

**DESCRIPTIONS OF IMMATURE STAGES OF *SCYMNUS (NEOPULLUS)*
SINUANODULUS YU AND YAO (COLEOPTERA: COCCINELLIDAE) WITH
NOTES ON LIFE HISTORY**

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Abstract

We describe for the first time immature stages of the *Scymnus* subgenus *Neopullus*; namely the egg, larval (4 instars), and pupal stages of *Scymnus (Neopullus) sinuanodulus* Yu and Yao (Coleoptera: Coccinellidae), which is indigenous to China. This lady beetle was imported to the USA for biological control of the hemlock wooly adelgid, *Adelges tsugae* Annand (Hemiptera: Adelgidae), a serious pest of hemlocks in eastern North America. The egg's anterior pole has a rosette of 4–11 cup-shaped and 13–20 semi-circular structures that are likely micropyles. Unlike the subgenera *Scymnus* and *Pullus*, a *Neopullus* larva lacks a retinaculum on its mandibles but has, in common, the antennae with 3 distinct segments, the maxillary palpi with 3 segments, and the labial palpi with 2 segments. The pupa is naked with transparent viscous droplets on the tips of setae and the larval exuvium attached only to the last abdominal segment. We also annotate morphological development and behavior of feeding, oviposition, and defense. Both larvae and adults of this small lady beetle exhibit defensive reflex bleeding of orange viscous droplets: the larva from thoracic tubercles and the adult from the femorotibial joints.

Scymnus (Neopullus) sinuanodulus Yu et Yao (Coleoptera: Coccinellidae) was first described from Yunnan, China, during searches for natural enemies of *Adelges tsugae* Annand (Hemiptera: Adelgidae) (Wang *et al.* 1997). It is one of six newly described species in the subgenus *Neopullus* (Yu *et al.* 1997, 2000). Because of its potential for biological control of *A. tsugae*, a severe pest of hemlocks in eastern USA, we imported *S. sinuanodulus* to a quarantine laboratory in the USA and studied its biology (Montgomery *et al.* 1997; Lu and Montgomery 1999, 2001). The eggs are laid in the spring and hatch in about 10 days. The larvae (4 instars) feed primarily on adelgid eggs and pupate in about 20 days. The new adults emerge from pupae in about 10 days, and feed on both adelgid eggs and nymphs (Lu and Montgomery 2001). This paper describes the morphological characters of egg, each larval instar, and pupa of *S. sinuanodulus*, and compares these to other Scymnini immatures. We also provide observations of the life history of *S. sinuanodulus* and its behavior of feeding, oviposition, and defense.

Materials and Methods

Immature and adult beetles were reared on adelgid-infested foliage of *Tsuga canadensis* (L.) in the spring of 1997 and 1998, from field-collected beetles shipped to the quarantine laboratory of USDA Forest Service, Northeastern Research Station at Ansonia, CT, during 1996–97. We first examined living specimens with light microscopes in quarantine, and removed some specimens killed in 70% ethanol from quarantine for further study with light and scanning

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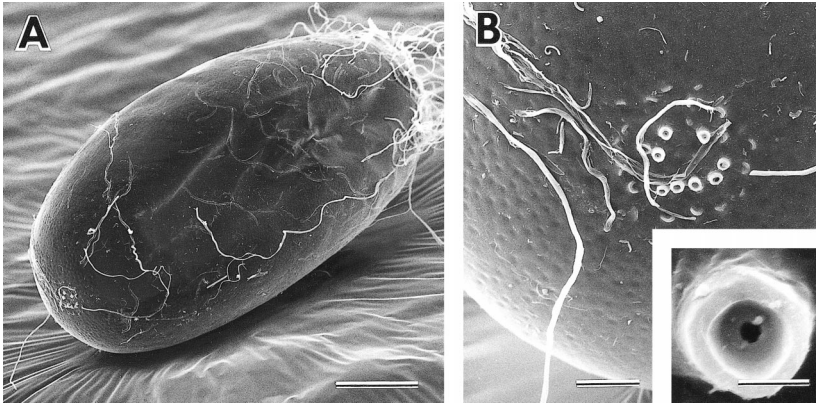


Fig. 1. Egg of *Scymnus sinuanodulus* (A) and its micropyle (B) with an inset of the tubular micropylar cup. Scale bars A = 100 μm , B = 20 μm , and inset = 2 μm .

electronic microscopes (SEM) (ETEC Co., Auto Scan). SEM specimen preparation followed the standard procedures of cleaning, dehydration, air-drying, mounting on support stubs, and sputter coating with gold.

Terminology followed Mazzini (1975) for egg, Sasaji (1968), LeSage (1991), and Rees *et al.* (1994) for larva, and Phuoc and Stehr (1974) for pupa. We describe only setae on tubercles or those useful for identification, and caution that some characters such as the setal base of the meso- and metanotum, and the pronotal plate pattern cannot be easily observed in live specimens. Voucher specimens are deposited in the Yale Peabody Museum, the U.S. National Museum of Natural History, and the Beijing Academy of Agricultural and Forestry Science.

Results

Egg (Fig. 1). Elongate oval, average length 0.57 ± 0.06 mm, average width 0.27 ± 0.02 mm ($n = 7$). Bright orange when young, turning duller with age and often with iridescent sheen (caused by separation of chorion from embryo, forming an air space) before hatching. Chorion bare with a membranous covering, shallow dimple-like depressions on exposed surface, and no such depressions on surface attached to substrate. Tube-like projections on exposed apical pole of 4–11 (mostly 7–9) cups arranged centrally in an irregular ring and surrounded by 15–20 semicircular walls (Fig. 1B). After hatching, chorion transparently white and often iridescent under light.

Larva (Table 1, Fig. 2). *General description* Body elongate fusiform, yellowish to reddish brown, and densely setaceous on head, thoracic plates, tubercles of thorax and abdomen, and on anal plates. Head including mouthparts and antennae dark brown; stemmata black; tibiotarsi dark brown, well-developed tubercles and plates of thorax and abdomen dark brown.

