 compared with 1830) and the proportions of the ovejector with the sphincters the longest element in *L. clelandi* (Smales 1995).

Since 1995 three additional species, *L. centralis* Smales, 2006 from *Petrogale lateralis* Gould, 1842, *L. territoriensis* Smales, 2006 from *M. bernardus* Rothschild, 1904 both from the Northern Territory and *L. bancrofti* (see Smales, 2006). *Labiosimplex mawsonae* can be readily distinguished from *L. centralis*, which has similar length spicules, because *L. centralis* has no gubernaculum a smaller genital cone, asymmetrically tipped spicules, a dorsal ray that bifurcates prior to giving off branches and a blunt female tail (Smales 2006). *Labiosimplex territoriensis* has shorter spicules (3855) and a shorter vagina vera (715) than *L. mawsonae* (see Smales 2006). *Labiosimplex turnbulli* with a similar form of the dorsal ray differs from *L. mawsonae* in having shorter spicules (5610-7750 compared with 7820-9350) smaller oesophago-intestinal diverticula, shorter deirids, smaller genital cone, longer dorsal lobe of the bursa, asymmetrical spicule tips, and differing proportions of the ovejector, the sphincters being the longest element (Smales & Chilton 1997). The occasional finding of additional branchlets on the dorsal ray as in *L. mawsonae* has also been noted in *L. centralis* (see Smales, 2006).

The most likely explanation for finding a single female labiostrongylin in the leg muscle of a macropod host, the specimen from Talbot, is that an error occurred during the dissection or labeling process. Adult filarioids may be found associated with leg muscle but never strongyloids.

In the material examined for this study *L. mawsonae* was found in a mixed infection with *L. irma* Smales, 1995 the only other labiostrongylin also known from *M. irma*. It can readily be distinguished from *L. irma*, however, by longer spicules (8397 compared with 5215), the shape of the bursa, the form of the dorsal ray, the form of the appendages on the genital cone, a longer female tail and shorter vagina vera (Smales 1995). Neither parasite species has been found in sympatric populations of the congeners of their host, *M. irma*.
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Labiosimplex camporum sp. nov.

Figures 18-33

MATERIAL EXAMINED

Holotype

Australia: Western Australia: ♂, Menzies (29°41'S, 121°02'E), 22 November 2008, I. Beveridge (WAM V7706). Host: Macropus rufus (Desmarest, 1822) (Marsupialia: Macropodidae); localisation: stomach.

Allotype

Australia: Western Australia: ♀, same data as holotype (WAM V7707).

Paratypes

Australia: Western Australia: 4 ♂, 12 ♀, same data as holotype (WAM V7708; SAMA AHC 45446).

Additional material studied

Australia: Western Australia: 10 ♂, 19 ♀, same data as holotype (SAMA AHC 45444, AHC 45448, AHC 45450, AHC 45451, AHC 45452); 1 ♂, 11 ♀, Karratha (20°53'S, 116°40'E), 7 August 1995, R. Martin (AHC 30519); 1 ♂, 1 ♀, 15 km S. of Roebourne (20°45'S, 116°59'E), 1 ♀, 21 km N. of Roebourne (20°53'S, 116°40'E), 2 ♀, 10 km N. of Fortescue River Roadhouse (21°11'S, 116°12'E), 2 ♀, 22 km N. of Fortescue River Roadhouse (21°08'S, 116°13'E); 12 ♀, 32 km N. of Fortescue River Roadhouse (21°01'S, 116°20'E); 3 ♂, 12 ♀, 47 km N. of Fortescue River Roadhouse (20°58'S, 116°23'E); 1 ♂, 2 ♀, 50 km N. of Fortescue River Roadhouse (20°57'S, 116°26'E); 1 ♂, 1 ♀, 65 km N. of Fortescue River Roadhouse (20°52'S, 116°32'E); 21 ♂, 12 ♀, 84 km N. of Fortescue River Roadhouse (20°48'S, 116°44'E); 4-8 June 2010, I. Beveridge (AHC 45796, AHC 45797 AHG 45800, AHC 45801 AHC 45802, AHC 45803, AHC 45804, AHC 45805, AHC 45806). Host M. rufus; localisation: stomach.


Prevalence: present in 9 of 10 M. rufus and 2 of 12 M. robustus from the Karratha region of Western Australia examined in 2010.

