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RESEARCH PAPER

The larval structures and bionomics of *Idgia iriomoteana* (Coleoptera: Prionoceridae)

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Abstract. The life cycle, bionomics and mature larval structures of the Japanese prionocerid species, *Idgia iriomoteana* Nakane, 1980 were investigated in captivity. The results showed that *I. iriomoteana* has the following characteristics: (1) the larval morph is less advanced in terms of miniaturization, and larvae pass seven larval molts before they pupate; (2) the life cycle is univoltine with summer, not winter, dormancy; (3) the first instar larvae are larger than the size of the egg, but foetomorphic larval instar (which is observed in the Melyridae: Malachiinae) is not shown. Based on comparison with melyrid species, the degree of miniaturization, dormancy behaviour, adaptation to the tropical and subtropical climates and the adaptive significance of a large first instar larva are all discussed. This study is the first to report the complete life cycle of a member of the family Prionoceridae.

Key words. Coleoptera, Cleroidea, Prionoceridae, melyrid lineage, life cycle, dormancy, foetometamorphosis, Japan, Oriental Region

Zoobank: http://zoobank.org/urn:lsid:zoobank.org:pub:F1A9A169-4124-4459-A715-6D580BBFF27E

Introduction

Prionoceridae Lacordaire, 1857 is a small, rarely studied family of Cleroidea that belongs to the melyrid lineage (Bocakova et al. 2016, Gimmel et al. 2019). Most species are associated with tropical and subtropical moist forests although some Palaearctic members live in xerothermic habitats (Geiser et al. 2016). In Japan, only one species, *Idgia iriomoteana* Nakane, 1980, is found on the Yaeyama Islands in the tropical rainforest climatic zone (Nakane 1980, Okushima 1994) and on Okinawa Island (Mizota & Azuma 1998). This species was previously treated as a junior synonym of *Idgia flavicollis* Redtenbacher, 1878 by Sato (1985); however, more recently, Mayor (2007) and Yoshitomi & Hayashi (2011) treated it as a separate species.

Prionocerid adults are pollen feeders whereas the larvae are carnivorous; the larvae are typically found in soil and under bark (Crowson 1964). Geiser et al. (2016) studied the molecular phylogeny of the family Prionoceridae and suggested a single origin of nocturnality with multiple transitions from nocturnal to diurnal lifestyle. They also suggested that the African and Arabian species of the family Prionoceridae represent two lineages, both of which have a tropical Asian origin. To date, the larval morphology of the following representatives has been described: *Lobonyx aeneus* (Fabricius, 1787); an unnamed species of *Idgia* Laporte, 1838; *Prionocerites tattriei* Lawrence, Archibald & Ślipński, 2008 from Eocene amber and *Idgia notaticollis* Pic, 1943 (Crowson 1964, Fiori 1971, Majer 1994, Lawrence et al. 2008, Asano et al. 2016). However, the biology and immature stages of Prionoceridae remain insufficiently explored.

In the present study, adult specimens of *I. iriomoteana* were collected from trees at the edge of a forest. The mature larval structures, bionomics and life cycles of this species are presented here. The mitochondrial cytochrome c oxidase subunit 1 gene of the sixth instar larva was also determined for use in future studies. Based on the observations herein, the duration of development was compared with that of another species of the melyrid lineage, *Astylus trifasciatus* (Guérin-Méneville, 1835) (Estrada & Solervicens 1997) from the subfamily Melyrinae, and with that of *Intybia pelegrini pelegrini* (Pic, 1910) from the subfamily Malachiinae, that has two foetomorphic

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larval instars (Asano 2021). The degree of advancement in miniaturization, dormancy behaviour, cold tolerance and the significance of large first instar larva in terms of egg size are discussed.

Material and methods

Seven adults of *I. iriomoteana* were collected on 14 and 15 March 2020 at Haiminaka (24°17′52.4″N 123°51″56.2″E) and Funauki (24°20′23.1″N 123°43′25.7″E), Taketomi town, Okinawa Prefecture, Japan. Adults were collected from the flower buds of *Turpinia ternata* Nakai (Staphyleaceae) and the leaves of leguminous plants at the forest edge using a sweep net. The adult specimens were transferred to plastic containers with the leaves and buds of *T. ternata* and inflorescence of *Argyranthemum frutescens* (L.) (Asteraceae). Their larvae were transferred to plastic containers and after the fifth molt were put into the containers separately. Containers were kept at room temperature. The specimens were provided with food (pollen for the adults, dead chironomid larvae for the larvae), and larval molts were checked every morning.

