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The host and geographical range of the grasshopper pathogen *Paranosema (Nosema) locustae* revisited

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Abstract

Host and geographical ranges are updated for the microsporidium *Paranosema locustae*; this pathogen was developed in the USA as a long-term microbial control agent of grasshoppers. Currently known to be susceptible to *P. locustae*, either naturally or experimentally, are 121 species of Orthoptera from North and South America, Africa, Australia, China, and India. Most belong to the Acrididae (112), and within this family, to the Melanoplinae (36), Oedipodinae (35), and Gomphocerinae (35). The host range of *P. locustae*, as presently understood, is based largely on morphology and could change if molecular techniques revealed cryptic species. The North American isolate is not only the best studied, but the one established after its introduction into Argentina, and produced and used in China: it can be considered a generalist pathogen. As such, *P. locustae* may have the ability to alter, through differences in host susceptibilities, the structure of grasshopper assemblages in areas where it was not present before. Long-term careful monitoring of key grasshopper species in areas of pathogen introduction/establishment may reveal such effects.

Introduction

Paranosema locustae is a spore-forming pathogen of the adipose tissue of orthopterans that was isolated, selected, and developed in the USA as a long-term microbial control agent of grasshoppers (Henry & Oma 1981, Johnson 1997, Lockwood *et al*. 1999). *P. locustae* belongs to the Microsporidia, a group of unicellular eukaryotes that are obligate intracellular parasites of animals and some protists (Wittner & Weiss 1999). Microsporidia were historically regarded as Protozoa or Archezoa, but recent studies at the molecular level have shown they are actually related to Fungi (Keeling & Fast 2002).

In North America, Steinhaus (1951) first noticed *P. locustae*, albeit without naming it, in 3 species of grasshoppers of the genus *Melanoplus* from Montana. Soon after, Canning (1953) described *P. locustae* as *Nosema locustae*, using diseased African migratory locusts, *Locusta migratoria migratorioides*, from a rearing colony at the Imperial College Field Station in London. Sokolova *et al*. (2003), while erecting the new genus *Paranosema* for another microsporidian pathogen of Orthoptera from the cricket *Gryllus bimaculatus*, transferred *N. locustae* to *Paranosema*, based on molecular and ultrastructural grounds, erecting the new combination *P. locustae*. Even more recently, Slamovits *et al*. (2004) proposed another new combination, *Antonospora locustae*; but Sokolova *et al*. (2005) provided reasons for favoring the name *P. locustae*.

One of several factors that permitted the selection of *P. locustae* for its development as a microbial control agent, is its wide host range among acridomorphs. While the host range of most Microsporidia is relatively narrow (Solter *et al*. 2005), host specificity is a species-based character in Microsporidia, that should be considered individually (Solter & Becnel 2003). The unusually broad host range of *P. locustae* was observed early in its development as a biocontrol agent (Henry 1969), and judged to be desirable (Henry 1977). This was because many grasshopper species are considered pests, and frequently, when outbreaks occur, more than one (and sometimes several) species are involved.

Henry (1969) provided the first list of hosts that he knew to be susceptible, which included 55 North American species, 53 of them acridomorphs, one cricket, and one tetrigid. Almost 2 decades later, Brooks (1988) presented a new list of worldwide susceptible insects, all of them Orthoptera, expanding the known host range of *P. locustae* to 95 species. Since then, additional work has been conducted on *P. locustae*, much of it outside of North America, in Argentina, China and South Africa. The present update compiles the current available knowledge on the host and geographical range of *P. locustae*. Caution should be exerted when assessing the currently known host range of *P. locustae* because it is largely based on morphological grounds. The possibility that a scrutiny of different isolates at the molecular level could reveal the occurrence of cryptic species cannot be ruled out.

