Journal of Asia-Pacific Entomology 19 (2016) 903–909

Contents lists available at ScienceDirect

Journal of Asia-Pacific Entomology

journal homepage: www.elsevier.com/locate/jape

Morphology of the immature stages of *Arge pagana* (Panzer, 1798) (Hymenoptera: Argidae) with notes on its biology

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ARTICLE INFO

Article history:
Received 8 April 2016
Accepted 22 August 2016
Available online 24 August 2016

Keywords:
Sawfly
Egg
Larva
Prepupa
Pupa
Morphology

ABSTRACT

The immature stages of the large rose sawfly *Arge pagana* (Panzer, 1798) were investigated using light and scanning electron microscopy. The egg is partly inserted into the tissue of twigs of *Rosa chinensis* (Jacq.). The chorion in the plant tissue is furnished with irregular polygonal network and aeropyles, but the exposed portion of chorion is glabrous and aporous. Ten to twelve micropyles were on the posterior pole of eggs. The eruciform larva bears five pairs of ventral prolegs on abdominal segments II–VI and a pair of anal prolegs on segment X. A pair of prominent stemmata is present on the lateral side of head dorsal to the 1-segmented antennae. Male larvae have five instars, but female larvae have six instars. When fully-grown, the larvae move to the ground and spin cocoons to pupate inside. The exarate and decticous pupae are yellow, taking the shape of the adults. This species completes four generations per year, overwintering as prepupae in cocoons. The durations of egg, larva, prepupa, and pupa are 10–15, 19–24, 8–12, and 3–5 days, respectively.

Introduction

Argidae, a cosmopolitan family of Hymenoptera, is composed of approximately 900 described species throughout the world (Taeger et al., 2010; Aguiar et al., 2013), and over 110 species have been reported from China (Shinohara et al., 2015). Previous research was mainly focused on the taxonomy of Argidae based on the adult stage or last-instar larvae (Smith, 1972; Gauld and Bolton, 1988; Saini and Thind, 1995; Wei, 1997; Shinohara and Hara, 2010b; Schmidt, 2012). The knowledge of immature stages, however, is still very limited in Argidae.

Descriptions on the immature stages of Argidae are mainly concentrated on the life history (Regas-Williams and Habeck, 1979; Shinohara and Hara, 2008, 2010a; Shinohara et al., 2011), habits (Adachi, 1981, 1983; Boraschi and Del Lama, 2004; Petre et al., 2007; Eiseman, 2015), and physiology (Petre et al., 2007; Chitgar et al., 2013; Boeve et al., 2014). Although several descriptions have been made of larvae (Gauld and Bolton, 1988; Smith, 1989; Liston et al., 2010), few publications present ultrastructural studies of the egg, prepupa, and pupa.

The large rose sawfly *Arge pagana* (Panzer, 1798) is a serious pest of *Rosa chinensis* (Jacq.), *Rosa multiflora* (Thunb.), *Rosa rugosa* (Thunb.), and *Rosa xanthina* (Lindl.), and is distributed in Asia and Europe (Gauld and Bolton, 1988; Smith, 1989; Huang et al., 1991; Saini and Thind, 1995). The larvae feed on leaves of its host plants and frequently cause defoliation (Huang et al., 1991). Because of their economic importance, previous research of *A. pagana* was mainly focused on its distribution, chemical control, larval physiology, and host ranges (Huang et al., 1991; Petre et al., 2007; Boeve et al., 2014). However, no detailed description has been made on the morphology of immature stages, despite the larva was separated from some other species of *Arge* by Lorenz and Kraus (1957) and hand-drawings of the egg, larva, pupa as well as adult were provided by Huang et al. (1991).

In this study, we investigated all the immature stages of *A. pagana*, including the egg, larva, prepupa, and pupa, using light and scanning electron microscopy for the first time in order to provide knowledge on the recognition of the immature stages of this species.

Material and methods

Adults of *A. pagana* were captured on the campus of Northwest A&F University (34°16′N, 108°4′E), Yangling, Shaanxi Province, China. The adults were reared in a net cage of 100 cm × 50 cm × 50 cm. Fresh twigs of *Rosa chinensis* (Jacq.) inserted in narrow-mouthed bottles filled with water were put in net cages for the sawfly females to oviposit. The twigs containing eggs were transferred to jars with water out of the cages. Fresh twigs with leaves were offered daily as food items for larvae. The sawflies were reared in the laboratory at temperature of 23 ± 2 °C. Photographs were taken with a Nikon D7000 digital camera (Nikon, Tokyo, Japan).

