Nematologica 24 (1978): 286-294. E. J. Brill, Leiden

GEOGRAPHICAL DISTRIBUTION AND HOST PREFERENCES OF *DELADENUS* SPECIES (NEMATODA: NEOTYLENCHIDAE) PARASITIC IN SIRICID WOODWASPS AND ASSOCIATED HYMENOPTEROUS PARASITOIDS

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A comprehensive study, involving over 22,000 dissections, has been made of the distribution of seven species of *Deladenus* parasitising 31 siricid and parasitoid hosts from 31 tree species and 29 countries. Geographical distribution may be wide, one nematode species being found throughout the holarctic and part of Asia, or it may be restricted, another species, for example, being found only in southeast U.S.A. An important factor governing nematode distribution is their degree of specificity to one or other of the two species of symbiotic fungi found associated with siricids.

Following the discovery in Australia of *Sirex noctilio* F., a serious pest of *Pinus radiata* D. Don, CSIRO carried out an extensive worldwide search for parasites and pathogens of this and related woodwasps, as part of a programme aimed at the control of this pest.

Apart from the many insect parasitoids collected (Taylor 1967, 1976; Kirk 1974, 1975a, b), seven new species of *Deladenus* were found (Bedding 1968, 1974). These nematodes have an extraordinary life history involving two life-cycles — one parasitic and usually resulting in sterilisation of siricid females, the other free-living, utilising as food the wood-rotting symbiotic fungus of siricids (Bedding 1967, 1972a, b).

One species of nematode, *Deladenus siricidicola* Bedding, is now being used extensively in the biological control of *S. noctilio* in Australia (Bedding & Akhurst 1974) and New Zealand (Zondag 1975).

Kirk (1974, 1975a, b) and Spradbery & Kirk (in prep.) describe in detail the results of comprehensive searches for and collections of siricid infested material from North America, Europe, Africa and Japan. Their work provides a unique opportunity for the most comprehensive study ever conducted on the geographical distribution and natural host specificity of a genus of insect parasitic nematodes.

MATERIALS AND METHODS

Adult siricids and parasitoids were obtained from infested wood held in cages until emergence occurred. Thousands of 1 m logs from over 100 localities in Europe, North Africa and Turkey were sent by Dr. J. P. Spradbery and Mr. A. A. Kirk (officers of CSIRO) to the CSIRO Sirex Unit at Silwood Park, U.K., where they were held under quarantine conditions in outdoor cages. Collections of wood made by the C.I.B.C. in North America, Pakistan and India and by the abovementioned officers in Japan and U.S.A. were held in the collecting region and live adult insects (siricids with wings and ovipositors amputated) were sent air express to the *Sirex* units at Silwood Park or Tasmania.

Of the many thousands of siricids emerging from collected timber, a total of 22,150 were dissected for nematodes. Because identification of parasitic stages to species level is not feasible, juvenile stages, dissected from the insect, were reared through to adult free-living nematodes. This was achieved by removing juvenile nematodes aseptically from their host and placing them on young axenic cultures of siricid symbiotic fungi (*Amylostereum areolatum* (Fr.) Boidin or *A. chailettii* (Pers. ex Fr.) Boidin, depending upon the siricid species) growing on plates of potato dextrose agar (Bedding & Akhurst 1974). Generally, cultures of nematodes were made from several specimens of each species of siricid from each locality and cross-breeding tests (Akhurst 1975) were used extensively where adult free-living nematodes were not readily classifible after preliminary morphological examination.

In most instances, the fungal preferences of the nematodes were readily determined because rapid growth, development and reproduction occurred on the usual host fungus whereas little if any development occurred on other fungi.

GEOGRAPHICAL DISTRIBUTION

The distributions of the seven species of *Deladenus* are shown in Table I and Figs. 1-3. *Deladenus wilsoni* Bedding is by far the most widely distributed, being found throughout the world wherever rhyssine parasitoids of siricids were collected.