Head transversely subpentagonal, broader than long, slightly narrowing basally, broadest in middle between stemmata; frontal suture distinct with 3 pairs of long setae within and 4 pairs outside of the “U” (medium and short setae not counted). Antennae typical of *Scymnus*, very small and 3-segmented, located in a socket at apex of each frontal suture branch; sclerotized ring of

Table 1. Measurements of head, prothorax, total length (from anterior head to posterior margin of abdomen), and tibiotarsi (mm) of *Scymnus sinuanodulus* larvae, with range and sample size (in parentheses) indicated.

In- star	Head		Prothorax		Total Length	Tibiotarsus		
	Width	Length	Width	Length		Front	Middle	Hind
1	0.22 ± 0.02	0.16 ± 0.01	0.29 ± 0.04	0.17 ± 0.04	1.15 ± 0.36	0.13 ± 0.01	0.14 ± 0.01	0.15 ± 0.01
	0.18~0.25 (29)	0.12~0.17 (29)	0.23~0.34 (29)	0.09~0.31 (29)	0.71~2.20 (29)	0.12~0.14 (8)	0.12~0.16 (8)	0.14~0.17 (8)
2	0.27 ± 0.01	0.20 ± 0.03	0.40 ± 0.04	0.26 ± 0.04	1.69 ± 0.35	0.16 ± 0.01	0.17 ± 0.01	0.18 ± 0.01
	0.26~0.30 (31)	0.14~0.25 (31)	0.32~0.55 (31)	0.17~0.34 (31)	0.81~2.38 (31)	0.14~0.16 (9)	0.14~0.17 (9)	0.15~0.20 (9)
3	0.33 ± 0.02	0.23 ± 0.03	0.50 ± 0.05	0.35 ± 0.08	2.20 ± 0.44	0.20 ± 0.02	0.23 ± 0.01	0.24 ± 0.01
	0.29~0.39 (61)	0.18~0.30 (61)	0.39~0.63 (61)	0.20~0.55 (61)	1.32~3.19 (61)	0.15~0.22 (13)	0.21~0.23 (13)	0.21~0.27 (13)
4	0.41 ± 0.02	0.29 ± 0.03	0.65 ± 0.05	0.47 ± 0.10	2.84 ± 0.59	0.26 ± 0.02	0.29 ± 0.02	0.31 ± 0.02
	0.37~0.44 (25)	0.25~0.36 (25)	0.57~0.78 (25)	0.34~0.67 (25)	1.89~3.95 (24)	0.21~0.30 (24)	0.25~0.31 (24)	0.25~0.34 (24)

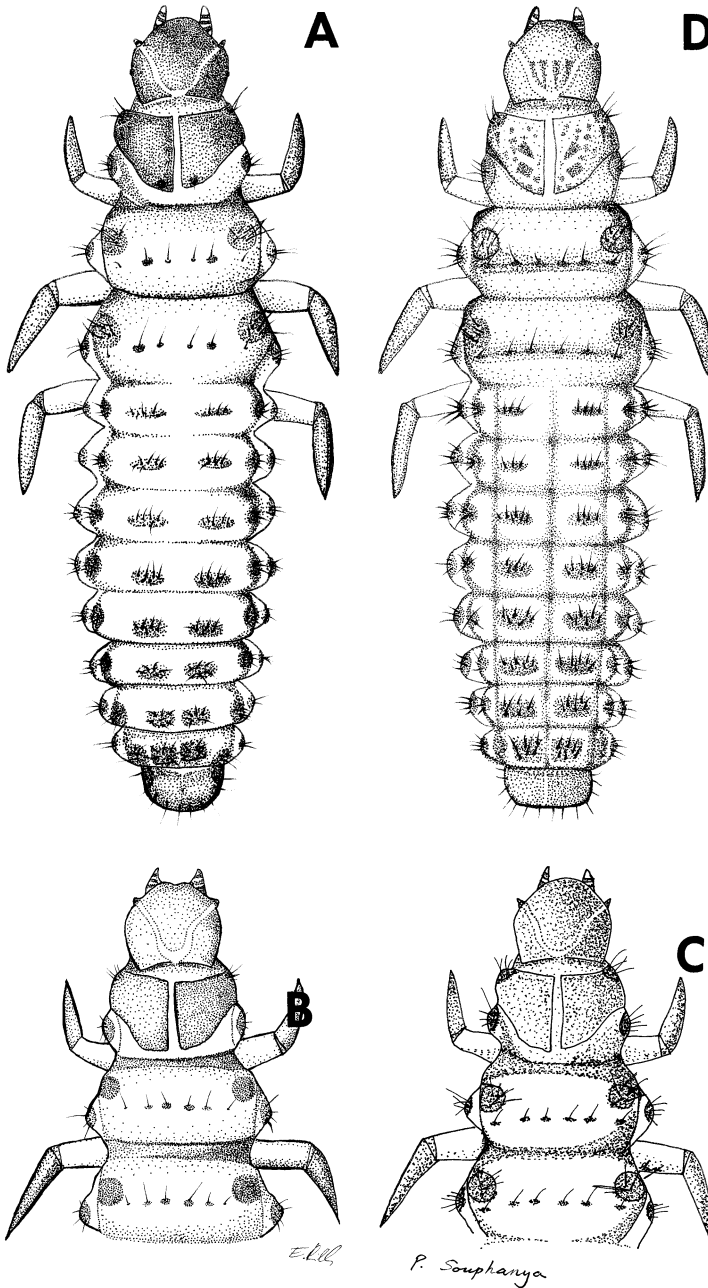


Fig. 2. Schematic dorsal views of *Scymnus sinuanodulus* larvae from 1st to 4th instars (A, 1st instar; B, 2nd instar; C 3rd instar; D, 4th instar).

