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Revision of the Japanese Species of *Chrysocharis* (Hymenoptera, Eulophidae), IV

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Abstract This paper deals with relationships among species-groups of *Chrysocharis* from the following three points of view: I. morphological similarities based on canonical discriminant analysis; II. morphoclines for 10 characters; III. parasite-host associations. It has been concluded that the species-groups associated with a lepidopterous genus, *Stigmella*, represent primitive forms of *Chrysocharis*, from which the Diptera-feeding groups have evolved through intermediate forms such as species-groups associated with multiple hosts.

Key words: Eulophidae; *Chrysocharis*; species-group; relationship.

Introduction

HANSSON (1985a, 1987, and personal communication) divided *Chrysocharis* into 12 species-groups. He did not analyze phylogenetic relationships among the species-groups cladistically, because of the lack of suitable characters uniting the members of each monophyletic group (HANSSON, 1985a). In this part, I took the following three approaches to understand the relationships among the 11 species-groups except the *moravica*-group: I. morphological similarities in quantitative characters analyzed by canonical discriminant analysis; II. construction of morphoclines; III. parasite-host associations. Thus, in the preceding three parts of this revision (IKEDA, 1995, 1996a, 1996b) the species-groups and species in each species-group are arranged according to their supposed taxonomic states.

Material and Methods

I have examined 57 species representing 11 of HANSSON's (1985a) 12 species-groups and more than ten species belonging to eight genera which are supposed to be closely related to *Chrysocharis* (Table 1).

I. *Morphological similarities in quantitative characters among the species-groups.*

In this analysis I used 26 species of *Chrysocharis* mostly from Japan, which cover nine species-groups, and some species of four allied genera for compari-

Table 1. List of the species examined and the number of specimens used for canonical discriminant analysis.

Species	Number of specimens
prodice-group	
C. prodice (Walk.)	10
C. pilicoxa (Thomson)	7
C. acoris (Walk.)	0
C. amasis (Walk.)	8
assis-group	
C. assis (Walk.)	10
C. truncatula Graham	0
amanus-group	
C. amanus (Walk.)	0
nigricrus-group	
C. argyropezae Graham	6
C. nigricrus (Thomson)	0
illustris-group	
C. albipes (Ashmead)	10
C. ujiyei Kamijo	10
C. illustris Graham	10
C. gemma (Walk.)	0
purpurea-group	
C. purpurea Bukowski	4
C. eurynota Graham	8
pentheus-group	
C. collaris Graham	0
C. nitetis (Walk.)	7
C. nautius (Walk.)	0
C. pentheus (Walk.)	8
C. laricinella (Ratz.)	0
C. paradoxa Hansson	0
C. nitidifrons Graham	0
C. budensis Erdős	0
C. debussyi Hansson	0
C. submutica Graham	10
C. nephereus (Walk.)	6
C. laomedon (Walk.)	6
C. tsugae Ikeda	0
C. lubrica Ikeda	0
mediana-group	
C. bestiola Hansson	0
C. nigra Ikeda	0
C. albicoxis (Erdős)	4
C. mediana Förster	0
C. chlora Graham	0
pubicornis-group	
C. pubicornis (Zett.)	10
C. liriomyzae Del.	6
C. polyzo (Walk.)	8
C. crassiscapus (Thoms.)	10
C. phryne (Walk.)	0
C. clarkae Yoshimoto	0
C. acutigaster Hansson	0
C. avia Hansson	0
C. orbicularis (Nees)	0
C. amyite (Walk.)	0
C. entedonoides (Walk.)	0
C. viridis (Nees)	10
C. sunosei Kamijo	2
C. chilo (Walk.)	10
C. pubens Del.	10
C. pilosa Del.	6
ainsliei-group	
C. oscinidis Ashmead	0
C. tristis Hansson	0
C. equiseti Hansson	0
C. ainsliei Crawford	0
C. caribae Bouček	3
idyia-group	
C. idyia (Walk.)	0
C. latifossa Hansson	0
Achrysocharoides spp.	10
(including *A. athys*, *A. splendens*)	
Derostenus sp.	7
Kratoysma sp.	3
Closterocerus trifasciatus	9
Entedon nomizonis	0
Entedon sp.	0
Pediobius acantha	0
P. crassicornis	0
P. spp.	0
Mestocharis sp.	0
Pleurotroppopsis spp.	0

son (Table 1). Only the females were analyzed, because males were rare or unavailable in some species. I measured 11 characters, namely head length (HL), head width (HW), head height (HH), eye height (EH), malar space length (MS), mouth opening length (MO), thorax length (TL), thorax width

