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Potential for classical biological control of the potato bug Closterotomus norwegicus (Hemiptera: Miridae): description, parasitism and host specificity of Peristenus closterotomae sp. n. (Hymenoptera: Braconidae)

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Abstract

The potato bug, Closterotomus norwegicus (Gmelin) (Hemiptera: Miridae) is an introduced pest of lucerne, white clover and lotus seed crops in New Zealand and a key pest of pistachios in California, USA. Efforts were made to identify potential biological control agents of C. norwegicus in Europe. A total of eight parasitoids, including six primary parasitoids from the genus Peristenus (Hymenoptera: Braconidae) and two hyperparasitoids from the genus Mesochorus (Hymenoptera: Ichneumonidae), were reared from C. norwegicus nymphs collected in various habitats in northern Germany. With a proportion of more than 85% of all C. norwegicus parasitoids, Peristenus closterotomae (Hymenoptera: Braconidae), a new species, was the most dominant parasitoid, whereas other parasitoid species only occurred sporadically. Peristenus closterotomae did not fit in the keys to any described species and is described as new to science. Parasitism caused by P. closterotomae was on average 24% (maximum 77%). To assess the host specificity of parasitoids associated with C. norwegicus, the parasitoid complexes of various Miridae occurring simultaneously with C. norwegicus were studied. Peristenus closterotomae was frequently reared from Calocoris affinis (Herrich-Schaeffer), and a few specimens were reared from Calocoris roseomaculatus (De Geer) and the meadow plant bug, Leptopterna dolobrata (Linnaeus) (all Hemiptera: Miridae). The remaining primary parasitoids associated with C. norwegicus were found to be dominant in hosts other than C. norwegicus. Whether nymphal parasitoids may potentially be used in a classical biological control initiative against the potato bug in countries where it is introduced and considered to be a pest is discussed.

Keywords: potato bug, Closterotomus norwegicus, Peristenus closterotomae, biological control, host specificity, California, New Zealand, pistachio, lucerne, white clover

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Introduction

The potato bug, Closterotomus norwegicus (Gmelin) (syn. Calocoris norvegicus) (Hemiptera: Miridae), is widely distributed throughout Europe, northern Africa and occidental Asia and is regarded as an introduced species in North America, Australia, New Zealand and Tristan da Cunha (Aukema & Rieger, 1999). First reported in New Zealand in the 1920s (Myers & China, 1928), today it occurs throughout the entire country and on the Chatham Islands but is absent from Wairarapa, Kaikoura and Stewart Island (Eyles, 1999). In New Zealand, this polyphagous mirid occurs on a wide variety of host plants (Eyles, 1999) and is regarded as a major pest of lucerne, white clover and lotus seed crops on the South Island (Macfarlane et al., 1981; Schroeder, 1995). Occasionally C. norwegicus causes feeding damage to asparagus (Watson & Townsend, 1981), cocksfoot seedling crops (McPherson, 1957; Eyles, 1999), hops (Ferro, 1976) and various vegetable crops (Chapman, 1976). In North America, C. norwegicus was first recorded in Quebec, Canada in the late 19th century (Provancher, 1886) and was later reported as a potato and strawberry pest in the maritime provinces of Canada (Pickett et al., 1944; Beirne, 1972; Kelton, 1982). In California, USA, C. norwegicus first appeared in the 1940s and has since spread throughout most of northern and central California (Rice & Bentley, 2005). Today C. norwegicus is considered a key pest of pistachio, Pistacia vera L. (Anacardiaceae) (Rice et al., 1985; Uyemoto et al., 1986; Purcell & Welter, 1990b; Rice & Bentley, 2005).

Generally, *C. norwegicus* inflicts feeding damage by piercing plant tissues, secreting digestive enzymes and pumping out the fluid plant material. In alfalfa, white clover and lotus, feeding results in the shrivelling of seeds and proliferation of secondary stems (Macfarlane *et al.*, 1981; Wightman & Macfarlane, 1982; Wightman & Whitford, 1982; Clifford *et al.*, 1983; Chapman, 1984; Schroeder *et al.*, 1998; Wheeler, 2000). Schroeder *et al.* (1998) demonstrated that feeding injury inflicted by *C. norwegicus* has the potential to significantly reduce white clover seed yield causing estimated losses of up to \$740 ha⁻¹. In pistachios, feeding during the soft-shelled stage produces necrotic lesions along the epicarp (Bolkan *et al.*, 1984). Uncontrolled populations of *C. norwegicus* can reduce pistachio yield significantly and cause losses as high as \$1660 ha⁻¹ (Welter & Purcell, 1988).

Potato bugs overwinter as eggs oviposited in woody plants or herbs (Kullenberg, 1944; Southwood & Leston, 1959; Purcell & Welter, 1990a) and thus, hedgerows and field margins are preferred overwintering habitats from which nymphs invade field crops in early spring (Afscharpour, 1960; Schroeder & Clifford, 1996). Therefore, suggested techniques for managing C. norwegicus include the removal and control of host plants in hedgerows adjacent to fields as well as the application of pesticides along the field edges (Hartley et al., 1982; Purcell & Welter, 1991; Schroeder et al., 1998; Rice & Bentley, 2005). However, ecological infrastructures, such as hedgerows and grass or wild flower strips, are essential for the development and efficiency of natural enemies of crop pests, providing refuges, hibernation areas, prey for juvenile stages of predators and essential food sources (e.g. nectar, pollen of flowering plants) for adult parasitoids and pollinators (Boller et al., 2004; Gurr et al., 2004). Furthermore, in New Zealand, only a few insecticides are currently registered for use in white clover seed crops, two of which are reported to reduce beneficial arthropods

such as lacewings and lyniphiid spiders (Schroeder & Chapman, 1995). In addition, insecticides available for use in flowering legume crops are limited in number due to concerns about the lethal effects they have on bee pollinators. In California, the most effective insecticide used against plant bugs, including *C. norwegicus*, is permethrin. However, permethrin is particularly harsh on beneficial insects (Hembree & Shrestha, 2005). Therefore, application of classical biological control may provide a more environmentally compatible approach for controlling *C. norwegicus*.

