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学位論文全文に代わる要約
Extended Summary in Lieu of Dissertation

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Name

学位論文題目：　The ontogeny of melyrid beetles (Cleroidea)
Title of Dissertation　（ジョウカイモドキ科（カッコウムシ科）の個体発生）

学位論文要約：
Dissertation Summary

On development of Exopterygota, the presence of a developmental stage, which is between embryonic and nymphal stages is well known as “pronymphal stage”. A developmental stage between embryonic and nymphal stages has been interrupted peculiar to Exopterygota. It is believed that pronymphal stage of Exopterygota is equivalent to larval stage of Endopterygota (Berlese’s theory), however, its truthfulness has been discussed for more than a century (Truman and Riddiford 1999, Sehnal *et al.* 1999, Konopová and Zrzavý 2005 etc.).

A German zoologist meanwhile found an existence of inactive and nonfeeding early stage between embryonic and larval stages in two cantharid beetles of a group Endopterygota, superfamily Elateroidea (Verhoeff 1917). This phenomenon was interpreted as an abnormal metamorphosis in holometamorphosis such as hypermetamorphosis, called “Foetometamorphosis” (Verhoeff 1917). However, subsequently, this phenomenon had been forgotten without progress of study and 100 years have passed from the suggestion of Verhoeff to the present day.

Recently, I found similar to inactive and nonfeeding early stage of above species in *Laius asahinai* Nakane, 1955 of malachiine beetles also on its biological study (Fig. 2). I wonder if such a strange phenomenon occurs, and was also interested in occurring similar phenomenon in two groups of Endopterygota, although melyrid lineage belongs in superfamily Cleroidea which is remote from elateroids. However, the ontogeny including early stage of melyrid lineage has been observed and reported in fragments so far (Evers 1960, Fiori 1971, Estrada and Solervicens 1997). Therefore, I studied the ontogenic development from oviposition to larval stage of seven species of melyrid beetles (Fig. 1); five malachiine species, a dasytine species and a rhadaline species; additionally, a clerid species as an out-group, their structures and biological information are described and are compared for elucidation the factor of the strange early stage and the evolution of ontogeny in this lineage.

Based on the results, it has been obtained many findings about oviposition and larval development of melyrid lineage. Similar oviposition patterns were shown among each species. Eggs were not covered by anything, and at each egg site, 3 to 43 eggs were laid within dead plants or clefts of rocks. Eggs of some species had high drought resistance. Although melyrid lineage is most miniaturized group in cleroids, egg size is usually about 1.0mm, which is no significant difference from other cleroid families, it is believed to some constraint. By contrast, clutch size is various, became smallest in cleroid lineage. Accordingly, it is believed that the miniaturization of body size brought to the miniaturization of clutch size in melyrid lineage. However, clutch size of malachiines is rather large than other subfamilies, it is because of having flexible abdominal sternites.

The growth pattern is very various, not uniform among melyrid lineage, and each subfamily have peculiar characteristics. An ancestral growth pattern which is generally shown in cleroids was shown only in rhadaline species in melyrid lineage.

Meanwhile, dasytine and malachiine species showed the appearance of egg-bursters and egg burst occurred

before the completion of larval morphogenesis. This is the homology of the subfamilies Dasytinae and Malachiinae.

However, dasytine species showed egg hatch after the completion of larval morphogenesis (larva after egg burst does not move, neither reacting to stimuli, such as light and water, and does not consume water). Hence, foetomorphic larval stage does not exist. This is peculiar characteristics of dasytines.

In contrast, malachiine species showed egg hatch before the completion of larval morphogenesis (larva after egg burst wiggles the upper half of the body in response to light and water and consumes water). Hence, foetomorphic larval stage exist (Fig. 3), and this stage is shown in all observed malachiine species. However, the larval morphogeneses of each body parts at the hatching and the number of molts until the completion of larval morphogenesis is not fixed in the malachiines. Also, malachiine species hatched most foetomorphic structure, mature larval body parts developed high functioning compared to other groups of cleroids conversely.