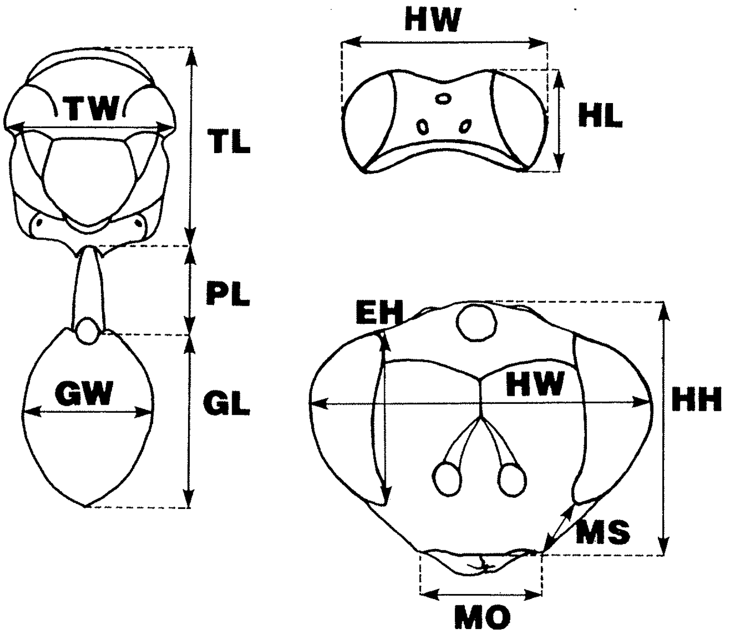


Fig. 1. Measurements of 11 characters in *Chrysocharis* and allied genera. For abbreviations, see material and methods.

(TW), petiole length (PL), gaster length (GL), and gaster width (GW) (Fig. 1). All measurements were ln-transformed and were analyzed using canonical discriminant analysis. This multivariate technique is used to demonstrate morphological differences among species-groups visually. This analysis creates new variates called canonical variates. Canonical variate 1 is the linear combination of the raw variates which maximizes the ratio of the among-group variation to the within-group variation, and canonical variate 2 is the one which maximizes the ratio under the constraint of no correlation with canonical variate 1 (SAS Institute, 1985; WILEY, 1981). The statistical analysis was performed with the SAS statistical program package in the Hokkaidô University Computing Center.

II. *Construction of morphoclines*

Morphoclines (MASLIN, 1952) were constructed for 10 characters. Polarities were determined by out-group comparisons or the characters' own peculiarities. Character states of some genera and species not available to my own study were based on authors. I follow SCHAUFF (1991) about what is to be regarded as the out-group of *Chrysocharis*, which contains *Derostenus*, *Kratoysma*, *Pediobius*, *Horismenus*, *Alachua*, *Entedon*, *Emersonella*, *Mestocharis*, *Holcopelte*, and *Pleurotroppopsis.*