Natural enemies of *C. norwegicus* have rarely been recorded in the literature. In Britain however, it has been reported that nymphs of *C. norwegicus* are parasitized by *Peristenus pallipes* (Curtis) (Hymenoptera: Braconidae) (Brindley, 1939). In general, *Peristenus* parasitoids attack early nymphal instars of mirids and kill their hosts in the late nymphal or adult stage (Loan, 1980). Members of the genus *Peristenus* have been described from various mirid hosts (Bilewicz-Pawinska, 1982; Loan, 1974; Haye, 2004) and the European *Peristenus digoneutis* Loan (Hymenoptera: Braconidae) has been used successfully for biological control of native *Lygus* plant bugs in North America (Day, 1996).

This paper describes the nymphal parasitoid guild composition of C. norwegicus in Europe, including the description of a Peristenus species new to science, that could potentially be used for classical biological control of the potato bug. Sampling in Europe was restricted to the area of Schleswig-Holstein, northern Germany, where C. norwegicus is known to be abundant in spring (Afscharpour, 1960) but does not cause severe damage to crops. Before exotic biological control agents can be introduced into foreign countries it is necessary to prove that the application of the agent will not cause a significant displacement of any native species within its natural habitat (e.g. ERMA New Zealand, 1999; Barratt & Moeed, 2005). Therefore, host specificity of parasitoids associated with C. norwegicus was investigated by studying their ecological host range, defined as the current and evolving set of host species actually used for successful reproduction in the field (Nechols et al., 1992; Onstad & McManus, 1996).

Materials and methods

Parasitoid guild composition, parasitoid emergence pattern, and parasitism of C. norwegicus

Between May and July 2001–2003, 27 samples of *C. norwegicus* nymphs were collected using a sweep net from various host plants at 18 localities in Schleswig-Holstein, northern Germany to define the nymphal parasitoid guild of *C. norwegicus*. Host plants sampled were chamomile (*Matricaria recutita* (L.) (Asteraceae), 12 sites), red clover (*Trifolium pratense* L. (Fabaceae), two sites), stinging nettles (*Urtica* spp. (Urticaceae), two sites), tansy phacelia (*Phacelia tanacetifolia* Bentham (Hydrophyllaceae), three sites) and grasses (one site). Since *Peristenus* larvae are known to frequently emerge from late nymphal instars and only rarely from teneral adults (Loan, 1980), exclusively fourth or fifth instar mirid nymphs were collected.

From each of the 27 samples, 20 to 50 nymphs were taken randomly and dissected for parasitism, whereas the remaining nymphs were taken into rearing. Samples of up to 50 nymphs were kept in 1.2 litre plastic containers fitted with removable Petri dishes on the bottom. The Petri dishes were

filled with moist vermiculite and separated from the container by a piece of gauze (mesh size 1.20 × 1.38 mm), which allowed nymphal parasitoids to gain access to the Petri dish for pupation (Drea et al., 1973). Closterotomus norwegicus nymphs were reared at 20°C, 70 RH and provided with organically grown beans and water as required. Larger samples consisting of up to 500 nymphs were kept in plastic buckets, of which the bottoms had been removed and replaced with gauze. Plastic funnels, terminating in vermiculite-filled Petri dishes, were attached to the bottom of the buckets in order to collect emerging parasitoid larvae that fell through the gauze. In September of each field season, after the last nymphs had disappeared in the field and parasitoid emergence had ended, Petri dishes containing the remaining parasitoid cocoons were removed and stored in an outdoor wooden shelter for overwintering. After cold storage for six months, overwintering parasitoid cocoons collected in 2001 were transferred into a climate chamber (20°C, 60% RH, 16h light) on 15 April 2002 to induce parasitoid emergence. Over a period of six weeks the emergence of parasitoids was checked daily. Cocoons obtained in 2002 were kept outdoors to monitor parasitoid emergence under natural temperature conditions in northern Germany and to examine whether parasitoid emergence is synchronized with the appearance of their host *C. norwegicus* in the field. Cocoons from 2003 were incubated in February 2004, but parasitoid emergence was not studied in detail. Emerged parasitoids were immediately transferred into 70% ethanol, after which they were critical point dried. Since in most cases the immature stages of Peristenus species found in dissections were morphologically indistinguishable (Bilewicz-Pawinska & Pankanin, 1974), morphological characteristics of the adults were then used to identify the parasitoid species responsible for the observed parasitism.

The abundance of parasitoids within the nymphal parasitoid guild of C. norwegicus was determined by calculating the total number of primary parasitoids and hyperparasitoids that emerged from all C. norwegicus samples collected for rearing. The proportion of each parasitoid species relative to the total number of parasitoids that emerged was then calculated. The impact of each parasitoid on C. norwegicus at individual sites was estimated by relating parasitism, as determined by dissections, with the parasitoid species composition, assessed from duplicate reared samples. For example, if 70% of dissected nymphs were parasitized and 80% of the reared parasitoids were species A and 20% species B, then the parasitism by species A was 56% and by species B was 14%. If hyperparasitoids emerged, percent parasitism by a primary parasitoid could not be estimated precisely because it was not possible to associate each hyperparasitoid with the primary parasitoid it had killed before.