TABLE I

List of countries from which Deladenus *species have been collected*

Country	*D. wilsoni*	*D. siricidicola*	*D. rudyi*	Country	*D. wilsoni*	*D. siricidicola*	*D. rudyi*
Australia	—	+	—	Morocco	+	+	—
Belgium	+	+	+	New Zealand	—	+	—
Bulgaria	+	—	+	Norway	+	+	+
Canada ****	+	—	—	Pakistan *	+	—	—
Corsica	+	+	+	Portugal	—	+	—
Czechoslovakia	+	+	—	Scotland	—	—	+
Eire	+	—	+	Spain	+	+	—
England	+	+	+	Sweden	+	+	—
France	+	+	+	Switzerland	+	+	+
Germany	+	+	—	Turkey	+	+	+
Greece	+	+	+	S.E. U.S.A. **	+	—	—
Hungary	+	+	+	S.W. U.S.A. ***	+	—	—
India	+	—	—	Wales	+	—	—
Italy	+	+	+	Yugoslavia	+	+	+
Japan	+	+	+				

* *D. imperialis* recorded from Pakistan
** *D. proximus* recorded from S.E. U.S.A.
*** *D. nevexii* and *D. canii* recorded from S.W. U.S.A.
**** *D. canii* recorded from Canada

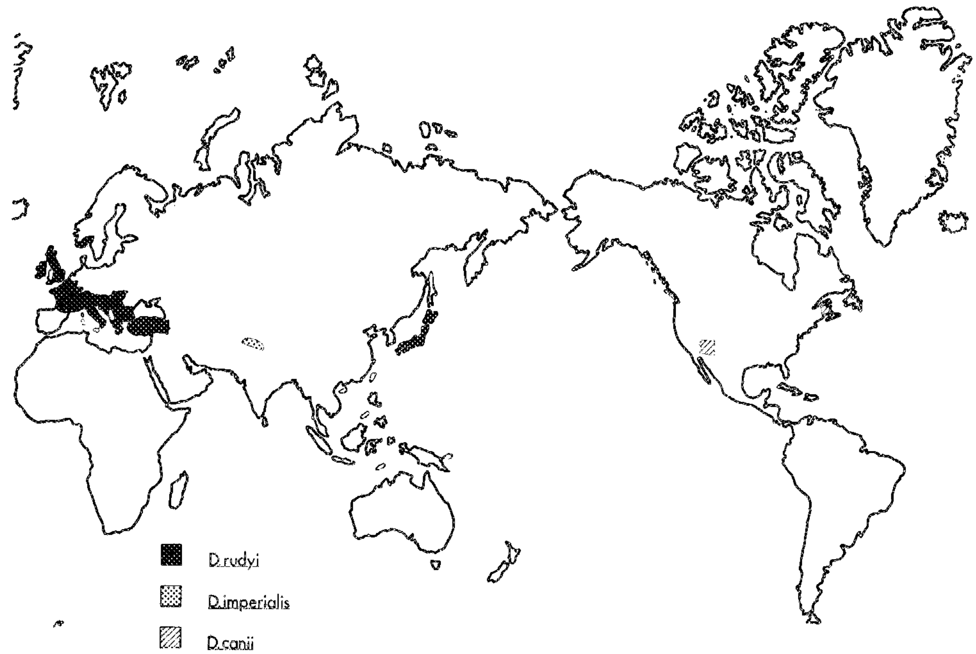

Fig. 1. Recorded distribution of *D. rudyi, D. imperialis* and *D. canii.*

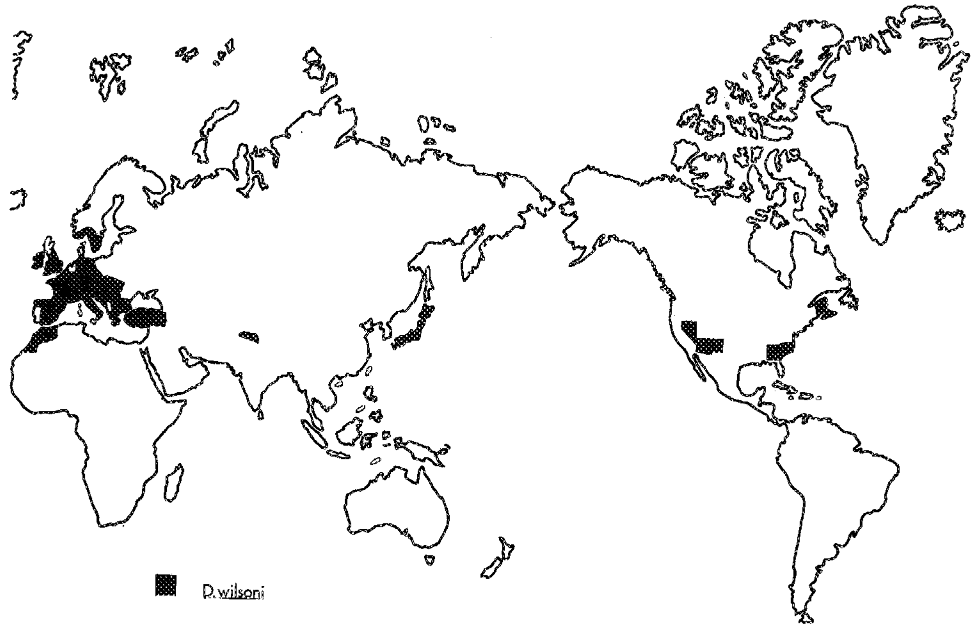

Fig. 2. Recorded distribution of *D. wilsoni.*

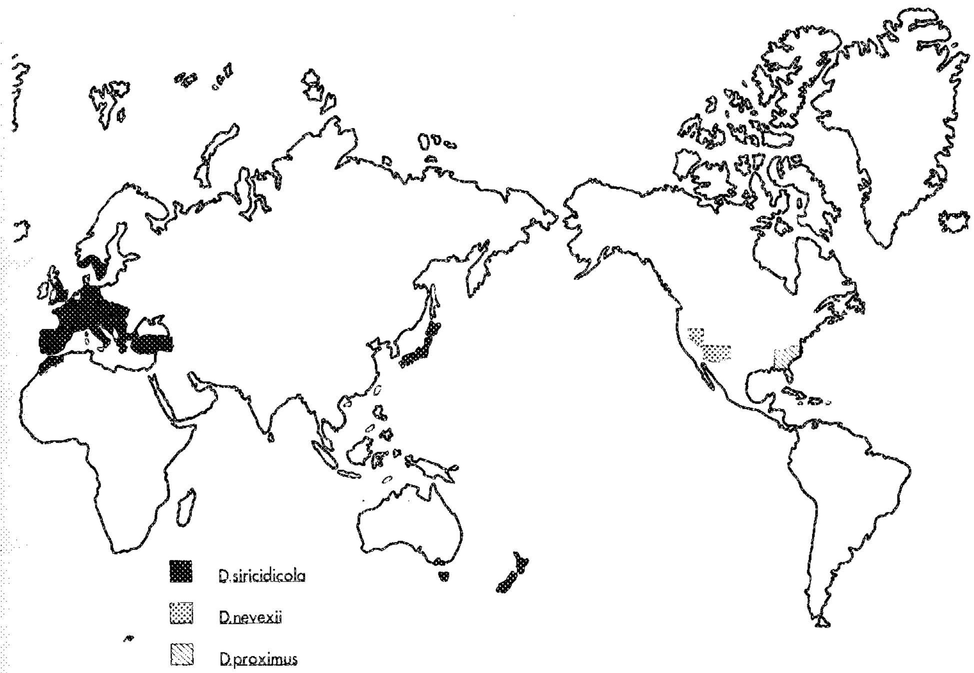

Fig. 3. Recorded distribution of *D. siricidicola, D. nevexii* and *D. proximus.*