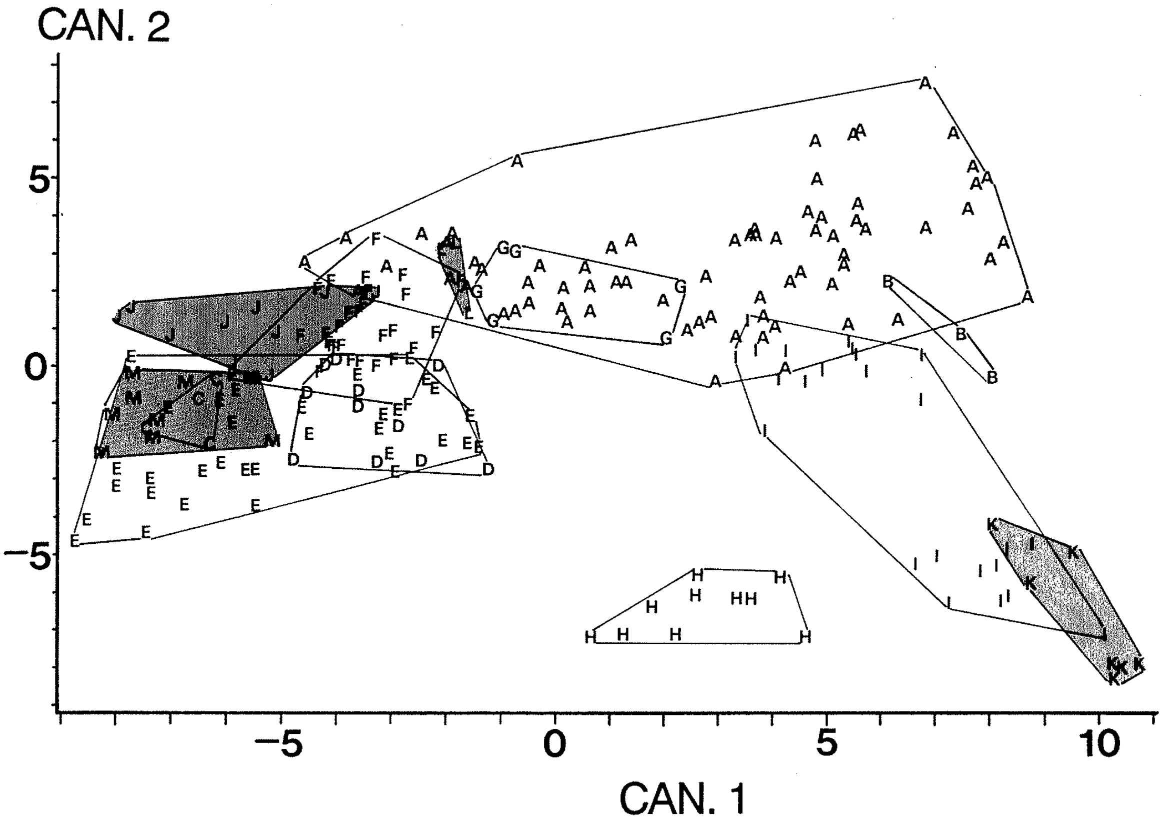


Fig. 2. Canonical variate 1 and 2 of individual specimens. Plots of the same species-group are enclosed with lines. A: the *pubicornis*-group. B: the *ainsliei*-group (*C. caribae*). C: the *mediana*-group (*C. albicoxis*). D: the *purpurea*-group. E: the *pentheus*-group. F: the *illustris*-group. G: the *nigricrus*-group (*C. argyropezae*). H: the *assis*-group (*C. assis*). I: the *prodice*-group. J: *Achrysocharoides* spp. K: *Derostenus* sp. L: *Kratoysma* sp. M: *Closterocerus trifasciatus.* Areas of allied genera of *Chrysocharis* (J, K, L, and M) are darkened.

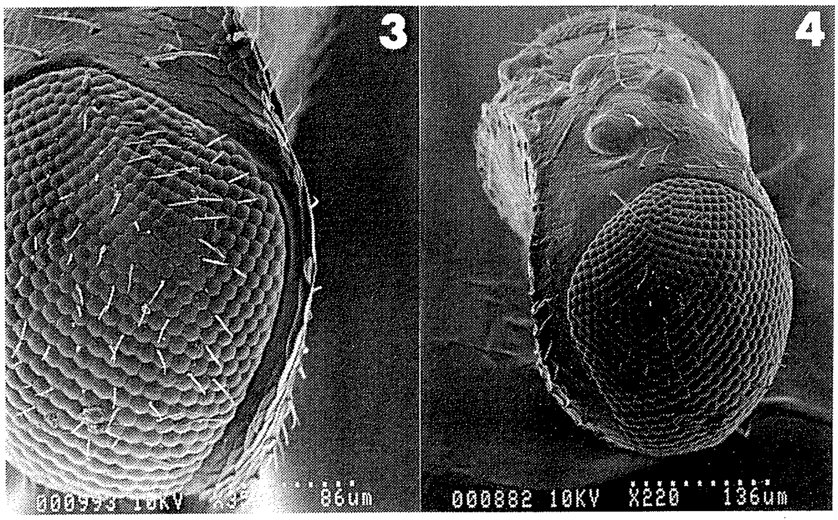
III. *Parasite-host associations*

The host records used are chiefly based on Hansson, 1985a and 1987.

Results

I. *Morphological similarities in quantitative characters*

Canonical variate 1 and 2 explained 51% and 18%, respectively, of the total variation. The following characters have absolute values of standardized canonical coefficients larger than one. Canonical variate 1: petiole length (3.9497), malar space length (−1.7698), gaster length (−1.5728), eye height (−1.2561) and mouth opening length (1.0375). Canonical variate 2: malar space length (2.6495), thorax length (−1.7206), mouth opening length (1.5887), and petiole length (1.2959). It is shown that petiole length and malar space length contribute to discriminate species more effectively than the other characters do.



Figs. 3–4. Head in lateral view.—— 3, *C. pubicornis* (the *pubicornis*-group), ♀, left side of head; 4, *C. prodice* (the *prodice*-group), ♀, right side of head.

Fig. 2 shows values of canonical variate 1 and 2 of individual specimens. Plots of the same species-groups are enclosed with lines. However, it is noted that canonical variates are not orthogonal.

