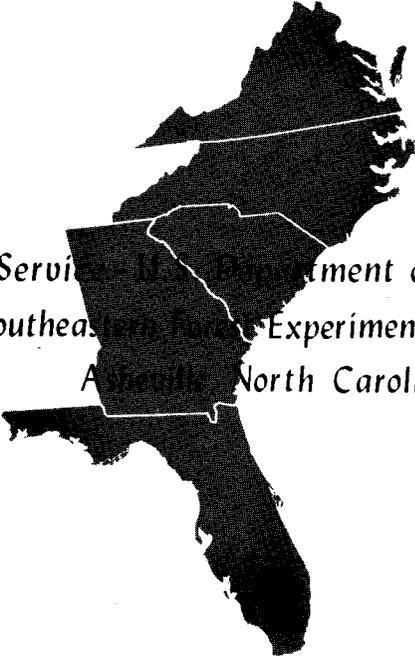


Current Knowledge of Monodontomerus dentipes (Dalman),
A Cocoon Parasite of Pine Sawflies

by

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Monodontomerus dentipes (Dalman), a European parasite of cocoons of pine sawflies, has been a key factor in the control of the introduced pine sawfly, Diprion similis (Hartig), in the United States and Canada. Several other Diprion and Neodiprion spp. have also been reported as hosts, and the sawflies which occur in the southeastern United States are possible targets for control by M. dentipes. During a recent study of the development and emergence of the parasite, a comprehensive survey of the literature on M. dentipes was made. The purpose of this review is to aid others in studying the insect so that its usefulness as an agent in the control of Neodiprion and Diprion spp. can be enhanced.

The original description of M. dentipes is generally credited to Dalman (1820) who described both sexes of the adult. A number of sources (Hartley 1923; Faure 1925; Sitowski 1929; de Fluiter 1933; Mokrezecki 1933; Scheidter 1934; Gahan 1941; Bucher 1948) incorrectly listed the description by Boheman (1833), based on a single female as having priority. Dalman named the parasite Torymis dentipedis and placed it in the family Pteromalidae, tribe Pteromalini. The species was transferred to Monodontomerus (Walker 1847), which at the time was in the family Callimomidae (Westwood 1833). The name Callimomidae has been permanently suppressed (Peck 1963). Monodontomerus has also been listed in the family Chalcididae (Howard and Ashmead 1898) but is presently in the family Torymidae (Gahan 1941). The species M. dentipes is synonymous with Torymus vicicellae Förster (Walker 1847) and M. viridaeneus Provancher (Burks 1963).

Several keys are available for the diagnosis of M. dentipes. Adults were separated from those of other Monodontomerus spp. by Gahan (1941) and Steffan (1952). A comprehensive list of references by species of Monodontomerus was provided by Burks (1963). Since there is little overlapping of the hosts of M. dentipes and other Monodontomerus spp., identification is simplified through the identification of the host, especially if the host is a diprionid sawfly (table 1). In North America, M. japonicus Ashmead and M. dentipes are the only Monodontomerus spp. which attack sawflies. The only record of M. japonicus on a North American sawfly is in Canada, where it was released against D. hercyniae (Hartig) (Finlayson and Finlayson 1958b). In the absence of further records of M. japonicus on D. hercyniae, it probably has not become established. M. dentipes was separated from other parasites of pine sawflies by Morris et al. (1937), Finlayson (1960a, 1960b, 1962, and 1963), Mertins (1967), and Mertins and Coppel (1971).

¹Hymenoptera: Torymidae.

Table 1.--Host families of Monodontomerus dentipes (Dalman) and some other Monodontomerus spp. with those parasites having host families in common with M. dentipes indicated by horizontal lines

Host	Parasite									
	<u>M. dentipes</u> (Dalman)	<u>M. aereus</u> Walker	<u>M. dianthidii</u> Gahan	<u>M. emarginatus</u> Gahan	<u>M. indiscretus</u> Gahan	<u>M. japonicus</u> Ashmead	<u>M. mandibularis</u> Gahan	<u>M. minor</u> (Ratzeburg)	<u>M. monteivagus</u> Ashmead	<u>M. obscurus</u> Westwood
HYMENOPTERA										
Apidae										X
Braconidae	X	X								
Chalcididae		X								
Cynipidae	X									
Diprionidae	X	-----X								
Ichneumonidae	X	X	-----					X		
Megachilidae			X	X			X			X
Sphecidae									X	
Tenthredinidae					X					
Vespidae									X	
LEPIDOPTERA										
Arctiidae		X								
Lasiocampidae		X						X		
Liparidae	X									
Lymantriidae	X	X								
Olethreutidae	X	-----							X	
Saturniidae								X		
Tortricidae	X	X	-----					X	X	
Zygaenidae	X									
DIPTERA										
Tachinidae	X	X								

Description of Adults

The most complete treatment of the morphology of the adults of M. dentipes is a detailed study by Bucher (1948). He included numerous drawings with descriptions of the internal and external anatomy of both sexes.