DIAGNOSIS

Very large robust nematodes; mouth opening surrounded by 6 prominent fleshy lips with distinct pulp cavities; 2 lateral lips, simple, bearing amphids, shorter than submedian lips; 4 submedian lips broadest proximally, bearing cephalic papillae on mid region; oesophagus long clavate; oesophago-intestinal diverticula medium sized, complexly bilobed; bursal lobes clearly delineated; dorsal trunk branching at 1/2 its length, bifurcating at or posterior to branching; spicules long, alate, with blunt tips; female tail tapering, blunt, conical; vulva immediately anterior to anus; vagina vera slightly sinuous; parasites of macropodid marsupials.

DESCRIPTION

Very large robust nematodes, grayish white when living, cuticle with fine transverse striations, cephalic extremity with 6 fleshy well developed lips with pulp cavities, 4 submedian lips ridged, as broad or broader at anterior end than base, bearing cephalic papillae on mid region, lateral lips simple, shorter than submedians, bearing amphids. Oral opening circular, buccal capsule very thick walled, cylindrical, wider than deep. Oesophagus long, clavate about 1/3.5 -1/5 body length. Deirids short, thread like, anterior to nerve ring encircling oesophagus at about 1/5-1/6 its length. Excretory pore posterior to nerve ring. Oesophago-intestinal diverticula complexly bilobed, medium sized, about as long as width of oesophagus.

Male

Length 38-60 (45) mm, width 850 -1190 (985). Buccal capsule 87-114 (104) wide by 80 -121 (105) deep. Nerve ring 1507-1955 (1673), deirids 837-1407 (993), excretory pore 2040-2720 (2288) from base of lips. Oesophagus 7140-13260 (8590) long. Bursa large, ventral lobes separate, lateral lobes longer. Ventro-ventral and latero-ventral rays apposed, same length, reaching margin of bursa; externo-lateral ray short, not reaching margin of bursa, medio-lateral and postero-lateral rays apposed, reaching margin of bursa; externo-dorsal arising close to lateral trunk, longer than externo-lateral, not reaching margin of bursa; dorsal trunk stout, bifurcating at about 1/2 its length, branching soon thereafter, branches not reaching margin of bursa. Spicules 6120-6970 (6559) about 1/7 body length, proximal ends irregularly knobbed, distal tips slightly curved, may be crossed, alae striated extending to tips. Gubernaculum more or less sub cordinate. Genital cone about 1/3 length bursa, anterior lip larger, conical, posterior lip smaller, reniform with paired irregularly multi-lobed appendages.

Female (measurements of 15 specimens)


REMARKS

All the specimens examined conformed to the diagnosis of the genus Labiosimplex given by Smales (2002). Some variability was noted in the shape of the
FIGURES 18–33  *Labiosimplex camporum* sp. nov. from *Macropus rufus*: 18, anterior end, male, lateral view; 19, cephalic extremity, male, dorso-ventral view; 20, cephalic extremity, female, optical section, lateral view; 21, proximal end; 22, lateral lip, female; 23, cephalic extremity, apical view; 24, spicules, distal tips; 25, oesophago-intestinal diverticula; 26, deirid; 27, gubernaculums, dorsal view, showing variations; 28, submedian lip, male; 29, dorsal ray; 30, bursa, apical view; 31, ovejector, dissected from body of female; 32, genital cone, dorsal view; 33, posterior end, female, lateral view; 34, tail tips, female, showing variations. Scale bars: 500 μm (Figures 18, 25); 100 μm (Figures 19, 20, 22, 23, 33); 50 μm (Figures 21, 24, 27, 28, 29, 32, 34); 25 μm (Figure 26); 200 μm (Figures 30, 31).