The *pentheus*-, *purpurea*-, and *mediana*-groups (*C. albicoxis*), and *Closterocerus trifasciatus* overlapped each other. The *pubicornis*-group overlapped the *prodice*-group partly, but was discrete from the *pentheus*-group. The *ainsliei*-group (*C. caribae*), the *nigricrus*-group, and *Kratoysma* sp. were included almost in the range of the *pubicornis*-group. The *illustris*-group was intermediate between the *pubicornis*- and *pentheus*-groups. The *prodice*-group was separated into two parts: one was formed by *C. amasis* and *C. pilicoxa*, which overlapped the *pubicornis*-group partly, and the other was represented by *C. prodice*, which overlapped *Derostenus* sp. The *assis*-group (*C. assis*) showed a unique morphology and was a little nearer to *C. prodice* than to the others.

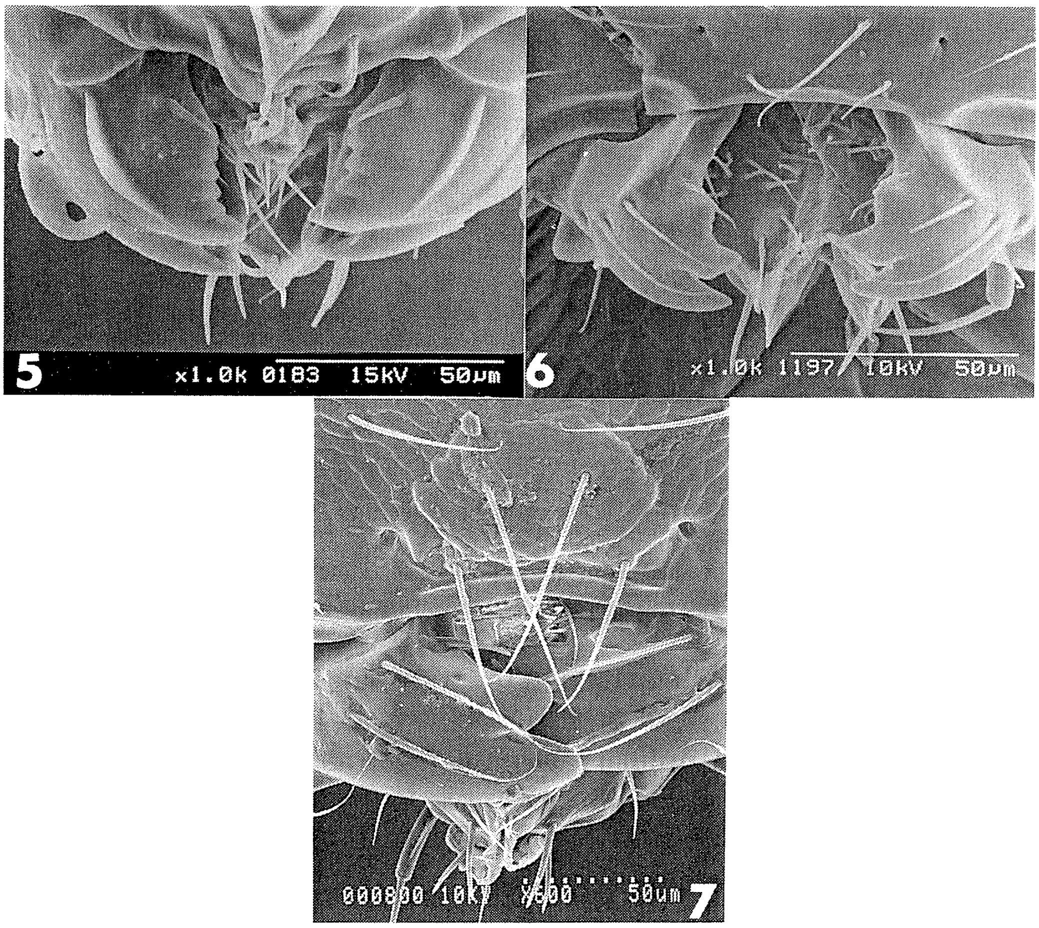
II. *Construction of morphoclines*

1. *Occipital margin*

The occipital margin changes in a series from an entirely rounded to an entirely carinated or edged occipital margin. The out-groups except some species of *Paracrias* (SCHAUFF, 1985; WOOLLEY & SCHAUFF, 1987) and *Horismenus* (BURKS, 1971; SCHAUFF, 1991) have a completely carinated or edged occipital margin. Thus the comparison suggests that the carinated or edged one is primitive.

2. *Upper and hind parts around compound eye* (Figs. 3, 4)

These parts are carinate (Fig. 3) or not (Fig. 4). Since most genera in the



Figs. 5–7. Mandibles.—— 5, *C. assis* (the *assis*-group), ♀; 6, *C. pentheus* (the *pentheus*-group), ♀; 7, *C. crassiscapus* (the *pubicornis*-group), ♀.

