On the Geographic Origin of the Wheat Stem Sawfly (Hymenoptera: Cephidae): A New Hypothesis of Introduction from Northeastern Asia

Evidence from newly recognized populations in Asia shows that the wheat stem sawfly, *Cephus cinctus* Norton, was introduced by human agency into North America from northeast Eurasia during the 19th century.

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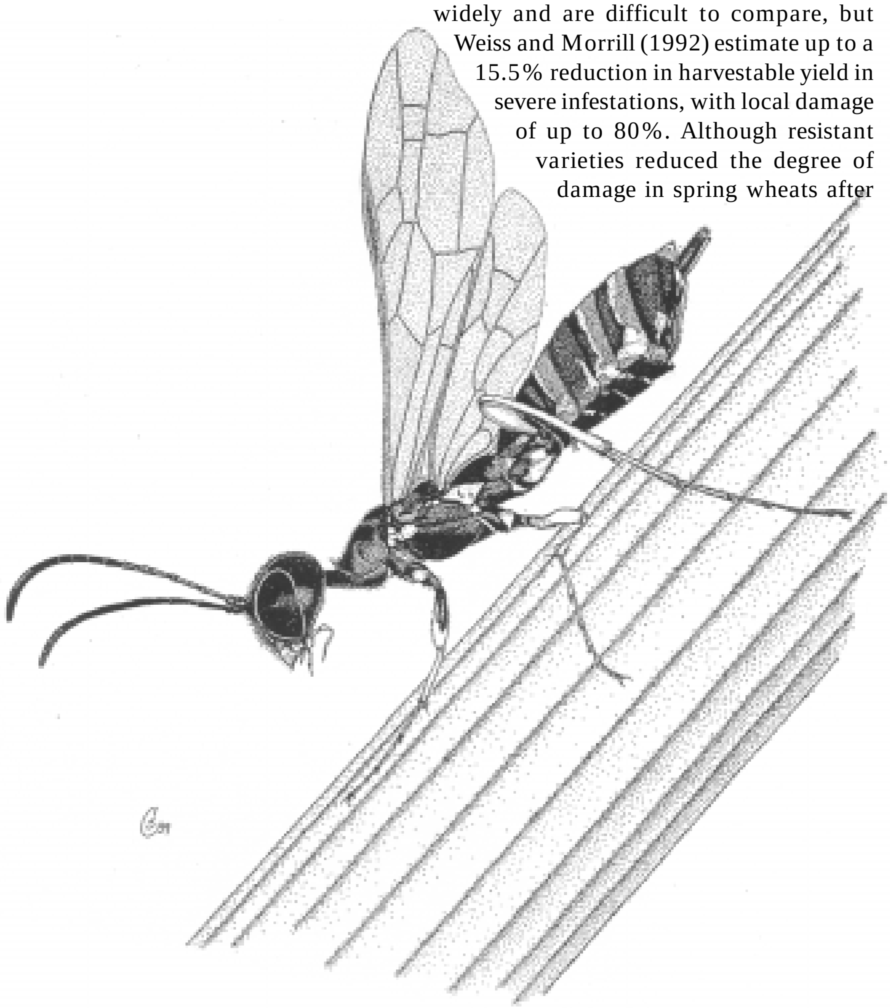
The wheat stem sawfly, *Cephus cinctus* Norton, is a brightly colored yellow and black cephid that mines the stems of grasses. The adult is a slow flier, and at up to 1 cm long it is an obvious and easily observed member of the Great Plains fauna. It has been a major pest of wheat and barley in the northern Great Plains of North America since 1895, when it was found damaging wheat in Manitoba and Saskatchewan (Wallace and McNeal 1966). Loss estimates vary widely and are difficult to compare, but Weiss and Morrill (1992) estimate up to a 15.5% reduction in harvestable yield in severe infestations, with local damage of up to 80%. Although resistant varieties reduced the degree of damage in spring wheats after the 1940s, lower yield potentials of those varieties, sporadic but significant damage in winter wheat, and a resurgence of damage in spring wheat have rekindled interest in this pest (Weiss and Morrill 1992 and references therein; Morrill et al. 1992a, 1992b). Blodgett et al. (1997) reported the wheat stem sawfly as the number one pest concern of Montana wheat growers. Currently, it is being incompletely controlled with resistant varieties, manipulation of planting dates, and occasional chemical treatments. Each of these strategies has the disadvantage of lowering potential yields, severely hurting profitability, and/or possibly contributing to environmental degradation.



Agricultural researchers in Canada and the United States have studied this pest continuously since the earliest reports of damage (Weiss and Morrill 1992). Throughout its long history in the literature, the wheat stem sawfly has been treated as a native North American species (Weiss and Morrill 1992), but, amazingly, no evolutionary investigations of this species or its lineage have been published. This has allowed the assumption that the wheat stem sawfly was a North American native to persist unchallenged.

When I first identified and then examined this assumption of native status, its inconsistency with existing data raised questions that resulted in this study. Those questions led to the recent discovery that wheat stem sawfly also occurs in Eurasia (Ivie and Zinovjev 1996), which strengthened my doubts about its origin.

Taken as a whole, the accumulation of information about wheat stem sawfly will no longer support its endemic status. It is time for a reexamination of those data in a modern evolutionary framework and for a resulting paradigm shift (i.e., that the wheat stem sawfly is an introduced species, carried by human agency from its home in northeast Asia to western North America in the last century).

My hypothesis that wheat stem sawfly was introduced is a radical departure from 100 years of unanimous conventional wisdom. A complete scenario of its origin as a native grass-feeding species, switching to cultivated cereals, has evolved from Criddle (1922) to an elaborate but completely unsupported form with Turnock (1971) (see Weiss and Morrill 1992). Examination of publications supporting this scenario reveals no evidence beyond the fact that wheat stem sawfly was first discovered and described in North America. The basic factual information available about wheat stem sawfly from past investigations can be summarized as follows.

History of Wheat Stem Sawfly Distribution

Wheat stem sawfly occurs widely across North America from Pennsylvania and Georgia to the Pacific (Table 1), being common in the prairies from Ohio west (Ries 1937, Smith 1979) (Fig. 1). North to south, it occurs from the Peace River District of Alberta to Texas (Wallace and McNeal 1966, Smith 1979; TAMU, collection codens used throughout can be found in the *Acknowledgments* section). Recently, Ivie and Zinovjev (1996) have reported that it also occurs in northeastern Asia, in Russia from the Altai to Kamtschatka, and in Hokkaido, Japan (Fig. 2).

Early Records

Norton (1872) described the wheat stem sawfly from Colorado. Records from Nevada (1872), California (1890), Montana (1890), Utah (1894), Manitoba (1895), Saskatchewan (1895), and Wisconsin (1898) followed (Riley and Marlatt 1891, Ashmead 1898, Wallace and McNeal 1966, ANSP) (Table 1; Fig. 1). The first damage was noticed in 1895 at Souris, Manitoba, and Moose Jaw, Saskatchewan (Fletcher 1896, Ainslie 1920) (Fig. 1). By 1910, wheat infestation had been reported from Montana and North Dakota (Ainslie 1920, Wallace and McNeal 1966). Today, economically important damage is concentrated in the northern Great Plains of Alberta, Saskatchewan, Manitoba, Minnesota, the Dakotas, Montana, and Wyoming (Wallace and McNeal 1966, Weiss and Morrill 1992).