Ecological host range

According to Wagner (1952), the family Miridae to which *C. norwegicus* belongs contains approximately 2000 species in the Palaearctic region (307 in Germany) and thus, the number of potential non-target hosts for parasitoids associated with *C. norwegicus* is immense. For practical reasons, the number of mirid host species investigated was therefore reduced, based on relatedness, spatial and temporal overlap as well as availability of target and non-target hosts in their natural habitats in the area of investigation,

Schleswig-Holstein, northern Germany (Kuhlmann et al., 2006). To define the ecological host range of C. norwegicus parasitoids, sweep net samples of late instar mirid nymphs from the subfamily Mirinae (21 species), Bryocorinae (one species), Orthotylinae (two species) and Phylinae (five species) were collected between May and August 2001-2003 from various host plants in natural or agricultural habitats in northern Germany (see table 3). Besides the host plants listed for C. norwegicus, other host plants sampled included black medick Medicago lupulina L. (Fabaceae), mugwort Artemisia vulgaris L. (Asteraceae), tansy Chysanthemum vulgare (L.) (Asteraceae), bladder campion Silene vulgaris (Moench) Garcke (Caryophyllaceae), hedge nettle Stachys silvatica L. (Lamiaceae), Atriplex lacinata L. (Chenopodiacae), various Apiaceae and oak trees (Quercus spp. (Fagaceae)). For non-target mirids, a similar rearing systems as described for C. norwegicus was used. However, for most non-target mirid species, the host plants from which they were collected (see table 3) were added to the rearing cages instead of beans because they would not accept any other food.

Results

Parasitoid guild composition, parasitoid emergence pattern, and parasitism of C. norwegicus

A total of 11,198 C. norwegicus nymphs were gathered from 27 collections conducted at 18 localities in northern Germany. From the 9996 nymphs taken into rearing, 1464 parasitoid cocoons were collected, from which 1142 (78%) parasitoids emerged either in the same year of collection or following overwintering. In total, eight parasitoid species were reared (table 1), including the primary parasitoids Peristenus relictus (Ruthe) (syn. P. stygicus), P. digoneutis Loan, P. orchesiae (Curtis), P. nitidus (Curtis), Peristenus sp. (all Hymenoptera: Braconidae) (det. H. Goulet and C. van Achterberg) and the hyperparasitoids Mesochorus curvulus Thomson and Mesochorus sp. (Hymenoptera: Ichneumonidae) (det. K. Zwakhals). However, the most commonly occurring species in all habitats sampled (fig. 1), with an overall proportion of 85.2%, was one which did not match any of the described species in the European key (Loan, 1974, 1979). Furthermore, this species was also the most widely distributed, occurring at all localities sampled (n = 18). This unrecognized European species is regarded as new and is formally named Peristenus closterotomae van Achterberg & Goulet (Hymenoptera: Braconidae). A morphological description is included below.

When overwintering cocoons were transferred to 20° C in mid-April 2002, adults of P. closterotomae emerged in the laboratory after 1–11 days $(5.9\pm1.9 \text{ days}, \text{ S.D.}, n=282)$ (table 2). Males emerged first, with females emerging shortly thereafter. Under natural temperature conditions in 2003, P. closterotomae emerged over a period of one month between the end of April and the end of May. During both years, no non-diapausing individuals were observed. In contrast, the majority of P. relictus and P. digoneutis adults did not enter diapause and emerged within the same year of collection (July). Diapausing P. relictus emerged after six to eight days of being transferred to the laboratory, whereas emergence outdoors was at the beginning of May. Other Peristenus species reared from C. norwegicus also emerged in May (outdoors), but numbers were not significant. Hyperparasitoids

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Table 1. Member species of the natural nymphal parasitoid guild of *Closterotomus norwegicus* in northern Germany from 2001 to 2003. Information is given on the nymphal parasitoid guild composition, number of sites at which parasitoids were discovered, and mean and maximum parasitism caused by single parasitoid species.

Parasitoid species	No. of sites $(n = 18)$	No. of specimens collected	Parasitoid guild composition (%)	Mean % parasitism	Maximum % parasitism
Braconidae					
Peristenus closterotomae van Achterberg & Goulet	18	973	85.2	24.1 ± 3.6	77.2
Peristenus relictus (Ruthe)	11	49	4.3	1.0 ± 0.3	6.7
Peristenus digoneutis Loan	10	40	3.5	1.1 ± 0.4	8.6
Peristenus orchesiae (Curtis)	1	1	0.1	<1	1.3
Peristenus nitidus (Curtis)	1	1	0.1	<1	0.3
Peristenus spp.	4	5	0.4	<1	2.7
Ichneumonidae					
Mesochorus spp.a	11	73	6.4	2.1 ± 0.5	7.3
Total		1142	100		

^aHyperparasitoids.

of the genus *Mesochorus* emerged 11–20 days (14.2 ± 3.5 days, S.D., n = 5) after transfer to 20°C. Under natural temperature conditions emergence was observed from 22 to 31 of May.

To be able to distinguish between P. closterotomae and the morphologically similar P. adelphocoridis, reared from the non-target Adelphocoris lineolatus (Goeze) (Hemiptera: Miridae), the emergence patterns of both species were compared. In contrast to P. closterotomae, P. adelphocoridis emerged much later in the laboratory, requiring 27-35 days (30.5 ± 8.9 days, S.D., n=5) of incubation prior to emergence. Under natural temperature conditions a similar difference between the emergence patterns was observed. Whereas the majority of P. closterotomae emerged in May 2003, only a single female of P. adelphocoridis emerged on 11 May, with the remaining specimens emerging much later, between 14 and 29 of June, 2003.

Mean parasitism of *C. norwegicus*, as determined by dissections, was $25.0\pm4.1\%$ (SE). However, total parasitism varied greatly between sites, reaching a maximum of 78%. Parasitism, exclusively by *P. closterotomae*, averaged $24.1\pm3.6\%$ (SE), whereas the maximum parasitism rate was 77.2%. Average parasitism by the remaining *Peristenus* species was 1.1% or less (table 1) and their maximum parasitism rates did not exceed 9%. Hyperparasitism by *Mesochorus* spp. averaged $1.8\pm0.5\%$ (SE).