Observations were made under a dissecting stereoscope (Olympus SZX7) and compound microscope (Nikon LABOPHOT and Olympus CH2). Photographs were taken with Canon Power shot D12 and EOS D7 digital cameras The examined specimen of the sixth instar larva was acquired by captive breeding and fixed on 24 November 2020. The larva was fixed in 70% ethanol. The head capsule, mouth parts, legs and urogomphi were removed and immersed in 10% KOH solution at room temperature for 24 hours.

In larval description, the terminology follows Asano et al. (2016), Šváchа & Lawrence (2014) in part, and the following abbreviations are used:

BL	length of body, from anterior margin of frons to apex of urogomphi;
BW	maximum width of body;
HL	maximum length of head capsule;
HW	maximum width of head capsule;
PL	maximum length of pronotum;
PW	maximum width of pronotum;
TL	maximum length of tibia;
UL	maximum length of urogomphi;
aa	anterior arm of tentorium;
ch	chorion;
eb	egg burster;
ex	larval exuvia;
pa	posterior arm of tentorium;
y	yolk.

Genomic DNA was extracted from a larval body using QIAGEN DNeasy Tissue Kit following the manufacturer's instructions. The partial fragment of mitochondrial cytochrome oxidase subunit 1 (COI) gene was amplified with the universal primers LCO1490 (5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′) and HCO2198 (5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′) (Folmer et al. 1994). PCR reaction was performed in a total volume of 20 µl containing 5 µl of KOD FX Neo Buffer, 4 µl of dNTP mix (2 mM each), 0.6 µl of each primer (10 µM), 0.4 µl of KOD FX Neo DNA polymerase, and 4 µl of template DNA, and 5.4 µl of water. The reaction temperature profile included the initial step at 94°C for 2 min followed by 35 cycles of 98°C for 10 s, 55°C for 30 s and 68°C for 30 s, and final extension step at 68°C for 5 min. PCR products (ca 700 bp) were purified from agarose gel and sequenced by Sanger sequencing.

The taxonomic vouchers and extracted DNA are tentatively deposited at Teiso kasei Co., Ltd., Shizuoka and will be preserved in the National Museum of Nature and Science, Tokyo, Japan.