basal segment $1/3$ as long as broad; 2nd segment about $1/4$ narrower than basal segment, sclerotized ring as long as basal segment or slightly shorter on inner surface; terminal segment distinctly shorter, $1/2$ as long as previous segments and $1/2$ as broad as 2nd segment, bearing 5–6 minute bud-like setae and a long, thick apical seta as long as all 3 segments combined; 2nd segment also with a long and stout seta on membranous apical area, described as sensorial appendage (Delucchi 1954), preapical (Sasaji 1968), or large spine-like seta (LeSage 1991), 4 times as thick as apical seta at base, as long as basal and 2nd segments combined. Stemmata slightly raised and smooth on surface, arranged in irregular triangle, 2 on dorsolateral edge behind antenna and 1 on lateral side below it (not visible dorsally). Labrum transversely rectangular and anteriorly distinctly emarginate. Maxillary palpi typical of *Scymnus*, long and 3-segmented; terminal segments as long as basal and 2nd segments combined, pointed apically, 3 times as long as broad at base; both maxillary palpifer and basal segment large and distinct. Mandibles with a tooth pointed at apex and a molar area and without retinaculum, similar to *Scymnus creperus* Mulsant (LeSage 1991). Labial palpi typical of *Scymnus*, 2-segmented but slightly longer compared with antennae, with terminal segment 3 times as long as basal segment, twice as long as broad at base. Labium similar to *Scymnus rufipes* F. (Binaghi 1941) and *Scymnus impexus* (Mulsant) (Delucchi 1954), rectangular, ligula fused with mentum, submental area more sclerotized and distinct than gular area, which is transversely narrow and indistinct.

Pronotum sub-trapezoidal with a pair of large triangular dorsal plates; anterior outer corner of each dorsal plate with 1 long seta surrounded by 4–8 medium and small setae; a round tubercle on dorsolateral area each posterior to dorsal plates, bearing 1 long seta at center surrounded by 4–8 medium and small setae. Mesonotum broader than pronotum with (1) a pair of lateral projections (posterior lobes of mesopleuron, Gorden and Vandenberg 1991), each bearing a round setose tubercle; (2) a pair of dorsolateral tubercles larger and more rounded than those of prothorax, and larger and more sclerotized than those on lateral projections; (3) a row of 6 fine setae posterior to midpoint, namely dorsal, dorsolateral, and lateral, each on a base becoming more distinct from sclerotization; all mesonotal tubercles with 1 long, 4–8 medium, and several small setae. Metanotum similar to mesonotum in structure but broader. Legs slender, femora and tibiotarsi cylindrical; tibiotarsi length slightly $>1/2$ head width, narrowing apically; similar to *S. impexus* (Delucchi 1954) in bearing 2 pairs of clavate apical setae and having claws distinctly thickened at base.

Abdomen of 9 segments. Segments 1–8 each with a pair of lateral projections and 3 pairs of distinct tubercles: dorsal and dorsolateral pairs on each tergite, and a lateral pair on lateral projections. Each tubercle bearing 1 long, and various shorter setae; dorsolateral and lateral tubercles nearly round, bearing more medium-length setae than dorsal tubercles; dorsolateral tubercles largest and most sclerotized; dorsal tubercles smallest and transversely narrow on basal segments, but becoming elliptical to round, and more distinct on apical segments, fused with each other on segment 8 in later instars. Segment 9 with a less sclerotized anal plate, which is slightly emarginate anteriorly and rounded on posterior margin, no lateral projections, bearing 8 long setae around its posterior margins and various medium setae dorsally. Underside of abdominal segments 1–8 each with a pair of small ventrolateral projections (not visible dorsally), bearing a medium seta on each tip, surrounded by 4

medium setae; segment 9 with only 4 setae in a row, outer 2 darker than inner 2, without ventrolateral projections.

First instar (Fig. 2A) is remarkably distinct from the later instars. The larva is translucent yellow in life, as are all newly molted instars. Its pronotal dorsal plates have a pair of setae on a distinctly darkened sclerotized base at the posterior inner corners. On the mesonotum and metanotum, only the dorsolateral pair of the row of 6 setae has a sclerotized base and is readily visible; the base of the dorsal pair is slightly larger than that of the lateral pair.

Second instar (Fig. 2B) is brownish yellow and turns darker and opaque with age. The distinct pigmentation and sclerotization of the pair of setae at the posterior inner corner of the pronotal dorsal plates are lost. On the mesonotum and metanotum, 2 pairs of setae are visible, but the degree of sclerotization between the pairs is reversed: the basal sclerotization of the dorsal pair is slightly larger than that of the dorsolateral pair; the distinction between the 2 pairs is relatively minor compared with that in the 1st instar. The lateral pair does not have a darkened sclerotized base and remains barely visible.

Third instar (Fig. 2C) is yellowish brown and opaque in life. All 6 setae on the mesonotum and metanotum are visible, with equal basal sclerotization. The dorsal tubercles on abdominal segment 8 become partially fused. Short, white, velvety wax appears as the instar nears its molt. This stage may be confused with the 4th instar.

Fourth instar (Fig. 2D) is reddish brown and opaque in life. There are 4 distinct short stripes of dark pigment on the frontal area of the head. The pronotal dorsal plate becomes speckled and blotched; at least 2 pairs of spots are recognizable on the posterior half; the more anterior pair is elongate triangular and the posterior pair are rectangular to oval. Each mesonotal and metanotal segment folds transversely along a line between the dorsolateral tubercles and the row of 6 setae; the fold is heavily sclerotized and dark brown. The short, white, velvety wax appears on all non-sclerotized areas, forming a grid pattern on the abdominal dorsum, contrasting strongly with the shiny, waxless, chocolate brown thoracic folds and abdominal tubercles. The head pigmentation, the pronotal mottling pattern, the mesonotal and metanotal folds, and the white velvety grid pattern of the abdomen distinguish the 4th instar from the 3rd.