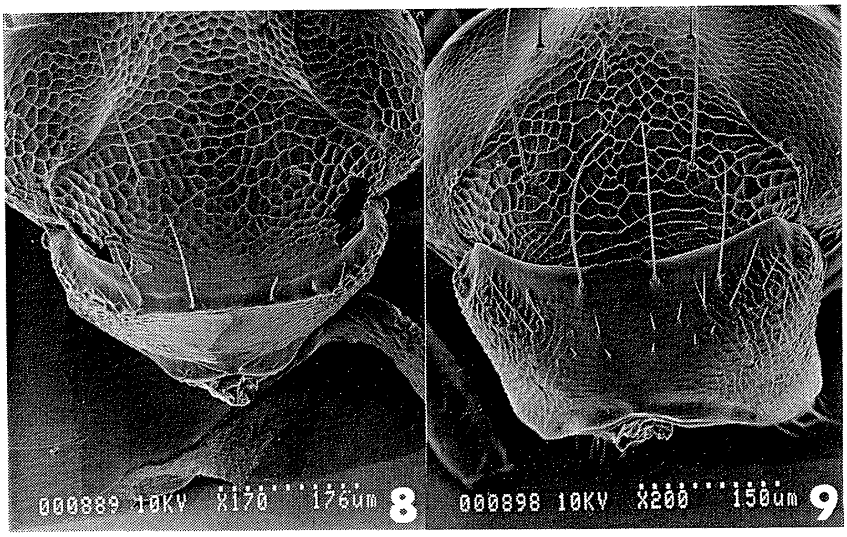
out-groups do not have the carina, the polarity should be: absence → presence. However, at least *Alachua* (Fig. 2 of SCHAUFF & BOUČEK, 1987), *Mestocharis* and *Pleurotroppopsis* have the carina.

3. *Frontal fork*

Four types of the frontal fork have been recognized: Y-shaped one, T-shaped one having complete arms, T-shaped one having short arms, and the fork having no arm. SCHAUFF (1991) regards the Y-shaped frontal fork as primitive. Because the loss of the arms is more likely than the acquisition of them, the frontal fork having no arms should be more advanced than the T-shaped one with short arms; and the T-shaped one having short arms should be more advanced than the T-shaped one with complete arms.

4. *Number of mandibular teeth* (Figs. 5, 6, 7)

There are three types of mandibles in *Chrysocharis*: multidentate (Fig. 5), tridentate (Fig. 6), and bidentate (Fig. 7), as designated by HANSSON (1985a).



Figs. 8–9. Pronotum and mesoscutum in anterodorsal view.——8, *C. laomedon* (the *pentheus*-group), ♀; 9, *C. crassiscapus* (the *pubicornis*-group), ♀.

The transition from the multidentate to the tridentate mandibles is conceivably gradual, because several small prominences defined by incisions between the third tooth and the two ordinary ones in the tridentate mandibles can be regarded as homologous with teeth. Decrease in dentation is more likely than increase, so that the multidentate type may be the most primitive and the bidentate type may be the most advanced.

The mandibles are used probably for two purposes, i.e. for feeding and for getting out of the skin and cocoon or the puparium of the host. The number of teeth may have a function for the second purpose. Furthermore, the tridentate mandibles may not necessarily be homologous among the species having them, because the third tooth of them varies in size and shape (HANSSON, 1985a). In this regard, the hypothesized polarity remains equivocal.

5. *Pronotum* (Figs. 8, 9)

HANSSON (1985a) recognizes three types of the pronotum. In type 1 a transverse carina is present and the area behind the carina is smooth (Fig. 8). Type 2 has no carina with the posterior area smooth. In type 3 the pronotum is completely reticulated with no carina. He regards the *pubicornis*-, *ainsliei*- and *idyia*-groups as belonging to type 3. However, I have found some species which have the smooth hind margin in these species-groups (Fig. 9); therefore I recognize only two types, one with a carina and the other without it.

The presence of the carina is probably primitive because the out-groups except *Paracrias* (SCHAUFF, 1985), *Mestocharis* (HANSSON, 1988) and *Holcopelte* (HANSSON, 1989) have the carina.