Results

Sixth instar larva of *Idgia iriomoteana* Nakane, 1980

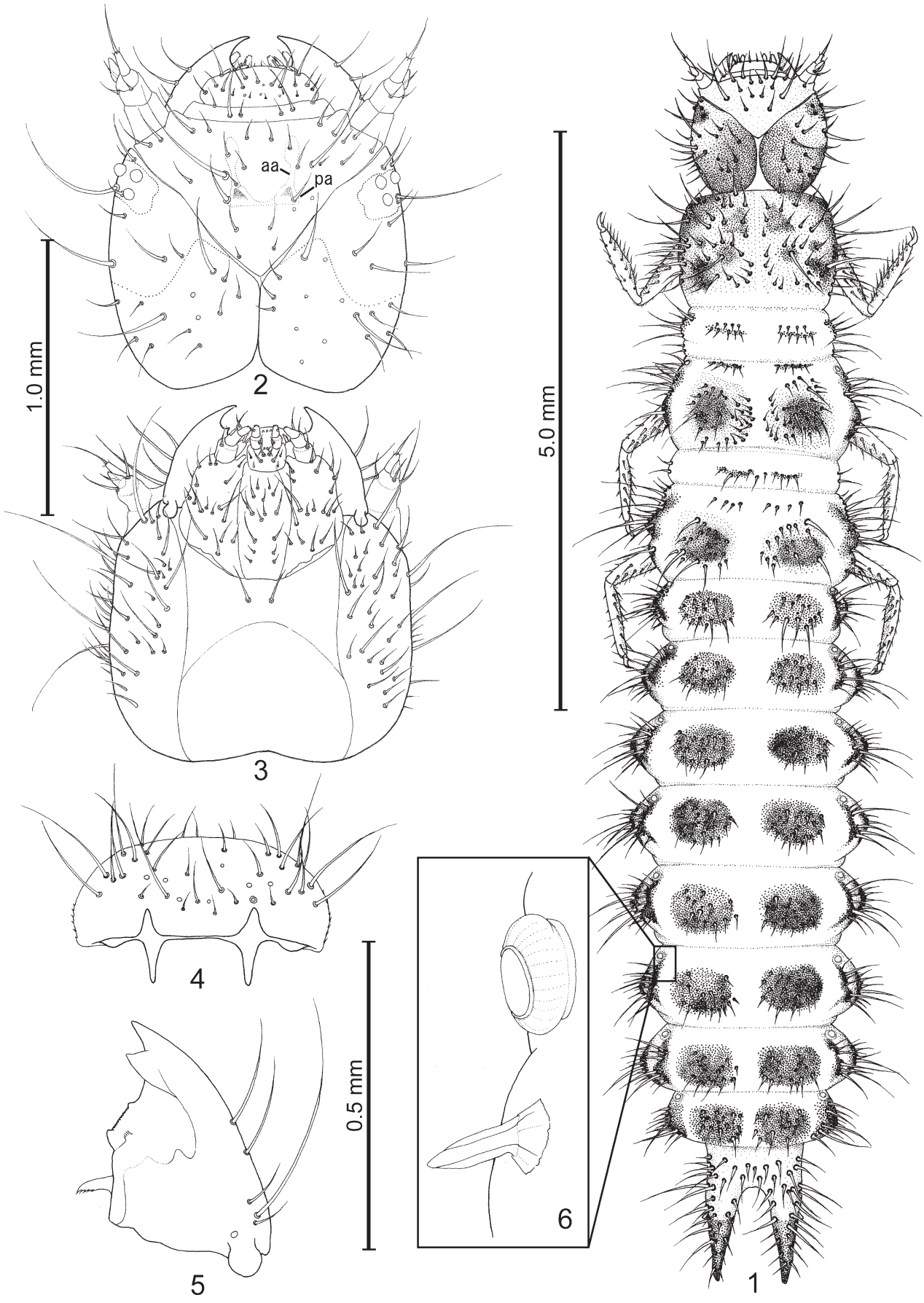
(Figs 1–6, 17)

Coloration. Head capsule light brown except for black middle part of epicranial plates and around stemmata. Body yellow except for markings of each segments. Prothoracic tergite pigmented light brown in most of dorsal part, black in each anterior angle portion, with three pairs of small black spots in middle parts. Arthrodial membrane of thoracic segments pigmented light brown in dorsal middle parts. Meso- and metathoracic tergite with three pairs of pigmented areas as follows: horizontal line-shaped pair on anterior margin, and pair of black large papillate markings in middle and on each side, respectively. Legs translucent. Abdominal tergites with pair of large black papillate markings in middle and on each side, respectively. Urogomphi yellow except for black apical portions (Fig. 17).