Newly molted 4th instar is brightly yellowish orange and immaculate with a shiny wet look. By hr 1 the body starts darkening and turns brown at 20°C. By hr 3 the head capsule, pronotum, and anal segment appear darker than the rest of the body. By hr 4, these 3 segments are distinctly darkened, as are the tibiotarsi; the head markings appear, and the tubercles are distinctly sclerotized and very shiny. By hr 7, the thoracic fold, connecting the row of 6 setae and the dorsolateral tubercles, appears on the mesonotum and metanotum, and gradually becomes as dark as the dorsolateral tubercles. By hr 10 after molting, the short, white, velvety wax covers the unsclerotized dorsal and dorsolateral areas of the thoracic and abdominal segments, forming the grid pattern. At this time all morphological characters are distinct. The wax becomes thicker, longer, and hair-like, forming a waxy cover. During the quiescent prepupal period, the larvae shorten and thicken.

Pupa (Fig. 3). Total length 2.78 ± 0.16 (n = 13 throughout). Larval exuvium attached to last abdominal segment. Body entirely yellowish, surface smooth without ornamentation, covered uniformly with coarse setae longer than lateral thickness of pronotum and arising on a slightly elevated cuticular ring; transparent viscous droplets often seen on setal tips.

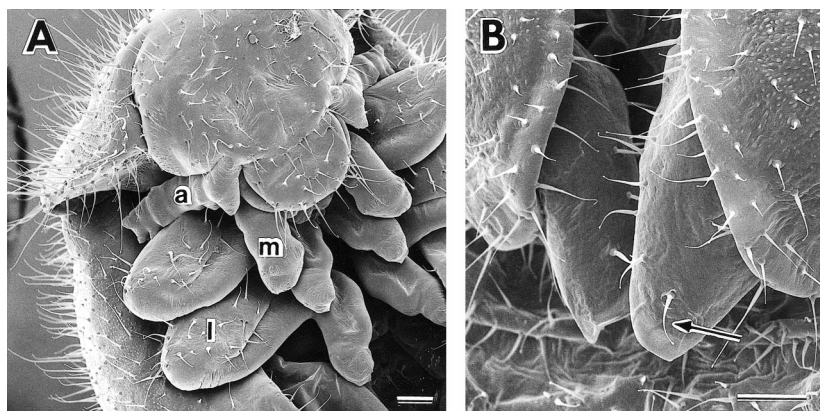


Fig. 3. Frontoventral view of pupa of *Scymnus simuanodulus* (A) with setae on hind wing indicated (B); **a**, antenna; **l**, posterior leg; **m**, maxillary palpus. Scale bars A, B = 100 μ m.

Head (Fig. 3A) width 0.50 ± 0.04 , length 0.49 ± 0.04 , opisthognathous, homogeneously sclerotized and setiferous, vertex invisible in dorsal view, broader than long. Epicranial and frontal sutures absent, but frontal area marked by a pair of depressions along midline. Eyes large, facets not well-defined, inner lateral portion of ocular suture only visible at certain light angles, distance across frontal area between eyes about 2 eye widths combined. Antennae long, as long as distance between eyes or length of lateral margin of pronotum, $1/3$ – $1/4$ longer than clypeolabrum. Antennal scape greatly enlarged, expanded caudad to a triangular process, at least $1/3$ broader than broadest antennal club, and convex with anterior surface glabrous. Antennal flagellum indistinct from antennal club, of subequal width in early stages with antennal club, basal 2 segments well developed and slightly expanded as in scape. Antennal club papillate, about $1/2$ length of flagellum, slightly increasing in width apically. Clypeolabrum $1/3$ broader than long, subquadrate, apical margin broadly rounded; clypeolabral suture seen as a slightly arched transverse depression all the way across. Mandibles simple and pointed at tip, no obvious tooth but with molar area developed. Maxillary palpus large, bulbous, elongate triangular, and glabrous; galea bulbous and subquadrate in dorsal view, subequal to base of maxillary palpus, lacinia right beneath galea, slender, and slightly pointed at tip. Labium bulbous with a distinct mentum, embraced by labial palpi and galea and lacinia of maxilla, apical margin broadly rounded; labial palpus bulbous, stout, short, and subquadrate, as broad as apical galea of maxilla, $1/2$ as long as maxillary palpus. Hypopharynx enlarged anteriorly, bracketed laterally by mandibles, and extremely slender at base between mandibles, like 3-leaf clover with a thread-thin stem.

Prothorax width 1.04 ± 0.06 , length 0.45 ± 0.09 , transverse, 3 times as broad as long, broader posteriorly; anterior margin continuous with vertex of head, emarginate so that anterior angles protruding to partially embrace head; posterior margin expanded into a broadly rounded basal lobe; lateral margin straight; surface smooth with setae of different lengths: long macrosetae, short macrosetae ($1/3$ shorter), and microsetae ($1/2$ – $1/4$ of macrosetae). Mesonotum almost rectangular, anterior margin barely longer than posterior, both concave,

but posterior margin with a slight protrusion in middle; scutellar area slightly elevated, triangular, often with a little dent on top. Metanotum trapezoidal, with a longitudinal depression through midline, tapering caudad; anterior margin slightly concave in middle, narrower than posterior margin, angles rounded; posterior margin sinuate, expanded posteriorly into a narrowly rounded basal lobe, angles long and pointed; both anterior and posterior angles with a broadly and slightly depressed proximate area.

Elytra elongate oval, bending ventrally to cover most of hind legs and abdominal 1st sternum (longer with age); lateral angle obtusely rounded and continuous with lateral margin; epipleuron long and narrow, slightly concave; apical angle pointed; elytral surface smooth and homogeneously setiferous, including apical and sutural margins. Hind wing less sclerotized, bulbous, and tapered apically; surface smooth and sparsely setiferous, mostly along anterior margins (Fig. 3B). Legs short and robust; femur and tibia confluent in flexed position, femoral surface setiferous; tarsus distinctly 3-segmented, last segment slender; procoxae separated by prosternum, distance between metacoxae twice as broad as that between procoxae.