Ecological host range

A total of 74,806 nymphs of 29 species belonging to the family Miridae were collected in order to estimate the ecological host range of parasitoids associated with the target $C.\ norwegicus$ (table 3). The dominant parasitoid in $C.\ norwegicus$, $P.\ closterotomae$, was reared from three other Mirinae hosts, including $Calocoris\ affinis$ (Herrich-Schaeffer), $Calocoris\ roseomaculatus$ (De Geer) and $Leptopterna\ dolobrata$ (Linnaeus) (all Hemiptera: Miridae). The proportion of $P.\ closterotomae$ reared from the common grass bug, $L.\ dolobrata$, relative to the total number of parasitoids that emerged from this species was $0.5\%\ (n=374)$. In comparison to $C.\ norwegicus$, the two hosts belonging to the genus Calocoris were relatively rare in the area of investigation. Thus, a much smaller number of parasitoids. A total of 21

parasitoids were reared from the 186 *C. affinis* nymphs collected, 17 of which were identified as *P. closterotomae* (81% of the nymphal parasitoid guild composition). Only a single specimen of *P. closterotomae* was obtained from *C. roseomaculatus*.

The remaining primary parasitoids associated with *C. norwegicus* were found more frequently in other mirid hosts (table 3). *Peristenus relictus* and *P. digoneutis* were the dominant parasitoids of *Lygus* spp. However, *P. relictus* also emerged regularly from *Megaloceraea recticornis* (Geoffroy), *Trigonotylus coelestialium* (Kirkaldy), *Plagiognathus chrysanthemi* (Wolff) and *Amblytylus nasutus* (Kirschbaum) (all Hemiptera: Miridae). *Peristenus orchesiae* and *P. nitidus* were dominant parasitoids of the mirids *Lygocoris pabulinus* (Linnaeus) (49%) and *Apolygus lucorum* (Meyer-Dür) (69%), respectively. *Peristenus* sp. was frequently reared from the mirid hosts *L. dolobrata* (67%) and *S. laevigata* (L.) (21%).

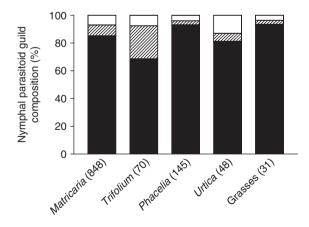


Fig. 1. Proportion of nymphal parasitoids when *Closterotomus norwegicus* nymphs were collected from different host plants. Parasitoids others than *Peristenus closterotomae* (■) are grouped as *Peristenus* spp. (□); *Mesochorus* spp. (□) represent the hyperparasitoids reared. Numbers in brackets represent the total number of parasitoids reared from nymphs collected from different host plants.

Table 2. Emergence of overwintered parasitoids reared from *Closterotomus norwegicus* and *Adelphocoris lineolatus* in the laboratory in 2002 at constant 20°C (incubation started 15 April 2002) and at outdoor temperatures in 2003 in Kiel, Germany.

Parasitoid species	No. non-	No. diapausing		Emergence after o	verwinte	ring
	diapausing ^c	using		2002 (laboratory)	2	003 (outdoors)
			п	Days until emergence after incubation	n	Emergence in the field
Peristenus closterotomae van Achterberg & Goulet	0	712	283	1–11	429	29 Apr-31 May
Peristenus relictus (Ruthe)	28	12	3	6–8	9	4–8 May
Peristenus digoneutis Loan	28	1	_	_	1	17 May
Peristenus orchesiae (Curtis)	0	1	1	5	_	_
Peristenus nitidus (Curtis)	0	1	_	_	1	11 May
Peristenus sp.	0	3	2	4–9	1	5 May
Mesochorus spp.a	16	29	5	11–20	24	22–31 May
Peristeous adelphocoridis Loan ^b	0	15	5	27–35	10	11 May–29 June

^aHyperparasitoids; ^breared from *Adelphocoris lineolatus*; ^cemerged within the same year of collection.

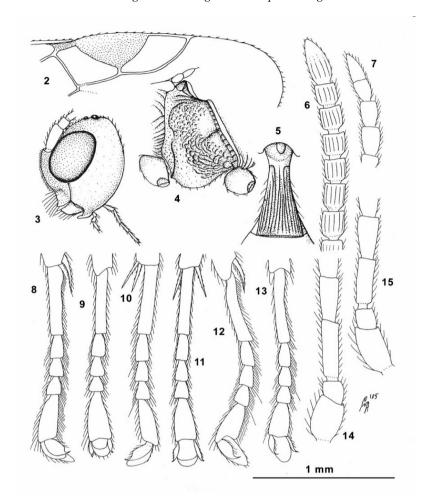
Peristenus closterotomae van Achterberg & Goulet, sp. n. (figs 2-11, 14, 15)