Related Species

The wheat stem sawfly is one of four North American species in the grass-mining tribe Cephini. This tribe is composed of over 50 described species in the Holarctic region, placed in three genera (Benson 1946). The Nearctic species are placed in one (Ries 1937), two (Middlekauff 1969), or three (Smith 1979, followed here) genera. Two species are known to have been introduced from Europe, the European wheat stem sawfly, *Cephus pygmeus* (L.), and the black grain stem sawfly, *Trachelus tabidus* (F.) (Wallace and McNeal 1966, Smith 1979). The fourth Nearctic species is *Calameuta clavata* (Norton), a poorly known species from the western United States (Middlekauff 1969), which is the sole Nearctic member of a speciose Palearctic genus (Smith 1979).

Phylogenetic Information

There is no worldwide revision of the species of Cephini or *Cephus*. Only regional faunal treatments

Fig. 1. Distribution of wheat stem sawfly (*Cephus cinctus* Norton) in the western United States and southwestern Canada (after Wallace and McNeal 1966, records added from Table 1), with points of early Russian contact (■), pre-1900 distribution records west of the Mississippi River (▲), pre-1910 economic reports (●). Selected railroad connections to the Pacific: red dashed – completed 1869, green dashed – completed 1873, orange dashed –completed 1880, blue dashed – completed to Saskatchewan 1882, to Pacific 1895, black solid – completed 1883, green solid – completed 1892.

(e.g., Gussakovskij 1935, Ries 1937, Takeuchi 1938, Verzhutskii 1966, Middlekauff 1969, Zhelochovtsev 1988) and a single world review (Muche 1981) have been published. Muche gives separate keys for Eurasia and North America without critical comparison of Nearctic and Eurasian forms. Muche stated his keys were largely literature-based and supplemented by specimens in Eberswalde and Berlin. No evolutionary or biogeographic analyses were presented.

Because of difficulty in obtaining access to collections in Europe during the Cold War, and ongoing problems obtaining specimens from former Soviet, Mongolian, North Korean, and Chinese territories in north Asia, the material needed to

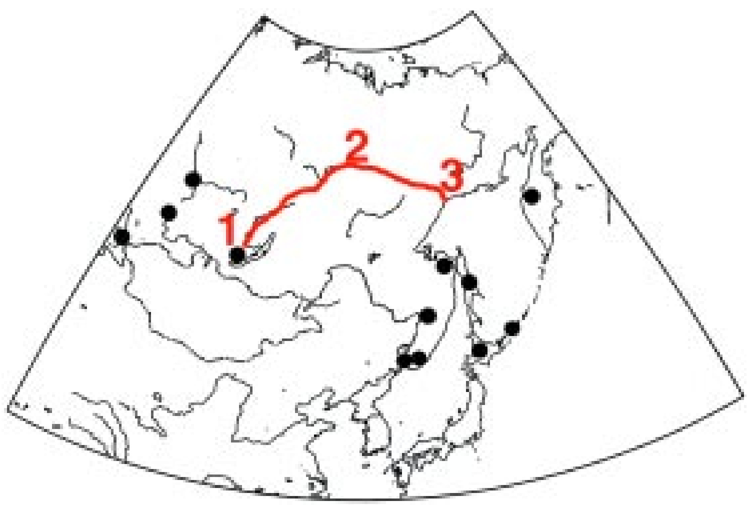


Fig. 2. Distribution records of wheat stem sawfly (*Cephus cinctus* Norton) in northeastern Asia (●). Overland route of supply for Russian North America during New Albion period (1812-1841): 1 – Irkutsk, 2 – Yakutsk, 3 – Okhotsk (after Chevigny 1965 and Gibson1976).

Table 1. **Earliest records of wheat stem sawfly by state, province, or island**

Area	Year	Source
Colorado	1872	Norton 1872
Nevada	1872	Riley and Marlatt 1891
California	1890	Riley and Marlatt 1891
Montana	1890	Riley and Marlatt 1891
Utah	1894	ANSP
Manitoba	1895	Wallace and McNeal 1966
Saskatchewan	1895	Wallace and McNeal 1966
Wisconsin	1898	Riley and Marlatt 1891
Washington	1901	Ries 1937
New Mexico	1902	ANSP
Wyoming	1905	Wallace and McNeal 1966
North Dakota	1906	Wallace and McNeal 1966
South Dakota	1906	Wallace and McNeal 1966
Oregon	1907	Webster and Reeves 1907
Alberta	1909	Hewitt 1910
Iowa	1910	Ainslie 1920
Minnesota	1914	Ries 1937
Nebraska	1915	Wallace and McNeal 1966
Missouri	1917	Ainslie 1920
Michigan	1920	Gahan 1920
Ohio	1922	Ries 1937
Vancouver Is.	1929	CNCI
Illinois	1930	Ries 1937
Texas	1932	TAMU
Idaho	1935	UICM
Arizona	1937	Ries 1937
Kansas	1937	Ries 1937
Ontario	1944	CNCI
Br. Columbia	1947	CNCI
Arkansas	1966	Wallace and McNeal 1966
Indiana	1971	USDA 1971
Pennsylvania	1971	USDA 1971
Virginia	1971	USDA 1971
Oklahoma	1981	OSEC
Georgia	1989	NMNH

Sources refer to citations or collection codens listed in the *Acknowledgments* section.

undertake a full revision of the genus has been difficult to assemble.

Host Data

The many recorded hosts of the wheat stem sawfly (Smith 1979) include several Holarctic grass genera with cultivated, feral, naturalized, and native species, including *Triticum* spp. (wheats), *Hordeum* spp. (barleys), *Secale cereale* L. (rye), *Agropyron* spp. (wheat grasses), *Elymus* spp. (rye grasses), *Bromus* spp. (brome grasses), and others (Wallace and McNeal 1966). Wheat stem sawfly shows little selectivity in oviposition choice, seemingly accepting any available stem of the correct size, including many where larvae will not mature, such as the solid-stem wheats, oats (*Avena sativa* L.), and even a non-grass in the case of flax (*Linum usitatissimum* L., Linaceae) (Farstad 1944, Wallace and McNeal 1966). Preferred hosts are wheat, rye, and other introduced Eurasian grasses with large diameter stems. Several native North American grasses support the species, but only the largest diameter stems of those species permit the survival of the wheat stem sawfly (e.g., see Criddle [1917] for *Agropyron smithii* Rydberg, Wallace and McNeal [1966] for *Hordeum jubatum* L. and *H. montanenses* Scribner, and Youtie and Johnson [1988] for *Elymus cinerus* Scribner & Merrill). A careful review of the literature indicates that the actual host species within the acceptable genera is not the critical factor in wheat stem sawfly preference. Indeed, the same host may be preferred in one year or locality, and not in another (Criddle 1917). For example, *Agropyron smithii* was considered such a good host for wheat stem sawfly that Seamans and Farstad (1938) objected to its recommendation for soil conservation use. Yet, Wallace and McNeal (1966) report that half the stems of *A. smithii* are too small to support wheat stem sawfly larvae. Criddle (1917) ties the acceptability of this grass as a host to rainfall. Another example of an exotic grass with high infestation rates is winter wheat, which usually is reported to be resistant but may have infestation of up to 80% in years when the wheat's development is delayed (Wallace and McNeal 1966, Weiss and Morrill 1992, Morrill et al. 1993).