Abdominal terga immaculate, closely opposed to one another without exposed conjunctivae; surface with 2 types of setae: macrosetae twice as long as microsetae; macrosetae usually consistent in location, in a group of 5–7 on each spiracle, or of 2–3 transversely aligned on each tergum; posterior tergum 8 slightly pointed. Pygidium bulbous, short, 4 times as broad as long, transversely truncate but slightly concave between urogomphi; surface densely setiferous. Urogomphi unbranched, cylindrical, and slender, as long as, or up to 1/2 longer than tergum 8, and slightly curved ventrally, with apical ends enlarged subspherically. Abdominal spiracles circular and normal. Abdominal pleura rhomboidal and densely setiferous, especially along outer lateral half in a group of 5–7 long setae. Abdominal sterna less setiferous.

Life History. When ovipositing, *S. sinuanodulus* first inspected the foliage, then extended the posterior abdominal segments and the ovipositor to probe substrates and to lay an egg. The egg was usually placed in an adelgid ovisac or a hemlock bud scale with the micropylar pole of the egg slightly exposed. When we changed foliage infested with adelgids daily, providing plenty of food and habitat, more than half of the eggs (17/30 in 4 days) were found under ovisacs and we did not see >2 beetle eggs in an ovisac; when crowded, we found up to 6 beetle eggs in an ovisac. Eggs, especially if beetles were crowded, were found also in stem cracks, in flower cones, under scale insects on hemlock needles, and on rough areas such as torn edges of the paperboard rearing container and gauze added to the rearing container.

Adults preyed on adelgid eggs by chewing, often leaving smeared egg contents or partially consumed eggs. The beetles fed first on eggs exposed outside an ovisac, then gradually penetrated until only their posterior abdomen was visible. The ovipositing adelgid often was pushed up, partially dislodging the stylet, and eventually died. When attacking adelgid adults and older nymphs, adult beetles first took a single bite, usually on the dorsum close to the thorax, causing dark brown hemolymph to ooze from the adelgid. The beetles imbibed the hemolymph and often chewed some of the body, but usually did not consume the adelgid entirely. Among 47 adelgid adults and older nymphs attacked, 80% were partially consumed or injured with considerable bleeding and subsequently died in 2 days, but 20% healed and survived. The beetles fed little on the active crawlers, which could easily escape when approached by the

beetle. The beetles did not consume dead adelgids, and cannibalized their own eggs only when adelgids were not plentiful.

We observed *S. sinuanodulus* larvae feeding on all stages of adelgids, but mostly on eggs and crawlers. When feeding on adelgid eggs, the larvae readily went deep into the ovisac and were completely covered by the ovisac. A larva would consume all or nearly all of the eggs before leaving an ovisac, leaving the wax cover intact but loosened. We found clusters of empty egg chorions in ovisacs attacked by beetle larvae, whereas ovisacs attacked by adult beetles did not have empty chorions. We saw the head and pronotum of beetle larvae often covered with empty egg chorions and adelgid wax tightly packed.

Although adelgid crawlers could usually escape encounters with adult beetles, *S. sinuanodulus* larvae effectively captured this active stage. We observed that the larvae used their long and distinctive maxillary palpi to grab and hold the adelgid crawlers during regurgitation. All instars first bit and immobilized the captured crawlers, and slowly sucked juice out of the crawlers. We could see the gut of the beetle larvae turning orange (the color of the crawler). Then, with maxillary palpi and forelegs, they held the crawler up overhead and regurgitated the orange contents back into the empty and transparent corpse of the crawlers. The flattened crawlers ballooned up and turned orange again. This process was repeated at least five times from 30 sec to 2 min, until the larva abandoned the empty corpse. When starved, 1st instar larvae fed on crawlers of the hemlock scale *Fiorinia externa* Ferris, regurgitating in the same way. The 1st instar beetle larva attacked the aestivating 1st instar adelgid nymph by turning the prey on its side, piercing the underside of the thorax near the stylet, and sucking out the hemolymph. Beetle larvae were cannibalistic only when starved for 1–2 days.

After feeding voraciously for 2–3 days, 4th instar larvae produced short, white, velvety wax over most of the abdomen. They then became inactive, slightly shorter and wider, and produced dark brown, sticky liquid from the anal segment. Some prepupae remained quiescent and hidden among the hemlock foliage, but others became active and crawled for several days. When the latter stopped crawling, some returned to the foliage for pupation, but others secreted long, silk-like threads of wax and pupated in the open under the wax. Prepupae attached themselves to a surface by the anal segment before pupation. Pupae are entirely immobile. The larval exuvium only partially covers the last abdominal segment of the pupa, more so ventrally; thus, the pupa is naked.

After emergence, new beetles were uniformly dull orange without elytral pattern. Some remained in the transparent pupal exuvia for 1–3 days until their bodies hardened. The elytral pattern did not develop fully at 20°C until after 2–3 weeks when it was damp, but took less than one week when it was very dry. It is important to remember in field identification that the coloration patterns take time to develop fully.

Beetles began mating one month after pupal ecdysis and mated repeatedly throughout the summer. Beetles held at 5°C during the winter months mated when warmed for a few minutes in the laboratory while we added hemlock foliage. Mating also occurred after beetles emerged from overwintering.

We frequently observed both larva and adult *S. sinuanodulus* to exude droplets of orange liquid when disturbed. The larvae released the liquid from the meso- and metathoracic tubercles and the adults from the joints between femora and tibiae of all legs. Both larvae and adults secreted the droplets from only one or two locations closest to the disturbed area.

Discussion

There are few reports on the external structure of coccinellid eggs. The membrane covering the egg of *S. sinuanodulus* is present in most other coccinellid tribes (Ricci and Stella 1988). Eggs detached from the substrate are often partially collapsed, probably because the membrane is torn, allowing loss of moisture. Ricci and Stella (1988) stated that all coccinellids had tube-like structures at the anterior pole, but contradictorily, they did not find external micropylar structures in Scymnini. The cup-like and semi-circular structures in *S. sinuanodulus* eggs appear to have circular openings at the center. We believe they are micropyles. The egg of *Adalia bipunctata* L. (Mazzini 1975) is less oval, more rough, has longer and more micropylar cups, and lacks the semicircular structures.