Others have described the external anatomy of the adults (Morris et al. 1937, Gahan 1941, and Mertins and Coppel 1971), and Mertins (1967) includes an illustration of both sexes. The remarks that follow are mainly from Bucher (1948).

M. dentipes is larger than most chalcids. Its size depends largely on the size of the host and on the number of individuals that develop in one cocoon. Females are about 4.1 mm from the front of the head to the tip of the extended ovipositor, which measures 0.7 mm. The males average 2.7 mm in length and can be distinguished from the females by differences in size, genitalia, and terminal abdominal segments. Associated structures, such as sensory plates, components of female genital armature, which function in investigating a host cocoon prior to oviposition, are useful secondary characteristics.

The parasite is dark green with a metallic sheen. The tibiae and tarsi are amber and eyes, red. The basal segment of the antenna is green and flagellum, black. The flagellum occasionally exhibits a metallic green sheen. The cuticle of the adults of M. dentipes is smooth and shiny with fine setae concentrated in the corners of irregular geometric patterns formed by tiny reticulations of the cuticle. The setae and reticulations may be reduced or absent at points of articulation of segments.

Description of Immature Stages

No comprehensive description exists for all the immature stages of M. dentipes. Mertins (1967) and Mertins and Coppel (1971) described the egg and late instar, but not the other instars or the pupa. Morris et al. (1937) described the egg, the final instar, and the pupa, and illustrated these stages. They did not describe the early instars.

The egg is approximately elliptical with tapered ends, the adhesive end being more acutely tapered than the end bearing the micropyle (Morris et al. 1937). The shape of the egg has been likened to that of a banana (Mertins 1967; Mertins and Coppel 1971). It is about 0.7 by 0.2 mm, glossy white, and covered with symmetrical rows of minute spicules (Morris et al. 1937).

The last instar is white and somewhat crescent shaped (Morris et al. 1937). It can be distinguished from the larvae of all other parasites of sawfly cocoons by its smooth, densely setiferous integument.

Cephalic structures and spiracles of the last instar of sawfly parasites are diagnostic characters (Finlayson 1960a, 1960b, 1962; Mertins 1967; Mertins and Coppel 1971). Morris et al. (1937) have illustrated the cephalic structure of the last instar of M. dentipes. The spiracles of the last instar of M. dentipes were described and illustrated by Mertins (1967).

The pupa of M. dentipes was described by Morris et al. (1937) as being initially pale yellow, changing later to glossy black. The ovipositor, adhering closely to the dorsal surface of the pupa, enables easy differentiation of the females of M. dentipes from other cocoon parasites. These authors did not distinguish the male of M. dentipes from other parasites of sawfly cocoons. No cocoon is formed by M. dentipes (Mertins and Coppel 1971).

GEOGRAPHIC DISTRIBUTION AND ITS RELATION TO HOSTS

Generally, the distribution of M. dentipes depends on the presence of sawflies of the family Diprionidae, although other groups are represented as hosts (table 2). Wherever M. dentipes occurs, the hosts are most commonly Diprion spp. and Neodiprion spp. Other Hymenoptera, Diptera, and Lepidoptera are also parasitized, but far less frequently.

Table 2.--Recorded hosts of Monodontomerus dentipes (Dalman)

Hosts	Locality	Source
DIPTERA		
Tachinidae		
<u>Arrhinomyia tragica</u> L. ¹	France	Rosenburg 1934
HYMENOPTERA		
Braconidae		
<u>Apanteles</u> sp.	Poland	Thompson 1944
<u>A. glomeratus</u> L. ²	France	Faure 1925, 1926; Thompson 1944
	Italy	Thompson 1944
<u>Meteorus versicolor</u> Wesmæl ³	Holland	de Fluiter 1933; Thompson 1944
Cynipidae	Sweden	Dalman 1820; Boheman 1833; Howard and Ashmead 1898
Diprionidae		
<u>Diprion</u> spp.	Poland	Mokrezecki 1933
	USA: New York	Viereck 1928; Gahan et al. 1928
<u>D. frutetorum</u> (Fabricius)	Canada: Ontario	Raizenne 1957; McGugan and Coppel 1962; Griffiths et al. 1971
	Czechoslovakia	Finlayson and Finlayson 1958a
<u>D. hercyniae</u> (Hartig) ⁴	Canada: New Brunswick	Baird 1938
	Nova Scotia	Baird 1938
	Ontario	Finlayson and Reeks 1936; Baird 1937, 1939; Peck 1951; Finlayson 1960b; McGugan and Coppel 1962
	Quebec	Finlayson and Reeks 1936; Baird 1938; Briand 1949; McGugan and Coppel 1962
	China	Peck 1963
	Germany	Peck 1963
	Holland	Peck 1963
	Poland	Peck 1963
	USA: Maine	Procter 1938
	Vermont	Dowden 1938
<u>D. pallidum</u> (Klug)	Czechoslovakia	Morris et al. 1937

continued

See footnotes at end of table.