For scanning electron microscopy (SEM), the eggs and larvae were fixed in Carnoy's solution for 12 h and preserved in 75% ethanol. After dehydration in a graded ethanol series, the samples were treated with tertiary butanol, freeze-dried for 3 h, sputtered coated with gold, and

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http://dx.doi.org/10.1016/j.aspen.2016.08.010
1226-8615/

examined with a Hitachi S-3400 N scanning electron microscope (Hitachi, Tokyo, Japan) at 15 kV.

Results

Adults

For the integration of its life cycle, we provide a brief description of the adults of *A. pagana*.

Female (Fig. 1): Head, thorax and legs black with bluish reflection. Wings also black. Forewings infuscated. Costa, stigma and venation dark brown. Abdomen yellow orange except for tergum I dark brown. Body length 8.70 ± 0.42 mm ($n = 20$). Forewing length 8.42 ± 0.16 mm ($n = 20$), with vein 3r-m extremely excurved. The top of 3rd cubital cell longer than its bottom. Antennae black with three antennomeres; flagellum much longer than pedicel and scape. Supraclypeal and frontal region with minute punctures. Compound eyes gray with bluish reflection. Head behind compound eyes slightly widened from above. Clypeus dark brown, emarginated anteromedially. Labrum and labium black. Mandibles and 5-segmented maxillary palps dark brown. Notauli present on mesonotum. Abdomen with golden pubescence and a little saw-like ovipositor. Lancet with 13 serrulae, not exposed until female begins depositing eggs.

Male (Fig. 1A): Similar to female in general form but smaller. Body length 6.74 ± 0.37 mm ($n = 6$). Forewing length 5.58 ± 0.12 mm ($n = 6$).

Eggs

The egg is elongate, reniform, 1.22 ± 0.087 mm long and 0.53 ± 0.062 mm wide ($n = 20$) (Fig. 2A). The newly deposited eggs are milky white and turn light green with embryonic development in several hours. Upon hatching, the black stemmata of the larvae are visible through the somewhat transparent chorion.

With SEM examination, the chorion in the plant tissues is furnished with irregular polygonal network, but the exposed portion is glabrous (Fig. 2A). Each polygon of the network has an independent, separated ridge whose top is slightly wave-like and sometimes not fully closed (Fig. 2B). There are one to two aeropyles on the ridges of some polygons (Fig. 2B). A foveolate protuberance is visible in the central region of the posterior pole and contains ten to twelve micropyles (Fig. 2C).

Larvae

The larva of *A. pagana* is eruciform, with three pairs of well-developed thoracic legs and six pairs of fleshy ventral prolegs on abdominal segments II–VI and XI (Fig. 3B and D). The head is hypognathous. The antennae on the lateral sides of the head are unsegmented and taper toward the apex (Fig. 4A and C). A prominent stemma is situated on the lateral side of the head dorsal to the antenna (Fig. 4A). The larval trunk is cylindrical, composed of three thoracic segments and ten abdominal segments, and furnished with scattered hairy black spots on each segment. The thoracic leg is 6-segmented with an acute tarsal claw (Fig. 5A). The prolegs are unsegmented (Fig. 5B), although the anal prolegs are stouter (Fig. 5C). Abdominal segments I–IX each have three annulets (Fig. 3B–D). The spiracles are present on the prothorax and the first eight abdominal segments. The tenth tergum bears a black sclerotized plate, with dense long setae at apex (Fig. 3D). The larvae undergo five or six instars and have similar morphological characteristics between different instars except the last instar.

First-instar larvae

The newly-hatched larvae are milky white except for the black stemmata and the black and white thoracic legs. The head capsule turns black and shiny in 30 min after hatching. The trunk turns green after the larva began feeding. The black spots on the trunk are blurry.

The width of head capsule is 0.63 ± 0.052 mm ($n = 20$). The body length is 3.42 ± 0.416 mm ($n = 20$).

The head is subglobose, sclerotized, and somewhat circular in frontal contour (Figs. 3A and 4A). The occipital foramen is rounded in outline. The setae are much denser on the lateral side than on the vertex. The ecdysial suture is unrecognizable for naked eyes. A curved epistomal suture is present between the frons and wrinkled clypeus, which bears four setae. A pair of anterior tentorial pits is readily visible near the two lateral ends of the epistomal suture (Fig. 4A). The one-segmented antennae are conical, each with six to eight sensilla basiconica and four sensilla placodea (Fig. 4C). The lateral stemma (Fig. 4A) is prominent and dorsal to the antenna.