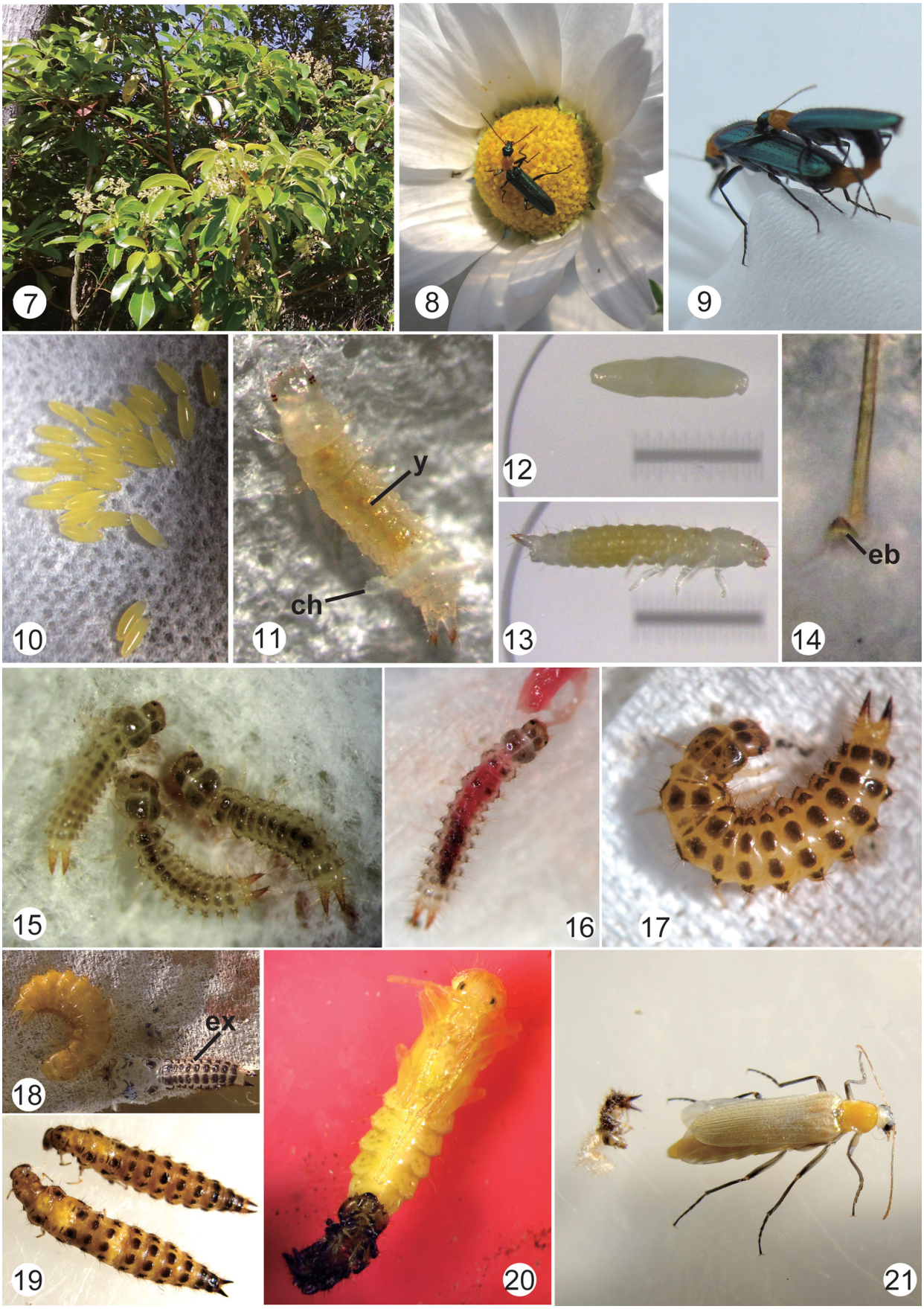
Structure. Measurements in mm (n = 1). BL: 10.7; HL: 1.05; HW: 1.23; PL: 1.05; PW: 1.36; PTL: 0.69; UL: 1.23. Head capsule square, with dense short setae; frons large, with 2 pairs of long setae; epicranial plate with 4 pairs of long setae (Fig. 2); tentorium with anterior and posterior arms (Fig. 2: aa, pa), dorsal arms obscurely visible. Labrum about 2.5 times as broad as long, with 11 pairs of setae and 3 pairs of pores (Fig. 4). Number of stemmata 5; anterior 3 arranged in transverse row and posterior 2.

Antennae 3-segmented; 2nd segment with conical sensorium and three long setae; 3rd segment with one long and 3 short setae (Fig. 3). Mandible bidentate, with sharp apical teeth; cutting edge distinctly denticulate, ventral margin side ridged, face ridged and provided with tooth, outer margin of face with 4 long and one short seta (Fig. 5). Maxillary palpi 3-segmented; 1st palpomere with short seta and pore; 2nd one with short seta and pore; 3rd one longer than preceding, with sensilla (Fig. 3). Labial palpi 2-segmented; 1st palpomere with short seta; 2nd with pore and sensilla (Fig. 3). Prementum with 4 pairs of setae (Fig. 3). Maxillary stipes and postmentum with dense short setae, the former with 16 setae, the latter with 18 pairs of setae (Fig. 3). Cardo invaginate behind stipes, only basal border seen ventrally (Fig. 3).