Table 2.--Recorded hosts of Monodontomerus dentipes (Dalman) (continued)

Hosts	Locality	Source
<u>Diprion pini</u> (L.)	Germany	Scheidter 1934; Thompson 1944
	Holland	Ritzema Bos 1919; Thompson 1944
	Poland	Sitowski 1929; Thompson 1944
	Sweden	Howard and Ashmead 1898
<u>D. polytomum</u> (Hartig)	Czechoslovakia	Kolubajiv 1934; Morris et al. 1937; Thompson 1944; Finlayson and Finlayson 1958b
	Germany	Morris et al. 1937
<u>D. similis</u> (Hartig) ⁶	Europe (general)	Gahan 1941; Dowden 1949
	Canada: Ontario	Baird 1939; Gahan 1941; Bucher 1948; Dowden 1949; Raizenne 1957; Sippell et al. 1960; Finlayson 1962; McGugan and Coppel 1962
	Quebec	Baird 1938; Finlayson 1962; McGugan and Coppel 1962
	China	Peck 1963
	Germany	Thompson 1944
	Holland	Hartley 1923; Thompson 1944
	Hungary	Gahan 1941; Peck 1963
	Poland	Sitowski 1929; Finlayson and Finlayson 1958a
	Sweden	Howard and Ashmead 1898
	USA: Connecticut	Britton and Zappe 1918; Gahan 1941; Dowden 1949
	Maine	Gahan 1941; Procter 1946
	Michigan	Gahan 1941
	New Jersey	Weiss 1917a, 1917b, 1918; Hartley 1923; Gahan 1941; Dowden 1949, 1962
	New York	Gahan 1941
	Ohio	Gahan 1941
	Pennsylvania	Hartley 1923; Gahan 1941; Dowden 1949, 1962
	Wisconsin	Shenefelt and Benjamin 1955; Dowden 1962; Mertins 1967; Mertins and Coppel 1971
<u>Neodiprion abietis</u> (Harris)	Europe (general)	Baird 1944
	Canada: Ontario	McGugan and Coppel 1962
	New Brunswick	Baird 1944; McGugan and Coppel 1962
<u>N. excitans</u> Rohwer ⁶	USA: Florida	Wilkinson, personal communication
<u>N. lecontei</u> (Fitch) ⁶	USA: Florida	Wilkinson 1969
<u>N. pinetum</u> (Norton)	Canada: Ontario	Raizenne 1957; McGugan and Coppel 1962
	Manitoba	Baird 1941; McGugan and Coppel 1962

continued

See footnotes at end of table.

Table 2.--Recorded hosts of Monodontomerus dentipes (Dalman) (continued)

Hosts	Locality	Source
<u>N. pratti banksianae</u> Rohwer	Canada: Ontario	Baird 1941
<u>N. p. pratti</u> Rohwer ⁶	USA: Virginia	Morris 1971
<u>N. swainei</u> Middleton	USA: Wisconsin	Becker and Benjamin 1964
Eulophidae		
<u>Dahlbominus fuscipennis</u> Zetterstedt ⁵	USA: Wisconsin	Mertins 1967; Mertins and Coppel 1971
<u>Tetrastichus xanthopus</u> (Ratzeburg) ⁷	Austria	Seitner 1927
Ichneumonidae		
<u>Exenterus amictorius</u> (Panzer) ⁵	USA: Wisconsin	Mertins 1967; Mertins and Coppel 1971
<u>Itopectis conquisitor</u> Say ⁵	USA: Wisconsin	Mertins 1967; Mertins and Coppel 1971
<u>Pimpla</u> sp. ⁷	Austria	Seitner 1927
<u>Therion giganteum</u> (Gravenhorst) ⁷	Austria	Seitner 1927
<u>Theronia atalanta</u> (Poda) ⁷	Austria	Seitner 1927
Vespidae		
<u>Ancistrocerus tigris tigris</u> (Saussure) ⁶	USA: Wisconsin	Coppel 1960
LEPIDOPTERA		
Liparidae		
<u>Euproctis chrysorrhoea</u> (L.) ⁹	Sweden	Howard and Ashmead 1898
Lymantriidae		
<u>Dendrolimus pini</u> (L.) ⁷	Austria	Seitner 1916, 1927; Hartley 1923
	Germany	Thompson 1944
<u>Nygmia phaeorrhoea</u> (Donovan) ¹⁰	USA: Idaho	Peck 1963
<u>Orgyia pseudotsugata</u> (McDonough) ^{10 11}	USA: Idaho	Bedard 1938
<u>Stilpnotia salicis</u> L. ³	Holland	de Fluiter 1933
<u>Porthetria dispar</u> (L.)	New England	Burgess 1915
Pieridae		
<u>Pieris brassicae</u> L. ³	France	Faure 1926

continued

See footnotes at end of table.