Host acceptability is thus influenced more strongly by the timing of plant maturity and stem diameter than species within the host genera (Wallace and McNeal 1966; see also Weiss and Morrill 1992, table 4). When the correct phenological stage of an acceptable host is available with the correct diameter of stems at the time the female is ovipositing, it becomes a preferred oviposition site. Subsequent survival of the larva would be related to a variety of factors, including stem solidness. Davis (1954) reports that damage does not occur farther south in wheat stem sawfly range because early maturation desiccates the immature larva. The damage belt within the range of wheat stem sawfly is probably the area where normal occurrence of susceptible wheat stems overlaps in time with the normal emergence of the adult sawflies. The use of delayed-planting dates to avoid this co-occurrence of susceptibility and pest presence (Weiss et al. 1987) is evidence that this is the case.

Therefore, it seems the critical aspect is the normal stem diameter. Especially in drought years, which are frequent in the Great Plains, cultivated grains and introduced grasses provide the vast majority of suitable stems.

Parasitoid Associates

Of the 10 parasitoids reported to infest wheat stem sawfly (Burks 1979, Carlson 1979, Marsh 1979), none seems to exert significant or consistent control (Wallace and McNeal 1966, Morrill et al. 1994, Morrill et al. 1998). Further, of these 10, eight are either known introductions (three), cases of mistaken host records (two), or generalists with a broad host range (three). Of the known introductions, two, *Scambus detritus* Holmgren (Ichneumonidae) and *Pediobius nigritarsis* (Thomson) (Eulophidae), are established species introduced in biological control efforts targeted at cephines and Hessian fly, *Mayetiola destructor* (Say) (Cecidomyiidae). The third, *Bracon terebella*

Wesmael (Braconidae), was also a biological control attempt targeted at cephines, but the wasp did not become established in the areas where it was purposely introduced. At the time of these biological control efforts, *Bracon terebella* and *Pediobius nigritarsis* were already present in eastern North American where they had been introduced accidentally with European cephines or Hessian fly (Salt 1931, Wallace and McNeal 1966, Burks 1979, Marsh 1979).

Other parasitoids associated with wheat stem sawfly are probably the result of misidentified hosts: *Eurytoma parva* Phillips (Eurytomidae) is a parasitoid of wheat jointworm, *Tetramesa* (=*Harmolita*) *tritici* (Fitch) (Eurytomidae), and *Eurytoma atripes* Gahan (Eurytomidae) attacks Hessian fly. Because each has been listed only once as a parasite of wheat stem sawfly (Burks 1979), and because the normal hosts also are found in grass stems, it seems safe to consider that the records of wheat stem sawfly parasitism by these species are mistaken.

Of the five remaining purportedly native parasitoids, three are generalists, one is a true specialist, and one is of uncertain status. Of the three generalists, two [*Eupelmus allyni* (French) (Eupelmidae) and *Eupelmella vesicularis* (Retzius) (Eupelmidae)] have over 30 known hosts in six orders. Included in the wide host ranges of both are reports of primary parasitism of the wheat stem sawfly as well as secondary parasitism of *Bracon cephi* (Gahan) (Braconidae), itself a parasitoid of wheat stem sawfly. Another generalist, *Pediobius utahensis* (Crawford) (Eulophidae), is poorly documented biologically. To date, it has been reported only from wheat stem sawfly (Burks 1979), but it also seems to have a wide but unreported host range. It has been reared in Idaho from seed heads of musk thistle (*Carduus nutans* L.) infested with *Rhinocyllus conicus* (Froelich) (Curculionidae) (J. B. Johnson, personal communication) and has been taken in Maine (Burks 1979), beyond the known range of any Cephini.

Bracon cephi is apparently a specialist on the wheat stem sawfly, having been reared repeatedly and exclusively from that host over a wide geographic range (Marsh 1979, Runyon et al. 2001). It is the only important species of parasitoid attacking this pest, although it is seldom effective as a control agent (Holmes 1982; Morrill et al. 1994, 1998). *Bracon cephi* and the following species are members of poorly known species-groups widespread in Eurasia. In all of the many citations reporting rearings of *B. cephi* from wheat stem sawfly, no specialist secondary parasitoid has ever been recorded.

The last species is difficult to characterize. *Bracon lissogaster* Muesebeck (Braconidae) must be considered, for the time being, a specialist on wheat stem sawfly, but this supposed association is troublesome. Reported only from Montana's Golden Triangle region (Somsen and Luginbill 1956, Marsh 1979, Morrill et al. 1994, Runyon et al. 2001), it apparently has been reared and recognized by only two research groups, both working in the same area. The first group, working between 1949 and 1956, discovered the species (Somsen and Luginbill 1956); the second is apparently the only other to rear the species, working from 1988 to date (Morrill et al. 1994, Runyon et al. 2001). It never has been reported by the Agriculture Canada researchers at Lethbridge, Alberta, just 75 km north of the Golden Triangle. Recently, it has been purposely released in new areas of Montana (Morrill et al 1998, Runyon et al. 2001).

Somsen and Luginbill (1956) reported on the biology of *B. lissogaster*, but the data were taken from specimens reared under artificial conditions. Larvae of the parasitoid were manually placed on wheat stem sawfly larvae after hatching in well slides. Actual oviposition on the host sawfly was only observed in chambers where wheat stem sawfly larvae had been introduced through cuts in the stems. This is hardly a natural situation. Somsen was with the Entomology Research Branch of the USDA Agricultural Research Service in Bozeman, MT, and specimens assembled by him and other USDA workers are deposited in the Montana State University Entomology Collection (MTEC). They are still arranged as they were by Lew E. Wallace when he incorporated them into his extensive reared collections. Specimens collected in 1951 from the original collection site in the Golden Triangle are split between two unit trays. The first of these contains seven specimens with the typed label "Dissected from wheat stems when in pupal stage. Reared through to adult in incubator. Remains of sawfly could not be found near them." In the second tray are four specimens with a similarly typed label, except the third sentence reads "Remains of sawfly found near parasites in each instance." Both series have determination labels from C.F.W. Muesebeck. No mention of the 1951 observations recorded in the MTEC are made in Somsen and Luginbill (1956) despite the authors' statement that pupation occurs "very close to the remains of the host." Although *B. lissogaster* can undoubtedly survive on wheat stem sawfly and can be reared from infested wheat stems (Morrill 1997, Runyon et al. 2001) it remains to be established if this is the normal host in the wild.

Of the five remaining purportedly native parasitoids, three are generalists, one is a true specialist, and one is of uncertain status.

A New Hypothesis

In forming a new hypothesis of geographic origin for the wheat stem sawfly, I examined the data accumulated by previous workers and continuously asked if their conclusions made sense in light of known evolutionary patterns. I found that the combination of these accumulated facts is best explained by the new hypothesis that wheat stem sawfly is not native to North America, as originally thought, but instead was introduced from Eurasia. I examined the following six general aspects of wheat stem sawfly information and evolutionary expectations: (1) Eurasian populations, (2) early collections, (3) hosts, (4) biogeography, (5) parasitoid associates, and (6) means and opportunity for introduction. At each juncture, I phrased a dependent hypothesis and null model that served to test the introduction model.

Eurasian Populations

If wheat stem sawfly is introduced from Eurasia, then populations must occur there. And they do! Examinations of collections in Eurasia resulted in the discovery of Asian populations of this sawfly (Ivie and Zinovjev 1996). This supports the hypothesis but does not by itself refute the native model—the species could be Holarctic. Therefore, more evidence is needed.