Description. Female. Holotype, length of body 3.8 mm, of fore wing 2.8 mm. Head. Antenna with 25 segments of which 6 subquadrate segments subapically (fig. 6), length of third segment 1.3 times fourth segment, third, fourth and penultimate segments 3.4, 2.2 and 1.0 times their maximum width (figs 6, 14); face 0.9 times higher than its minimum width, its minimum width 2.7 times height of eye, with long whitish pilosity obscuring its regularly punctate surface, with interspaces about equal to diameter of punctures; face in lateral view slightly convex (fig. 3); clypeus mainly smooth except for a few punctures, rather flat and wide; frons densely setose and punctate (but less densely dorsally), with interspaces about equal to diameter of punctures, but OOL (distance from lateral ocellus to nearest eye margin) area interspaces wider, with a distinctly developed regular median carina, dorsally rugose; vertex distinctly above upper level of eye, largely smooth, with few fine punctures; length of maxillary palp 0.6 times height of head, fifth (=apical) segment 1.5 times longer than fourth segment; length of posterior side of stemmaticum 1.8 times lateral side; OOL: diameter of posterior ocellus: POL (distance between inner margins of posterior ocelli) = 6:3:9; in dorsal view length of eye 1.1 times length of temple; temples subparallel-sided behind eyes and somewhat narrowed posteriorly, and sparsely punctate laterally; occipital carina largely present dorsally (up to of upper level of eye) but narrowly interrupted medio-dorsally, and ventrally joining hypostomal carina; hypostomal flange large and flexed under mandible; length of eye in lateral view 3.4 times length of malar suture or space; length of malar space equal to basal width of mandible; antennal socket near level of ventral 0.3 of eye. Mesosoma. Length of mesosoma 1.4 times its height; side of pronotum largely rather coarsely vermiculate-rugose, dorsally smooth with some punctures; area of precoxal sulcus widely and coarsely vermiculate-rugose but anteriorly mainly punctate and up to scrobe, without a crenulate and curved groove; remainder of mesopleuron coarsely punctate but speculum widely smooth (fig. 4); pleural sulcus coarsely crenulate; mesosternal sulcus shallow and widely crenulate; notauli distinctly and completely impressed, moderately coarsely crenulate; lateral lobes of mesoscutum with some rows of rather coarse punctures and middle lobe moderately punctate with interspaces much wider than diameter of punctures, largely setose and shiny; scutellar sulcus with one strong carina; scutellum mainly smooth (except some striae anteriorly) and with a distinct smooth semicircular medio-posterior depression; propodeum nearly completely reticulate-rugose. Wings. Fore wing: basal and subbasal cells regularly but much sparser setose than apical cells; 1-M 1.8 times vein m-cu; vein 1-R1 complete, 0.5 times as long as pterostigma and 1.1 times width of pterostigma (fig. 2); pterostigma 2.1 times longer than wide; distance from apex of marginal cell to wing apex 2.4 times vein 1-R1; vein r twice longer than wide, wider than vein SR1 and just behind middle of pterostigma; r:SR1+3-SR:2-SR=2:34:19; vein m-cu slightly postfurcal (right wing: fig. 2) or interstitial (left wing); 1-CU1:2-CU1=2:19; 1-CU1 rather widened and oblique. Hind wing:1-M:1r-m:2-SC+R=10:11:8. Legs. Hind coxa largely smooth except for some microsculpture; length of femur, tibia and basitarsus of hind leg 4.4, 10.4 and 7.0 times their maximum width; hind tibia parallel-sided apically; outer and inner hind tibial spur equal, 0.4 times as long as hind basitarsus; second-fourth segments of fore and middle tarsi comparatively slender, normally setose and telotarsus 1.7 times wider than third segment in dorsal view, length of second, third and fourth segments of fore tarsus 1.7, 1.4 and 1.1 times their maximum width in dorsal view, respectively (figs 8, 9); fore tarsus similar to middle tarsus (figs 10, 11); fore femur moderately slender. Metasoma. First tergite gradually widened posteriorly (fig. 5), its length 1.7 times its apical width, its surface coarsely regularly striate and baso-laterally distinctly striate; spiracle of first tergite near basal 0.6 of tergite; ovipositor sheath just visible, pointed apically, hardly protruding. Colour. Black; antenna (except yellowish scapus and pedicellus and brown third segment) and metasoma (but three basal tergites blackish) dark brown; hind coxa blackish-brown; clypeus dark brown, but medially chestnut brown; hind tibia apically and tarsus slightly brownish, remainder of legs, tegulae and palpi pale brownish-yellow; veins of hind wing and basal half of fore wing yellowish, remainder of veins largely brownish; pterostigma basally and anteriorly yellowish-brown, remainder of pterostigma and parastigma dark brown; base of mandible narrowly infuscate.

Table 3. Ecological host range of nymphal parasitoids associated with Closterotonus norwegicus and their relative abundance (%) in the nymphal parasitoid guilds of mirid hosts collected in Schleswig-Holstein, northern Germany.

	Host species	Host plants ^a	No. nymphs	No. of			% Peristenus	S)			% Mesochorus
utifier (Fallén) Sv 274 (1) 38 - 5 invelatus (Gezez) MI 635 (11) 35 - - - is (Herrich-Schaeffer) U, Av 1217 (13) 86 - - - - is (Herrich-Schaeffer) U, Av 117 (13) 86 21 -			collected (No. of sites)	parasitoids reared	closterotomae	relictus	digoneutis	orchesiae	nitidus	sb.	sbb.
Interclatest (Goezee)	Bryocorinae Dicyphus globulifer (Fallén)	Sv	274 (1)	38	ı	ιv	I	ı	ı	I	ı
incolatus (Goeze) MI 635 (11) 35 - - rum (Meerrch-Schaeffer) U, Av 1217 (13) 86 - - - rum (Meerrch-Schaeffer) U, Av 1217 (13) 86 - - - - maculatus (De Geer) A TP, Mr, G, Pt, U 11,198 (18) 1142 85 4 4 - moreogenes (Geneim) TP, Mr, G, Pt, U 11,198 (18) 174 -	Mirinae: Mirini										
Principality (New-Dark) N. Av. 1217 (13) 86 14 14 14 (2) 14	Adelphocovic lineoletus (Cooze)	M		ς, Γ	ı	I	ı	ı	ı	ı	ď
Experiment (Authority) A. Mr. G. Pt. U. 1.21 (13) 80 3 Timis (Modeller) To, AV. 1.21 (13) 80 3 4 4 Semanculatus (De Geer) A 14 (2) 21 8 4 4 semanculatus (De Geer) A 11,198 (18) 1142 85 4 4 4 abulituus (Eabricus) U 47,76 (31) 409 - 4	Anethrocolis intechnius (Socze)	TT A		3 8	I	ļ	*	=		l	۶ ر
This (Herrich-Schaeffer)	Apolygus tucorum (Meyer-Dur)	U, AV		90	ı	1 '		4	69	I	97
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	Amblytylus nasutus (Kirschbaum)	U	1289 (8)	38	1	79	ı	ı	1	I	က

*Only single specimens reared. ^aA, Apiaceae; Al, Atriplex lacinata L.; Av, Artemisia vulgaris L.; Cv, Chrysanthenum vulgare (L.); G, Gramineae; Ml, Medicago lupulina L.; Mr, Matricaria recutita (L.); Pt, Phacelia tanacetifolia Bentham; Q, Quercus spp.; Sv, Silene vulgaris (Moench) Garcke; Tp, Trifolium pratense L.; U, Urtica spp. ^bHyperparasitoids.



