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World Review of the Parasitoids of the Southern Green Stink Bug, *Nezara viridula* (L.) (Heteroptera: Pentatomidae)

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World Review of the Parasitoids of the Southern Green Stink Bug, *Nezara viridula* (L.) (Heteroptera: Pentatomidae)

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ABSTRACT A survey of published and unpublished information was used to compile a list of insect parasitoids recorded emerging from *Nezara viridula* (L.) in the field worldwide. Fifty-seven species among two families of Diptera and five families of Hymenoptera are recorded; 41 are egg parasitoids. No hyperparasitoids are known. Most species are not closely associated with *N. viridula*, although some are well adapted and the status of others is unclear. Six species of Nearctic and Neotropical Tachinidae are well adapted to adult *N. viridula* and could become established in new areas; they also attack large nymphs. There are no effective parasitoids specific to nymphs. The scelionid *Trissolcus basalis* (Wollaston), probably of Old World origin, is the most widespread egg parasitoid and now occurs with *N. viridula* in the New World, coastal Africa, southern Europe, Pakistan, Australia, New Zealand, and some Pacific islands. Unique complexes of egg parasitoids occur in parts of Africa and eastern Asia. Based on the distribution of the genus *Nezara* and its species' color polymorphs and egg parasitoid complexes, *N. viridula* is considered to be of Ethiopian origin. African and Asian egg parasitoids in the genera *Trissolcus*, *Telenomus*, and *Gryon*, plus six New World Tachinidae, should be considered for establishment against *N. viridula* elsewhere.

KEY WORDS Insecta, *Nezara viridula*, parasitoids, biological control

THE SOUTHERN green stink bug, *Nezara viridula* (L.), is one of the most important insect pests of agricultural crops in the world. Its high vagility and polyphagous feeding habits, combined with passive spread via international commerce, have enabled the insect to become widely established around the world. It presently occurs in most of the warmer regions, damaging a wide variety of fruit, nut, grain, and vegetable crops (DeWitt & Godfrey 1972, Todd & Herzog 1980). With the expansion of soybean production in the warmer regions of the Americas during the last two decades, and of other crop hosts elsewhere, *N. viridula* has become the focus of intensified research on control measures. The insect invaded California's Sacramento Valley in 1986 and now poses a serious threat to several crops throughout the state (Hoffman et al. 1987). As cropping patterns of susceptible cultivated plants change, *N. viridula* will continue to become increasingly important worldwide.

Because it is a known emigrant to areas outside Africa and eastern Asia, there have been several attempts to establish parasitoids in newly invaded areas, primarily in the Pacific Basin (Wilson 1960, Rao et al. 1971). The programs in Hawaii and Australia have been considered very successful (DeBach 1962, Clausen 1977, Caltagirone 1981), largely because of the establishment of the egg parasitoid *Trissolcus basalis* (Wollaston) (Scelionidae). *Trichopoda pennipes* (F.) and *T. pilipes* (F.) (Tachinidae) from the Americas have been released as part of the same projects but have become established only in Hawaii. Clausen (1977) and Luck (1981) have reviewed the various importation programs for which information was available. Classical biological control programs currently are active in the southern United States, Argentina, Chile, Brazil, Taiwan, New Zealand, South Africa, and Cape Verde, Africa.

Both *T. basalis* and *T. pennipes* occur with *N. viridula* in the United States, but the host continues to be a major pest where its range overlaps with those of soybean and other susceptible crops. Although attempts have been made to establish new parasitoids in the United States (Lee 1979, Jones et al. 1983, 1985, Jones 1984, Orr 1985), generally the species imported have been the result of fortuitous opportunities rather than the result of organized efforts from classically planned programs.

This paper presents the known parasitoids of *N. viridula* worldwide. The information may suggest new sources of parasitoids for distribution to new areas. Pathogens and predators are not considered here. Native predators are important mortality factors (Panizzi & Slansky 1985). There are no known records of significant pathogen epizootics in this species. However, searches for pathogens are in progress by Brazil and the United States Department of Agriculture.

The parasitoid species listed include those emerged from field-collected hosts reported in the literature and from unpublished data of my own

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and others. Scientific names reflect the current accepted status for each taxon. The list of known parasitoids (Table 1) is arranged in systematic order and includes geographic range, a brief and somewhat subjective description of known host relations, followed by the most pertinent references.

The text is arranged according to the host stage attacked and is an initial attempt to separate casual associations from those having current and potential use as biological agents against *N. viridula*. The geographic origin of *N. viridula* is also discussed.

Results and Discussion

Fifty-seven species among two families of Diptera and five families of Hymenoptera are recorded from *N. viridula* worldwide (Table 1). Some of the species names may be synonyms. Parasitoids have been reported from all three life stages.