We suspect that the tiny, but distinct, seta at the posterior inner corner of the pronotal dorsal plate of the 1st instar of *S. sinuanodulus* may be an egg burster because it disappears after the 1st stadium. Ricci and Stella (1988) describe four types of egg bursters; however, the pronotal seta in *S. sinuanodulus* is simple in structure, does not fit any of the four types, and may work with other structures in bursting the chorion.

Many larvae in the tribe Scymnini have waxy coverings (Pope 1979). *Scymnus* (*Neopullus*) *sinuanodulus* is similar to *Pseudoscymnus tsugae* Sasaji and McClure (Cheah and McClure 1998) in producing a waxy cover only in the 4th instar. In contrast, *S. (Pullus) impexus* and *Scymnus (Scymnus) nigrinus* Kugelann, which also feed on adelgids, have waxy covers in every larval instar (Delucchi 1954; Vohland 1996). Wax covers on lady beetle larvae provide protection against carabids and ants but not against larger coccinellids that prey on wax-covered aphids (Volkl and Vohland 1996). Larvae of *S. impexus* spin a waxy, cocoon-like structure before pupating (Delucchi 1954), whereas *S. sinuanodulus* never formed a cocoon, secreting at most a few long strands of wax.

We found exuvia of *S. sinuanodulus* near the adelgids, frequently in the adelgid ovisacs and thus difficult to see. We often found the exuvia of all instars close together, especially if adelgid populations were dense. But exuvia of *S. impexus* larvae are seldom found near the adelgid population because molting occurs in protected areas in the tree bark (Delucchi 1954).

Extra-oral digestion is common in Scymnini (Delucchi 1954; Hagen 1962; Hodek and Honek 1996). Some *Scymnus* larvae feed on aphids by holding them off the substrate and swinging them back and forth until the struggling aphids are exhausted (Yang and Zheng 1991). Although *S. sinuanodulus* larvae did not swing their heads, they did regurgitate while holding adelgid crawlers up. Elevating the prey may facilitate digestion or may prevent prey from escaping. Aphidophagous coccinellids have two modes of feeding (Ricci and Stella 1988): extra-oral digestion, leaving the empty exoskeleton of the prey, or chewing, consuming the prey entirely. Delucchi (1954) observed that the 1st instar of *S. impexus* pierced and regurgitated adelgid eggs, but older instars did not exhibit this behavior. We observed older *S. sinuanodulus* larvae regurgitating as well as chewing their prey.

Reflex bleeding is a common defensive mechanism in Coccinellidae (Hagen 1962; Hodek and Honek 1996; King and Meinwald 1996). Although it is the largest coccinellid genus, there are few reports of defensive behavior in *Scymnus*. Delucchi (1954) observed reflex bleeding in *S. (Pullus) impexus*, but Pas-

teels *et al.* (1973) did not detect alkaloids in Scymnini and found that birds ate the beetles exhibiting the defensive behavior. Whether or not the fluid contains alkaloids or other defensive chemicals, the location of reflex bleeding by the larvae is unusual because it is not the same as any of the locations of reflex bleeding described by Ricci and Stella (1988). The difference in locations of reflex bleeding between larvae of *S. sinuanodulus* and other Scymnini species may be interesting in revealing the phylogenetic relationships of the tribe. This reflex bleeding may explain, in combination with the habit of feeding under an adelgid ovisac, why the younger instar larvae do not have a protective waxy cover.

The prepupa is a distinct stage in *S. sinuanodulus*. Although prepupae are generally defined as inactive (Costa and Vanin 1985) or quiescent (Majerus 1994), we consider larvae that stop feeding, exude anal liquid, and become immobile for 1–2 days as prepupae, even though they may later initiate crawling. A high percentage of *S. sinuanodulus* prepupae crawled in our laboratory, but many of these died (Lu and Montgomery 2001). We do not know where the larvae would pupate in nature, but suggest that their behavior may be similar to *S. impexus*, whose mature larvae descend from the upper to the lower part of the tree and pupate on the tree trunk about 3 m above the ground (Delucchi 1954). Prepupal crawling may be a mechanism for dispersal away from the larval feeding site or finding a protected site for pupation.

Pupae of *S. sinuanodulus* are naked. We observed the last larval exuvium covering a pupa only when it failed to complete development to adult. Statements by LeSage (1991), Majerus (1994), and Hodek and Honek (1996) that the last larval molt completely covers the pupa of Scymnini contradict Phuoc and Stehr's (1974) comprehensive work on Coccinellidae pupae. Pupae of other species in Scymnini are naked (Binaghi 1941; Cheah and McClure 1998; Phuoc and Stehr 1974). Only Chilacorini and Noviini have pupae enclosed completely in their last larval exuvia; in Hyperaspini, the last larval exuvia cover only the ventral surface (Phuoc and Stehr 1974). Wax was not observed on *S. sinuanodulus* pupa, unlike *Scymnus (Neopullus) hoffmanni* Weise, whose pupa is partially covered with wax (Yang and Zheng 1991). The coarse setae with transparent viscous droplets may be a defensive adaptation.

The only pupa of *Scymnus* described in detail is *S. (Pullus) creperus* (Phuoc and Stehr 1974). The head vertex of *S. sinuanodulus* pupa is invisible in dorsal view, unlike *S. creperus*. In *S. creperus* the antenna is short, extending about 1/3 of the distance between the eye and the widest lateral margin of the pronotum (Phuoc and Stehr 1974). In *S. sinuanodulus* the antenna is long, extending to 1/3 of the lateral margin of the pronotum. The basal lobe of the pupal pronotum of *S. sinuanodulus* is small and does not form a larger tubercular lobe as it does in *S. creperus*. The hind wing of *S. creperus* pupae is glabrous, but in *S. sinuanodulus* there are sparse setae on the anterior margin. The subspiracular macrosetae on the abdominal terga are 5–7 per group in *S. sinuanodulus* and 2 per group in *S. creperus*.