Both *D. siricidicola* (20 countries) and *Deladenus rudyi* Bedding (15 countries) are widely distributed in Europe and Japan. *D. siricidicola* was accidentally introduced into New Zealand with *S. noctilio* and has been liberated in Australia from 1970 onwards. *Deladenus proximus* Bedding was found only in southeast U.S.A. and *Deladenus nevexii* Bedding only in southwest U.S.A. while *Deladenus canii* Bedding occurred in southwest U.S.A. and Canada.

INSECT HOST PREFERENCES

D. siricidicola, and *D. rudyi, D. nevexii, Deladenus imperialis* Bedding and *D. wilsoni* readily infect and develop in several species of *Sirex* and the related genus *Urocerus* (Bedding, *in prep.*) although their natural host range is much more restricted. However, extensive laboratory trials have shown that, although infective nematodes of all seven species will enter parasitoid larvae in the laboratory (and also occasionally in the field), with the exception of *D. wilsoni,* these invariably fail to develop. *D. wilsoni* develops in rhyssines but not in *Ibalia* species. The infective stage of this species is in fact rarely formed in the presence of siricid larvae, and so siricid larvae are seldom parasitized in nature. However, one strain of *D. wilsoni* was found producing high levels of parasitisation in a Turkish population of *U. gigas.*

The natural occurrence of different species of *Deladenus* (and a species from a related but undescribed genus) in various siricid and associated hymenopterous

TABLE II

Siricid hosts of Deladenus *spp.*

Insect host	Symbiotic fungus	*D. siricidicola*	*D. wilsoni*	*D. rudyi*	*D. imperialis*	*D. nevexii*	*D. canii*	*D. proximus*	*Undescribed genus*	Geographical location
Sirex noctilio	*Amylostereum areolatum*	+								Europe, Australia, New Zea
S. juvencus	,, ,,	+	+							Europe
S. nitobei	,, ,,	+								Japan
S. cyaneus	,, ,,	+								Europe
S. juvencus	*Amylostereum chailettii*			+						Japan
S. cyaneus	,, ,,		+	+		+	+			Europe, North America
S. longicauda	,, ,,					+				North America
S. imperialis	,, ,,				+					Pakistan
S. californicus	,, ,,								+	North America
S. edwardsii	,, ,,							+		North America
S. nigricornis	,, ,,							+		North America
Urocerus gigas	,, ,,		+	+						Europe, North America
U. augur	,, ,,			+						Europe
U. californicus	,, ,,					+				North America
U. albicornis	,, ,,					+				North America
U. japonicus	,, ,,			+						Japan
U. antennatus	,, ,,			+						Japan
Xeris spectrum	*	+		+		+				Europe, North America, Jap
X. morrisoni	**					+				North America

* No symbiotic fungus but usually associated with other siricid species having *A. areolatum* or *A. chailettii*
** No symbiotic fungus but usually associated with other siricid species having *A. chailettii*

TABLE III

Occurrence of D. wilsoni *in parasitoid species*

Insect host	Geographical source
Rhyssa alaskensis	U.S.A.
R. amoena	Europe
R. crevieri	Canada
R. himalayensis	India
R. hoferi	U.S.A.
R. howdenorum	U.S.A.
R. jozana	Japan
R. lineolata	U.S.A., Canada
R. persuasoria	Canada, Europe, Japan, Morocco, Turkey, U.S.A.
Megarhyssa nortoni quebecensis	Canada
Pseudorhyssa sternata	Europe
P. approximator	Europe

parasitoids is recorded in Tables II and III. Only successful parasitism, as opposed to the presence of undeveloped infective stages in the insect haemocoel, has been listed.

Both *D. wilsoni* and *D. siricidicola* have been found producing juveniles in *Serropalpus barbatus* (Schall.), a beetle commonly associated with siricids.