Host range and distribution

Table 1 shows, by continent, family, and subfamily, all the species reported to be susceptible, either naturally or experimentally, to *P. locustae*, which at present total 121. Of these, 112 species are Acrididae, and the remaining 9 susceptible species belong to the families Romaleidae (3), Gryllidae (1), Oecanthidae (1), Tetrigidae (1), Tettigonidae (1), and Pyrgomorphidae (2). Among the Acrididae, susceptible species are in the subfamilies Acridinae (2), Calliptaminae (1), Catantopinae (2), Cyrtacanthacridinae (5), Copiocerinae (1), Eyprepocnemidae (3), Gomphocerinae (23), Melanoplinae (36), Oedipodinae (35), Oxyinae (3), and Tropidopolinae (1). Based on the host species involved in the natural infections (ecological host range, Solter *et al*. 2005), on the natural and induced (after field applications) prevalences, the results of laboratory bioassays (physiological host range, Solter *et al*. 2005), and on the intensity of infections (spore loads per individual), it appears that species in the subfamilies Melanoplinae, Oedipodinae, and Gomphocerinae are generally more susceptible than species in other subfamilies (Canning 1953; Henry 1969; Henry *et al*. 1973; Ewen 1983; Lockwood 1988; Whitlock & Brown 1991; Bomar *et al*. 1993; Wang & Yu 1994; Yuhua 1997; Lange 2003 a, b). It is important to note that in the earlier literature on host range of *P. locustae* (Henry 1969), most species that by then were treated as Cyrtacanthacridinae are now considered to be within the Melanoplinae.

P. locustae has been reported to be native in North America, India and South Africa (Henry 1969, Ewen 1983, Srivastava & Bhanotar 1985, Raina *et al*. 1987, Whitlock & Brown 1991). It has been mentioned for the Irkutsk region of Russia (Issi & Lipa 1968), but later apparently treated by Issi & Krylova (1987) as a different species, *Nosema chorthippi*. However, aside from the original description by Canning (1953), virtually all available knowledge on *P. locustae* comes from research on the North American isolate, while the records for India were poorly diagnosed.

The North American isolate of *P. locustae* has become established after its introduction in the Pampas of Argentina (Sokolova & Lange 2002, Lange 2003a, Lange & De Wysiecki 2005), and it is produced and used in China for the control of grasshoppers and locusts (Long 1995, Wangpeng *et al*. 2001, Shi & Njaqi 2004). Unfortunately, the fate of introductions conducted in other countries, such as Australia, Cape Verde, Mali, Niger, and Mauritania has not been explored.

The present update shows the significant, relatively recent, expansion in host and geographical ranges of *P. locustae*, mostly as a result of applied use. Due to the extremely wide host range acknowledged at present for *P. locustae*, this microsporidium clearly qualifies as a generalist pathogen. In assessing the significance of this, those infections recorded in field-collected individuals, either naturally (labeled as **N** in Table 1), or as induced infections following an introduction or augmentation event (labeled as **I** and **A** in Table 1), are of particular relevance. Although the physiological host range can be used as an indicator of ecological host range, it needs to be carefully observed and evaluated. When forced into experimental hosts during bioassays, some microsporidia are known to develop atypical infections that are not likely to occur or persist in the field (Solter *et al*. 2005).

A generalist pathogen has the ability to alter, through differences in host susceptibilities, the structure of insect assemblages when established in areas where it was not present before (Bonsall 2004). In this sense, regular, long-term monitoring in grasshopper communities of Argentina and China should prove very informative in the long run. Key grasshopper species, in terms of known or potential susceptibility, rareness, and range of geographical distribution, should be designated within areas of pathogen establishment and surroundings. Careful attention should be paid in future surveys to their populations and eventual infection status.

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Table 1. Species of Orthoptera, by continent, family, and subfamily, known to be susceptible to *Paranosema locustae*. **(N)** natural infection in a wild host, **(I)** infection in a wild host after an introduction event of the pathogen, **(E)** experimental infection resulting from a laboratory bioassay, **(S)** spontaneous infection in a host rearing facility, **(A)** infection in a wild host after application in a general area where *Paranosema locustae* is known to be native.