A comparison of the hatching behavior of malachiines with dasytines suggested that the presence of the foetomorphic larval stage is directly attributable to the appearance of egg-bursters and egg burst occurred before the completion of larval morphogenesis, and wiggling the upper half of the body immediately after egg burst. This characteristic is peculiar to malachiines.

Beetles generally form the egg-bursters and rupture chorion after the completion of larval morphogenesis (Crowson 1981), above growth patterns of malachiine and dasytine species are very unusual in the order Coleoptera (Fig. 4).

The results the applying ontogenic synapomorphy of melyrid lineage and peculiar characteristics of each subfamilies to a molecular genealogical tree (Bocakova *et al*. 2012), it is suggested that the gradual evolutions of ontogeny; 1) miniaturization of the body size and corresponding clutch size decreased, 2) first hypermorphosis of the embryos (increasing in size), 3) clutch size increased, 4) second hypermorphosis of the embryos (increasing in size) and corresponding hypermorphosis of the larvae (increasing in morphogenetical potency) occur in melyrid lineage (Fig. 5).

In consequence, oviposition and larval growth pattern were diversified, and the strange early stage, foetomorphic larval stage was secondary acquired by malachiines in this course of evolution, i. e. foetomorphic larval stage is differ from “pronymphal stage” of Exopterygota in its origin.

This phenomenon is able to interrupt an unusually metamorphosis in holometamorphosis such as hypermetamorphosis. This result agrees with the suggestions of Verhoeff (1917). Additionally, it follows from foetomorphic larval stage being malachiine synapomorphy, its directly attribution and the development after this stage, foetomorphic larval stage is neither embryonic stage nor larval stage, it may conclude the between of both, “prolarval stage” which were suggested of Verhoeff (1917).

The subfamily Malachiinae is proposed the most modern and successful group in the superfamily Cleroidea (Crowson 1964). They also live in the extreme arid environments. There is possibility that the compatibility of three essentially conflicting characteristics, “miniature body size”, “hypermorphosis of embryos and larvae” and “large clutch size” brings about an advantage of the extreme environments. As a result, malachiine species became able to grow up plant-independent and it allows adaptation to various environments.

This study revealed that “prolarval stage” is possible to obtain in Endopterygota, although, pronymphal stage has been interrupted peculiar developmental stage of Exopterygota at this time. “Miniaturization of body size”, “hypermorphosis”, and “clutch size increased” are definitely not rare evolutions. I wander if “prolarval stage” of Endopterygota occurred in the two beetle taxa is just an exceptional case. Observations of hatching and early stage in Endopterygota are too little to be able to determine it still now.

In future, the carefully inspections its diffusibility and homology of cuticles to pronymph is necessary. I am sure that its result affect discussion on Berlese’s theory.

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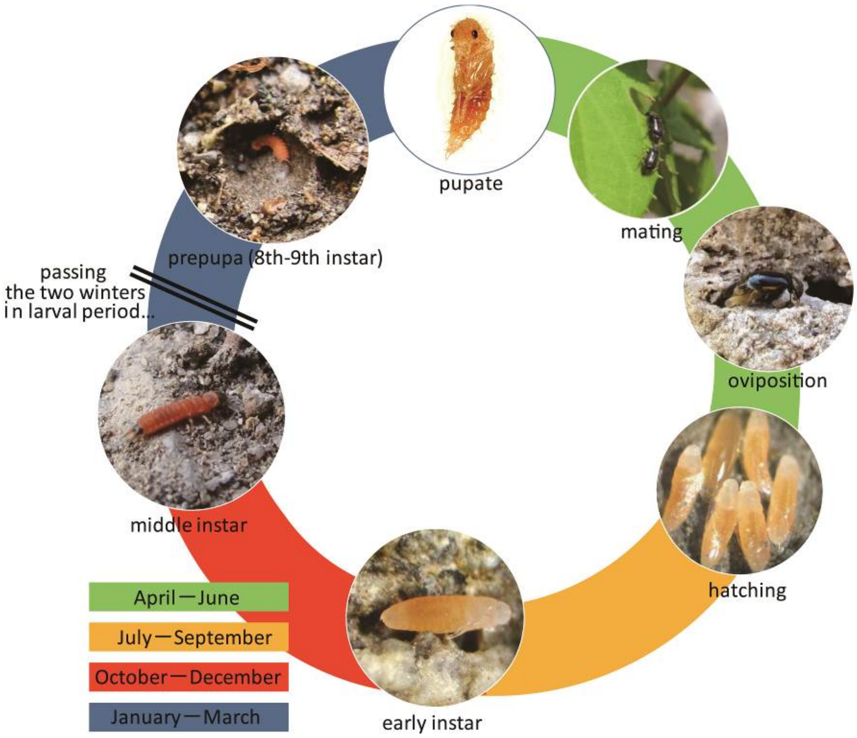