Table 2.--Recorded hosts of *Monodontomerus dentipes* (Dalman) (continued)

Hosts	Locality	Source
Tortricidae		
<i>Cydia pomonella</i> L. ¹	France	Rosenburg 1934
<i>Tortrix viridana</i> (Girard)	Sweden	Howard and Ashmead 1898
Zygaenidae		
<i>Zygaena filipendulae</i> L.	Sweden	Howard and Ashmead 1898
<i>Z. occitanica</i> de Villers	France	Hartley 1923

¹ *M. dentipes* is hyperparasitic on *Cydia pomonella* L. through *A. tragica*.

² *M. dentipes* is hyperparasitic on *Pieris brassicae* L. through *A. glomeratus*.

³ *M. dentipes* is hyperparasitic on *Stilpnotia salicis* L. through *M. versicolor* (de Fluter 1933).

⁴ Early North American references to *D. hercyniae* mistakenly identified it as *D. polytomum* (McGugan and Coppel 1962).

⁵ *M. dentipes* is both a primary parasite and a hyperparasite of *D. similis*. *D. similis* is a secondary host through *D. fuscipennis*, *E. amictorius*, and *I. conquisitor*.

⁶ *M. dentipes* was released against these hosts in a biological control effort of the USDA Forest Service. No recoveries have been made to date.

⁷ *M. dentipes* is hyperparasitic on *Dendrolimus pini* through these species (Seitner 1927).

⁸ *M. dentipes* was reported as a primary parasite of *A. tigris tigris* inhabiting empty cocoons of *D. similis*.

⁹ As *Porthesia chrysoorrhoea* L.

¹⁰ Peck (1963) believes these hosts indicate *M. aereus*, not *M. dentipes*.

¹¹ As *Hemerocampa pseudotsugata*.

M. dentipes is native to the Palearctic region of the world and distributed exclusively in the Holarctic region (table 3). Although *M. dentipes* is found throughout the Palearctic region, only a single locality record exists for China (Gahan 1941). *M. dentipes* has been reported throughout northern and central Europe. Records from France and Austria list nonsawfly hosts exclusively. Peck (1963) believed these hosts suggested the parasite was identified incorrectly and was *M. aereus* Walker, not *M. dentipes*. In Europe, *Diprion pini* (L.) and *D. polytomum* (Hartig) are the most frequently parasitized hosts.

In the Nearctic region, *M. dentipes* occurs in the United States and Canada, primarily east of the Great Plains. *M. dentipes* was accidentally introduced into the United States as a parasite of the sawfly, *D. similis*, which subsequently became the most frequently attacked host in this country. *M. dentipes* was first reported in Connecticut around 1910 (Britton 1915, Britton and Zappe 1918) and shortly after in New Jersey (Weiss 1917a, 1917b, 1918; Hartley 1923; Gahan 1941; Dowden 1949). By 1922, *D. similis* was effectively parasitized by *M. dentipes* in a minor infestation near Philadelphia, Pennsylvania (Hartley 1923), which marked the southernmost extension of the parasite's distribution at that time. In later years, the parasite was reported on the same host in Maine, Michigan, Ohio, and Wisconsin, and on other *Diprion* spp. in Maine, Vermont, and New York (table 4). West of Wisconsin, a single record exists of *M. dentipes*, and two lepidopterous hosts are listed (Bedard 1938).

Table 3.--Palearctic distribution of Monodontomerus dentipes (Dalman)

Continent and country	Hosts	Source
ASIA		
China	<u>Diprion hercyniae</u> (Hartig)	Peck 1963
	<u>D. similis</u> (Hartig)	Peck 1963
EUROPE		
(general)	<u>Diprion pini</u> (L.)	Steffan 1952
	<u>D. similis</u>	Gahan 1941; Dowden 1949
	<u>D. sertifer</u> Geoffroy	Steffan 1952
Austria	<u>Dendrolimus pini</u> L. ¹	Seitner 1916, 1927
	<u>Tetrastichus xanthopus</u> (Ratzeburg) ¹	Seitner 1927
	<u>Pimpla</u> sp. ¹	Seitner 1927
	<u>Therion giganteum</u> (Gravenhorst) ¹	Seitner 1927
	<u>Theronia atalanta</u> (Poda) ¹	Seitner 1927
	<u>Rhogas</u> sp. ¹	Seitner 1927
Czechoslovakia	<u>D. frutetorum</u> (F.)	Finlayson and Finlayson 1958b
	<u>D. palladium</u> Klug	Morris et al. 1937
	<u>D. polytomum</u> (Hartig)	Kolubajiv 1934; Morris et al. 1937; Thompson 1944; Finlayson and Finlayson 1958a
France	<u>Apanteles glomeratus</u> L. ²	Faure 1925, 1926; Thompson 1944
	<u>Arrhinomyia tragica</u> L. ³	Rosenburg 1934
	<u>Cydia pomonella</u> L. ³	Rosenburg 1934
	<u>Pieris brassicae</u> L. ³	Faure 1925
	<u>Zygaena occitanica</u> de Villers	Hartley 1923
Germany	<u>D. hercyniae</u>	Peck 1963
	<u>Diprion pini</u>	Scheidter 1934; Thompson 1944
	<u>D. polytomum</u>	Morris et al. 1937
Holland	<u>D. hercyniae</u>	Peck 1963
	<u>D. similis</u>	Hartley 1923; Thompson 1944
	<u>Diprion pini</u>	Ritzema Bos 1919; Thompson 1944
	<u>Meteorus versicolor</u> Wesmael ⁴	de Fluiter 1933; Thompson 1944
	<u>Stilpnobia salicis</u> L.	de Fluiter 1933

continued

See footnotes at end of table.