Prothorax large, oblong, strongly sclerotized, with dense short and long thick setae on pronotum (Fig. 1). Mesothorax large and wide. Prescutum with 9 pairs of short setae on pigmented part in middle. Scutum with 2 pairs of strongly sclerotized parts on anterior and middle



Figs 1–6. Larval structures of *Idgia iriomoteana* Nakane, 1980. 1 – habitus; 2 – head in dorsal view; 3 – head in ventral view; 4 – labrum; 5 – left mandible ventrally; 6 – spiracle and membranous appendage. Abbreviations: aa – anterior arm of tentorium; pa – posterior arm of tentorium.



Figs 7–20. Photographs of *Idgia iriomoteana* Nakane, 1980. 7 – adult habitat; 8 – adult feeding on inflorescence of *Argyranthemum frutescens*; 9 – mating; 10 – eggs; 11 – hatching; 12 – egg immediately before hatching; 13 – first instar larvae immediately after hatching; 14 – egg burster and seta of prothorax; 15 – pigmented first instar larvae; 16 – feeding of a first instar larva (dead chironomid larvae); 17 – summer dormancy (6th instar); 18 – 6th larval molt (exuvia of 6th instar and 7th instar larva); 19 – molting failure; 20 – pupa with exuvia of the 7th instar larval cuticle; 21 – eclosion. Abbreviations: ch – chorion; eb – egg burster; ex – exuvia; y – yolk.

portions; former pair horizontal and each part with 5 short setae; latter pair large, each part with dense short setae and 3 long setae (Fig. 1). Epipleuron with membranous appendage in lateral portions. Metathorax large and wide. Prescutum with 5 pairs of short setae on pigmented part in middle. Scutum with 2 pairs of sclerotized parts on anterior and middle portions; former pair with 4 short setae on each part, latter pair large, each part with dense short setae and with 3 or 4 long setae (Fig. 1).

Abdomen with 9 tergites, the last (= IX) one bearing pair of urogomphi (Fig. 1). Tergites I–VIII each with two pairs of strongly sclerotized large protrusions arranged in transverse row having dense short and long stout setae, respectively (Fig. 1); the middle pair of protrusions with one pore and one a membranous appendage on each side (Fig. 6). Urogomphi elongate, subparallel, straight and not curved upwards, slightly dentate on outer margin, dorsal surface with dense short and 9 or 10 pairs of long setae and pair of membranous appendages in middle (Fig. 1). Spiracles dome-shaped (Fig. 6).

Legs elongate, with dense short strong setae. Femora elongate, with several long setae interiorly. Claw slender, with single short seta (Fig. 1).

Differential diagnosis. The larva of *Idgia notaticollis* Pic, 1943 (Asano et al. 2016) and *I. iriomoteana* in the current study share the following distinguishing characteristics: strong setae covering body, large frons, mandibles with stout and short prostheca, large prothorax, distinguishable prescutum with setae, pigmented sclerites of tergites, presence of membranous appendages on thoracic abdominal segments, long femur, and long and straight urogomphi, compared with those in other families of the melyrid lineage.

DNA barcode. The partial COI sequence is available from GenBank under the accession number MZ686961.

Larval development and bionomics. Adults were observed gathering on the flower buds of *Turpinia ternata* and leaves of leguminous plants at the forest edge (Fig. 7); they moved rapidly among the buds. The larvae were not found at the same location. A pupa of *Idgia notaticollis* was collected from the stem of bamboo (Asano et al. 2016); however, there was no bamboo in the surrounding area.

Adult specimens were maintained in captivity. Mating behaviour was observed in March when the males mounted the backs of the females (Fig. 9). A female laid 38 eggs on 17 March 2020. Eggs were not covered by any substance but were laid in a cluster on the surface of tissue paper (Fig. 10). The abdomen of females with eggs showed little swelling and the abdominal tergites and sternites were completely sclerotized; in contrast, the abdomens of malachiines are swollen with eggs, and several abdominal tergites and sternites are mostly membranous but partly sclerotized as small plates (Asano 2021). The adults lived in captivity (at most) until 4 May 2020 and during this time fed only on the pollen of *Argyranthemum frutescens* (Fig. 8).