The mouthparts are of the mandibulate type (Fig. 4A). The well-developed labrum is about as board as long, rounded laterally and deeply emarginated anteromedially (Fig. 4A). The mandibles are very stout, broad at the base, bearing one curved seta on the outer surface. The maxillary palp (Fig. 4A and B) comprises three palpomeres, with one short seta near the anterolateral margin of the first joint, which is twice as long as the second joint. The distal joint is conical and slightly shorter than the second joint. The stipe is very board and bears two lateral setae. The mentum is slightly shorter than the submentum. The labial palp consists of three palpomeres (Fig. 4B). Between the labial palps is a conspicuous cross-shaped salivary orifice surrounded by numerous irregular micropapillae (Fig. 4D).

The thoracic legs are 6-jointed and are furnished with several long setae on each joint (Fig. 5A). The prolegs are unsegmented (Fig. 5B), and bear seven to nine setae. The anal prolegs (Fig. 5C) are closer to each other than the preceding prolegs.

Last feeding instar larvae

The width of head capsule is 1.94 ± 0.093 mm ($n = 20$). The body length is 18.64 ± 0.817 mm ($n = 20$).

Compared with the preceding instars, the head is yellow and the trunk is yellowish green, with black spots readily visible on the trunk (Fig. 3C and D).

Fig. 1. Adults of *Arge pagana*. (A) A pair in copula, with the female on the left; (B) a female deposits eggs facing downward; (C) a female deposits eggs facing upward.

Prothorax (T1)

A pair of prominent prothoracic shields and large brown spiracles are present on the first thoracic segment that is composed of two annulets. On the dorsum of the first annulet is a pair of black spots close together near the middorsal line. Below the spiracle is a pair of surpedal lobes whose apex is black and setaceous. The lateral side of the first annulet possesses a pair of large spots. A pair of dorsal black spots and a pair of subdorsal black spots are present on the second annulet, with the subdorsal spots roughly three times as large as the dorsal spots.

Mesothorax (T2)

The mesothorax has three annulets, each of which is provided with a pair of dorsal black spots and a pair of subdorsal spots. The dorsal black spots are almost the same as the subdorsal spots in size and shape on the first annulet. The first annulet is thinner with the black spots closer to each other than the second annulet. The third annulet has an additional pair of large lateral black spots. The surpedal lobes on T2 are slightly larger than those on T1.

Metathorax (T3)

The first annulet on T3 is different from that on T1 and T2 in that a pair of lateral black spots is present and the three pairs of black spots on the first annulet of T3 are smaller. The black spots on the second and third annulet of T3 are similar to those on T2 in number and distribution, but the dorsal black spots on the second and third annulet of T3 are smaller. The surpedal lobes on T3 are nearly the same as those on T2.

Abdominal segment I (A1)

On the first annulet, the dorsal pair of black spots is almost the same as the subdorsal pair in size and shape. The lateral pair is wanting. The second and third annulet each are furnished with three pairs of black spots, i.e. an additional pair of black spots is present on the lateral side of the second and third annulet. The distance between the dorsal pair on the first annulet is the shortest among the distances on the three annulets. The distance is slightly greater on the third annulet than on the second annulet. The subspiracular lobes on A1 resemble the surpedal lobes on T3, but is smaller.

Abdominal segments II–VIII (A2–A8)

The black spots on A2–A8 exhibit a similar pattern. The first annulet on each of these segments bears a pair of lateral black spots that is absent on the first annulet of A1. The distributions of the black spots on the second and third annulets of these segments are similar to that on A1. The distance between the dorsal black spots on the first annulet is approximately 1.5 times as long as on the second annulet. The dorsal black spots on the second annulet are slightly closer than those on the third annulet. A2–A8 each are furnished with a pair of peculiar subspiracular lobes, which are black, setaceous at their apexes and more prominent than those on A1.

Abdominal segment IX (A9)

The intersegmental fold between A8 and A9 is clear and A9 is more slender than A8. The distinct difference between A9 and the preceding segments lies in the absence of spiracles and black subspiracular lobes. The black spots on the first and third annulet are of little difference between A9 and A8, although the spots on A9 are smaller. On the second annulet of A9 are a dorsal pair and a subdorsal pair of black spots, but the lateral pair is wanting.