Geographic distribution, family, subfamily, species, and infection type	References
North America (western USA, southern Canada)	
Acrididae	
Cyrtacanthacridinae	
Schistocerca americana **(E)**, *S. nitens* (= *vaga*)**(E)**	Henry 1969
Gomphocerinae	
Aeropedellus clavatus **(N)**, *Ageneotettix deorum* **(N)**, *Amphitornus coloradus* **(A)**,*Aulocara ellioti* **(N)**, *Aulocara* (=*Depranopterna*) *femoratum* **(A)**,*Bruneria brunnea* **(N)**,*Chorthippus curtipennis* **(N)**, *Cordillacris occipitalis* **(A)**, *Mermiria bivittata* **(N)**, *Opeia obscura*, **(N)**, *Phlibostroma quadrimaculatum* **(N)**, *Psoloessa delicatula delicatula* **(N)**	Henry 1969, Ewen 1983, Henry 1971, Henry & Oma 1974,
Melanoplinae	
Bradynotes obesa **(N)**, *Hesperotettix viridis viridis* **(N)**, *Hypochlora alba* **(E)***Melanoplus alpinus* **(N)**, *M. bivittatus* **(N)**, *M. borealis borealis* **(N)**, *M. bowditchi canus* **(E)**, *M. confusus* **(N)**, *M. cuneatus* **(N)**, *M. dawsoni* **(N)**, *M. differentialis* **(N)**, *M. femurrubrum* **(N)**, *M. foedus foedus* **(N)**, *M. gladstoni* **(E)**, **M. infantilis (N)**, *M. keeleri luridus* **(E)**, *M. lakinus* **(A)**, *M. occidentalis* **(N)**, *M. packardii* **(N)**, *M. sanguinipes sanguinipes* **(N)**, *Oedaleonotus enigma* **(N)**, *Phoetaliotes nebrascensis* **(N)**,	Henry 1969, Steinhaus 1951, Ewen 1983, Henry & Oma 1974, Bomar *et al.* 1993
Oedipodinae	
Arphia conspersa **(N)**, *A. pseudonietana* **(E)**, *Camnula pellucida* **(N)**,*Conozoa wallula* **(N)**, *Cratypedes neglectus* **(N)**, *Dissosteira carolina* **(N)**, *D. spurcata* **(N)**, *Encoptolophus costalis* **(E)**, *Hadrotettix trifasciatus* **(N)**, *Metator nevadensis* **(N)**, *M. pardalinus* **(N)**,*Spharagemon equale* **(A)**, *S. collare* **(A)**, *Trachyrhachys kiowa* **(N)**, *Trimerotropis sp.***(N)**,*T. fontana* **(N)**, *T. gracilis* **(N)**, *T. inconspicua* **(N)**, *T. latifasciata* (=*laticinta*) **(N)**, *T. pallidipennis* **(N)**, *Xanthippus corallipes* **(N)**	Henry 1969, Ewen 1983, Canning 1962,Henry *et al*. 1973, Bomar *et al.* 1993
Romaleidae	
Romaleinae	
Brachystola magna **(N)**	Henry 1969
Gryllidae	
Gryllinae	
Gryllus sp. **(E)**	Henry 1969
Oecanthidae	
Oecanthinae	
Oecanthus sp. **(A)**	Bomar *et al.* 1993
Tetrigidae	
Undetermined sp. **(E)**	Henry 1969
Tettigoniidae	
Tettigoniinae	
Anabrus simplex **(N)**	Henry & Onsager 1982
South America (western Pampas and northwestern Patagonia, Argentina)	
Acrididae	
Acridinae	
Allotruxalis gracilis **(I)**	Lange 2003a
Cyrtacanthacridinae	
Schistocerca cancellata **(E)**	Lange *et al*. 2000, Sokolova & Lange 2002, Lange 2003b
Copiocerinae	
Aleuas lineatus **(E)**	Luna *et al.* 1981
Gomphocerinae	
Euplectrotettix schulzii **(I)**, *Laplatacris dispar* **(E)**, *Rhammatocerus pictus* **(I)**, *Staurorhectus longicornis* **(I)**	Lange 2003a, Luna *et al.* 1981
Melanoplinae	
Baeacris punctulatus **(I, E)**, *B. pseudopunctulatus* **(I, E)**, *Dichroplus conspersus* **(E)**, *D. elongatus* **(I,E)***D. maculipennis* **(I, E)**, *D. pratensis* **(I)**, *D. schulzi* **(E)**, *D. vittatus* **(I)**, *Leiotettix pulcher* **(I)**,*Neopedies brunneri* **(I)**, *Ronderosia bergi* **(E)**, *R. forcipata* **(I)**, *Scotussa daguerrei* **(I)**, *S. lemniscata* **(I)**	Lange 2002, Lange 2003a,b; Luna *et al.* 1981 Sokolova & Lange 2002
Oedipodinae	
Trimerotropis pallidipennis **(E)**	Lange, unpublished results
Romaleidae	
Romaleinae	
Diponthus argentinus **(I)**, *Zoniopoda tarsata* **(I)**	Lange 2003a