Early Collectors

The late date of description and aspects of initial damage reports raised the first red flag in this investigation. How could a brightly colored, easily collected, 1 cm long insect that feeds in such an obvious way on wheat, and occurs as far east as the Atlantic coast, go undescribed until 1872, and unnoticed in wheat until 1895?

Several hypotheses come to mind: (1) no collectors worked in wheat stem sawfly habitats; (2) specimens were seen but discarded because collectors were uninterested in Cephidae; (3) originally it occurred only in the West, and it did not reach the eastern states and provinces until later; or (4) it was introduced.

Thomas Say, America's first native entomologist, lived and collected within today's wheat stem sawfly range at New Harmony, Indiana, from 1826 to 1834 (Weiss and Ziegler 1931). Say was interested in pests of cultivated cereals, as evidenced by his detailed description of the Hessian fly, its life history, and one of its parasitoids [*Homoporus destructor* (Say), Pteromalidae] (Say 1817, Weiss 1936). Say also had collections from farther west (Fig. 3). He received specimens from Thomas Nuttall, who in 1811 collected along the Missouri River from eastern Missouri into the center of today's wheat stem sawfly damage area in North Dakota (Cassagrande 1985). Say himself collected in what is now prime wheat stem sawfly habitat on his trips with Major S. H. Long's expeditions—the first through the Missouri-Platte-Arkansas River valleys in 1819-1820 (Weiss 1936, Cassagrande 1985), the second through the Mississippi-Red-Rainy River Valleys of Minnesota and Manitoba in 1823 (Weiss 1936). These trips lasted for a minimum of an entire season, up to multiple years. Today, it would be difficult for an avid insect collector to retrace any one of either Nuttall's or Say's trips and bordering on impossible to make all three without stumbling onto this sawfly, yet Say did not report the species.

Perhaps specimens were collected but not described because Say was not interested in the group? This idea is refuted solidly by the fact that Say did describe hartigiine cephids when they were available: *Cephus abbreviatus* (now in *Janus*) from the first Long Expedition, *Xiphydria basalis* (a synonym of *J. abbreviatus*), and *Cephus trimaculaus* (now in *Hartigia*) (Smith 1979).

Charles Valentine Riley, another of America's premier early entomologists, was the Missouri State Entomologist from 1868 to 1878 (Osborn 1937). Although he was based in an area where wheat stem sawfly occurs today and obviously was interested in species that attack crop plants, Riley never mentioned it during those years. In addition to his own legendary field work, he was a teacher at the University of Missouri and Kansas State College during this period, where he had the opportunity to view many student collections (Mallis 1971). The Riley collection, now at the National Museum in Washington, DC, contains no wheat stem sawfly. In later years, Riley and Marlatt (1891) described *Cephus occidentalis* from Wisconsin, a synonym of *C. cinctus*, while dealing with damage by other Cephini. It is logical to expect that if wheat stem sawfly was there to be found, Riley would have reported the species and its damage from Missouri and/or Kansas.

The chronology of range documentation for the species is almost perfectly opposite of what would be expected of a native transcontinental species (Table 1). Instead of the usual discovery of these species in eastern North America, where most entomologists, departments of entomology, and museum collections were located, and a gradual filling in of records from western regions, wheat stem sawfly was first found in the West. A pattern emerges of early finds in the west-central part of the range, gradually extending northwest, south, and, finally, east. By 1910, the majority of western states and provinces had accumulated records, yet of the 10 infested states and provinces east of the Mississippi, only Wisconsin had records before 1920. It was not documented in the Ohio Valley until the 1920s, with no eastern seaboard records until the 1970s.

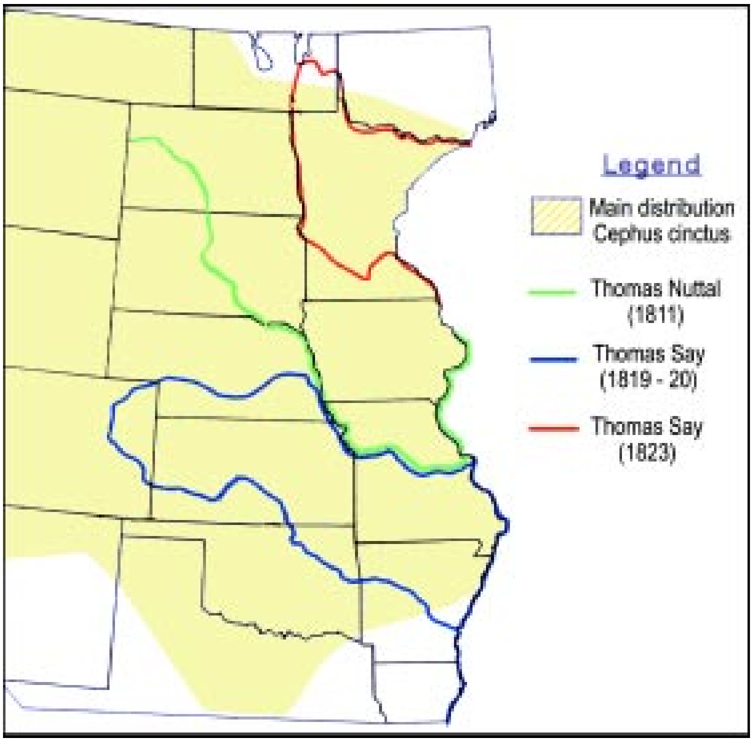


Fig. 3. Routes of early insect collectors in central portion of wheat stem sawfly range: green – Thomas Nuttall (1811); blue – Thomas Say (1819-20); red – Thomas Say (1823).

This pattern is indicative of a species spreading from west to east. Because Nuttall and Say did not find it on their travels, wheat stem sawfly must have spread from even farther west. Reports in the literature claim it is a poor flier (Weiss and Morrill 1992), so its current range is likely to be the result of dispersal through human agency.

In the literature, there are a few direct hints that wheat stem sawfly was not generally distributed even when the early reports of damage were published. Criddle (1922), a 1946 map of Montana (Montana Agricultural Experiment Station, unpublished data), and Davis (1953) all document spread of the species into newly infested areas. If the species was native, the sawfly would have shown up when wheat was first grown within its range, rather than spreading there. Yet, the first reports of damage were generally long after wheat was first grown in an area. A strain specific to cereals could explain this phenomenon, but there is no evidence of such a host-specific strain (Lou and Bruckner 1995). On the contrary, reports of the sawfly moving back and forth from "wild" (see below) grasses to grain crops are common (Wallace and McNeal 1966, Weiss and Morrill 1992 and references therein).

Hosts

It seems clear that the native grass community is not the focus of the wheat stem sawfly population. Several Eurasian grasses are feral or naturalized within wheat stem sawfly range, where they function as hosts, and many authors have confused these with natives. As an example, Davis (1948) listed nine hosts specifically as natives, yet six of those are introduced (USDA 1982). Technically more accurate but also frequently misinterpreted is the approach of Wallace and McNeal (1966), who list the following "wild" hosts of wheat stem sawfly: *Agropyron caninum* (L.) Palisot de Beauvois, *A. cristatum* (L.) Gaertner, *A. elongatum* (Host) Palisot de Beauvois, *A. intermedium* (Host) Palisot de Beauvois, *A. repens* (L.) Palisot de Beauvois, and *Bromus inermis* Leyss. All of these examples, and several others in their list, were introduced into North America from Eurasia (USDA 1982), yet the mistaken idea that these species were the original hosts in North America has been repeated so often as to become ingrained in the literature (Weiss and Morrill 1992 and references therein).