Abdominal segment X (A10)

A10 lacks annulets. The most prominent character of A10 is a large black sclerotized anal plate on the distal part of the dorsum. Only two pairs of small black spots are present on this segment. The subdorsal pair is slightly larger and darker than the lateral pair.

When fully-grown, the last feeding instar changes to the prepupal stage (a non-feeding stage). The prepupae enter the ground (or the debris on the soil) and spin double-walled cocoons (Fig. 6) to pupate inside.

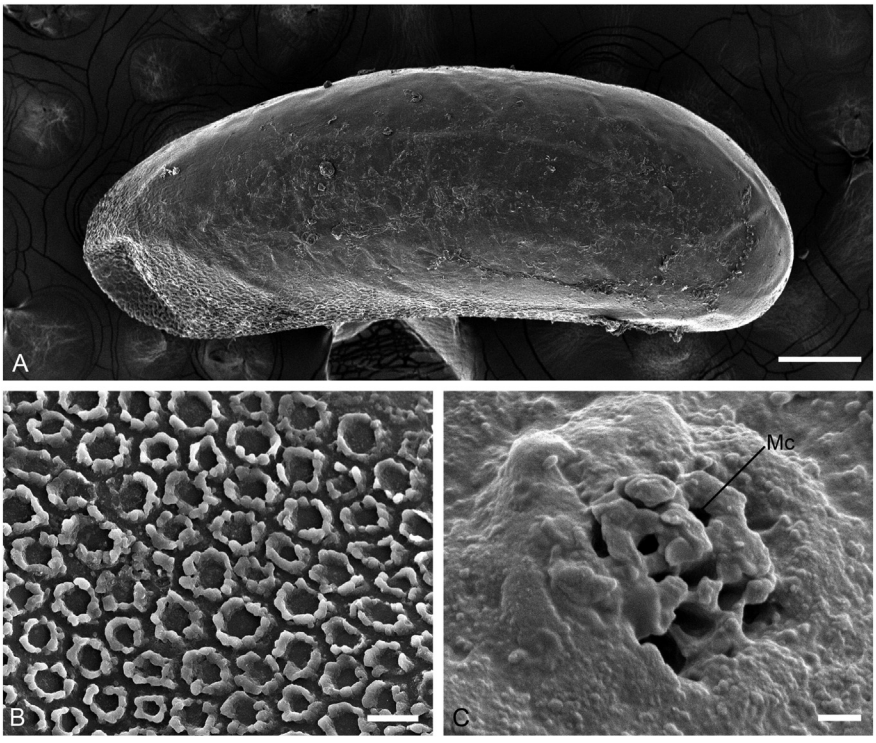

Fig. 2. Eggs of *Arge pagana*. (A) An egg habitus; (B) magnification of the chorion, showing the polygonal network; (C) the posterior pole, showing micropyles (Mc) on the foveolate protuberance. Scale bars: (A) = 150 μm; (B) = 20 μm; (C) = 2 μm.