Egg Parasitoids. Of the five families of Hymenoptera recorded as emerging from the eggs of *N. viridula*, the Scelionidae is the most important. The scelionid, *T. basalis*, is both the most important and the most widely distributed species. It is frequently recorded from several other pentatomids but is clearly most closely associated with *N. viridula* (Cumber 1964, Thomas 1972, Jones 1979, Buschman & Whitcomb 1980, Ferreira 1980, 1986, Jones 1984, Orr et al. 1984, 1986, Temerak & Whitcomb 1984). *Trissolcus basalis* is the dominant egg parasitoid of its primary host in the Americas, the Mediterranean Basin, the Middle East, and Pakistan, and has been established in Hawaii, Australia, New Zealand, and other Pacific islands as part of biological control programs (Lever 1941a, Wilson 1960, Davis 1964, 1967, Rao et al. 1971). Although widely distributed, *T. basalis* appears to be confined primarily to coastal areas within its range. This species was introduced into Taiwan (Su & Tseng 1984) and Argentina (Crouzel & Saini 1983) from cultures imported from Hawaii and Australia, respectively. Chile recently imported this parasite from Brazil for possible release (E. Zúñiga, personal communication). A culture of *T. basalis* from Morocco has been imported and studied in the U.S.S.R. for comparison with other *Trissolcus* spp. (Shapiro et al. 1975). Numerous studies have been published on the biology and behavior of *T. basalis*, and research is continuing (Miller 1928, Kamal 1937, Noble 1937, Wilson 1961, Ganesalingam 1966, Thomas 1972, Shapiro et al. 1975, Sales et al. 1978, Powell & Shepard 1982, and others).

Nine other egg parasitoids have been recorded from *N. viridula* in the Americas. *Telenomus cristatus* Johnson (Scelionidae), recently described from *N. viridula* eggs from Florida and Trinidad (Johnson 1984a), has since been recovered from another pentatomid, *Acrosternum hilare* (Say), in Louisiana soybeans but not from *N. viridula* eggs in the same fields (Orr et al. 1986). There is no evidence that other New World records indicate more than incidental relationships with *N. viridula*.

Ooencyrtus spp. (Encyrtidae) have been reported from *N. viridula* eggs throughout most of the range of this pentatomid, but are never a major component of the parasitoid complex. Most species are known to have a broad host range within the Heteroptera. *Ooencyrtus submetallicus* (Howard) occurs in Florida, the West Indies, Brazil, and Argentina (Howard 1898, Myers 1931, Buschman & Whitcomb 1980, de Santis 1985, Ferreira 1986). This species was imported from the West Indies into Louisiana, Hawaii, Australia, and New Zealand (Wilson 1960, Davis & Krauss 1963, Davis 1967, Lee 1979), but failed to become established. Lee (1979) concluded that *O. submetallicus* was inferior to *T. basalis* in dispersal and host-finding ability in soybeans in Louisiana.

Four other *Ooencyrtus* spp., including *O. malayensis* Ferrière, *O. trinidadensis* Crawford, and *O. nezarae* Ishii, have been imported and evaluated in a quarantine facility in the United States and shown to attack at least 20 species of native Pentatomidae, Coreidae, and Rhopalidae (Jones et al. 1983, unpublished data). These species were not released because of their wide host range and lack of evidence of effectiveness in their native regions. *Xenoencyrtus rubricatus* Riek is known only from a single recovery from *N. viridula* eggs in Australia (Riek 1962). A related species, *X. niger* Riek, was successfully cultured on *N. viridula* eggs from a single captured female and subsequently reared and released in New Zealand and Hawaii, but has not been recovered from field-collected host eggs (Riek 1962, Davis 1967, Clausen 1977).

Anastatus spp. (Eupelmidae) are only rarely reported from *N. viridula*. The host range of *Anastatus* spp. frequently includes more than one insect order. Species that attack *N. viridula* produce only males; females can be produced only in larger host eggs (Hokyo & Kiritani 1966b, Rao et al. 1971, Genduso 1976, unpublished data). Augmentative releases of an *Anastatus* sp. are routinely made in China against the lichee stink bug, *Tessaratoma papillosa* Drury (Tessaratomidae); the parasitoids are mass-produced in large Lepidoptera eggs (Ming-Dau et al. 1974).

Adair (1918) reported the recovery of a *Pteromalus* sp. (Pteromalidae) from *N. viridula* in Egypt. Ferriera (1981, 1986) recovered the eurytomid *Neorileya* sp. in low numbers from *N. viridula* eggs in Brazilian soybeans. Pteromalids and eurytomids have been reported as occasional hyperparasitoids, but there are no records of demonstrated hyperparasitism in *N. viridula*.

A unique complex of Japanese egg parasitoids of *N. viridula* has been studied in detail (Kiritani & Hokyo 1962, 1970, Hokyo & Kiritani 1963, 1966a,b, Kiritani et al. 1963, Hokyo et al. 1966, Nakasuji et al. 1966, Kiritani & Sasaba 1969). *Trissolcus mitsukurii* (Ashmead) and *Telenomus chloropus* Thomson (as *T. nakagawai* Watanabe) occur together in Japan and are important mortality factors of both *N. viridula* and the oriental stink bug,

Table 1. Parasitoids of the southern green stink bug, *Nezara viridula* (L.)