Fig. 1. Life cycle of malachiines in the temperate areas of Japan.

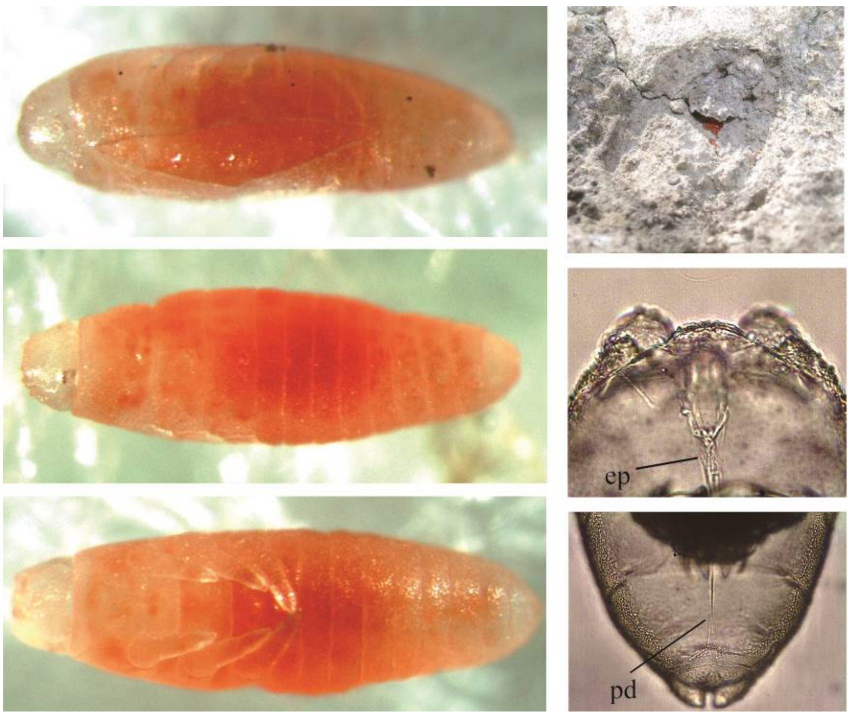

Fig. 2. Hatching and 1st instar of *Laius asahinai*

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