FUNGAL SPECIFICITY

Although not particularly insect-host specific, *Deladenus* species are highly fungal specific. Bedding (unpubl.) has shown that although limited feeding may occur on several fungi, nematode reproduction is restricted even within the genus *Amylostereum*: only *D. wilsoni* will feed and reproduce significantly on both the symbiotic fungi associated with siricids — *A. chailettii* and *A. areolatum*; *D. siricidicola* is specific to *A. areolatum* and *D. canii, D. rudyi, D. nevexii, D. proximus* and *D. imperialis* are specific to *A. chailettii.* The experimental results are borne out in results from the field, as recorded in Table II.

TREE SPECIFICITY

The relevant data are summarised in Table IV. Because it was expedient in many cases to consign several hymenopterous parasitoids to a container, it has

TABLE IV

Occurrence of Deladenus *spp. in various tree species*

	D. rudyi	*D. wilsoni*	*D. canii*	*D. nevexii*	*D. imperialis*	*D. siricidicola*	*D. proximus*	New genus undescribed
Abies alba	+	+						
balsamea			+					
borisii regis	+							
bornmulleriana	+	+						
cilicia	+							
concolor		*		+				
equitrojani	+							
firma	+	*						
homolepis	+							
pindrow					+			
sachalinensis	+	*						
Cedrus atlantica		+						
Chamaecyparis obtusa	+	*						
Cryptomeria japonica	+	*						
Larix decidua		+				+		
Picea abies	+	+				+		
sitchensis		+				+		
engelmanni		*	+					
Pinus brutia						+		
densiflora		*				+		
echinata		*					+	
elliottii		*					+	
palustris		*					+	
pinaster						+		
pinea						+		
ponderosa		*						+
radiata						+		
sylvestris		+				+		
taeda		*					+	
thunbergii						+		
virginiana		*					+	

* Uncertain, see text.

not always been possible to identify with certainty the tree source of a host containing *D. wilsoni*. Where doubt exists an asterisk (*) is inserted in the table.

DISCUSSION

Much of the information on the geographical distribution of nematodes pertains to important plant parasitic species, and this has almost certainly been very confused by the tremendous interchange of plants throughout the world in historic times. On the other hand, the present geographical distribution of *Deladenus* species parasitising siricids has possibly been little affected by man apart from the introduction of *D. siricidicola* into New Zealand and Australia, and may therefore contribute to an understanding of the geographical distribution of important sections of the Nematoda.

D. wilsoni is remarkable for its occurrence in all parts of the holarctic where rhyssine parasites of *Sirex* were found. Of the other six species, three are confined to the nearctic region and the rest to the palearctic. This separation is mainly a function of geographical isolation, since four of the species concerned have the same species of insect host, *S. cyaneus*, in common to both regions, and three of these utilise the same fungus, *A. chailettii*, (*S. cyaneus* is occasionally associated with *A. areolatum* and can then be parasitised by *D. siricidicola*). The existence of a separate species in Pakistan may reflect speciation in geographical isolation.

The geographical distributions of *D. rudyi* and *D. siricidicola* in Europe, Turkey and Japan appear to be coincident, but the two species are completely separated by their specificity to different fungi. Since *Urocerus* species are only associated with the symbiotic fungus *A. chailettii*, these are never parasitised by *D. siricidicola* and likewise *S. juvencus* and *S. noctilio*, which are only associated with *A. areolatum*, are not parasitised by *D. rudyi*. *S. cyaneus*, which is associated with either symbiotic fungus, and *Xeris spectrum*, which utilises symbiotic fungi from other siricids (Spradbery, pers. comm.), may be parasitised by either *D. rudyi* or *D. siricidicola* in Europe, depending upon which symbiotic fungus is present; this and the ability of five *Deladenus* species tested to parasitise various siricid species in the laboratory, indicates the species of siricid host is of little direct importance for these nematodes. There is however the possibility that *D. canii*, which has only been found in *S. cyaneus*, even when *Xeris* species are present in the same tree, is more insect-host specific.