Parasitoid taxa	Geographic range	Known host relations	Selected references
DIPTERA			
Tachinidae			
Gymnosoma clavata (Rohdendorf)	Palearctic, Israel	One record ex *N. viridula*	Herting 1960
Gymnosoma rotundata (F.)	Palearctic	Wide host range; attacks *Nezara* spp. in Japan	Kiritani et al. 1963, Kiritani & Sasaba 1969
Bogosia antinorii Rondani	Ethiopian	Recorded ex *N. viridula;* other hosts unknown	Greathead 1966, 1971, Barraclough 1985
Trichopoda pennipes (F.)	North America, Hawaii	Well adapted to *N. viridula*	Drake 1920, Todd & Lewis 1976, Jones 1979, Buschman & Whitcomb 1980, McPherson et al. 1982
Trichopoda pilipes (F.)	West Indies, Hawaii	Well adapted to *N. viridula*	Myers 1931, Nishida 1966, Davis 1967
Trichopoda lanipes (F.)	Southern USA	One record ex *N. viridula;* attacks other species	Drake 1920
Trichopoda giacomellii (Blanchard)	Argentina	Well adapted to *N. viridula*	Liljesthröm 1980, 1981
Trichopoda gustavoi (Mallea)	Argentina	Well adapted to *N. viridula*	Mallea et al. 1968
Trichopoda nigrifrontalis (Blanchard)	Argentina	Descr. ex *N. viridula;* other hosts unknown	Blanchard 1966
Trichopoda sp.	Uruguay	One record ex *N. viridula*	Guido & Ruffinelli 1956
Eutrichopodopsis nitens Blanchard	Brazil, Colombia, Argentina	Well adapted to *N. viridula*	Gastal 1977a,b, Ferreira 1984
Ectophasiopsis arcuata (Bigot)	Chile	Well adapted to *N. viridula*	E. Zúñiga, personal communication
Cylindromyia rufifemur Paramonov	Australia	One record ex *N. viridula*	Cantrell 1984
Sarcophagidae			
Sarcodexia innota (Walker)	Southern USA	Two records ex *N. viridula;* wide host range as primary parasitoid and scavenger	Drake 1920, Temerak & Whitcomb 1984
HYMENOPTERA			
Pteromalidae			
Pteromalus sp.	Egypt	One record ex *N. viridula*	Adair 1918
Eurytomidae			
Neorileya sp.	Brazil	Recorded ex *N. viridula;* other hosts unknown	Ferreira 1981, 1984, 1986
Eupelmidae			
Anastatus japonicus Ashmead	East Asia	Lepidoptera, Heteroptera; produces only males in *N. viridula*	Kiritani & Sasaba 1969, Hokyo & Kiritani 1966b
Anastatus dasyni Ferrière	Malaysia	Pentatomidae, Coreidae; described ex *N. viridula*	Van der Vecht 1933
Anastatus sp.	Thailand	Emerged ex imported eggs of *N. viridula*	W. Jones, unpublished data
Anastatus sp.	Southern USA	Two records ex *N. viridula*	W. Jones, unpublished data
Encyrtidae			
Hexacladia hilaris Burks	USA	One record ex *N. viridula*	Buschman & Whitcomb 1980
Ooencyrtus nezarae Ishii	East Asia	Coreidae, Pentatomidae, Plataspidae; not uncommon on *N. viridula* in Japan	Hokyo & Kiritani 1966b
Ooencyrtus submetallicus (Howard)	West Indies, Central and South America	Pentatomidae, Coreidae	Harland 1917, Gahan 1927, Lee 1979, de Santis 1985, Ferreira 1986
Ooencyrtus malayensis Ferrière	Malaysia, Philippines	Pentatomidae, Coreidae, Lepidoptera	Van der Vecht 1933, Jones et al. 1983
Ooencyrtus trinidadensis Crawford	West Indies, Argentina	Pentatomidae, Coreidae	Davis & Krauss 1963, Davis 1967, de Santis 1985
Ooencyrtus sp.	Brazil	One record ex *N. viridula*	Ferreira 1986
Ooencyrtus sp.	Thailand	Emerged ex imported eggs of *N. viridula*	W. Jones, unpublished data
Ooencyrtus sp.	Philippines	One record; possibly is *O. malayensis*	Corpuz 1969
Ooencyrtus sp.	France	One record; recovered ex other pentatomids	W. Jones, unpublished data
Ooencyrtus sp. (spp.?)	Southern USA	Taxonomy and host range not known	Drake 1920, Buschman & Whitcomb 1980, W. Jones, unpublished data
Xenoencyrtus rubricatus Riek	Australia	Described ex *N. viridula;* not recorded since	Riek 1962