6. *Number of setae on lateral part of propodeum*

The number of setae on the lateral part of propodeum varies from 2 on the

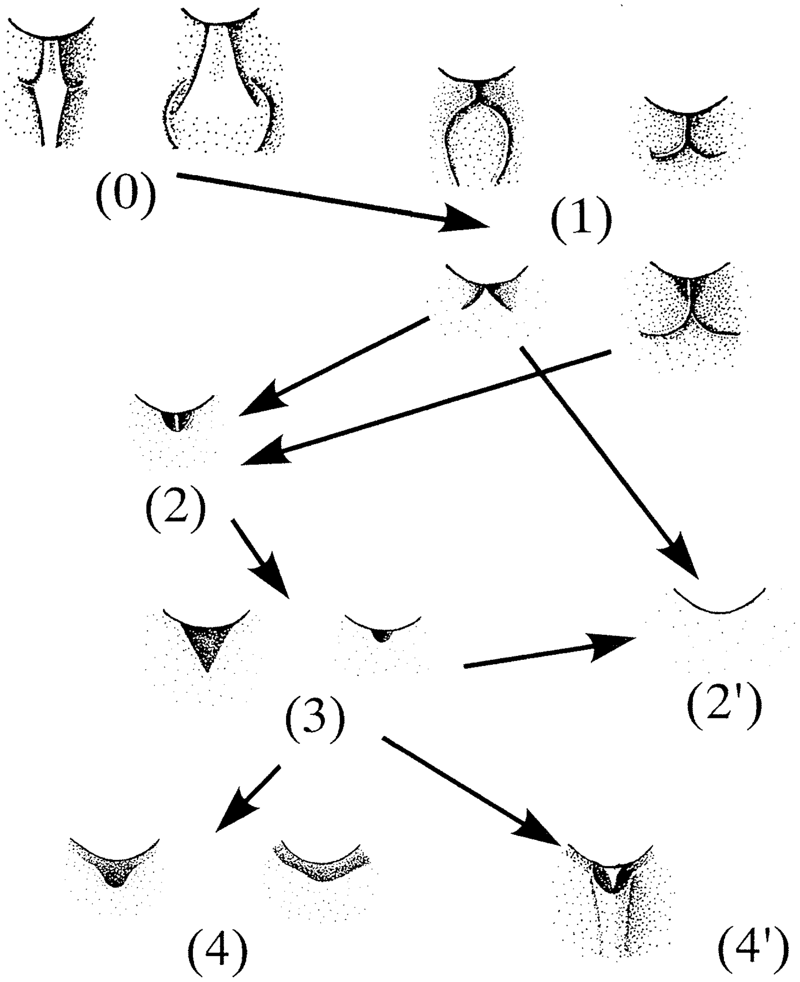


Fig. 10. Morphocline for the sculpture on the anteromedian part of the propodeum in *Chrysocharis.* (0): median carina; (1): V-, Y-, and anchor-shaped sculptures; (2): fovea divided medially; (2′): smooth, without sculpture; (3): fovea; (4): area along anterior margin of propodeum depressed; (4′): fovea divided medially, and area along anterior margin of propodeum weakly depressed.

callus to 27 on the callus and the area inside the spiracular sulcus (HANSSON, 1985a). The callus with 2 setae is frequently seen in the out-groups and other genera allied to *Chrysocharis*, and, therefore may be primitive. However, genera with many setae are also scattered in *Alachua* (SCHAUFF & BOUČEK, 1987), *Entedon* (KAMIJO, 1988), *Mestocharis* (HANSSON, 1988), and *Pleurotroppopsis* (KAMIJO, 1977b, 1990); therefore, the hypothesized polarity remains equivocal.

7. *Sculpture on anteromedian part of propodeum* (Fig. 10)

The sculpture of the anteromedian part of the propodeum is probably useful for making a morphocline as shown in Fig. 10. The median carina and plicae are variable intraspecifically in many species. However, the median carina is stable in the *illustris*-group and is also seen most frequently in the out-groups. Therefore, the state seen in the *illustris*-group may be primitive.

8. *Number of funicular segments*

The funicle is, 3- or 5-segmented. I postulate the 3-segmented funicle as primitive, because it is seen most frequently in the out-groups at least in the female. However, the female of *Pediobius* shows both types and the 2-segmented ones (BOUČEK, 1965). *Mestocharis* (HANSSON, 1988), *Holcopelte* (HANSSON, 1989), and *Emersonella* (BOUČEK, 1977) belong to the 5-segmented type and the female of *Paracrias* (SCHAUFF, 1985) to the 2-segmented.

9. *Setae on underside of costal cell and submarginal vein*

Some species have a complete row of setae on the underside of the costal cell, while other species have a short basal row of setae on the underside of the submarginal vein. These rows may be homologous, because the basal part of the complete row lies on the underside of the submarginal vein.

There are successive states from the occurrence of some basal setae to the presence of a complete row (rarely two) of setae. The former state may be primitive, because most genera in the out-groups have setae at most in the basal half of the submarginal vein. So far as I have examined, *Pleurotroppopsis* and *Entedon* among the out-group genera have exceptional species with complete rows of setae on the costal cell or the submarginal vein.

10. *Length of postmarginal vein*

The relative length of the postmarginal vein varies largely among species; *C. aegyptiensis* has the shortest one (0.9 times as long as the stigmal vein), while *C. arctica* has the longest one (4.3 times) (HANSSON, 1985a). The shortest type may be primitive, because in many genera of the out-groups the postmarginal vein is shorter than, and in other genera at most twice as long as, the stigmal vein. *Pleurotroppopsis* includes species with the postmarginal vein more than twice as long as the stigmal vein (KAMIJO, 1977b).