Nevertheless, I examined the hypothesis that wheat stem sawfly originally attacked native grasses and became obvious only after it switched to cultivated hosts. If this were true, wheat stem sawfly and its parasitoids would be well adapted to native grasses within its range and an integrated part of the grassland ecosystem. Natural selection would drive it toward maximizing host acceptability, especially in the absence of other cephine competitors. Of course, other limiting factors and selective pressures undoubtedly are involved, but being able to survive on the available stems is an obvious primary selection pressure. That selection for host stem size is important is shown by the fact that wheat stem sawflies preferentially infest the larger diameter stems even in cultivated small grains where virtually all stems are acceptable (Weiss and Morrill 1992). Yet, wheat stem sawflies can survive to adulthood in only the few largest diameter stems of native grasses (Criddle 1917, Wallace and McNeal 1966 and references therein, Youtie and Johnson 1988).

The fact that the stems of many cultivated, feral, and naturalized Eurasian grasses in North America have an average diameter in the optimal host range for wheat stem sawfly, while native grasses are smaller than optimal, suggests it is best adapted to Eurasian hosts. This observation has been available for many years. In 1917, Criddle observed about the truly native grass *A. smithii* (chosen as the original host by many scenarios, see Weiss and Morrill 1992) that "In times of drought its stems seldom attain the size sufficient to accommodate the sawfly larva, but under ordinary weather conditions at least a third of such stems are available..." In the same paper, he observed about the introduced Eurasian grass *A. repens* (which he and others referred to as "wild") that "Instead of providing 50% of suitable stems under normal weather conditions, as does *A. smithii*, *A. repens* produces almost a hundred percent." In dry years, wheat stem sawfly would literally starve on the truly native hosts. That the presence of these new grasses could so profoundly affect the optimal and acceptable host size in such a short time is highly unlikely.

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Another problem is with the timing of the hypothesized host transfer. Wheat stem sawfly was found on wheat at Souris, Manitoba, and Moose Jaw, Saskatchewan, in 1895; Kulm, North Dakota, in 1906; Minot, North Dakota, in 1907; and at Bainville, Montana, in 1910 (Wallace and McNeal 1966) (Fig. 1). Thus, in the space of 10-15 years, records appeared on wheat in spots separated by 400 km. Wheat cultivation started in southern Manitoba in 1812 (Morton 1957) but did not reach North Dakota's Drift Prairie (Kulm) until the 1870s (Robinson 1966), the Missouri Slope of Minot until about 1890 (Robinson 1966), and Montana's High Line around Bainville until after 1900 (Hoye 1976). By 1875, Manitoba and far-eastern North Dakota were major wheat producers (Morton 1957, Robinson 1966), whereas in eastern Montana production did not start until around 1900 (Hamilton 1957). If we accept the wheat stem sawfly as a native that switched to small grains (Weiss and Morrill 1992 and references therein), these data beg the question "why, if it took 80 years for local wheat stem sawfly to switch in Manitoba, did it take less than 10 years in Bainville, Montana?" If a biotype evolved that switched to cultivated hosts, why did the species switch over so much of its range in so synchronous a way (15 years) after such unequal exposure? These questions would have to be answered with a dispersal scenario of 25-40 km per year, which disagrees with the published dispersal capabilities of the species (Weiss and Morrill 1992). Therefore, if we use the scenario of biotype evolution to explain the problems with host preference noted above, that scenario would still require that the new strain be spread by human commerce in order to be found so widely in such a few years.

Therefore, the introduction hypothesis is more parsimonious. Both the evolution of a new biotype from a native species and the introduction of a pre-adapted exotic require human-assisted dispersal, but, under the view that the actual species of host is unimportant compared with the simple availability of an acceptable stem, no biotype evolution or switching per se is required by the new hypothesis. Further, there is no biological or genetic evidence available to support the biotype scenario (Lou and Bruckner 1995).

Finally, the incidence of higher rates of parasitism in "wild" (i.e. native) grasses than in cultivated grains is used repeatedly (Weiss and Morrill 1992 and references therein) to claim the original hosts were those wild grasses. The data simply do not support this. Smooth brome (*Bromus inermis*), introduced in the 1890s (USDA 1982), is one of the grasses in which wheat stem sawfly has the highest parasitism rates (Criddle 1922, Wallace and McNeal 1966); and *Agropyron trachycaulum* (Link) Malte ex A. F. Lewis, also with high recorded parasitism (Wallace and McNeal 1966), occurs in both North America and Eurasia (USDA 1982). Lastly, Morrill et al. (1994) reported very high parasitism (albeit rarely) in the exotic wheat! It appears that confusion of feral and naturalized grasses with native grasses has colored the conclusions of several previous workers.

Biogeography

At the beginning of this study, the lack of balance between Palearctic and Nearctic *Cephus* diversity was a key fact driving the discovery of Asian populations. In light of that discovery, the new pattern was still curious. Therefore, the hypothesis was tested that the biogeographic pattern exhibited by wheat stem sawfly and its relatives is consistent with a native species.

If the wheat stem sawfly is native to North America, its newly discovered Asian populations require that it be considered a Holarctic species. However, most Holarctic species exhibit very different distribution patterns from that of wheat stem sawfly. The vast majority of accepted Holarctic species follows the amphiatlantic, amphiberingian, transarctic, transboreal, and Vancouveran distributions (Lindroth 1957, 1968; Benson 1962; Hamilton 1983; Muona 1984; Pielou 1991; see Scudder 1979, Noonan 1988, and Wheeler and Henry 1992 for excellent reviews and further references). These patterns are amazingly consistent for diverse groups, with the above reviews showing examples from the Coleoptera, Hymenoptera, Hemiptera, Homoptera, Lepidoptera, and even mammals as large as the moose. Benson (1962) reviewed Holarctic sawfly distributions and found the naturally Holarctic species shared these same patterns.

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Hamilton (1983) presents an extensive review of these Holarctic distributions versus Nearctic endemic patterns using Cicadellidae as an exemplar taxon. His data are totally inconsistent with the assertion that wheat stem sawfly is a native insect in North America. He records the distribution of a number of putatively natural transboreal and transarctic distributions. In mapping the distributions of the transboreal and transarctic versus temperate endemic species (maps 1-5), he clearly shows the boreal forest restrictions of the natural transboreal distributions and the contrasting North American endemics. None of the transboreal species extends far into the Great Plains, even in the prairie provinces. None of the ranges of these transboreal species comes even close to the distribution pattern of wheat stem sawfly. It seems that in general the species that have been able to maintain specific identity between Asian and North American populations have a southern distribution boundary roughly at the edge of the boreal forests. Wheat stem sawfly is distributed distinctly south and east of this belt. Turnbull (1979) suggests that species with this southern bicontinental distribution are unlikely to be native. Wheat stem sawfly, with its basically prairie distribution, clearly does not fit the Holarctic species pattern.