Table 3.--Palearctic distribution of Monodontomerus dentipes (Dalman) (continued)

Continent and country	Hosts	Source
Hungary	<u>D. similis</u>	Gahan 1941; Peck 1963
Italy	<u>A. glomeratus</u>	Thompson 1944
Poland	<u>Apanteles</u> spp.	Thompson 1944
	<u>A. glomeratus</u> ²	Mokrezecki 1933
	<u>Diprion</u> spp.	Mokrezecki 1933
	<u>D. hercyniae</u>	Peck 1963
	<u>Diprion pini</u>	Sitowski 1929; Thompson 1944
	<u>D. similis</u>	Sitowski 1929; Finlayson and Finlayson 1958b
	<u>P. brassicae</u>	Mokrezecki 1933
Sweden	Cynipid wasps	Dalman 1820; Boheman 1833; Howard and Ashmead 1898
	<u>Diprion pini</u> ⁵	Howard and Ashmead 1898
	<u>D. similis</u> ⁶	Howard and Ashmead 1898
	<u>Euproctis chrysorrhoea</u> L. ⁷	Howard and Ashmead 1898
	<u>Tortrix viridana</u> (Giraud)	Howard and Ashmead 1898
	<u>Zygaena filipendulae</u> L.	Howard and Ashmead 1898

¹ M. dentipes is a hyperparasite of Dendrolimus pini L. through these species (Seitner 1927).

² M. dentipes is a hyperparasite of P. brassicae through A. glomeratus.

³ M. dentipes is a hyperparasite of C. pomonella through A. tragica.

⁴ M. dentipes is a hyperparasite of S. salicis through M. versicolor (de Fluiter 1933).

⁵ As Lophyrus pini L.

⁶ As Lophyrus similis Hartig.

⁷ As Porthesia chrysorrhoea L.

Table 4.--Nearctic distribution of *Monodontomerus dentipes* (Dalman)

Locality	Hosts	Source
NORTH AMERICA		
(general)	<i>Diprion</i> spp.	Peck 1951
	<i>D. hercyniae</i> (Hartig)	Peck 1951
	<i>D. similis</i> (Hartig)	Peck 1951
	Diptera	Peck 1951
	<i>Orgyia pseudotsugata</i> (McDonnough) ¹	Peck 1951
	<i>Petalodes unicolor</i> (Wesmael)	Peck 1951
	<i>Porthetria dispar</i> L.	Burgess 1915
Canada		
(general)	<i>D. similis</i>	McGugan and Coppel 1962
	<i>Neodiprion sertifer</i> (Geoffroy)	Finlayson 1960a
	<i>N. virginianus</i> complex	McGugan and Coppel 1962
Manitoba	<i>N. pratti banksianae</i> Rohwer	Baird 1941; McGugan and Coppel 1962
New Brunswick	<i>D. hercyniae</i> ^a	Baird 1938, 1939
	<i>N. abietis</i> (Harris)	Baird 1944; McGugan and Coppel 1962
Nova Scotia	<i>D. hercyniae</i>	Baird 1938
Ontario	<i>D. frutetorum</i> (F.)	Raizenne 1957; McGugan and Coppel 1962; Griffiths et al. 1971
	<i>D. hercyniae</i>	Finlayson and Reeks 1936; Baird 1937, 1939; Peck 1951; Finlayson 1960b; McGugan and Coppel 1962
	<i>D. similis</i>	Baird 1939; Gahan 1941; Bucher 1948; Dowden 1949; Raizenne 1957; Sippell et al. 1960; Finlayson 1962; McGugan and Coppel 1962
	<i>N. abietis</i>	McGugan and Coppel 1962
	<i>N. pinetum</i> (Norton)	Raizenne 1957; McGugan and Coppel 1962
	<i>N. pratti banksianae</i>	Baird 1941
	<i>N. sertifer</i>	Finlayson 1960a; McGugan and Coppel 1962; Lyons 1964; Griffiths et al. 1971
	<i>Rhyacionia buoliana</i> (Schiffermüller)	Watson and Arthur 1959; McGugan and Coppel 1962
Quebec	<i>D. hercyniae</i> ^a	Finlayson and Reeks 1936; Baird 1938, 1939; Briand 1949; McGugan and Coppel 1962
	<i>D. similis</i>	Baird 1938, 1939; Finlayson 1962; McGugan and Coppel 1962

continued

See footnotes at end of table.