The morphoclines examined here are summarized in Table 2, and the distributions of the varying states in the species-groups in Table 3.

III. *Parasite-host associations*

The 10 species-groups of *Chrysocharis* excluding the *moravica*- and *mediana*-groups can be clustered into the following three by their host associations: groups associated with Diptera (mainly Agromyzidae) (*pubicornis*-, *ainsliei*-, and *idyia*-groups), groups feeding on *Stigmella* (Lepidoptera, Nepticulidae) (*prodice*-, *assis*-, and *amanus*-groups), and groups associated with various insect groups (*nigricrus*-, *illustris*-, *purpurea*-, and *pentheus*-groups). The *moravica*- and *mediana*-groups are not treated in this section because the hosts have not been known sufficiently.

According to NOWAKOWSKI (1962), only five percent of leaf-mining

Table 2. Morphoclines constructed for 10 characters of *Chrysocharis.*

Character	Character states and polarity
1. Occipital margin.	entirely carinated or edged (0) → partly carinated or edged (1) → entirely rounded (2)
2. Upper and hind parts of compound eye.	carina absent (0) → carina present (1)
3. Frontal fork.	Y-shaped (0) → T-shaped (1) → with short arms(2) → without arms (3)
4. Number of mandibular teeth.	many (0) → three (1) → two (2)
5. Pronotum.	carina present (0) → carina absent, hind margin smooth (1)
6. Number of setae on lateral propodeum.	2 (0) → 3–5 (1) → 6–10 (2) → 11– (3)
7. Sculpture on propodeum.	See Fig. 10.
8. Setae on underside of costal cell and submarginal vein.	occurring basally (0) → forming a complete row (1)
9. Number of funicular segments.	2 (1′) ← 3 (0) → 5 (1)
10. Postmarginal vein/stigmal vein.	0.5–1.0 (0) → 1.0–2.0 (1) → 2.0–3.0 (2) → 3.0– (3)

→ shows polarity.

Table 3. Distribution of character states in *Chrysocharis.* Numbers of characters and character states correspond to those in Table 2 and Fig. 10.

Species-groups	Character No.									
	1	2	3	4	5	6	7#	8	9	10##
prodice-group	0. 1. 2.	0.	0.	0.	0.	0. 1.	3. 4.	0.	0.	1. 2.
assis-group	2.	0.	0. 1.	0.	0.	0.	1. 3.	0.	0.	2.
amanus-group	2.	0.	1.	0.	1.	0.	3.	0.	0.	2.
nigricrus-group	2.	0.	0.	0. 1.	0.	1. 2. 3.	1.	1.	0. 1.	1. 2.
illustris-group	1. 2.	0.	0.	1.	0.	0. 1. 2.	0. 2.	0. 1.	0.	2. 3.
purpurea-group	0. 1.	0.	0. 1.	1.	0.	0. 1.	3.	0.	0.	2.
pentheus-group	1. 2.	0.	0.	1.	0.	0.	1. 2. 2′.	0. 1.	0.	1. 2.
mediana-group	2.	0.	0.	1.	1.	0.	3. 2′.	0.	0. 1′.	1. 2.
pubicornis-group	0. 1.	1.	0. 1. 2.	2.	1.	0. 1. 2. 3.	1. 3. 4. 4′.	0. 1.	0. 1.	1. 2. 3.
ainsliei-group	1.	1.	0. 1. 2. 3.	2.	1.	0. 1. 2.	3. 4. 4′.	0.	0.	1. 2.
idyia-group	1. 2.	1.	0.	2.	1.	0. 1. 2.	3.	0.	0.	0. 1.
moravica-group	1.	?.	0.	?.	0.	0. 1.	3.	0.	0.	1.

#. Some character states after HANSSON, 1985a, 1985b, and 1987.

##. Character states after HANSSON, 1985a, 1985b, and 1987.