Table 1. Continued

Parasitoid taxa	Geographic range	Known host relations	Selected references
Scelionidae			
Psix lacunatus Johnson & Masner	Asia, Australia	Pentatomidae, Scutelleridae; ex *N. viridula* in Pakistan	Johnson & Masner 1985
Psix striaticeps (Dodd)	Africa, India	Pentatomidae; recorded once ex "*Nezara*"	Fouts 1934, Johnson & Masner 1985
Telenomus chloropus Thomson	Palearctic	Pentatomidae; *Nezara* spp. in E. Asia; thelytokous form in Japan	Kiritani & Hokyo 1962, Hokyo & Kiritani 1963, Johnson 1984a
Telenomus cyrus Nixon	Java, Philippines, Taiwan	Descr. ex *N. viridula;* host relations unknown	Nixon 1937, Taiwan Agricultural Research Institute 1984, M. Shepard, personal communication
Telenomus gifuensis Ashmead	East Asia	Pentatomidae, Coreidae; not well adapted to *N. viridula*	Hidaka 1958, Hokyo & Kiritani 1963
Telenomus mormideae Costa Lima	South America	One record ex *N. viridula;* attacks other pentatomids	Ferreira 1986
Telenomus podisi (Ashmead)	North and South America	Pentatomidae; not well adapted to *N. viridula*	Buschman & Whitcomb 1980, Orr et al. 1985
Telenomus seychellensis Kieffer	East Africa	Attacks other spp.; may be common on *N. viridula*	Nixon 1935, Croix & Thindwa 1986
Telenomus cristatus Johnson	Southern USA, West Indies	Known only ex *N. viridula* and *Acrosternum hilare* (Say)	Johnson 1984a, Orr et al. 1986
Trissolcus aloystisabaudiae (Fouts)	East Africa	Reportedly common on *N. viridula* in cotton	Fouts 1930, Chiaromonte 1931, Paoli 1933
Trissolcus basalis (Wollaston)	N. and S. America, S. Europe, Africa, Hawaii, Australia, New Zealand, Fiji	Most important parasitoid of *N. viridula* outside central Africa and eastern Asia	Miller 1928, Kamal 1937, Lever 1941b, Buschman & Whitcomb 1980, Ferreira 1980, Orr et al. 1986
Trissolcus brochymenae (Ashmead)	N. and S. America	Recorded ex *N. viridula;* attacks other pentatomids	Johnson 1984b
Trissolcus hullensis (Harrington)	North America, Venezuela	Recorded ex *N. viridula;* attacks other pentatomids	Johnson 1985a
Trissolcus lepelleyi (Nixon)	Central Africa	Descr. ex *N. viridula*, an apparently common host	Nixon 1966, Le Pelley 1979
Trissolcus lodosi (Szabó)	Turkey	Descr. ex *N. viridula;* nothing else known	Szabó 1981
Trissolcus maro Nixon	Southern Africa	*N. viridula* is only known host	Nixon 1935, Croix & Thindwa 1986
Trissolcus mitsukurii (Ashmead)	Japan	Important parasitoid of *N. viridula* in Japan	Kiritani & Hokyo 1962, Hokyo & Kiritani 1963
Trissolcus scuticarinatus (Costa Lima)	South America	One record ex *N. viridula;* attacks other pentatomids	Ferreira 1986
Trissolcus sipius (Nixon)	East Africa	Descr. ex *N. viridula* but not reported since	Nixon 1936
Trissolcus solocis Johnson	Florida, Mexico	Recorded ex *N. viridula;* attacks other pentatomids	Buschman & Whitcomb 1980, Johnson 1985a
Trissolcus thyantae Ashmead	Eastern N. America	Recorded ex *N. viridula;* attacks other pentatomids	Johnson 1985b
Trissolcus sp.	Taiwan	Recorded ex *N. viridula;* host relations unknown	Taiwan Agricultural Research Institute 1984
Gryon fulviventris (Crawford)	Africa, Asia	Pentatomoidea; attacks *N. viridula* only in Thailand	Anderson 1919, Dry 1921, W. Jones, unpublished data
Gryon obesum Masner	Southern USA	One record ex *N. viridula;* attacks other pentatomids	Buschman & Whitcomb 1980, Masner 1983
Gryon sp.	Laos	One record ex *N. viridula;* may be *G. fulviventris*	Grist & Lever 1969, Dean 1978a,b
Gryon sp.	India	One record ex *N. viridula*	Yadava et al. 1982

N. antennata Scott, in rice. *Ooencyrtus nezarae* Ishii frequently occurs in low numbers, and *Anastatus japonicus* Ashmead has been reported from *N. viridula* eggs. Some of the *A. japonicus* reported by Hokyo et al. (1966) may have been *A. gastropachae* Ashmead (Y. Hirose, personal communication). *Trissolcus mitsukurii* is known only from Japan.