Table 4.--Nearctic distribution of Monodontomerus dentipes (Dalman) (continued)

Locality	Hosts	Source
U.S.A.		
Connecticut	<u>D. similis</u>	Britton and Zappe 1918; Britton 1920; Gahan 1941; Dowden 1949
Florida	<u>N. lecontei</u> (Fitch) ^a	Wilkinson 1969
Idaho	<u>O. pseudotsuga</u> ¹	Bedard 1938
	<u>Nygmia phaeorrhoea</u> (Donovan)	Bedard 1938
Maine	<u>D. hercyniae</u>	Procter 1938
	<u>D. similis</u>	Gahan 1941; Procter 1946
Michigan	<u>D. similis</u>	Gahan 1941
New Jersey	<u>D. similis</u>	Weiss 1917a, 1917b, 1918; Hartley 1923; Gahan 1941; Dowden 1949, 1962
New York	<u>Diprion</u> spp.	Viereck 1928; Gahan et al. 1928
	<u>D. similis</u>	Gahan 1941
Ohio	<u>D. similis</u>	Gahan 1941
Pennsylvania	<u>D. similis</u>	Hartley 1923; Gahan 1941; Dowden 1949, 1962
Vermont	<u>D. hercyniae</u>	Dowden 1962
Virginia	<u>N. pratti pratti</u> Rohwer ^a	Morris 1971
Wisconsin	<u>Ancistrocerus tigris tigris</u> (Saussure) ⁴	Coppel 1960
	<u>D. similis</u>	Shenefelt and Benjamin 1955; Dowden 1962; Mertins 1967; Mertins and Coppel 1971
	<u>N. swaini</u> Middleton	Becker and Benjamin 1964

¹As Hemerocampa pseudotsugata.

²Early North American references to D. hercyniae mistakenly identified it as D. polytomum (McGugan and Coppel 1962).

³M. dentipes was released against these hosts in 1969-1970 through the biological control program of the USDA Forest Service. It has not been recovered to date.

⁴M. dentipes was listed as a primary parasite of A. tigris tigris, common inhabitants of cocoons of D. similis.

In Canada, M. dentipes has been released against pine sawflies in biological control programs in Ontario, Quebec, Manitoba, Nova Scotia, New Brunswick, and Prince Edward Island (table 4). In Ontario, D. similis is common and more frequently attacked than any other potential host. However, in Quebec and the Maritime Provinces, D. hercyniae is the most abundant sawfly and the most heavily parasitized.

Generally, in the Nearctic region, M. dentipes is concentrated in coastal regions. The distribution of the parasite extends along the Atlantic coast from Pennsylvania to Quebec, and westward along the Great Lakes to Wisconsin and Manitoba. Recent releases against sawflies in the southeastern United States (Wilkinson 1969; Morris 1971) have provided an opportunity for the range of M. dentipes to be extended southward as far as Florida, however, establishment has not yet been determined.

HOSTS

Included among the known hosts of M. dentipes are six families of Hymenoptera, one family of Diptera, and five families of Lepidoptera (table 2). Among the various families that have been reported are: Diprionidae, Braconidae, Ichneumonidae, Eulophidae, Vespidae, and Cynipidae in the order Hymenoptera; Tachinidae in the order Diptera; and Liparidae, Lymantriidae, Zygaenidae, Tortricidae, and Pieridae in the order Lepidoptera.

Hymenoptera of the family Diprionidae are the predominant hosts throughout the distribution of M. dentipes. Of this family, six species of Diprion and five species of Neodiprion, with two additional Neodiprion spp. as potential hosts, are parasitized, the former genus being by far the more common host. In the Palearctic region, M. dentipes attacks N. sertifer (Geoffroy) and six species of Diprion; only the genus Diprion is recorded as a host in Asia. D. hercyniae and D. similis have been reported as hosts of M. dentipes in China (Peck 1963). The principal hosts of M. dentipes in Europe, where the parasite is more common, appear to be Diprion pini and D. polytomum (table 3). D. similis and D. hercyniae have also been reported, but less frequently. D. frutetorum (F.) and D. pallidum Klug have been listed as hosts by Finlayson and Finlayson (1958a) and Morris et al. (1937), respectively.

In the Nearctic region, the hosts of M. dentipes include three Diprion species and five Neodiprion species (table 4). Here the host complex of M. dentipes differs from that of Europe in that D. polytomum, Diprion pini, and D. pallidum are absent.² N. pinetum (Norton), N. pratti pratti Rohwer, N. p. banksianae Rohwer, and N. swaini Middleton, in addition to the single Neodiprion sp. attacked in Europe, N. sertifer, are attacked. N. excitans Rohwer and N. lecontei (Fitch) are potential hosts in the United States. In North America, as in the Palearctic region, Diprion spp. are the principal hosts. D. similis and D. hercyniae are the most frequently parasitized hosts in Canada. D. similis predominates in southern Ontario and D. hercyniae, in Quebec and the Maritime Provinces. Occasionally, M. dentipes parasitizes D. frutetorum, N. pinetum, N. sertifer, and the N. virginianus complex in Canada (table 4). In contrast, D. similis is almost the exclusive host of M. dentipes in the United States, although the parasite has been reported infrequently on D. hercyniae and N. sertifer as well (table 4).