Perhaps wheat stem sawfly is simply a rare exception to these patterns? If so, the rest of the genus might provide insights into the biogeographic origin of the species. I therefore looked into the question "does *Cephus* have a pattern typical of a Holarctic distribution in areas south of the transboreal belt?" The answer is a resounding no—the distribution of *Cephus* diversity simply does not fit the normally expected Holarctic patterns exhibited by supraspecific taxa. Ancestral Holarctic species that occurred south of the boreal belt usually have evolved into sister-species pairs (Ball and Negre 1972). Further, these species were pushed south during the Pleistocene glacial maxima, rebounding both latitudinally and altitudinally during the interglacials (Devender and Spaulding 1979, Mielke 1989). The result is a pattern of widespread northern species and southern species of restricted range (Ball and Negre 1972, Devender and Spalding 1979, Halfter 1987). Because it has a much larger area and more southern mountains than the Nearctic, the Palearctic could be expected to have more species resulting from these events, but some level of balance should be expected.

In the Palearctic, *Cephus* exhibits a pattern of several widespread species in the northern and central regions and of many species with small ranges in the southern parts of the region: the Crimea-Caucasus, Iberia, North Africa, the Levant, and Korea-Japan. The alleged Nearctic element (wheat stem sawfly) is very different, with only a single very widespread species. None of the expected southern species has been discovered.

Two Holarctic cephid genera do have the expected distributions: in the tribe Harigiini *Hartigia* has 18 species, 12 Palearctic and 6 Nearctic; *Janus* has 19 species, 4 in North America (Benson 1946; Smith 1979, 1986).

The story is different for the tribe Cephini. The Cephidae are among the oldest groups of Hymenoptera, with fossil members from the Lower Cretaceous (sister-group relationships indicate a Jurassic origin) (Gauld and Bolton 1988). However, the Cephini is relatively recent (Benson 1946), being exclusively associated with the Pooidae (Benson 1946, Smith 1979), which did not appear until the Miocene (Thomasson 1987). All genera of the tribe occur in the Palearctic where they are relatively speciose.

Besides wheat stem sawfly, *Calameuta clavata* is the only member of the tribe purportedly native outside the Palearctic, occurring on the west coast of North America. It is a poorly known species (Middlekauff 1969), but from the parallels with wheat stems sawfly I strongly suspect it is also an introduced species. This hypothesis should be tested by comparing it with *Calameuta* spp. from the Palearctic.

Important to the interpretation of these biogeographic data are the origins of the other Cephini in North America. Fully 50% (both of the other pest species) are known to be introduced from Europe.

In summary, the lack of balance in the biogeographic distribution of *Cephus* and the Cephini, the anomalies of distribution of wheat stem sawfly, and the documented introduction by humans of other grain-feeding species of *Cephus* do not support the assumption that wheat stem sawfly is a native insect.

Parasitoid Associates

Ecological relationships of a species in its environment include not only its hosts but its predators as well. Although the larvae and pupae of wheat stem sawfly are protected from most predators by the stems in which they bore, parasitoid guilds attacking plant tissue-boring insects are usually large and diverse (Salt 1931, Askew and Shaw 1986, Kato 1994). Thus, numerous generalist and specialist primary and secondary parasitoids would be expected for such a taxonomically isolated but easily located member of a fauna. Therefore, a normal complement of parasitoid associates would be hypothesized for wheat stem sawfly if it is native in North America.

As noted above, one-half of the parasitoids recorded from wheat stem sawfly are known to be either introduced (*B. terebella*, *S. detritus*, and *P. nigritarsis*) or associated mistakenly with wheat stem sawfly (*E. atripes*, *E. parva*). This leaves five purportedly native parasitoids: three generalists (*E. allyni*, *E. vesicularis*, and *P. utahensis*) and two possible specialists (*B. cephi* and *B. lissogaster*).

As native species, the two *Bracon* species have taxonomic, biogeographic, and parasitoid problems of their own. Both are members of Eurasian or Holarctic lineages. As discussed above, the exclusive association of *B. lissogaster* with wheat stem sawfly is not certain. Even assuming both are specialists on wheat stem sawfly, they lack the expected specialized secondary parasitoids. The generalists *E. allyni* and *E. vesicularis* are the only secondary parasitoids reported for *B. cephi*, and none is known for *B. lissogaster*. In contrast, a congeneric parasitoid of the European wheat stem sawfly, *Bracon terebella*, has four secondary parasitoids in England (Salt 1931).

Two Eurasian braconid parasitoids (*Bracon terebella* and *Heterospilus cephi* Rohwer) and an eulophid (*Pediobius nigritarsis*) have been introduced accidentally into eastern North America with their hosts, the European wheat stem sawfly and/or the black grain stem sawfly (Wallace and McNeal 1966, Marsh 1973), showing the propensity of braconid and other parasitoids to be introduced with host stem sawflies.

To confound the issue, the taxonomy of *Bracon* species is so poorly understood that comparison of *B. cephi* or *B. lissogaster* to Eurasian species is difficult without a revision. Siberian specimens of wheat stem sawfly are rare in collections, so it is not surprising that their parasitoids have received less attention than those in North America.

Plant-mining insects tend toward large parasite assemblages, with many parasitoid species tied to a microhabitat rather than to a particular species (Askew and Shaw 1986).

In light of the accidentally introduced confamilial species and the lack of specialist secondary parasitoids, it is likely that at least *B. cephi* was introduced with its host. *Bracon lissogaster* is likely to be either the normal parasitoid of a different native insect or is itself also introduced.

As another way of examining this hypothesis, how does the parasitoid guild of wheat stem sawfly compare with those of other sawflies and plant-mining insects? Plant-mining insects tend toward large parasite assemblages, with many parasitoid species tied to a microhabitat rather than to a particular species (Askew and Shaw 1986). Therefore, some generalist parasitoids would be expected to be preadapted to exotic species that appear in that microhabitat. For instance, Kato (1994) found 10 specialist and 14 generalist parasitoids attacking an agromyzid leaf-miner. Leaf-mining and gall-feeding sawflies showed similar patterns (Askew and Shaw 1986).

It is in total guild richness that the inconsistency appears between wheat stem sawfly's parasitoid load and those of native elements of a fauna. The eight leaf-mining sawflies reported by Askew and Shaw (1986) (leaf-mining being the most similar situation to the stem-mining *Cephus* spp.) had an average of 12.4 parasite species (range of 6-18). In the only equivalent study of a Eurasian *Cephus*, Salt (1931) found 13 parasitoid associates of *C. pygmeus* in England, showing general agreement with what would be expected. Given that the island fauna of Great Britain is rather depauperate compared with a continental fauna (Hammond 1984), the number of parasitoid associates of wheat stem sawfly occurring in North America is far below what is expected for a native species.

The numbers of primary and secondary parasitoids, and the mix of generalists and specialists, are more indicative of an introduced species than a native.

Means and Opportunity for Introduction

Obviously, an introduced species must have had a source population that was subject to exchange

The farming by the Russians and the ranching by the Spanish and Mexicans provided many introduced grasses (Hendry 1931), so appropriate hosts would have been standing ready for infestation.

with the point of introduction at some time before discovery in the new area. There are several reasons to consider the hypothesis that "the wheat stem sawfly did not have the means and opportunity to be introduced" to be refutable.