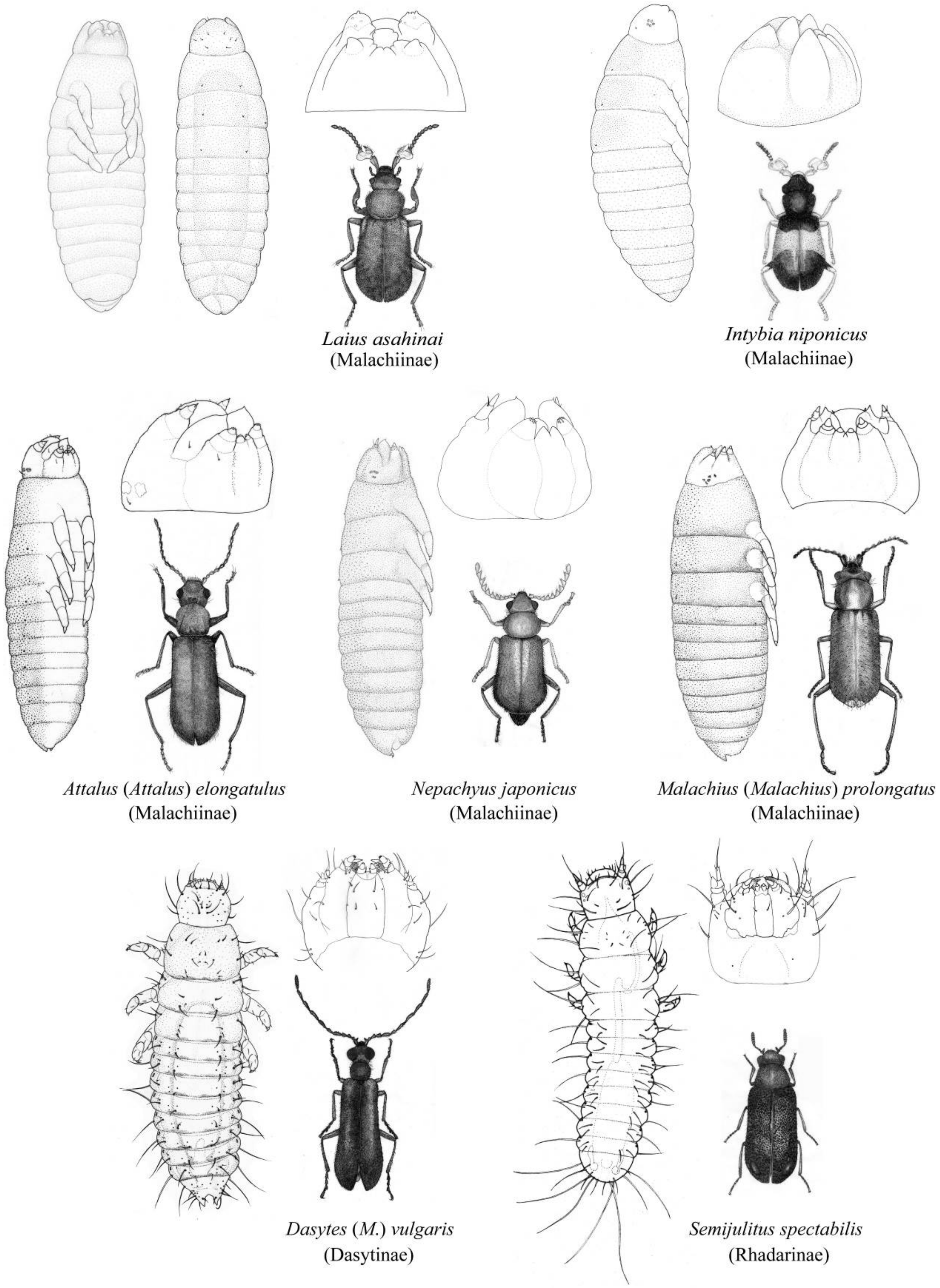

Fig. 3. 1st instar of melyrid beetles

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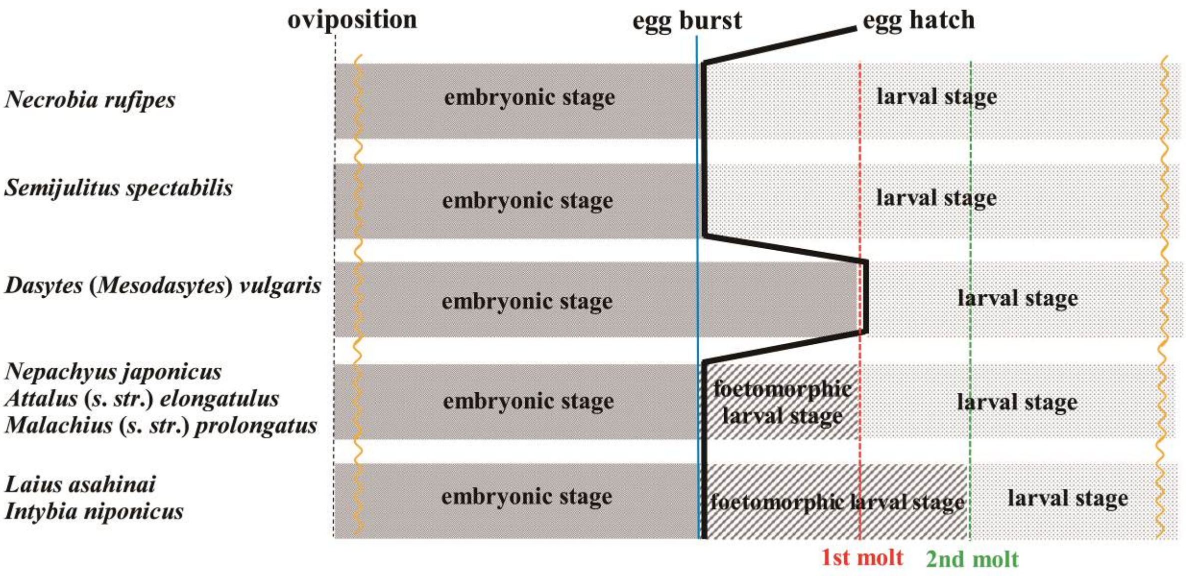