The taxonomy of *Telenomus chloropus* has been discussed recently by Johnson (1984a). *T. chloropus* is a common polyphagous parasitoid of pentatomid eggs across the Palearctic Region, but it apparently attacks *Nezara* spp. only in Thailand, Korea, and Japan. The Japanese form is uniquely thelytokous, rarely producing males; the continental populations are arrhenotokous, yet all forms are morphologically similar (Johnson 1984a). In the laboratory, Korean males readily attempt matings with uniparental Japanese females, but the females do not respond and matings are unsuccessful (unpublished data). The Japanese form has been released in Australia (Field 1984), Hawaii (Clausen 1977), and the United States (Jones 1980, Jones et al. 1983, Orr 1985) but has not become established, possibly because of its high humidity requirement for successful emergence (Orr et al. 1985). Both *T. mitsukurii* and *O. nezarae* have recently been imported and released in Brazil (Kobayashi & Cosenza 1987). The *T. basalis* reportedly released in Australia from Japan (Clausen 1977) was evidently *T. mitsukurii*. T. Kobayashi (personal communication) has recorded *Trissolcus japonicus* (Ashmead) and *Telenomus hakonensis* Ashmead from the eggs of *N. antennata* in Japan, but these parasitoids have not been reported from *N. viridula*.

Thailand has a slightly different complex of egg parasitoids. The most abundant species received in shipments from explorers in Thailand was the scelionid *Gryon fulviventris* (Crawford), not previously recorded from *N. viridula* (unpublished data). *Gryon fulviventris* (as *Dissolcus fulviventris* Mayr, *Hadronotus fulviventris* (Mayr), *H. antestiae* Dodd, and *G. antestiae* (Dodd), all synonymized by Mineo 1979) occurs from Africa through India, Thailand, southern U.S.S.R., and Malaysia, where it has been recorded from many species of Pentatomidae, Scutelleridae, and Coreidae but never previously from *Nezara* spp. Whitfield & Cameron (1932) reported that African *G. fulviventris* readily parasitized and developed in *Nezara* eggs but adults could not emerge successfully. Eggs of both *N. viridula* and *Piezodorus hybneri* (Gmelin) imported from Thailand were heavily parasitized by *G. fulviventris* (unpublished data). The parasitoid should be of interest in South America where *Piezodorus guildinii* Westwood, together with *N. viridula*, seriously damage soybeans but do not share the same native egg parasitoids. As with *T. chloropus*, biotypes evidently exist across the broad geographic range of *G. fulviventris*. The eggs from Thailand also were parasitized by *T. chloropus*, *O. nezarae*, and *Anastatus* sp. (Jones et al. 1983, unpublished data). The *Gryon* sp. reported from *N. viridula* eggs in Laos (Grist & Lever 1969, Dean 1978a,b) and India (Yadava et al. 1982) may be *G. fulviventris*.

Telenomus cyrus Nixon (1937) was described from specimens emerged from a *N. viridula* egg mass collected in Java and has recently been collected from *N. viridula* eggs in the Philippines (M. Shepard, personal communication). *Telenomus cyrus* was the most important egg parasitoid of *N. viridula* in soybean, jute, and rice in central Taiwan (Taiwan Agricultural Research Institute 1984). Maximal parasitism was 19% in soybean, 0.1% by a *Trissolcus* sp.

Telenomus gifuensis Ashmead, a common parasitoid of several Japanese pentatomids, has been recovered from *N. viridula* eggs (Kiritani & Sasaba 1969). Similarly, *Telenomus podisi* Ashmead in eastern North America, a common egg parasitoid of many North American pentatomids, has been recorded emerging from *N. viridula* eggs (Buschman & Whitcomb 1980, Orr et al. 1985, unpublished data). Field-collected egg masses that have yielded *T. podisi* usually also yield *T. basalis* in larger numbers (Orr et al. 1984, 1986). Both *Telenomus* spp. rarely emerge from *N. viridula* eggs exposed in the laboratory (Thames 1954, unpublished data).

At least six Scelionidae have been described or recorded from *N. viridula* eggs in Africa. These parasitoids include *Trissolcus aloysiisabaudiae* (Fouts), *T. basalis*, *T. lepelleyi* (Nixon), *T. maro* (Nixon), *T. sipius* (Nixon), and *Telenomus seychellensis* Kieffer. Croix & Thindwa (1986), in the only study of egg parasitoids of *N. viridula* in Africa, reported an average of 74% parasitism in Malawi on macadamia by *T. maro* and *T. seychellensis*. This is the first mention of *T. maro* since its description by Nixon (1935) from southern Africa. Paoli (1933) reported that *T. alloysiisabaudiae* was very common on *N. viridula* eggs in Somalia, completely destroying many egg masses. Both *T. lepelleyi* and *T. sipius* were described from *N. viridula* eggs in East Africa. During 1961, *T. seychellensis* and *G. fulviventris* were shipped from Pakistan to both Australia and Trinidad but failed to breed in the laboratory (Rao et al. 1971). The original hosts in Pakistan were not specified.

Psix striaticeps (Dodd) (Scelionidae), known from tropical Africa to India, has been recorded from *N. viridula*. *Psix lacunatus* Johnson & Masner is widely distributed in Asia and Australia and has been recorded from *N. viridula* eggs only in Pakistan (Johnson & Masner 1985). Nothing can be concluded from the other scattered host–parasitoid records.