The combination of the following characters seems common to Scymnini and *Scymnus* larvae: elongate body with only either tubercles (verruca) or strumae; last instar dorsum covered with a white, wax-like exudation; head subquadrate (never strongly transverse), frontal suture, if present, U-shaped as opposed to Y-shaped; stemmata normal; 3-segmented antennae less than 3 times as long as wide; maxillary palpi 2–3 segmented with terminal segment

wide (length <3 times width), mandibles with mola and only 1 tooth or slightly bidentate at apex; lack of complete fusion of cardines, stipes, submentum, and mentum; each abdominal tergum entire, not divided transversely, without pores (repugnatorial glands [LeSage 1991], foramina of secretory glands [Savoiskaya and Klausnitzer 1973], or intersegmental pores [Rees *et al.* 1994]); abdominal segments 1–8 dorsally with 3 pairs of tubercles, or strumae or clusters of a few large setae; segment 9 with posterior margin rounded.

There are six subgenera of *Scymnus*: *Scymnus* Kugelann, *Pullus* Mulsant, *Neopullus* Sasaji, *Didion* Casey, *Mimiopullus* Fursch, and *Parapullus* Yang (Pang and Yu 1993). Presently, we do not have sufficient information to construct a key to separate *Scymnus* larvae to subgenera. Sasaji (1968) separated Japanese members of subgenus *Scymnus* from *Pullus* by the presence of three pairs of distinct tubercles on abdominal segments 1–8 in *Scymnus*. But *Scymnus* (*Scymnus*) *frontalis* (F.) depicted by Gorden and Vandenberg (1991) does not have that character. The proportional size of the 3rd segment of the antenna of *S. (Neopullus) sinuanodulus* is smaller than shown for *S. (Pullus) creperus* by LeSage (1991), but is similar to that of *S. (Pullus) impexus* (Delucchi 1954), *S. (Scymnus) nigrinus* (Savoiskaya and Klausnitzer 1973), *Scymnus (Pullus) posticalis* Sicard (as *Scymnus hilaris* Motschulsky) (Sasaji 1968), *Scymnus (Scymnus) paganus* Lewis (Sasaji 1968), and *Scymnus (Pullus)* sp. (Rees *et al.* 1994). The number of minute setae on the terminal segment and the proportions of other segments seem to vary among the species rather than subgenera. As a rule the basal antennal segment is shorter than the 2nd segment among coccinellids (Savoiskaya and Klausnitzer 1973); but these antennal segments are about equal in length in both *S. (Neopullus) sinuanodulus* and *Pullus*. The labium of *S. (Neopullus) sinuanodulus* is more rectangular than that of *Scymnus (Pullus) collaris* Melsheimer (LeSage 1991) and *S. (Pullus)* sp. (Rees *et al.* 1994); the gular area is much shorter than *S. (Scymnus) paganus* in Sasaji (1968). The dorsal tubercles of the meso- and metanotum of *S. (Neopullus) sinuanodulus* are not raised and there is only one pair of lateral tubercles on the lateral projections, unlike *Scymnus (Pullus) fraternus* LeConte (as *Scymnus haemorrhous* LeConte), which has raised dorsal tubercles and two pairs of lateral tubercles (LeSage 1991).

Keys to tribes and genera of Coccinellidae larvae (Sasaji 1968; Savoiskaya and Klausnitzer 1973; LeSage 1991; Rees *et al.* 1994) may not correctly place *Scymnus (Neopullus)* larvae. Contrary to key couplet 8 in LeSage (1991), the legs of *S. sinuanodulus* larvae are not truncate, but are slender and the tibiotarsi are pointed, similar to the legs of *Pullus auritus* Thunberg and *Scymnus rufipes* F. depicted in Binaghi (1941). The mandibular mola of *S. sinuanodulus* is not as distinct as that of *S. (Pullus) creperus* depicted in LeSage (1991) and does not have a retinaculum like *S. (Pullus) impexus* depicted in Delucchi (1954). Because it lacks a retinaculum, we could not place *S. sinuanodulus* in *Scymnus*, using key couplet 17 of Rees *et al.* (1994). We further caution that the frontal suture and the sclerotization of thoracic plates are distinct in each instar of *S. sinuanodulus*, *contra* couplets 70 (17) and 78 (77) of Savoiskaya and Klausnitzer (1973) for *Scymnini*, respectively for each character.

Generic definitions of Sasaji (1968), Savoiskaya and Klausnitzer (1973), and Rees *et al.* (1994) can be used to separate *S. sinuanodulus* from larvae of other coccinellid genera found on hemlock. It can be distinguished from *P. tsugae* by the 3 antennal and 2 labial segments of the former and only one antennal

and labial segment of the latter. Larvae of non-Scymnini genera on hemlock do not have waxy covering in any instar and usually are black and have spiny tubercles. Superficially, Scymnini larvae on hemlock could be confused with *Laricobius* (Coleoptera: Derodontidae) larvae because both have waxy covering. *Laricobius* can be separated from *Scymnus* larvae by longer antennae of 3 segments and 6 stemmata on each side of the head for the former, and barely visible antennae and only 3 stemmata for the latter.