Benson (1962) summarizes data on 31 species of sawflies introduced across the Atlantic, suggesting packing materials and ballast as the means of transport for several species. Two of those 31 introduced species are congeneric or contribal with the wheat stem sawfly, and their documented histories of introduction provide insight into the means of introduction for wheat stem sawfly. The stem-feeding habits of the wheat stem sawfly, the European wheat stem sawfly, and the black grain stem sawfly are virtually identical (Wallace and McNeal 1966). The European wheat stem sawfly first was reported in North America in 1887 attacking wheat in New York and eastern Canada (Comstock 1889, Wallace and McNeal 1966). Comstock (1889) recognized the species as introduced. The black grain stem sawfly, initially named as new (*Calamenta* [sic] *johnsoni* Ashmead), was found in New Jersey in 1899 and later correctly identified as a well-known species from western Europe (Gahan 1920, Wallace and McNeal 1966).

Thus, some members of the genus are obviously subject to dispersal by human activities (Benson 1962, Wallace and McNeal 1966), and the wheat stem sawfly presumably could have been introduced via the same mechanisms by which the two European species were introduced. The adult is rather delicate and short-lived, and the egg and young larvae are found only in growing grass stems. Older larvae and pupae occur in straw and root stubs and are the most likely stages transported to North America. Straw was an important packing and bedding material for both humans and domestic stock in the nineteenth and early twentieth centuries. Salt (1931) showed that, in an English field harvested with a mechanical scythe, 8-13% of European wheat stem sawfly larvae were "harvested" with the wheat straw. Also, because not all stems break (Morrill et al. 1992b), these late larvae and pupae occasionally could survive in straw harvested by sickle. Further, stems of barley often are not cut (Farstad and Platt 1946, Anonymous 1947), making barley straw even more likely to contain the sawfly. None of these studies addressed the survival of sawflies in straw, but Holmes' (1953) statements indicate the reports that wheat stem sawflies overwinter only in stubs may be the result of no one looking elsewhere.

Propagules also could occur in stubs attached to medicinally important wheat and wheat grass (*Agropyron* spp.) roots. A common medicine during the eighteenth and nineteenth century was a diuretic tea made from these roots (Crenllin and Philpott 1989), so root bundles could be expected in a ship's medical supplies and as trade goods to new colonies. Thus, there were ample means for introduction.

What opportunities existed for a species of *Cephus* to be transported from northeastern Asia to western North America? In the late eighteenth century, the Russian America Company extended its fur trade to Alaska (Gibson 1976). Supply was overland from the Company base in Irkutsk, via Yakutsk to Okhotsk (Fig. 2). Ships from Okhotsk then transported goods to New Archangel (now Sitka, Alaska) (Gibson 1976). Because the lines of supply were so long and difficult, an agricultural colony, New Albion, was founded in 1812 on the California Coast about 100 km north of San Francisco. With headquarters at Ross (now Fort Ross) and a port at Port Rumiantsev (Bodega Bay) (Gibson 1976, Lightfoot et al. 1993), the settlement extended 15 km inland to Chernykh Rancho (Freestone) (Gibson 1976). This colony of Imperial Russia continued until 1841, raising wheat, barley, rye, and other crops as well as cattle (Gibson 1976); hunting and trading furs; and even building small coastal ships (Gibson 1976, Lightfoot et al. 1993). The outpost of up to 800 people was sophisticated enough to have houses with glass windows, a windmill, a hot house, and three threshing floors (Bancroft 1886, Essig 1953, Gibson 1976, Lightfoot et al. 1993). Russian-era traded goods from Eurasia that were recovered at Fort Ross also included glass bottles, porcelain, stoneware, creamware, and earthenware (Lightfoot et al. 1993). These items were breakable, and were most likely brought from Russian Asia packed in straw.

The settlement was supplied with these and other manufactured goods via the old Irkutsk-Okhotsk-Sitka route (Fig. 2). Goods were packed in Irkutsk in the winter, carted in spring to the Lena, and floated to Yakutsk during high water in 4-6 weeks. During late spring and summer, the goods were repacked for mule trains headed to Okhotsk, arriving after 2-4 months passage, usually from mid-June to mid-August. This trade was large enough to employ 10,000 to 15,000 packhorses annually (Gibson 1976).

At Okhotsk, freight was loaded on ships that left in late August or early September for New Archangel, usually arriving in October. From there, a single ship each year continued to Bodega, arriving in November to supply New Albion (Gibson 1976).

This transportation schedule fits well with the biology of wheat stem sawfly. Straw and root bundles containing larvae probably could be obtained almost anywhere along the Asian trade route (Fig. 2), and contaminated ballast was probably available at the port. The larvae mature in summer, before the stems dry, and would have been ready for transport when straw was ready to harvest. Also, the cool, moist conditions on the ship would have encouraged survival. When spring came the contagion would have reached the California coast. Once in California, the farming by the Russians and the ranching by the Spanish and Mexicans provided many introduced grasses (Hendry 1931), so appropriate hosts would have been standing ready for infestation. Middlekauff (1969) reports wheat stem sawfly throughout the general area of New Albion. Both wheat stem sawfly and its parasitoids, and perhaps *Calameuta clavata* as well, could have easily arrived this way.

Other opportunities also could have arisen for introduction. Traffic between the west coast of North America and China after the Opium War (1840-1842), and with Japan after the second visit of Admiral M. C. Perry (1854), linked these areas with California (Muscatine 1975). Wheat stem sawfly's known Asian distribution (not yet reported from China) is rather distant from major trading points, but it is possible that one of these countries actually served as the source or a source of introduction.

How could the species go from the California coast to expand across the continent? After several years of construction, the Central Pacific and Union Pacific Railroads connected California with the East in 1869 (Warman 1898). Construction involved hundreds of stock animals (Warman 1898) and left a ribbon of disturbed soil with Eurasian weedy grasses stretching across North America. During and after construction, straw in the form of stock bedding and packing material was moved East daily from California. An adult sawfly that flew into a train car could have been transported hundreds of miles by the next day and found a hospitable habitat awaiting. Ainslie (1920) recognized the association of wheat stem sawfly with railroad right-of-ways during life-history investigations in 1911-1912 (Fig. 4).

Not surprisingly, the first collections of wheat stem sawfly from California (Alameda), Nevada, and Colorado were from along the route. No report of wheat stem sawfly was made from any area before a rail connection was established with California (Fig. 1). The connection from the Union Pacific into Manitoba was in 1873 (Morton 1957), into Saskatchewan in 1882, and across Canada to the Pacific in 1895 (Richards 1969). The Utah and Northern line reached western Montana in 1880, and Bozeman was on the Northern Pacific line in 1883 (Paullin 1932, Houston 1933). Thus, the means of dispersal to all early localities was available to the wheat stem sawfly several years before detection.

Conclusion

All of the evidence seems consistent with the hypothesis that the wheat stem sawfly is an introduced species in North America.

Discussion

Lindroth (1957) proposed five rules of thumb to distinguish obviously anthropophilic immigrant species. These rules are of little use when used to evaluate pestiferous species. Turnbull (1979), when speaking of the Canadian fauna, states that "it is not difficult to imagine an exotic species that meets none of these (Lindroth's) conditions. There are pest species with a history of introduction that is but vaguely understood, that have spread across the continent, have invaded native environments, have attacked native plants, and do not show any clear dimorphism of form, but are nevertheless believed to have been introduced recently. The larch sawfly, *Pristiphora erichsonii* [(Hartig) (Tenthredinidae)], is one such species, and the oriental fruit moth, *Grapholitha molesta* [(Busck) (Tortricidae)] is another" [bracketed material added]. To this group I might add the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), a species that spread across western North America in just a few years during the 1980s (Morrison et al. 1988).