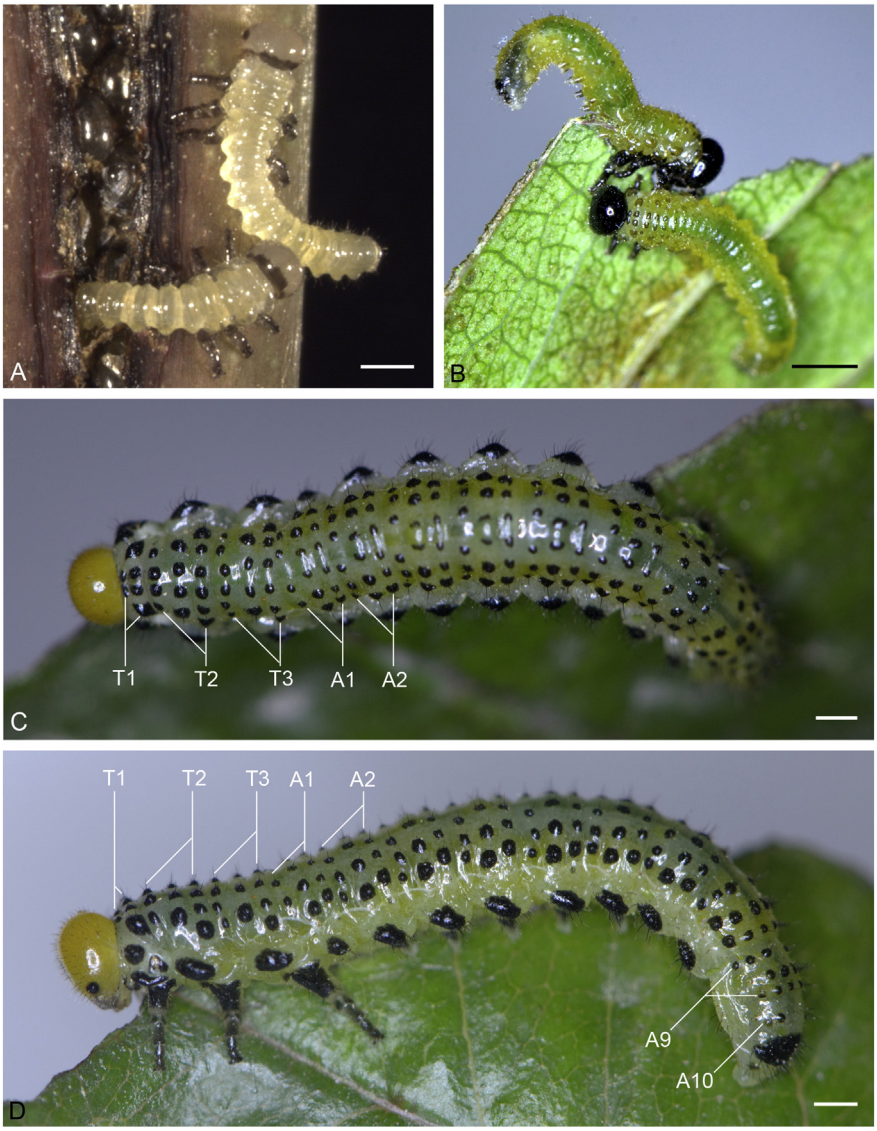

Fig. 3. Larvae of *Arge pagana*. (A) First-instar larvae; (B) second-instar larvae; (C) dorsal view of last feeding instar larva; (D) lateral view of last feeding instar larva. Scale bars: (A), (C) and (D) = 1 mm; (B) = 0.5 mm.

Prepupae

The prepupa is fusiform, taking the color of the last feeding instar larva except for A9 and A10 turning yellow (Fig. 7A–C). The width of head capsule is 1.92 ± 0.086 mm (n = 10). The body length is 9.62 ± 0.528 mm (n = 10). On the vertex is a quasi-trapezoidal black depression (Fig. 7A and B). Compared with the feeding larval stage, the mandibles of prepupa (Fig. 7A) become slender, thinner at the base, more like the pupal mandibles than the larval mandibles. The brown spiracles on the prothorax and the first eight abdominal segments (Fig. 7B) are more prominent than those of the last feeding instar larvae. The thoracic legs and abdominal prolegs bend to the midventral line (Fig. 7A).

Pupae

The pupa is exarate and decticous, and yellow except for the darkish compound eyes (Fig. 7D–F). The body trunk takes the shape of the adult. The width of head capsule is 1.83 ± 0.072 mm (n = 7). The body length is 9.14 ± 0.462 mm (n = 7).

The compound eyes are prominent, brown at first and turning gray or black soon. On the vertex are three brown ocelli arranged in a triangle (Fig. 7F). The antennae extend to T3 (Fig. 7D and E). The flagellum is composed of only one flagellomere, but much longer than scape and pedicel. A pair of five-segmented slender maxillary palps extends to T2.

Three pairs of legs and two pairs of wing-pads (Fig. 7D and E) are present on the thorax. Fore tarsi and wing-pads extend to A1. Middle tarsi extend to the distal part of A3, and hind tarsi to A6.

The abdomen is fusiform, with eight pairs of brown spiracles (Fig. 7E and F) clearly visible on the first eight segments. The depressions between the abdominal segments are readily distinguishable except that between A9 and A10.

Biology

Arge pagana is multivoltine, completing four generations per year and overwintering as prepupae in cocoons on the ground at central Shaanxi Province, China.

The mating behavior occurs from 10:00 to 14:00 during the day. During mating, the male grabs the female abdomen with his hind legs and the pair in copula maintains an end-to-end position (Fig. 1A).