Throughout Europe and the Nearctic region, M. dentipes has been reported on Lepidoptera and Hymenoptera other than Diprionidae (tables 3 and 4). Collectively, records of nonsawfly hosts are insignificant when compared numerically to records of sawfly hosts. However, they are an important factor in the host relationships of M. dentipes. M. dentipes has been recorded on three species of Braconidae and an unspecified species of Ichneumonidae. Similarly, only a few cases of M. dentipes parasitizing cynipid wasps have been reported from Europe. In addition, there are two North American records of the parasite on Tachinidae (Burgess 1915; Peck 1951). Many of the records of M. dentipes on nonsawfly Hymenoptera and Tachinidae refer to M. dentipes as a hyperparasite of a pine sawfly or lepidopterous host. The only records of M. dentipes parasitizing Lepidoptera in North America are from Idaho, where it was reported by Bedard (1938) from Nygmia phaeorrhoea (Donovan) and Orgyia pseudotsugata (McDonnough). Dendrolimus pini L. is the only lepidopterous host from Europe which has been parasitized widely by M. dentipes.

²Prior to 1941, when D. hercyniae was correctly identified by Smith (1941) as the species involved in Canadian infestations, populations of this sawfly were believed to be conspecific with those of the European species D. polytomum. As such, several early sources incorrectly refer to D. hercyniae as D. polytomum (McGugan and Coppel 1962).

Life History and Host Relationships

Morris et al. (1937) and Mertins (1967) are the only authors who have touched on a variety of topics related to the life cycle of the parasite, M. dentipes. In their studies, they included mating and oviposition, hatching of the eggs, maturation of larvae, pupation, emergence from the host cocoon, longevity of adults, and host relationships of M. dentipes. Mertins and Coppel (1971) revised the material pertaining to host relationships that Mertins (1967) had provided. They omitted much of the detailed information about M. dentipes that Mertins (1967) had included.

The stages in the life cycle of M. dentipes were described initially by Morris et al. (1937). These workers were unable to rear M. dentipes in the laboratory so their description was based on observations in the field and on field-collected material. The female of M. dentipes usually laid five or six (maximum, 15) eggs in a single host cocoon. The larvae fed externally on the prepupa of the sawfly host, devouring it completely. The larvae matured after 3 to 4 weeks. M. dentipes overwintered as prepupae, or, if weather were favorable, developed immediately into pupae. In April, when overwintering individuals pupated, the pupal stage lasted 3 weeks. During the summer, when other individuals pupated, the pupal stage was shorter. Four or five (maximum, 12) adults of M. dentipes emerged per host cocoon. Emergence of the first generation of adults occurred in May, although adults were found in the field into September. A full month elapsed between the emergence of the first and last insects from one cocoon.

Mertins' (1967) observations agree essentially with those of Morris et al. (1937). However, Mertins provided additional information about the Wisconsin parasites of D. similis. He reared M. dentipes from field collected cocoons of D. similis and studied the behavior, oviposition, and longevity of the parasite under unspecified laboratory conditions. M. dentipes took 28 days to develop from eggs to adults. Larvae hatched within 3 days of oviposition, fed on the host for 8 days, then were quiescent for 3 additional days before defecating. Afterwards, the larvae tended to position themselves in a single layer around the host cadaver and cocoon walls, all facing in the same direction. They pupated within 2 days after defecation and emerged 9 to 13 days later. No cocoons were formed. Mean emergence from 100 parasitized cocoons was 7.74 (range, 1-22). The sex ratio was 1.16 females per male. Males emerged up to a day before the females. A male would cut an exit hole in the host cocoon, emerge, and wait near the opening for a female to emerge. Then, beating his wings intermittently, he would follow her, climb on her back, tap her head with his antennae, and eventually attempt copulation. Males usually remounted until successful. Copulation lasted 15 to 20 seconds. Adult males lived 9.8 days while females lived 30.6 days in the laboratory when fed sugar water.

The host relationships of M. dentipes are often complex and potentially confusing since the range of its activities spans that of a primary parasite to possibly that of a semi-scavenger. On its most important hosts, the pine sawflies, it can act directly as a primary parasite, or indirectly as a hyperparasite and Coppel (1960) reported M. dentipes as a primary parasite of the solitary wasp, Ancistrocerus tigris tigris (Saussure), inhabiting empty cocoons of D. similis. In some circumstances, it can even compete successfully in a multiparasitic situation.