species of the Agromyzidae live on arborous angiosperms, and three quarters have been connected with "shrubs". It seems that he meant herbs by "shrubs". Judging from the host records of MEYRICK (1968) and the biological and ecological comments given by DAVIS (1987), members of the major families of leaf-mining Lepidoptera except Elachistidae (WAGNER, 1987) mine leaves of trees. Most hymenopterous leaf-miners (Tenthredinidae, Heterarthrinae) are also associated with trees (SMITH & MIDDLEKAUFF, 1987). As for coleopteran leaf-miners, the Japanese species of Rhynchaeninae (Curculionidae) so far as known all mine leaves of trees, except for one species parasitizing gall-making aphids (MORIMOTO, 1984); in the Japanese species of leaf-mining Buprestidae (*Trachys* spp. and *Habroloma* spp.) so far as known, 24 species feeds on leaves of trees, whereas only 4 species feed on those of herbs (KUROSAWA, 1959, 1976, 1985a, 1985b), although members of Hispinae of Chrysomelidae seem to prefer herbs (JOLIVET, etc., 1988). HANSSON (1985a) states that most leaf-mining Diptera are associated with herbs, and that most coleopterous, hymenopterous and lepidopterous leaf-miners with shrubs and trees. KATO (1987) also states that, while most dipterous leaf-miners feed on herbs, lepidopterous leaf-miners generally mine trees rather than herbs. It is generally accepted that herbs evolved mainly in the Tertiary, while trees had already been well diversified in the Cretaceous; therefore, most dipterous leaf-miners should have evolved later than other leaf-miners. The parasites of most dipterous leaf-miners (Diptera-feeding groups) may also have appeared later than the parasites of other miners associated with trees.

The family Nepticulidae is considered to be a primitive group among the leaf-mining Lepidoptera (COMMON, 1990). The parasites of Nepticulidae (*Stigmella*-feeding groups), therefore, may have originated before the appearance of parasites of other lepidopterous leaf-miners.

The family Eriocraniidae is considered as the most primitive group in the leaf-mining Lepidoptera (HERING, 1951; COMMON, 1990). *C. nephereus* is the only species that parasitizes eriocraniids (HANSSON, 1985a). However, since it is highly polyphagous (HANSSON, 1985a), this host association does not necessarily indicate that *C. nephereus* is the most primitive form in the *Chrysocharis* species attacking Lepidoptera.

Discussion

The *pubicornis*-, *ainsliei*-, and *idyia*-groups (Diptera-feeding groups) share the following character states: bidentate mandibles; upper and hind parts around the compound eye with a carina; pronotum without a transverse carina; fore margin of the propodeum with a shallow depression. The former three states support the view that Diptera-feeding groups are derived. The polarity of the last character was not determined.

In some quantitative characters the *pubicornis*-group is similar to the *illustris*-group, and partly to the *prodice*-group and also to the *nigricrus*-group. On the other hand, these three species-groups have the transverse carina of the pronotum, and the mandibles are multidentate in the *prodice*-group and the *nigricrus*-group (*C. argyropezae*). In these two characters the *pubicornis*-group does not seem to be particularly close to the *illustris*-, *prodice*-, and *nigricrus*-groups. It is the opinion here adopted that the similarity in the quantitative characters has no phylogenetic significance.

HANSSON (1985a) states that the *prodice*-, *assis*- and *amanus*-groups (*Stigmella*-feeding groups) share several character states such as the multidentate mandibles, enlarged third anellus of the male, narrow malar space, more T-shaped frontal fork, subtruncate forewings, acuminated dorsellum (*amanus*- and *assis*-groups) and the presence of a pale subbasal spot on the male gaster (*amanus*- and *prodice*-groups). However, the polarities of these characters except the mandibles were not determined. Judging from the morphocline of the number of mandibular teeth, these species-groups may be primitive in *Chrysocharis.* This view is supported by their hosts.

C. amasis and *C. pilicoxa*, of the *prodice*-group, are similar to some species of the *pubicornis*-group, which is considered as a derived species-group; on the other hand, *C. prodice* is more similar to *Derostenus* sp. than to *C. amasis* and *C. pilicoxa* in quantitative characters. Again this similarity in quantitative characters does not agree with the morphocline of the number of the mandibular teeth.

Although morphoclines in the sculpture of propodeum and the length of postmarginal vein suggest the primitiveness of the *illustris*-group and also of the *idyia*-group, there are no other characters in support.

In conclusion, the states of the mandibular teeth, pronotum, and the upper and hind parts around the compound eye, and the parasite-host association suggest that the *Stigmella*-feeding groups are primitive forms of *Chrysocharis*, from which the groups associated with dipterous miners evolved through forms having multiple hosts.

Derostenus, *Kratoysma*, *Achrysocharoides*, and *Closterocerus*, genera of *Chrysocharis*-complex, are each similar to some species or some species-groups of *Chrysocharis* in some quantitative characters, but not in other characters. This suggests frequent occurrence of parallelism and convergence in quantitative characters, too. It seems that parallelism and convergence may have more likely taken place within the genus *Chrysocharis* than between genera in those characters; therefore, morphological similarities in quantitative characters have little phylogenetic significance.

Many morphoclines were also useless for phylogenetic analysis. Probably the characters used in this study have changed complicatedly both within and among species-groups. Indeed, parallelism and convergence, and even reversal must have taken place frequently in organisms' evolution.

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