Eggs hatched 12 days after oviposition. This species did not have a foetomorphic larval stage, in contrast to malachiines that undergo one or two instar stages as inactive and non-feeding foetomorphic larval stage. Embryos grew much larger immediately before the egg burst, becoming 1.6-times as long as the chorion (Figs 12, 13). They were positioned straight rather than curled and their abdominal segments folded accordion-like in the chorion. Eggs from the same cluster began to burst simultaneously. First instars ruptured and removed the thin chorion from the larval head to the thorax; they then emerged from the chorion completely and began walking and feeding (Fig. 16). The yolk was still present immediately after hatching (Fig. 11). First instar larvae consumed dead chironomid larvae that were provided for them, but did not prey on each other. Markings on the head, thorax and abdomen pigmented within 1 hour after hatching (Fig. 15). The first molt began 22–29 days after hatching. Thereafter, the growth of ten larvae that fed only on dead chironomid larvae was closely observed; they underwent seven larval molts before pupation (Table 1). The second molt occurred 15–25 days after

Table 1. The dates and lapsed days of larval development of *Idgia iriomoteana* Nakane, 1980, the soft winged flower beetles *Astylus trifasciatus* (Guérin-Méneville, 1835) and *Intybia pelegrini pelegrini* (Pic, 1910).

Events	***Astylus trifasciatus**** (Estrada & Solervicens 1997)		***Intybia pelegrini*** overwintering generation (Asano 2021)		***Intybia pelegrini*** 2nd generation (Asano 2021)		***Idgia iriomoteana*** (this study)	
Oviposition	8 Oct, 1994	0	25 Jul, 2019	0	1 Jul, 2019	0	17 Mar, 2020	0
Hatching	26 Oct, 1994	16	30 Jul, 2019	5	7 Jul, 2019	6	30 Mar, 2020	13
1st molt	27 Oct, 1994	18	31 Jul, 2019	6	8 Jul, 2019	7	21 Apr, 2020	35
2nd molt	1 Nov, 1994	27	1 Aug, 2019	7	10 Jul, 2019	9	13 May, 2020	57
3rd molt	26 Nov, 1994	64	unconfirmed	–	30 Jul, 2019	29	2 Jun, 2020	104
4th molt	27 Dec, 1994	108	27 Aug, 2019	33	unconfirmed	–	29 Jun, 2020	134
5th molt	26 Jan, 1995	146	19 Sep, 2019	56	15 Aug, 2019	45	15 Jul, 2020	120
6th molt	9 Mar, 1995	204	absent	↓	absent	↓	28 Oct, 2020	225
7th molt	16 Sep, 1995	418	absent	↓	absent	↓	absent	↓
8th molt	15 Dec, 1995	516	absent	↓	absent	↓	absent	↓
Prepupation	unconfirmed	–	8 May, 2020	288	25 Aug, 2019	55	10 Jan, 2021	299
Pupation	31 Jul, 1996	745	13 May, 2020	293	28 Aug, 2019	58	14 Jan, 2021	303
Eclosion	15 Aug, 1996	760	23 May, 2020	303	3 Sep, 2019	64	4 Feb, 2021	324

**Astylus trifasciatus* was observed in the southern hemisphere.

the first molt (13 to 16 May 2020); the third molt occurred 17–25 days after the second molt (2 to 7 June 2020) and the fourth molt occurred 22–39 days after the third molt (29 June to 11 July 2020). The larvae molted at around the same time up to the fourth molt; however, the timing of the fifth molt varied among specimens. Specifically, four specimens molted from 15 to 30 July, one specimen molted on 14 August, two specimens molted on 16 and 27 September, respectively, and three specimens molted from 14 to 24 October (all in 2020). The time difference of the final sixth molt among the specimen was not as large as for the fifth molt; the sixth molt occurred from 28 October to 24 November 2020. The larval exuvia was thick and firm (Fig. 18). The final seventh instar larvae often bit the tissue paper. These larvae became the prepupae from 10 January 2021 and pupated from 14 January 2021; two specimens pupated on 14 and 31 January, five specimens pupated from 3 to 25 February (Fig. 20), whereas two pupae died due to molting failure of the final instar cuticles (Fig. 19). Eclosions then began from 4 February 2021: first, a male eclosed on 4 February; next, two females eclosed on 10 and 11 February, respectively; finally, a male and female eclosed on 3 March (Fig. 21). The pupal stage lasted for 8–21 days.