Morris et al. (1937) reported that M. dentipes was always a primary parasite on D. polytomum. Mertins (1967) reared M. dentipes most often as a primary parasite from his Wisconsin collections of D. similis. However, from a group of 100 parasitized D. similis cocoons he examined, M. dentipes was at least associated with another parasite species in seven cases. Under such circumstances, M. dentipes attacked Exenterus amictorius (Panzer), Itopectis conquisitor (Say), and Dahlbominus fuscipennis (Zetterstedt) (Mertins 1967). Mertins and Coppel (1971) extended the list of primary parasites of D. similis attacked by M. dentipes to include Diplostichus lophyri (Townsend). The relationship of M. dentipes to the parasites listed was thought to be facultative.

Mertins (1967) also reported that M. dentipes could compete successfully in a multiparasitic relationship on D. similis. During the summer months, adults of M. dentipes emerge constantly with the females ovipositing in new sawfly cocoons, so that the parasitism of sawflies is cumulative as the summer progresses (Morris et al. 1937). If the population of M. dentipes increases sufficiently by the time the second generation of sawflies forms cocoons, M. dentipes may attack sawfly cocoons already parasitized by other individuals of M. dentipes or by some other species of parasite (Mertins 1967). Secondary parasitism, multiparasitism, or superparasitism may occur. M. dentipes usually survives in either case. Mertins (1967) seldom found dead M. dentipes in cocoons that had also been attacked by another species of parasite. In one instance, Mertins observed both Eupelmella vesicularis (Retzius) and M. dentipes emerging from the same host cocoon. In addition, Mertins (1967) and Mertins and Coppel (1971) reared M. dentipes from the same host cocoon with E. amictorius, E. vesicularis, Gelis tenellus (Say), Habrocytus thyriderigis Howard, and Amblymerus verditer (Norton). However, this was a rarity.

In addition, M. dentipes may be a semi-scavenger. Mertins (1967) reported, in his work on the Wisconsin parasites of D. similis, that M. dentipes developed once on the remains of a sawfly left after the development of an ichneumonid parasite. He was unable to discern whether M. dentipes had attacked the sawfly cocoon during or after the development of the ichneumonid. Since the time of parasitism by M. dentipes was the crucial factor, he was unable to eliminate the possibility that the relationship had been multiparasitic originally.

M. dentipes is versatile in the host relationships it can assume. Regardless of what that relationship proves to be, the extent to which the females of M. dentipes can successfully attack pine sawflies is determined by the location in the soil or duff where the host sawfly forms its cocoon. For instance, D. polytomum, D. similis, and D. hercyniae are heavily parasitized by M. dentipes. They occur in the same areas with N. sertifer in Europe and North America, but N. sertifer is seldom attacked on either continent. In the first record of M. dentipes on N. sertifer in Canada, only one host cocoon produced the parasites (Finlayson 1960b) and subsequent reports are similarly meager (Griffiths et al. 1971; Lyons 1964).

M. dentipes was not effective against N. sertifer because the parasite could not reach the cocoons of N. sertifer in the mineral soil (Lyons 1964). Lyons (1964) reported that fewer than 3 percent of the N. sertifer at Chatsworth, Ontario, cocooned above the mineral soil, although a conflicting report exists (Morris and Cameron 1935). In contrast, D. polytomum, D. hercyniae, and D. similis all cocoon above mineral soil; D. polytomum and D. similis, on the host tree and nearby shrubs; and D. hercyniae, in the surface litter (McGugan and Coppel 1962).

The extent to which M. dentipes parasitizes a given host may also depend on physical and physiological characteristics of the host cocoon or host prepupa. The parasite is able to distinguish between the larch sawfly, Pristiphora erichsonii (Hartig), which is not known to be a host of M. dentipes, and N. lecontei, which is successfully parasitized by M. dentipes in the laboratory (Drooz and Fedde 1972). The ability of M. dentipes to differentiate between these hosts, which are very similar in appearance, is evident at both the cocoon and prepupal levels.

SUMMARY AND SUGGESTIONS FOR FURTHER STUDY

Most publications referring to M. dentipes pertained primarily to its hosts or distribution until 1937, when Morris et al. described the parasite along with others of D. polytomum in Europe. When the importance of M. dentipes in the control of D. similis in the United States and Canada was realized, the number of host and locality records of this insect mushroomed. Mertins (1967) recently made the second major contribution to knowledge about the life history and host relationships of M. dentipes.

Since M. dentipes is potentially useful for biological control of Neodiprion spp., which cocoon above ground, in the southeastern United States, additional studies are needed on the parasite's ability to function in such a capacity. There is a need for more understanding of the physiological responses to environmental factors for this parasite, as well as of natural food of the adults and the parasite's behavior and ability to select hosts. If M. dentipes is to be employed successfully against sawflies of the genus Neodiprion, much more about the biology of the parasite must be understood.

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A literature review on Monodontomerus dentipes (Dalman), including the systematics, morphology, hosts, distribution, and life history of the sawfly cocoon parasite.



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