Figs 2–15. *Peristenus closterotomae* sp. n. (female, holotype: figs 2–11, 14, 15; male, paraytype from Lindhöft, Germany: figs 7, 15) and P. adelphocoridis Loan (figs 12, 13) from Probsteierhagen, Germany: 2, pterostigma and marginal cell of fore wing; 3, head, lateral aspect; 4, mesopleuron, lateral aspect; 5, first metasomal tergite, dorsal aspect; 6, 7, apex of antenna; 8, fore tarsus, lateral aspect; 9, fore tarsus, dorsal aspect; 10, middle tarsus, lateral aspect; 11, middle tarsus, dorsal aspect; 12, fore tarsus, lateral aspect (P. adelphocoridis); 14, 15, basal segments of antenna (Scale: figs 1–3, $1.0 \times$ scale-line; fig. 4, $1.1 \times$; figs 5, 6, 13, 14, $2.1 \times$; figs 7–10, $1.6 \times$; figs 11, 12, $1.9 \times$).

Male. Similar to female, antenna more densely bristly setose subapical segments normal, its third segment about 2.2 times as long as wide (figs 7, 15); height of face 0.7–0.8 times higher than its minimum width, minimum width of face about equal to height of eye; fore and middle tarsi more slender than of female.

Variation. Antenna of females (n = 310) with 22 (0.3%), 23 (6%), 24 (55%), 25 (38%) or 26 (0.7%) segments; antenna of males (n = 443) with 24 (0.7%), 25 (6.3%), 26 (34%), 27 (46%), 28 (12%) or 29 (1%) segments; antenna of females with 6–9 more or less moniliform segments; length of penultimate antennal segment of female 1.0–1.4 times its width; scapus and pedicellus brownish-yellow, rarely in males dark brown, third segment dark brown in males and yellowish-brown in females, which may have also the fourth and sometimes more or less following segments yellowish or pale brownish; vein r of fore wing 1–2 times longer than wide; vein m-cu of fore wing interstitial, shortly antefurcal or postfurcal; distance from apex of marginal cell to wing apex 2.4–3.2 times vein 1-R1; vein 1-R1 of fore wing 0.4–0.5 times as long as pterostigma and 1.1–1.2 times width of pterostigma;

pterostigma of female 2.1–2.6 times longer than wide; tegulum brownish-yellow or yellowish-brown; hind tibia rarely distinctly infuscate dorso-apically.

Material examined. A name bearing type is fixed for *P. closterotomae* from a type series consisting of 901 specimens, 508 males (3) and 393 females (\$\partial{\Phi}\$). The holotype and part of the paratypes listed below are deposited in The Nationaal Natuurhistorische Museum, Leiden, Netherlands (RMNH). The remaining paratypes are housed in the Canadian National Collection (CNC), Agriculture and Agri-Food Canada, Eastern Cereal and Oilseed Research Centre, Ottawa, Ontario, Canada.

Holotype, ♀. The holotypes bears the following labels: Germany, Lütjenbrode, 54° 21′ 52″ N 11° 01′ 49″ E, coll. 14.vi.2001, em. 23.iv.2002, clover-vetches field B2, T. Haye// ex: *Closterotomus norwegicus* (Gmelin), L4, det. T. Haye, 2001// *Peristenus* near *pallipes* "spring black mtcx, det. H. Goulet, 2003".

Paratypes (457\(\gamma + 425\(\delta\)). If not indicated differently, all paratypes were reared from the host *Closterotomus norwegicus*