Seasonal occurrence. Adults were collected in the field on 14 and 15 March. Oviposition was observed on 17 March. The period from oviposition to pupation was 303–332 days. Larvae were inactive and the fifth larval molt stagnated in summer (Fig. 17). The duration of the sixth instar varied among specimens. In captivity, specimens passed the winter as the final seventh instar or pupal stage; they pupated and eclosed from January to March of the following year.

Discussion

Larval molts and structure. *Idgia iriomoteana* passed seven larval instars until they pupated without foetomorphic larval instars. One more larval instar was observed than is found in the malachiine species *Intybia pelegrini* and *Intybia takaraensis* (Asano 2021). The durations of the particular larval instars, from the first to the fifth, were also longer than those in *I. pelegrini* (Table 1). The respective instar period of *Intybia* species was prolonged only in the final (sixth) instar (Asano 2021) relative to that of *Idgia iriomoteana*. These differences may be influenced by the miniaturization and simplification of the larval body structures in malachiines.

Larvae of *I. iriomoteana* have large body size and complex body structures compared with the malachiine species. 'Simplification of the tentorium', 'absence of most sclerites and extremely weak sclerotization of the integument in larvae' and 'dramatic reduction in the number of ommatidia and sensilla' are described as the miniaturization effects (Polilov 2015). Larvae of *I. iriomoteana* have the following distinguishing characteristics: five stemmata, a distinguished tentorium, thick and firm cuticles, many pigmented sclerites, many long setae, and a large head and prothorax. In contrast, malachiine species have the following characteristics: four stemmata, an inconspicuous tentorium, thin and weak cuticles, minimally pigmented sclerites, scarce long setae, and a narrow head capsule and prothorax. Then, the results can be interpreted that malachiine species are advanced in terms of miniaturization and simplification, whereas prionocerid species are less advanced.

The total duration of larval stage and the durations of particular larval instars of the melyrine species *Astylus trifasciatus* which inhabits the rural area near the Clarillo River in Río Clarillo National Reserve of Chile together with *I. iriomoteana* are also longer than in *I. pelegrini pelegrini*. *Astylus trifasciatus* larvae pass nine instars until they pupate (Estrada & Solervicens 1997) (Table 1). It is interpreted that the long-term larval development of this species (Table 1) is caused by the climate conditions of this area (Estrada & Solervicens 1997). Mature larvae of *A. trifasciatus* also have large body (approximately 20 mm in the final instar) and many long setae throughout the whole body (Estrada & Solervicens 1997). There is also the possibility that *A. trifasciatus* is less advanced in terms of miniaturization and simplification compared with the malachiine species. Thus, there is the possibility that the degree of the miniaturization and simplification of the larval body structures is also related to the number of larval instars and the duration of larval stage.

Life cycle and dormancy. The larval molt and consumption of *Idgia iriomoteana* stagnated in mid-summer; however, the larval molt, pupation and consumption did not stagnate in winter.

***Summer dormancy*.** Larvae molted at around the same time until the fourth molt, however, the timing of the fifth molt varied among specimens. Most larvae passed the summer in the fifth or sixth instar, and the larval molts stagnated (Fig. 17). Consequently, the duration of the fifth instar was extended up to 117 days, although the duration of each larval instar from the first to fifth was about 20–30 days. The larvae became active again in mid-September, at which point the larval molt resumed.

The melyrid species *Astylus trifasciatus*, *Intybia pelegrini pelegrini* and *Intybia takaraensis* did not show the stagnation of consumption and molts in summer (Estrada & Solervicens 1997, Asano 2021) (Table 1). Additionally, a period of dormancy was not always necessary for the ontogenetic development of some malachiine species to proceed. The larvae that hatched in early summer became adults during that summer or in early autumn of the same year, and the time between hatching and pupation was only 40–60 days. Asano (2021) suggested that these species are potentially bivoltine, at least in temperate zones. In the present study, such shortening of larval developmental duration and multivoltinism were not observed in the ontogeny of *I. iriomoteana*.

Overwintering. *Idgia iriomoteana* showed the sixth larval molt from late October to November (Fig. 18). The final (seventh) instar larvae passed early and mid-winter, with pupation beginning in January and eclosion beginning in February of the following year.