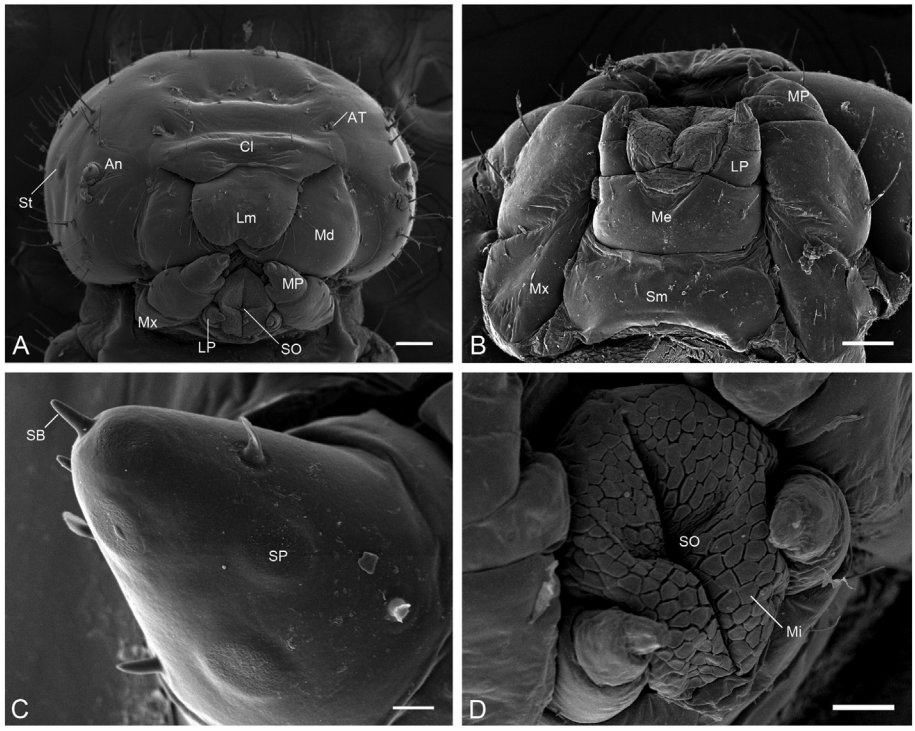

Fig. 4. Head of first-instar larvae of *Arge pagana*. (A) Head, ventro-frontal view; (B) mouthparts, posteroventral view; (C) antenna (An); (D) salivary orifice (SO). AT, anterior tentorial pit; Cl, clypeus; Lm, labrum; LP, labial palp; Md, mandible; Me, mentum; Mi, micropapillae; MP, maxillary palp; Mx, maxilla; SB, sensillum basiconicum; SP, sensillum placodeum; Sm, submentum. Scale bars: (A) = 60 μm; (B) = 40 μm; (C) = 4 μm; (D) = 20 μm.

Oviposition takes place from 11:00 to 17:00 based on our observation of 36 females in the laboratory. Thirty-two females deposited their eggs facing downward (Fig. 1B) and four females deposited their eggs facing upward (Fig. 1C). All females inserted their eggs in the tissue near the tip of the twigs. The eggs were deposited in two rows and were arranged in an inverted V-shape. The spawning marks are shuttle-shaped and turn brown in a day. The twigs broke off easily as a result of egg enlargement due to the embryonic development in the tissues. The egg duration lasts 10–15 days.

Upon hatching, the larvae crawled forward with body stretched (Fig. 3A) until crawling out of the twig tissue under the force of stretching. This process lasts 12–30 min. The young larvae stay together for about an hour before feeding in a group along the freshly emerged leaf edges. Third- and later instar larvae live individually and feed on older leaves as well. The male larvae have five instars, but the female larvae have six instars (n = 35). The duration of the larval stage is 19–24 days. The cocoons were aggregated together on the ground under the litter (Fig. 6). *Arge pagana* stays in the cocoon for 12–16 days, with 8–12 days as the prepupal stage and 3–5 days as the pupal stage. Upon emergence, the compact inner wall of some cocoons (6 of 35 cocoons observed) disintegrates, leaving the adult visible through the net-like outer wall.

Discussion

As in other insects, morphological studies of immature stages play an important role in pest control of *A. pagana* and the taxonomic and phylogenetic analyses in sawflies (Van Emden, 1957; Meier and Lim, 2009). To our knowledge, this paper represents the first attempt to study the ultramorphology of the egg and larvae of *A. pagana*.