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(Gmelin), collected and determined by T. Haye: $42^{\circ}_{+}+43^{\circ}_{\circ}$: (RMNH, CNC), Germany: Lindhöft, 54° 27′ 32″ N 09° 58′ 37″ E, coll. 30.v., 13.vi. and 26.vi.2001, em. between 3.v. and 26.v.2003, margin of winter canola, L1-L3; 1132+943: (RMNH, CNC), Germany: Achterwehr, 54° 187′ 44″ N 09° 57′ 44″ E, coll. 19.vi., 25.vi., 30.vi. and 4.vii.2001, and 12.vi. and 3.iv.2002, em. between 16.iv. and 24.iv.2002, and between 12.v. and 23.v.2003, fallow field, L5; 11♀+23♂: (RMNH, CNC), Germany: Rastorf, 54° 16′ 09″ N 10° 17′ 11″ E, coll. 11.vi., 23.v., 30.v. and 27.vi.2001, and 9.vi. 2002, em. between 16.iv. and 23.iv.2002, and between 3.v. and 13.v.2003, margin of winter canola; 12: (RMNH), Germany: Kaköhl, 54° 16′ 53″ N 10° 40′ 30″ E, coll. 14.vi.2001. em. 19.iv.2002, grassland, L4; 4♀+2♂: (RMNH, CNC), Germany: Osterrönfeld 54° 17′ 56″ N 09° 42′ 24″ E, coll. 19.vi.2001, and 3.vi.2002, em. between 19.iv. and 23.iv.2002, and between 3.v. and 13.v.2003, ruderal site, L5; 93\(\times + 141\delta\): (RMNH), Germany: Schleswig-H., Kiel-Holtenau 54° 22′ 76″ N 010° 07′ 96″ E, coll. 25.vi.2003, em. ii.2004, on Phacelia tanacetifolia, RMNH'04; 49 + 33: (CNC), Germany: Osdorf, 54° 25.484'N 10° 01.349'E. coll. 13.vi.2003, em. ii.2004, grass land; 23♀+8♂: (CNC), Germany: Plön, 54° 10′ 25″ N 10° 23′ 11″ E, coll. 14.vi.2002, em. between 3.v. and 14.v.2003, on Urtica; $4^{\circ}_{+}+7^{\circ}_{\circ}$: (CNC), Germany: Schwedeneck, 54° 28′ 26″ N 10° 05′ 32″ E, coll. 6.vi. and 7.vi.2002, em. between 6.v. and 24.v.2003, on Matricaria; 49 + 63: (CNC), Germany: Scharnhagen, 54° 26′ 28″ N 10° 07′ 03″ E, coll. 10.vii.2001, and 7.vi.2002, em. between 21.iv. and 23.iv.2002, and between 6.v. and 21.v.2003, on Lolium perenne (2001) and Phacaelia (2002); 85♀+39♂: (CNC), Germany: Kochendorf, 54° 29′ 03″ N 09° 45′ 35″ E, coll. 2.vi.2002, em. between 3.v. and 26.v.2003, on Matricaria; 13: (CNC), Germany: St. Peter Ording, $54^{\circ}\,20'\,12^{''}\,N$ 08° $35'\,53^{''}\,E,$ coll. 2.vii.2001, em. 21.iv.2002, coastal grass land; $2^{\circ}+1_{\circ}$: (CNC), Germany: Felm, $54^{\circ}24'36''$ N 10° 03′ 09″ E, coll. 25.vi.2003, em. ii.2004, fallow field, Matricaria; 6♀+5♂: (CNC), Germany: Sophienhof, 54° 12′ 30″ N 10° 20′ 19″ E, coll. 14.vi.2002, em. between 3.v. and 17.v.2003, on Matricaria; 9[°] +11[°] (CNC), Germany: Schnaap, 54° 28.800′N 09° 46.243′E, coll. 23.vi.2003, em. ii.2004, fallow field, Matricaria; 132 + 93: (CNC), Germany: Lütjenbrode, 54° 21′ 52″ N 11° 01′ 49″ E, coll. 27.v., 6.vi., 14.vi., 15.vi.2001, and 4.vi. and 9.vi.2003, em. between 17.iv. and 24.iv.2002, and between 7.v. and 31.v.2003, red clover (2002), clover – vetches field (2003) 14♀+17♂: (CNC), Germany: Kragholm, 54° 48.481'N 09° 34.770'E, coll. 27.vi.2003, em. ii.2004, mustard field; 7♀+2♂: (CNC), Germany: Dagebüll, 54° 43′ 57″ N 08° 42′ 49″ E, coll. 17.vi.2002, em. between 12.v. and 31.v.2003, on Matricaria; $11^{\circ}+16^{\circ}$: (CNC), Germany: Brux, $54^{\circ}16'41''$ N 09° 51′ 55″ E, coll. 19.vi.2002, em. between 6.v. and 19.v.2003, on Matricaria; 1 \updownarrow + 1 \circlearrowleft : (CNC), Switzerland: Vue des Alpes, coll. 25.vii.1999, em. 9.v.2000, H.D. White, ex: C. norwegicus, det. H. White, 1999; 2^o: (CNC), Switzerland, near Grenchenberg, coll. 2000, em. 8.v.2001, H.D. White, ex: Calocoris roseomaculatus (DeGeer), det. H. White, 2000; 12: (CNC), Germany: Osterönfeld, 54° 17′ 56″ N 09° 42′ 24″ E, coll. 19.vi.2001, em. 22.iv.2002, T. Have, ruderal site, ex: Calocoris roseomaculatus (DeGeer), det. T. Haye, 2001; $2^{\circ}_{+}+1_{\circ}$: (CNC), Germany: Eidertal, $54^{\circ} 13' 35'' N$ 10° 01′ 51″ E, coll. 5.vii.2001, em. between 20.iv. and 21.iv.2002, T. Haye, on Urtica, ex: Calocoris affinis (Herrich-Schaffer) or Closterotomus norwegicus (Gmelin), det. T. Haye, 2001; 12+23: (CNC), Germany: Grevenkrug, 54° 13′ 35″ N 10° 01′ 51″ E, coll. 5.vii.2001, em. 24.iv.2002, T. Haye, on Urtica, ex: Calocoris affinis (Herrich-Schaffer), det. T. Haye, 2001; $4^{\circ}_{+} + 2^{\circ}_{-}$: (CNC), Germany: Rosenfelder See, 54° 16′ 50″ N 10° 15′ 51″ E, coll. 7.vii.2001, em. 22.iv.2002, T. Haye, river bank, ex: Calocoris affinis (Herrich-Schaffer), det. T. Haye, 2001; 1♀+1♂ (CNC), Germany: Niebüll, 54° 17′ 56″ N 09° 42′ 24″ E, coll. 17.vi.2002, grass, em. 13.vi.2003,

T. Haye field margin, ex: *Leptopterna dolobrata* (Linnaeus), det. T. Haye, 2002.

Comments. Peristenus closterotomae is very closely related to *P. adelphocoridis* Loan (Hymenoptera: Braconidae), 1979, from which it differs mainly biologically (see above), but there are some minor differences in the shape of the fore and middle tarsal segments (figs 8 and 9 vs. figs 12 and 13), and the new species has the shape of the middle tarsus similar to that of the fore tarsus (figs 10, 11). It seems likely that *Peristenus closterotomae* is synonymous with *Peristenus (Euphorus) pallipes* (Curtis) (Hymenoptera: Braconidae) recorded to attack *C. norwegicus* in Britain (Brindley, 1939).