Melyrid beetles passed the winter in the mature larval stage (Fiori 1971, Estrada & Solervicens 1997, Asano 2021); the larval molt and consumption stagnated in mid-

Table 2. The length of eggs and first instar larvae and the maximum clutch size of the species of the melyrid lineage.

Family	Species	Clutch size (maximum)	Egg (mm)	1st instar larva (mm)	References
Cleridae (outgroup)	*Neohydnus hozumii*	7	0.97	0.90	unpublished data
Rhadalidae	*Semijulistus spectabilis*	4	0.90	0.75	Asano (2019b)
Prionoceridae	*Idgia iriomoteana*	38	1.24–1.27	2.12	this study
Melyridae	*Psilothrix viridicaeruleus*	40	1.18–1.23	1.10–1.30	Fiori (1971)
	Dasytes vulgaris	8	0.85–1.10	1.03	Asano (2016)
	Holzschuhus yoroensis	21	0.65	0.75	Asano (2019a)
	Malachius prolongatus	38	1.00–1.10	0.87–0.93	Asano (2017)
	Axinotarsus pulicarius	about 30	0.80–0.90	0.90–1.00	Evers (1960)
	Attalus elongatulus	43	0.80	0.90–1.00	Asano (2018)
	Nepacyus japonicus	18	0.70–0.80	0.75–0.80	Asano (2014)
	Laius asahinai	14	0.80	0.84	Asano & Kojima (2013)
	Intybia niponicus	25	0.80	1.16	unpublished data
	Intybia takaraensis	15	0.80–0.85	0.88–0.90	Asano (2021)
	Intybia pelegrini pelegrini	19	0.80–0.82	0.77–0.83	Asano (2021)

-winter. A long-lasting final larval instar, which passed the winter, was shown in the melyrid species *A. trifasciatus*, *I. pelegrini pelegrini* and *I. takaraensis* (Estrada & Solervicens 1997, Asano 2021) (Table 1). In the current study, such stagnation of consumption and larval molts in winter was not observed in the ontogeny of *I. iriomoteana*.

Most prionocerid species are associated with tropical and subtropical moist forests (Geiser et al. 2016); however, a prionocerid larva was found in the Eocene amber associated with the Hat Creek Coal Formation, Kamloops Group, British Columbia, Canada (Lawrence et al. 2008). The mean annual temperature in the early Eocene was likely over 10°C warmer than today (Westerhold et al. 2020).

Potentially, *I. iriomoteana* has an univoltine life cycle with dormancy in summer; their life cycle may adapt to the tropical and subtropical climates. In contrast, their life cycle may not adapt to the north of subtropical climate necessary for winter dormancy in the larval stage. For these reasons, this species may now be distributed only in the relatively warm Ryukyu Islands.

Large first instar larva. The first instar larvae of *I. iriomoteana* are about 1.6-times as long as the chorion (Figs 12, 13) that contains the larvae with straight posture. Similarly, the phenomenon in which embryos grow larger in the chorion also occurs in melyrid beetles, but not to the extent as in *I. iriomoteana*. The eggs of melyrids are filled with embryos immediately before egg bursting (Asano 2013, 2014, 2016, 2017, 2018, 2019a,b, 2021) and the body lengths of the first instar larvae immediately after hatching are similar or larger than the length of the chorion (Table 2). It is possible that this phenomenon is a particular characteristic of the sister families Melyridae and Prionoceridae (Table 2). However, the first instar larvae of melyrid beetles burst the chorion in foetomorphic states and their larval morphogenesis continues after egg bursting (i.e., foetometamorphosis); it is completed after one or two larval molts (Asano 2013, 2014, 2016, 2017, 2018, 2019a,b, 2021). In contrast, *I. iriomoteana* completes larval morphogenesis before egg bursting, the large first instar larvae are shrunken in the chorion with their abdominal segments folded like accordion. They differ from above-mentioned melyrid species in these respects.

Large eggs have the advantage of producing large first instar larvae safely; however, the disadvantage of large eggs is a reduced clutch size, i.e., large newborn larva is incompatible with large clutch size. However, these results suggest that large first instar larvae occurring without reduced clutch sizes by the upsizing of eggs has taken place in different ways among two families which are foetometamorphosis and accordion-like folding of abdominal segments.

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