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Literature Cited

- Binaghi, G. 1941.** Gli stadi preimaginali del *Pullus auritus* Thunb. e dello *Scymnus rufipes* Fabr. morfologia, notizie ecologiche ed apparati genitali (Col. Coccinellidae). Estratto delle Memorie della Societa Entomologica Italiana 20:148–161.
- Cheah, C. A. S.-J., and M. S. McClure. 1998.** Life history and development of *Pseudoscymnus tsugae* (Coleoptera: Coccinellidae), a new predator of the hemlock woolly adelgid (Homoptera: Adelgidae). Environmental Entomology 27:1531–1536.
- Costa, C., and S. A. Vanin. 1985.** On the concepts of “pre-pupae,” with special reference to the Coleoptera. Revista Brasileira de Zoologia 2(6):339–345.
- Delucchi, V. 1954.** *Pullus impexus* (Muls.) (Coleoptera, Coccinellidae), a predator of *Adelges piceae* (Ratz.) (Hemiptera: Adelgidae), with notes on its parasites. Bulletin of Entomological Research 45:243–278.
- Gorden, R. D., and N. Vandenberg. 1991.** Field guide to recently introduced species of Coccinellidae (Coleoptera) in North America, with a revised key to North American genera of Coccinellini. Proceedings of the Entomological Society of Washington 93:845–864.
- Hagen, K. S. 1962.** Biology and ecology of predaceous Coccinellidae. Annual Review of Entomology 7:289–326.
- Hodek, I., and A. Honek. 1996.** Ecology of Coccinellidae. Kluwer Publisher, Boston, Massachusetts.
- King, A. G., and J. Meinwald. 1996.** Review of the defensive chemistry of coccinellids. Chemical Review 96:1105–1122.
- LeSage, L. 1991.** Coccinellidae (Cucujoidea) [pp. 485–494]. In: Immature insects, Volume 2 (F. W. Stehr, editor). Kendall / Hunt Publishing Company, Dubuque, Iowa.
- Lu, W., and M. E. Montgomery. 1999.** Comparative biology of three *Scymnus* lady beetles (Coleoptera: Coccinellidae): predators of *Adelges tsugae* (Homoptera: Adelgidae) [p. 188]. In: Proceedings: symposium on sustainable management of hemlock ecosystems in eastern North America, Durham, New Hampshire, June

- 22–24, 1999 (K. A. McManus, K. S. Shields, and D. R. Souto, editors). U.S. Department of Agriculture, Forest Service, General Technical Report NE-267. Newtown Square, Pennsylvania.
- Lu, W., and M. E. Montgomery. 2001.** Oviposition, development, and feeding of *Scymnus* (*Neopullus*) *sinuanodulus* (Coleoptera: Coccinellidae): a predator of *Adelges tsugae* (Homoptera: Adelgidae). *Annals of the Entomological Society of America* 94:64–70.
- Majerus, M. N. 1994.** Ladybirds. Harper Collins Publishers, London, United Kingdom. xvi + 367 pp.
- Mazzini, M. 1975.** Sulla fine struttura del micropilo negli insetti. Ultrastruttura dell'uovo di *Adalia bipunctata* L. (Coleoptera: Coccinellidae). *Redia Giornale di Zoologia* 56(3):185–191.
- Montgomery, M. E., S. M. Lyon, W. Lu, D. Yao, and H. Wang. 1997.** Developing biological control technology: evaluation of the feeding range of predacious beetles [pp. 28–33]. *In: Resource technology 1997: Beijing international symposium proceedings.* China Forestry Publishing House, Beijing.
- Pang, X., and G. Yu. 1993.** Validity of *Scymnus* (*Parapullus*) Yang with description of a new species (Coleoptera: Coccinellidae) from Taiwan. *The Coleopterists Bulletin* 47:228–231.
- Phuoc, D. T., and F. W. Stehr. 1974.** Morphology and taxonomy of the known pupae of Coccinellidae (Coleoptera) of North America, with a discussion of phylogenetic relationships. *Contributions to the American Entomological Institute* 10(6):1–125.
- Pasteels, J. M., C. Deroe, B. Tursch, J. C. Braekman, D. Daloze, and C. Hoorele. 1973.** Distribution et activités des alcaloïdes défensifs des Coccinellidae. *Journal of Insect Physiology* 19:1771–1784.
- Pope, R. D. 1979.** Wax production by coccinellid larvae (Coleoptera). *Systematic Entomology* 4:171–196.
- Rees, B. E., D. M. Anderson, D. Bouk, and R. D. Gordon. 1994.** Larval key to genera and selected species of North American Coccinellidae (Coleoptera). *Proceedings of the Entomological Society of Washington* 96:387–412.
- Ricci, C., and I. Stela. 1988.** Relationship between morphology and function in some Palearctic Coccinellidae [pp. 21–25]. *In: Ecology and effectiveness of aphidophaga: proceedings of an international symposium, Teresin, Poland, August 31–September 5, 1987* (E. Niemczyk and A.F.G. Dixon, editors). SPB Academic Publishing, The Hague, The Netherlands.
- Sasaji, H. 1968.** Descriptions of the coccinellid larvae of Japan and the Ryukyus (Coleoptera). *Memoirs of the Faculty of Education, Fukui University* 18(2):93–135.
- Savoiskaya, G. I., and B. Klausnitzer. 1973.** Morphology and taxonomy of the larvae with keys for their identification [pp. 36–55]. *In: Biology of Coccinellidae* (I. Hodek, editor). Junk, The Hague, Academia Prague.
- Vohland, K. 1996.** The influence of plant structure on searching behavior in the ladybird, *Scymnus nigrinus* (Coleoptera: Coccinellidae). *European Journal of Entomology* 93:151–160.
- Volkl, W., and K. Vohland. 1996.** Wax covers in larvae of two *Scymnus* species: do they enhance coccinellid larval survival? *Oecologia* 107:498–505.
- Wang, H., D. Yao, G. Li, C. Zhang, L. Li, H. Guo, and D. Zhao. 1997.** Investigation on hemlock woolly adelgids and its natural enemies in China [pp. 41–46]. *In: Resource technology 1997: Beijing international symposium proceedings.* China Forestry Publishing House, Beijing.
- Yang, J.-W., and R.-F. Zheng. 1991.** A preliminary study of the bionomics of *Scymnus* (*Neopullus*) *hoffmanni* Weise [pp. 72–78]. *In: Proceedings of the symposium on coccinellids in China* (Huang *et al.* editors). Shanghai Science and Technology Press, Shanghai.
- Yu, G., D. Yao, and H. Liu. 1997.** The Coccinellidae collected from *Tsuga* with *Adelges tsugae* Annand (Homoptera: Adelgidae). *Scientia Silvae Sinicae* 33(5):432–440.

Yu, G., M. E. Montgomery, and D. Yao. 2000. Lady beetles (Coleoptera: Coccinellidae) from Chinese hemlocks infested with the hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae). *The Coleopterists Bulletin* 54:154–199.

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