gubernaculum (fig 27) and the position of the branches of the dorsal ray relative to its bifurcation (figs 29, 30) but there were no consistent differences between specimens collected from the same host or from different hosts, neither conspecifics nor congeners. Using the key of Smales (1995) the worms came close to either *L. aridus*, with flaps on the distal ends of the lips, but with vestigial oesophago-intestinal diverticula also occurring in *M. rufus*, or *L. robustus* with a pair of irregularly multi lobed appendages on the posterior lip of the genital cone but with spicules shorter than 6000, occurring in *M. robustus*. *Labiosimplex camporum* sp. nov., although having submedian lips broadest distally, is a much larger worm than *L. aridus* with females up to 120 mm long compared with 30 mm long and has medium sized oesophago-intestinal diverticula. *Labiosimplex camporum* further differs from *L. aridus* in spicule length, 6120-6970 compared with 5200-5800, vagina vera length, 1360-2550 compared with 620, and the morphology of the genital cone (Smales 1995). The submedian lips of *L. camporum* are broader distally than those of *L. robustus* and the oesophago-intestinal diverticula are smaller and more complex than those of *L. robustus*. Further, *L. camporum* has shorter spicules than *L. robustus* (4300-5500 compared with 6120-6970), a longer vagina vera (1360-2250 compared with 1000-1400) and smaller eggs (167-178 by 74-81) compared with 215-275 by 70-90. The form of the ovejector with vestibule and infundibula about the same length as compared with the vestibule the smallest element also distinguishes *L. camporum* from *L. robustus* (Smales 2006).

The three species of *Labiosimplex* described since 1995 are all much smaller worms than *L. camporum* and neither *L. arnhemensis*, *L. centralis* nor *L. turnbulli* have either sub median lips or oesophago-intestinal diverticula with the morphology found in *L. camporum* (see Smales 2006; Smales and Chilton 1997). They can be further distinguished as follows: *L. arnhemensis* has shorter spicules (4080-4760 compared with 6120-6790) and vagina vera (935-1615 compared with 1360-2250); *L. centralis* is lacking a gubernaculum and has simple bifid appendages on the posterior lip of the genital cone; *L. turnbulli* differs in the morphology of the dorsal ray, branching prior to bifurcation and the genital cone, with simple bifid appendages on the posterior lip, has asymmetrical spicule tips a sinuous vagina vera and shorter eggs (150-162 by 85-95 compared with 167-178 by 74-81).

The only other species of *Labiosimplex* known from *M. rufus* and *M. robustus*, *L. longispicularis*, has been found in this study in the same localities in Western Australia as *L. camporum*. The two species can be easily distinguished by the length of spicule, 6120-6970 compared with 10500-14000, the morphology of the spicule tips, asymmetrical in *L. longispicularis*, the form of the dorsal ray, branching at about the level of bifurcation for *L. camporum*, prior to bifurcation in *L. longispicularis*, the form the appendages on the posterior lip of the genital cone, complex for *L. camporum*, bifid for *L. longispicularis*, the shape of the female tail, shorter and more blunt in *L. camporum* and the length of the vagina vera, 1360-2550 compared with 2600-4000 for *L. longispicularis*.

*Labiosimplex camporum* has been found only in hosts collected from the Karratha region of Western Australia and not in more southern localities. This suggests that its geographic distribution may be limited to more northern populations of *M. rufus* and *M. robustus*. The much higher prevalence in *M. rufus* suggests that infections in *M. robustus* may represent occasional events in hosts that are in sympathy with *M. rufus*.

**DISCUSSION**

The findings from this study indicate that *L. kungi* and *L. longispicularis* have a continental distribution, occurring in association with populations of *M. rufus*, *M. robustus* and *M. fuliginosus*. By contrast *L. occidentalis* is restricted to western and *L. major* and *L. lateralabellosus* restricted to eastern populations of *M. fuliginosus*. Similarly, *L. camporum* is restricted to western populations of *M. rufus* and *M. robustus* and *L. aridus* to central and eastern populations of *M. rufus*.

As has been noted for other cloacinine nematodes the patterns that best describe host parasite relationships between *Labiosimplex* and its macropodid hosts may encompass both colonization and co speciation processes (Beveridge and Chilton 2001). For example *L. longispicularis* occurs in both *M. fuliginosus* and *M. rufus*, a possible colonization event. By contrast the occurrence of *L. camporum* in western populations and *L. aridus* in central and eastern populations of *M. rufus* suggests a co speciation event. A low prevalence of *L. camporum* in those western populations of *M. robustus* that are in sympathy with *M. rufus* suggests occasional infection events. The finding of two species of *Labiosimplex* in populations of *M. irma* may be indicative of co speciation within disjunct host populations.

More sampling throughout the range of each of the host species is needed before any putative distribution and diversification patterns of these parasites can be confirmed.

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**REFERENCES**


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