Nymph Parasitoids. The nymphal stages of Pentatomidae are generally free from significant attack by parasitoids. Certain Braconidae and Stylopidae are recorded as nymph or nymph–adult parasitoids of a few Pentatomidae, but none has been reported from *Nezara* spp. *Hexacladia hilaris* Burks (Encyrtidae) has been recovered occasionally from *N. viridula* in the southern U.S. and Puerto Rico (Buschman & Whitcomb 1980, F. D. Bennett, personal communication). Its only other recorded host is the pentatomid *Acrosternum hilare* (Burks 1972, Jones 1979).

Six related Diptera (Tachinidae: Phasiinae) in the New World frequently deposit eggs on the larger *N. viridula* nymphs but are better adapted to the adult stage of their hosts (Capelouto 1949, Mallea et al. 1968, Gastal 1977b, Buschman & Whitcomb 1980, Liljesthröm 1981, Ferreira 1984, and others). These species are discussed below.

Adult Parasitoids. Tachinidae are the only known parasitoids that attack adult *N. viridula*. In Japan, *N. viridula* is parasitized by *Gymnosoma rotundata* (F.), a widely distributed tachinid in the Palearctic Regions and known from many hosts. Up to 5% parasitism has been recorded by Kiritani et al. (1963). This species also attacks *N. antennata* in Japan and Korea (Kiritani et al. 1963, unpublished data). Outside of Japan, there are no published records of tachinids regularly attacking *N. viridula* in the Palearctic and Indo-Malayan Regions. *Gym-*

nosoma clavata (Rohdendorf) is recorded once from *N. viridula* in Europe (Herting 1960).

In the Ethiopian Region, *N. viridula* adults are attacked by *Bogosia antinorii* Rondani. Greathead (1971) referred to an unsuccessful attempt to establish this parasitoid in Australia from specimens collected in Kenya. This tachinid is widespread in eastern and southern Africa and its only recorded host is *N. viridula* (van Emden 1945, Barraclough 1985).

In the New World, where *N. viridula* is a known immigrant, it is sometimes heavily attacked by six related species—*T. pennipes* in the United States; *T. pilipes* in the West Indies; *T. giacomellii* (Blanchard) and *T. gustavoi* (Mallea et al. 1968) in Argentina; *Eutrichopodopsis nitens* Blanchard in Argentina, Brazil, and Colombia; and *Ectophasiopsis arcuata* (Bigot) in Chile. Each of these native parasitoids has successfully exploited an exotic host and each is now more abundant on *N. viridula* than on native hosts.

Trichopoda pennipes in North America is actually a complex of biotypes or cryptic species. In the east, the native hosts of *T. pennipes* are the squash bug, *Anasa tristis* DeGeer, several other coreids, and some pentatomids (Arnaud 1978). In California, *T. pennipes* attacks only a pyhrrhocorid and a largid and will not oviposit on squash bugs (Sabrosky 1955, Dietrick & van den Bosch 1957). In the southeast, the parasitoid attacks several coreids. It is regularly taken from the native pentatomid *Acrosternum hilare* and only occasionally from pentatomids other than *N. viridula* (Drake 1920, Schoene & Underhill 1933, Eaton 1975, Jones 1979, Buschman & Whitcomb 1980, Eger & Ables 1981, McPherson et al. 1982, Menezes et al. 1985).

In the West Indies, *T. pennipes* is replaced by the closely related *T. pilipes* (Myers 1931, Guimarães 1971, Arnaud 1978). Both species, variously reported as *T. pennipes* or *T. pennipes pilipes* (F.), have been imported into Hawaii, Australia, and other Pacific islands for attempted establishment against *N. viridula* (O'Conner 1950, Wilson 1963, Davis 1967, Michael 1981). Both species are now established in Hawaii, but *T. pilipes* is more important (Davis 1967). South Africa has recently imported *T. pennipes* from Florida for attempted establishment (F. D. Bennett, personal communication).

Eutrichopodopsis nitens is an important parasitoid of *N. viridula* in Brazil and parts of Argentina; its biology and host relations are similar to those of the previous two species (Gastal 1977a,b, Ferreira 1984). *Trichopoda giacomellii* was recorded parasitizing 100% of *N. viridula* adults for three consecutive generations in an uncultivated area near Buenos Aires (Liljesthröm 1981). *Ectophasiopsis arcuata* regularly attacks *N. viridula* in Chile and has successfully been established on this host on Easter Island (E. Zúñiga, personal communication).

Two other tachinids, *Trichopodopsis nigrifrontalis* Blanchard (1966) in Argentina and *Cylindromyia rufifemur* Paramonov (1956, cited by Cantrell 1984) in Australia, have been described from adults reared from *N. viridula* but have not subsequently been reported from this host. *Trichopoda lanipes* (F.) has been recorded once from *N. viridula* in Florida (Drake 1920). The identity of *Trichopoda* sp. recorded from *N. viridula* in Uruguay (Guido & Ruffinelli 1956) is unknown. Panizzi & Slansky (1985) refer to other tachinids recorded from *N. viridula* in Brazil by Lima (1940) and Silva et al. (1968), but I was unable to see these publications.