Fig. 4. Growth process.

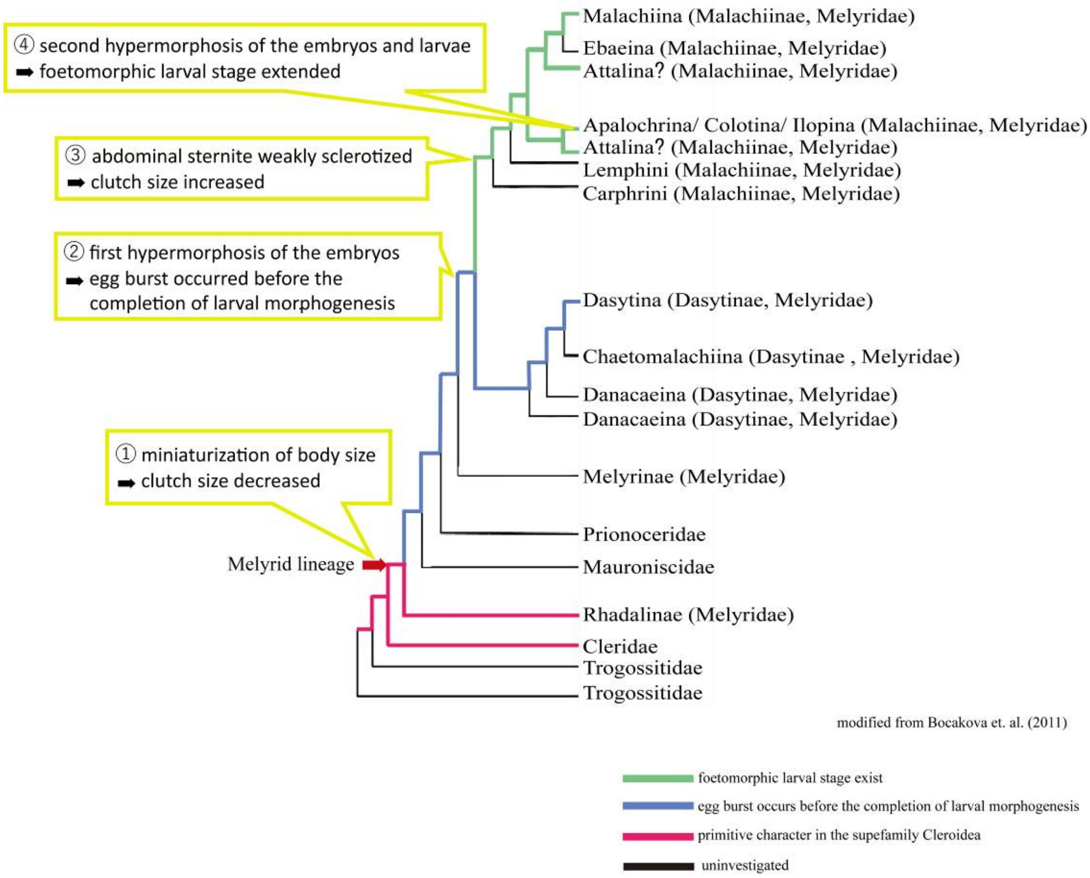

Fig. 5. Ontogenic evolution of melyrid lineage.