In *A. pagana* the egg portion inserted into the tissues of host plants is furnished with irregular polygonal network and aeropyles, but the exposed portion is glabrous (Fig. 2). This condition also occurs on the eggs of the gall wasp *Diplolepis rosae* (Linnaeus) (Cynipidae) (Bronner, 1985; Vårdal et al., 2003). Bronner (1985) thought that the specialized structure of *D. rosae* eggs functions as an anchor. Vårdal et al. (2003)

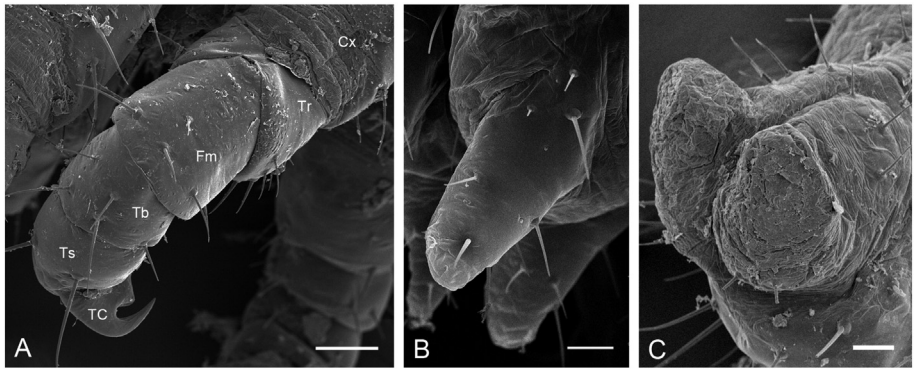

Fig. 5. Legs and prolegs of first-instar larvae of *Arge pagana*. (A) Prothoracic leg; (B) abdominal proleg V; (C) anal prolegs (AL). Cx, coxa; Fm, femur; Tb, tibia; TC, tarsal claw; Tr, trochanter; Ts, tarsus. Scale bars: (A) = 50 μm; (B) and (C) = 30 μm.

Fig. 6. Cocoons of *Arge pagana* on the soil, with debris removed.

suggested that the porous region facilitates the exit of the larva hatching and permits chemical exchange between the embryo and the plant. In our opinion, the network on the specialized region of eggs in *A. pagana* can increase the strengthness of the eggshell to protect the eggs from being damaged while the egg is inserted into the plant tissues. An alternative possibility is that it can strengthen the adhesion between the eggs and the plant tissue. The porous portion may also function as gas exchange and retain humidity suitable for the embryonic development because aeropyles are only present on this concealed portion of the eggs. The exposed glabrous portion is aporous, likely to reduce water evaporation from eggs to the dry atmosphere.

Hymenopteran larvae have a tendency to reduce the antennae (Gauld and Bolton, 1988; Beutel et al., 2008). The antennae are 6- to 7-jointed in the more primitive sawflies, such as Xyelidae and Pamphiliidae, but are one-segmented in more derived Siricidae (Yuasa, 1922; Gauld and Bolton, 1988; Beutel et al., 2008). In Tenthredinoidea, the larval antennae of most species are 3- to 5-jointed (Yuasa, 1922; Bird, 1927; Wong and Szlabey, 1986; Gauld and Bolton, 1988). The larval antennae of *A. pagana*, however, consist of only one segment. This supports the viewpoint of Schulmeister et al. (2002) that Argidae represents a more derived family in Tenthredinoidea.

The type of body ornamentation and number of prolegs are variable within the family Argidae and can be used in the separation of genera and species in this family (Smith, 1972). For example, *Arge hasegawae* (Takeuchi) and *A. gracilicornis* (Klug) are very similar to each other in the young larvae, but can be readily distinguished through the ground color and spots on the trunk of their last-instar larvae (Shinohara et al., 2011). The ground color of the last instar trunk is greenish white in *A. gracilicornis*, pale violet purple in *A. hasegawae* (Shinohara et al., 2011), but yellowish green in *A. pagana*. In contrast to *A. hasegawae*,