In contrast to the wide geographical distribution of *D. rudyi* and *D. siricidicola* and the very wide distribution of *D. wilsoni*, the narrow geographical ranges of *D. nevexii, D. proximus* and *D. imperialis* are perhaps surprising. Insect host specificity, climatic factors or even host tree specificity may well play an important part in these geographical limitations.

Although each nematode species (with the exception of *D. wilsoni*) is, in general, found in a separate group of tree species this is probably not the result of any direct tree/nematode interaction. Obviously geographical factors may determine which tree species and which nematode species are present in an area.

Palearctic nematodes are thus found in different tree species from nearctic nematodes (except in the case of exotic introductions such as *P. radiata* which is host to *D. siricidicola*) and the Asiatic *D. imperialis*. It is likely that the restriction of *D. proximus* and its five species of host trees to southeastern U.S.A. is a function of climate and isolation. However, no such geographical or climatic factors can explain the strikingly distinct range of host tree species of *D. siricidicola* and *D. rudyi*, which have been recorded from ten and eleven tree species respectively with only one, *Picea abies*, in common, since both nematode species occupy the same geographical and climatic regions. This is almost certainly the result of the species of tree determining the insect species present (Kirk 1974, 1975; Kirk & Spradbery, in prep.) which in turn determines which fungus occurs. (The siricid species infesting a particular tree species may of course also be related evolutionarily to the species of symbiotic fungus concerned). The wide geographical distribution of *D. wilsoni* and its presence in so many different tree species (if it is confirmed) may reflect its ability to utilise both species of symbiotic fungi.

We suggest that the strong specific dependence of the nematodes on either or both of the symbiotic fungi associated with siricids is part of a mechanism that has evolved to maintain the link with the host insects. Whereas many other mycetophagous nematodes feed readily on a variety of fungal species, the *Deladenus* species parasitising siricids and rhyssine parasitoids are highly specific. Though dead trees supply an abundant substrate for various fungi which are a potential food source for mycetophagous nematodes, to be successful the nematode population requires mechanisms for dispersing to fresh trees. For the *Deladenus* species this problem is overcome by their being transported by an insect to a fresh fungal culture in a new tree; moreover, they can also increase many thousandfold in numbers within the body of the transporting agent that is also usually the initiator of a new fungal infection.

The authors thank Dr. J. P. Spradbery, Mr. A. A. Kirk, Dr. F. Wilson and Mr. T. Woolcock for providing material and data; Mr. V. P. Rao, Mr. M. A. Ghani and Mr. D. C. Lloyd of the C.I.B.C. for sending material from India, Pakistan and Canada respectively; the many assistants who over the last decade helped with dissections and rearing of nematodes for identification.

ZUSAMMENFASSUNG

Die Parasitierung von siriciden Holzwespen und assoziierten Hymenopteren durch Deladenus-*Arten* (*Nematoda: Neotylenchidae*) *I. Geographische Verbreitung und Wirtsbevorzugungen*

In einer umfassenden Untersuchung über die Verbreitung von sieben *Deladenus*-Arten, die 31 siricide parasitäre Hymenopteren aus 31 Baumarten und 29 Ländern befallen, wurden 22000 Insekten seziert. Die geographische Verbreitung kann sehr weit sein, wobei eine Nematodenart in der gesamten Holarktis und Teilen von Asien auftritt. Sie kann aber auch sehr begrenzt sein, wenn eine Art z.B. nur im Südosten der U.S.A. gefunden wird. Ein wichtiger Steuerungsfaktor für die Verbreitung der Nematoden ist der Grad der Spezifizität ihrer Beziehungen zu der einen oder der anderen der beiden Pilzarten, die man als Symbionten mit Siriciden assoziiert findet.

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Accepted for publication: February 21, 1978.