Origin of *N. viridula*

The southern green stink bug is assumed to have originated from the eastern Palearctic or Indo-Malayan Regions (Yukawa & Kiritani 1965, Kiritani 1971, DeWitt & Godfrey 1972, Todd & Herzog 1980). Based on Freeman's (1940) review of the known *Nezara* spp., Jones & Powell (1982) suggested that the Ethiopian Region was more likely the area of origin. Following a further examination of other species in the genus *Nezara* and the distributions of *N. viridula* polymorphs and closely associated parasitoids, I propose that *N. viridula* is of Ethiopian origin.

Freeman (1940) recognized 10 species and several distinct color forms in *Nezara:* the cosmopolitan *N. viridula*, the oriental *N. antennata*, and eight species confined to continental Africa and Madagascar. Azim & Shafee (1978) have described a new species from India closely related to an African *Nezara;* they provided a new key to the eleven species. L. R. Rolston (personal communication) presently considers 20 species names to be valid, with all but seven confined to Africa. Although an historical–biogeographical analysis of the genus *Nezara* would help pinpoint the origin of the genus, the fact that the bulk of the species in the genus are African tends to discount a southeast Asian point of radiation.

Adult *N. viridula* have distinct genetically controlled color polymorphs that occur together in varying ratios in various regions (Freeman 1940, Servadei 1967, Kiritani 1970, Singh 1973, Schmitz 1978, and others). Based on an analysis of the frequency distribution of these polymorphs, Yukawa & Kiritani (1965) concluded that the insect probably originated from southeastern Asia. The presence of a unique complex of effective parasitoids tends to support their conclusion. However, they overlooked the work of others showing evidence of the significant occurrence of the same polymorphs in other areas of the world. Furthermore, all or nearly all African *Nezara* spp. also possess each of the polymorphs recorded in East Asian *N. viridula*. Most, if not all, color polymorphs commonly occur in *N. viridula* populations from sub-Saharan Africa through the Mediterranean Basin east to China (Freeman 1940, Servadei 1967, Singh 1973, Schmitz 1978, Chen 1980, Singh & Rawat 1982, and others). All but one of the African *Nezara* species reviewed by Freeman possess similar polymorphs and some may have additional morphs not known in *N. viridula*. Only in areas where *N. viridula* is a known invader, such as the Americas, Australia, and certain Pacific islands, are some of the major polymorphs not similarly represented.

The present review of the parasitoids of *N. viridula* shows that those species most closely associated with this host (excluding the adapted tachinids in America) are generally concentrated in Japan and Africa, each region possessing completely different complexes. Outside these regions, *N. viridula* is parasitized by native, adventive, or introduced species. *Trissolcus basalis* is well established in the Americas, probably via parasitized egg masses among imported plant material. This species is the most important parasitoid of *N. viridula* outside most of Africa and Asia and, although it is sometimes recovered from the eggs of other pentatomids, it does not occur outside the geographic range of its primary host. Johnson (1985a) noted that New World specimens of *T. basalis* showed much less morphological variation than those from Africa, an indication of an Old World if not an African origin.

Between the eastern Mediterranean and China, the little information available shows that a variety of species of *Psix*, *Trissolcus*, *Telenomus*, *Gryon*, and *Ooencyrtus* have been reported from *N. viridula* eggs, but there is no distinguishable pattern or a defined complex in any one area. *Trissolcus lodosi* was recently described from *N. viridula* eggs in Turkey (Szabó 1981), but little or nothing is known about this species or other parasitoids from Greece, Asia Minor, and the Middle East. A Pakistan strain of *T. basalis* has been imported and established in Australia (Wilson 1963) and the polyphagous and widespread *P. lacunatus* has been recorded from *N. viridula* there (Johnson & Masner 1985). The original hosts of the *T. seychellensis* and *G. fulviventris* shipped from Pakistan for release against *N. viridula* in the West Indies and Australia (Rao et al. 1971) were not reported. Because neither species was successfully reared in the laboratory, the two parasitoids may have been collected from other hosts. Singh (1973) reported no parasitoids in life-table studies of *N. viridula* in India.

In Africa, there are at least six Scelionidae known to be associated with *N. viridula*—*Trissolcus aloysiisabaudiae*, *T. basalis*, *T. lepelleyi*, *T. maro*, *T. sipius*, and *Telenomus seychellensis*. Although *T. seychellensis* is known from other African pentatomids, it and *T. maro* are important natural control agents of *N. viridula* in Malawi (Croix & Thindwa 1986), whereas *T. lepelleyi* is its normal parasitoid in Kenya (Le Pelley 1979). *Trissolcus aloysiisabaudiae* is important on *N. viridula* in cotton in Somalia (Chiaromonte 1931, Paoli 1933). *Trissolcus sipius* is known only from *N. viridula* eggs in Kenya. *Trissolcus basalis* is distributed only along coastal areas, whereas the others have been reported primarily from the central and eastern half of the continent. Although *T. basalis* has been imported into South Africa from New Zealand, Australia, and recently from the United States, there is evidence that it already occurred there prior to importations (Giliomee 1958, Greathead 1971).