Asia (Rajasthan and Vidarbha, India; Inner Mongolia, Hainan and Qinghai, China)	
Acrididae	
Cyrtacanthacridinae	
Schistocerca gregaria (**N**)	Srivastava & Bhanotar 1985
Gomphocerinae	
Chorthippus fallax (**I**), *Chorthippus* sp. (**I**),*Myrmeleotettix palpalis* (**I**), *Dasyhippus barbipes* (**I**), *Gomphocerus licenti* (**I**)	Long 1994, Ma *et al.* 2005
Oedipodinae	
Angaracris rhodopa (**I**), *A. barabensis* (**I**), *Bryodema luctuosum luctuosum* (**I**), *Locusta migratoria manilensis* (**E, I**), *Oedaleus asiaticus* (**I**)	Long 1994, Wang & Yu 1994; Yuhua 1997Long 1994, Long *et al.* 2001, Raina *et al.* 1995,Shi & Njaqi 2004, Ma *et al.* 2005
Oxyinae	
Hieroglyphus sp. (**N**), *Oxya chinensis* (**I**)	Raina *et al.* 1987, Liu & Yan 2000, Zang *et al* 2001
Australia (laboratory production)	
Acrididae	
Cyrtacanthacridinae	
Valanga irregularis (**E**)	Moulden 1981
Europe (locust rearing facilities in England)	
Acrididae	
Cyrtacanthacridinae	
Schistocerca gregaria (**S**)	Canning 1953, 1962
Oedipodinae	
Locusta migratoria migratorioides (**S**)	Canning 1953, 1962
Africa (Karoo, South Africa)	
Acrididae	
Acridinae	
Acrida bicolor (**E**)	Henry *et al.* 1985
Calliptaminae	
Acorypha glaucopsis (**E**)	Henry *et al.* 1985
Catantopinae	
Cryptocatantops haemorrhoidalis (**E**), *Diabolocatantops axillaris* (**I, E**)	Henry *et al.* 1985
Eyprepocnemidinae	
Cataloipus cymbiferus (**E**), *Cataloipus fuscocerulipes* (**I, E**), *Heteracris haterti* (**E**)	Henry *et al.* 1985
Gomphocerinae	
Krassauria amabile (**E**), *K. angulifera* (**E**)	Henry *et al.* 1985
Oedipodinae	
Acrotylus longipes (**I, E**), *Aiolopus longicornis* (**E**), *A. simulatrix* (**E**), *Locustana pardalina* (**N**), *Oedaleus nigeriensis* (**I,E**), *O. senegalensis* (**I,E**) *Pseudosphingonotus savigni* (**I,E**), *Sphingonotus canariensis* (**I,E**)	Henry *et al.* 1985, Habtewold *et al.* 1995, Whitlock & Brown 1991
Oxyinae	
Hieroglyphus daganensis (**E**)	Henry *et al.* 1985
Tropidopolinae	
Homoxyrrhepes punctipennis (**E**)	Henry *et al.* 1985
Pyrgomorphidae	
Pyrgomorphinae	
Pyrgomorpha cognata (**I, E**), *Zonocerus variegatus* (**E**)	Henry *et al.* 1985