Discussion

This paper provides information on parasitism of the potato bug *C. norwegicus* and its nymphal parasitoid guild composition in Europe, including the description of a species new to science. The emergence patterns of parasitoids associated with *C. norwegicus* after finishing diapause as well as their ecological host range is also presented. The overall aim of the study was to evaluate the potential for classical biological control of *C. norwegicus* using European nymphal parasitoids, because members of this parasitoid guild have already been used successfully for biological control of another mirid pest (*Lygus lineolaris* (Palisot de Beauvois) (Hemiptera: Miridae)) in North America (Day, 1996). Surveys for egg or adult parasitoids of *C. norwegicus* were not conducted; however, the chance to identify target specific biological control agents is considered limited.

In northern Germany, the emergence of the univoltine P. closterotomae in spring was well synchronized with the peak abundance of small instar nymphs of its univoltine host C. norwegicus in the field, which is usually observed between mid May and the beginning of June in northern Germany (Afscharpour, 1960). The synchronization of parasitoid emergence and the presence of early host instars is essential, because it has been shown that Peristenus parasitoids oviposit more successfully into early instars (Drea et al., 1973; van Steenwyk & Stern, 1976; Loan, 1980). Peristenus relictus and P. digoneutis, which were occasionally reared from C. norwegicus, emerged primarily in July within the same year of collection when *C. norwegicus* nymphs were not present in the field. Both species are well known to be dominant parasitoids of their bivoltine host Lygus rugulipennis Poppius (Bilewicz-Pawinska, 1982; Haye et al., 2005) and therefore, C. norwegicus is not considered an important host.

For *Peristenus* species that are morphologically difficult to separate it has been suggested to estimate the average time required for an adult to emerge from its cocoon after the cocoon has been transferred from cold storage to room temperature (Haye, 2004; Day, 2005). In the laboratory as well as under natural temperature conditions, the emergence of *P. closterotomae* hardly overlapped with the emergence of the closely related species, *P. adelphocoridis*, which occurs in the second half of June when early instars of its host *A. lineolatus* are present in the field and small nymphs of *C. norwegicus* are absent. Besides the minor morphological differences to *P. adelphocoridis*, the distinct difference in the emergence patterns of both *Peristenus* species indicate that *P. closterotomae* is indeed a separate species.

Of the six primary parasitoids reared from *C. norwegicus*, *P. closterotomae* was by far the dominant species within the pest's nymphal parasitoid guild, comprising an overall proportion of 85%. Thus, it had the highest impact on the pest and may yet show promise for a biological control initiative. The dominance of *P. closterotomae* in all habitats sampled suggests that this parasitoid species might have an impact on *C. norwegicus* populations not only in cultivated fields, but also on alternative host plants in adjacent natural habitats that may serve as reservoirs for the polyphagous pest.

According to the susceptibility hypothesis elucidated by Hawkins (1994), hosts that are not concealed or hardly protected by the plant parts they infest suffer from higher parasitism rates since they are more easily located by their parasitoids. Furthermore, Hawkins et al. (1993) stated that empirical data suggest an association between maximum parasitism rates of parasitoids and their success in biological control. In particular, parasitoids causing maximum parasitism rates of above 40% are more likely to be successful in biological control than those causing parasitism rates of less than 25%. Nymphs of C. norwegicus are hardly protected while feeding on their host plants and accordingly, suffer from high rates of parasitism by P. closterotomae (maximum 77%). Therefore, the susceptibility hypothesis implies that this species may be highly successful as a biological control agent.

When searching for biological control agents in the area of origin of the pest, field surveys are an important first step in identifying the species with the narrowest host range (Cock, 1986). Since the dominant P. closterotomae is not present in the parasitoid complexes of most mirid hosts investigated (table 3), its ecological host range is likely to be rather restricted. Closterotomus norwegicus has been placed in the genus Calocoris until the former subgenus Closterotomus has been accorded generic status (Rosenzweig, 1997). Thus, the recording of P. closterotomae from Calocoris affinis and Calocoris roseomaculatus is in accordance with the findings of Pemberton (2000) who stated that the more closely related the non-target species is to the pest, the more likely it is to be attacked. However, the development of P. closterotomae from the Stenodemini host, L. dolobrata, was unexpected as this species is assumed to be less closely related to the target.

In New Zealand, the subfamily Mirinae, to which C. norwegicus belongs, comprises 74 species of which 68 are native (Eyles, 2001). The genus, Closterotomus Fieber, comprises 31 species in the Palaearctic (Aukema & Rieger, 1999). However, the introduced C. norwegicus is the only species of this genus in New Zealand. Since none of the genera attacked in Europe are native to New Zealand (Eyles, 2001), the risk of non-target effects by P. closterotomae is likely to be low. In North America, the genus Closterotomus comprises only two species, the introduced C. norwegicus and the holoarctic C. fulvomaculatus (Gmelin); two indigenous species are also recorded from the genus Calocoris, C. texanus Knight and C. barberi Henry & Wheeler (Henry & Froeschner, 1988; Maw et al., 2000). The genus Leptopterna contains three species; the introduced L. ferrugata (Fallén) and L. dolobrata, and the indigenous L. amoena Uhler. However, from all species listed L. amoena is the only native species that occurs in California and the maritime provinces of Canada, where the potato bug is recorded as pest. Although P. closterotomae is rather specific, there have been a few cases in the past where biological control agents that were

considered to be monophagous, or were expected to have a rather restricted host range in the area of origin, were later found to attack several other host species in the area of release (Brower, 1991; Barratt et al., 1997). Therefore, conclusions regarding host specificity can rarely be made exclusively from field data collected in the area of origin of the biological control agent (van Lenteren et al., 2003). Laboratory tests to assess whether any of the mirid species native to New Zealand or North America would be attacked by P. closterotomae under a variety of test conditions would therefore be the next essential step to determine whether the release of *P. closterotomae* against *C. norwegicus* is likely to be environmentally safe. The remaining six Peristenus species listed for C. norwegicus can probably be eliminated as candidates for biological control at this early stage because they are primarily associated with mirid species other than C. norwegicus and their impact on the target is expected to be low.

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