The occurrence of *N. viridula* in Japan may be a modern phenomenon, and the presence of unique, well-adapted egg parasitoids may have evolved through long association there with the closely related oriental stink bug, *N. antennata*. The first record of *N. viridula* in Japan was in 1879 (the first New World record was in 1798), but the insect was not recorded again until found in mixed populations with *N. antennata* in 1952 (Hasegawa 1954), and it did not become a pest until about 1955 (Kiritani 1971). Clausen (1931) listed *N. viridula* as an agricultural pest in Japan, but the species was more likely the almost identical *N. antennata*, which was not listed. Kiritani et al. (1963) have documented the modern replacement of *N. antennata* by *N. viridula* in parts of Japan, attributing the phenomenon to changing rice cultivation practices and competitive displacement through interspecific matings. At present, *N. antennata* in Japan is confined primarily to colder latitudes and higher elevations where *N. viridula* is poorly adapted for survival, yet the parasitoids shared among both *Nezara* spp. occur throughout the range of each. Cultures from two shipments of *T. mitsukurii* imported from Japan were each lost by the third generation, apparently due to failure of adequate numbers of adult parasitoids to emerge successfully from the eggs in the laboratory (unpublished data). In Brazil, Kobayashi & Cosenza (1987) compared acceptance and successful emergence of an indigenous population of *T. basalis* with Japanese *T. mitsukurii*. Their results showed that *T. basalis* parasitized about 90% of exposed *N. viridula* eggs, with 60% successful adult emergence, compared with about 70% parasitism by *T. mitsukurii* and 40% emergence.

Summary and Conclusions

Although 57 parasitoids are recorded as using *N. viridula* as a host, many of these associations are incidental; either some species are rare or they are more closely associated with other hosts or habitats. No nymphal parasitoids are well adapted to *N. viridula*.

No known effective parasitoids of adult *N. viridula* are known outside the Western Hemisphere. In the Americas, at least six tachinids have become well adapted to *N. viridula* since it became established about two centuries ago—*Trichopoda pennipes* in the United States, *T. pilipes* in the West Indies, and *T. giacomellii*, *T. gustavoi*, *E. nitens*, and *E. arcuata* in South America. The biologies of these tachinids are apparently similar, and each species is closely associated with *N. viridula* within their respective geographic ranges (Nishida 1966, Mallea et al. 1968, Shahjahan & Beardsley 1975, Gastal 1977a,b, Liljesthröm 1981, Harris & Todd 1982, Ferreira 1984). Both *T. pennipes* and *T. pilipes* have been successfully established against *N. viridula* in Hawaii; *T. pilipes* is the more effective species (Davis 1967). The role of *Bogosia antinorii* on *N. viridula* in Africa requires further investigation.

The American tachinids should be able to exert some degree of pressure on *N. viridula* populations in Africa and Asia where this pentatomid is also a pest. Hokkanen (1983) recently concluded that, after an estimated 150–200-yr association with *T. pennipes* in the New World, Florida populations of *N. viridula* have evolved a 10% better reproductive success in resisting attack than host populations from Italy not previously exposed to this parasitoid. A comparative study of the six trichopodine tachinids should be made to determine which species would be the most effective if established in previously unexposed host populations.

Egg parasitoids are the most important biocontrol agents of *N. viridula*. There are 41 species among five families of Hymenoptera recorded emerging from *N. viridula* eggs. Like some of the species reported attacking nymphs and adults, several egg parasitoids have been recorded only once, and some undoubtedly are poorly adapted to *N. viridula*. Others are evidently well adapted but have not been investigated. The taxonomy and biosystematics of the African *Trissolcus* spp. need to be studied.

The Ethiopian Region is proposed as the origin of *N. viridula*, and an ecological evaluation of parasitoids there is highly warranted. The present examination of world parasitoids of *N. viridula* clearly shows that several untried sources remain for introduction and establishment for enhanced biological control of *N. viridula* in the world.

Addendum

Following acceptance of this manuscript, I found that Hokkanen (1986) had published a similar paper with similar conclusions. His list of 27 parasitoids included three species referred to by Herting (1971) and not listed here in Table 1: the tachinid *Gymnosoma kuramanum* Matsumura in Japan (Takano 1956), the encyrtid *Ooencyrtus fecundus* Ferrière & Voegelé in Morocco (Voegelé 1961), and the eulophid *Pleurotropitiella albipes* Blanchard in Argentina (Esquivel 1950).

Hokkanen also found that *N. viridula* probably originated from the Ethiopian Region, basing his conclusion on an examination of the distribution of closely associated parasitoids, the frequency of occurrence of color polymorphs, and the distribution of other species of *Nezara*. These results add further evidence that future classical biological control programs against the southern green stink bug should be based on a thorough examination of African parasitoids as the most likely candidates for establishment in other areas.

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