Benson (1962) suggested three criteria for identifying introduced sawflies. Wheat stem sawfly matches two of these: (1) recent appearance followed by epidemic numbers, and (2) attachment to introduced plants. Benson also notes that a high proportion of introduced sawflies (greater than one-half) exhibit thelyotokous parthenogenesis in the non-native populations. Wheat stem sawfly has repeatedly had initial populations that exhibit thelyotoky (Farstad 1938, Mackay 1955), indicating founding populations. Indeed the pest was present in Alberta for many years before a male was found.

Whitehead and Wheeler (1990) provide a discussion of other criteria appropriate to this case. Their first test, the temporal/geographic test, supports the adventive status of wheat stem sawfly. Their criterion "if earlier collections made at the place of first appearance were negative" seems in line with the data presented above. Their second test, unnatural disjunction, carries the criterion "does it belong to an extralimital group?" This also fits with the case here. For an example similar to the case of wheat stem sawfly, see their treatment of *Asciodema obsoletum* (Fieber) (Miridae) (Whitehead and Wheeler 1990, Wheeler and Henry 1992).

There are many examples of species being described as native and later discovered to be introduced: the coffee leaf-miner, *Leucoptera coffeella* (Guérin-Méneville) (Lyonetiidae) (Green 1984); the sweetclover weevil, *Sitona cylindricollis* Fåhraeus (Curculionidae) (Bright 1994); a widespread dung-inhabiting hydrophilid, *Sphaeridum scarabaeoides* (L.) (Hydrophilidae) (Smetana 1976); and an important Canadian elaterid pest, *Agriotes obscurus* (L.) (Elateridae) (Becker 1956), are well known examples.

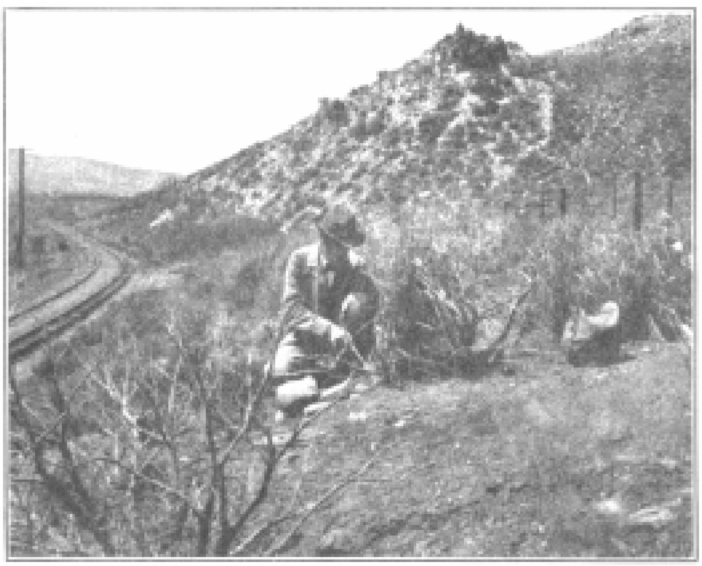

Fig. 4. Photograph from Ainslie (1920), published with the caption "Plants of *Elymus condensatus* growing along the railroad right of way. The natural habitat of the western grass-stem sawfly in Utah."

Other examples are particularly relevant to the current study. The pest named *Calamenta* [sic] *johnsoni* Ashmead was discovered to be the introduced black grain stem sawfly a decade later (see Gahan 1920 for a discussion). *Heterospilus cephi* Rohwer, a parasitoid of the European wheat stem sawfly, is another example. In a situation parallel to the North American name of wheat stem sawfly being older than the Asian name (Ivie and Zinovjev 1996), *H. cephi* originally was described from North America in 1925. The discovery of a 1960 European name that proved to be a junior synonym was used to hypothesize its introduction (Marsh 1973).

Turnbull (1979) suggests that many of the so-called Holarctic distributions of species in temperate, human-modified environments are actually human-facilitated introductions, a suspicion I share. Insect introductions from Europe are relatively well studied (e.g., Lindroth 1957, Benson 1962, Turnbull 1979, Larson and Langor 1982, Hamilton 1983, Wheeler and Henry 1992), but there is a decided lack of documentation of similar exchanges between northeast Asia and North America.

Most of the world's insect systematists are concentrated along the shores of the North Atlantic. Although there is a smaller concentration on the shores of the northern Pacific, scientists from North America and Japan long have been excluded from mainland northeast Asia. Even those Western scientists who attempt to do modern revisions of Holarctic taxa have a difficult time obtaining material from the eastern Palearctic. These collections are relatively small and are concentrated in places where colleagues have trouble making loans by mail because of mail systems that are too uncertain to risk using, too expensive relative to hard-pressed budgets, or too burdened by bureaucratic rules that hamper them with restrictive export/import regulations.

With the increasing importance and openness of the northwestern Pacific Rim to U.S. and Canadian trade, an increase in introductions is likely to occur. Introductions of Asian gypsy moth, *Lymantria dispar* (L.) (Lymantriidae), via ships from Siberia (USDA 1993, Campbell 1997) may be just the most obvious of new immigrants accompanying expanded trade across the North Pacific. It is important that collections and revisions that address the faunas of both sides of the Northern Pacific be increased as soon as possible to be able to identify both existing introduced populations and new ones.

Correct identification of these introductions is critical to identify appropriate candidates for biological control efforts, predict source areas for biological control agents, and even to avoid the possibility of unknowingly using scarce resources to conserve rare populations of non-native species.

My conclusion that wheat stem sawfly is a species introduced from northeast Asia is still a hypothesis. As such, there are dependent hypotheses that can be used to refute this conclusion: (1) if *Bracon cephi* is not found to be conspecific with Asian populations (If *B. lissogaster* is found to be an obligate parasitoid of wheat stem sawfly, it can be added to this hypothesis); (2) if wheat stem sawfly in North America does not exhibit a subset of the Asian population's maternal (i.e., mitochondrial) DNA; and (3) if wheat stem sawfly in North America does not have less total and geographic variation in nuclear DNA than its Asian populations; then the introduction hypothesis would be refuted.

If the *Bracon* species proves to be North American endemic specialists on wheat stem sawfly, it must be concluded that the host also was here and therefore native. Revisions and biological investigations of the *Bracon cephi* and *B. lissogaster* groups will be required to use this test.

Wheat stem sawfly usually exhibits the normal haplo-diploid sex determination system of the Hymenoptera with arrhenotokous production of males (Mackay 1955), but all-female thelyotokous populations are known (Farstad 1938, Mackay 1955). How this ability affects the normal hymenopteran selection pressures that maintain heterozygosity in order to produce females (Croizer 1977) will have to be investigated before genetic diversity can be used to refute the hypothesis. But, in any case, an introduced population should have less than the full complement of native variability. Because only a few individuals, when placed in the context of a species stretching across nearly 90° of Eurasian latitude, could have made the journey, and since 175 years or less of evolutionary time have occurred in the interim, introduced genetic diversity must be less than native. This restriction would apply to both nuclear and mitochondrial elements. Because there is no reason to assume a single introduction event, source, or individual, some variation in North America is not a successful refutation. Although support might be possible with relatively small Asian samples, refutation will require a large effort.

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