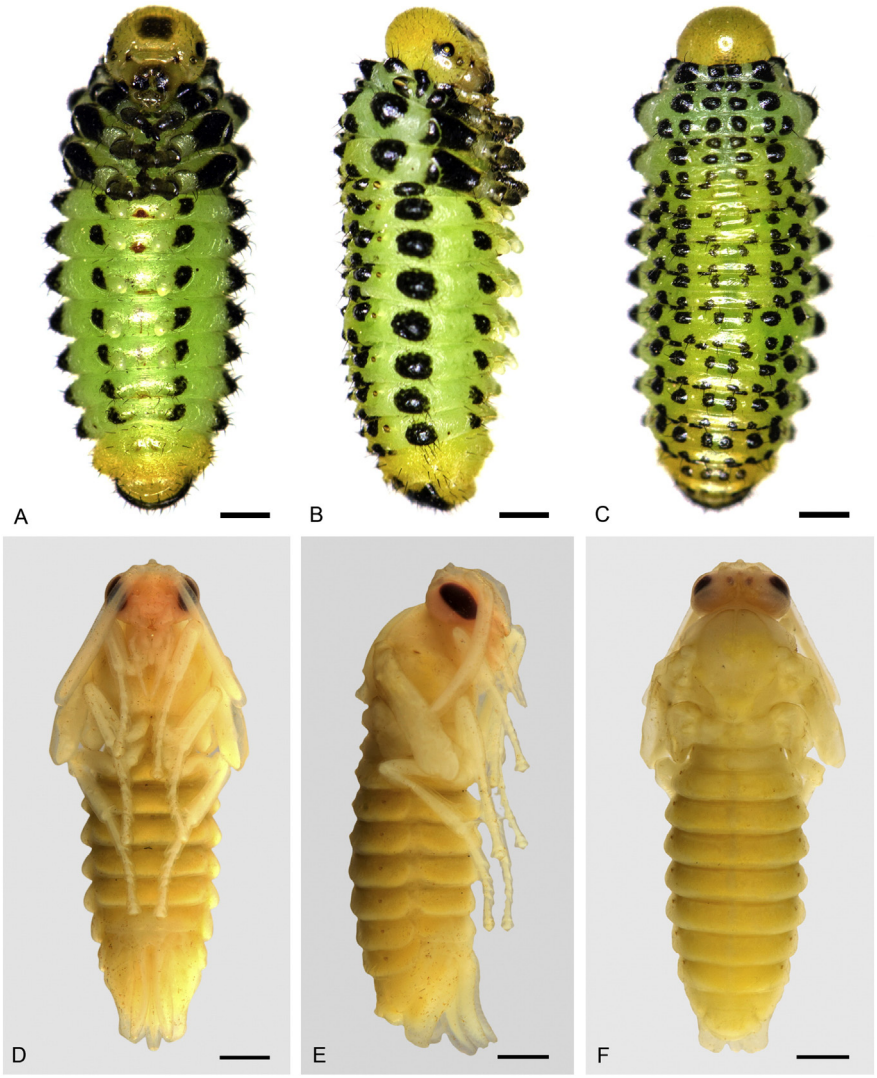

Fig. 7. Prepupa and pupa of *Arge pagana*. (A)–(C) Prepupa in ventral, lateral, and dorsal views; (D)–(F) female pupa in ventral, lateral, and dorsal views. Scale bars = 1 mm.

large dark yellow spots are absent on the trunk of the last instar in *A. pagana*. Prolegs are present on A1–A8 and A10 in *A. humeralis* (Beauvois), A2–A6 and A10 in *A. hasegawae*, A2–A7 and A10 in *Sterictiphora serotina* (Smith), A2–A9 and A10 (single anal proleg) in *S. krugii* (Cresson), and A4–A8 and A10 in *Atomacera decepta* (Rohwer) (Smith, 1972; Regas-Williams and Habeck, 1979; Shinohara et al., 2011). The number of prolegs in *A. pagana* is the same as in *A. decepta* and *A. hasegawae* even though the distribution and appearance are different.

In Symphyta the larvae usually have 4–6 instars with the male having one less instar than the female (Gauld and Bolton, 1988). Regarding the larvae of *A. pagana*, Huang et al. (1991) report that most of the larvae have five instars, and the rest have six instars at Guangzhou, Guangdong Province in tropical China. Based on our investigation, however, only a quarter (24.3%) of larvae ($n = 35$) have five instars, and the remaining have six instars at central Shaanxi Province in temperate China. Through rearing we found that all the larvae with six instars emerged as females, and all the larvae with five instars emerged as males. The vast difference in the sex ratio is likely due to the environmental differences between the temperate and tropical populations in *A. pagana*.

Acknowledgements

We thank Tao Li and Yu Yang for assistance in collecting the insects, Ji-Shen Wang and Lu Jiang for assistance in taking photographs, Ze-Jian Li for confirming the identification of the species. We also thank Bei-Bei Zhang, Li-Xuan Kou, Shuang Xue, Wei Du, and Yan-Qing Hu for comments on the early draft of the manuscript. Special thanks are due to two anonymous referees for valuable comments and suggestions on the revision of the manuscript. This research was supported by the National Natural Science Foundation of China (grant no. 31372186).

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