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Preliminary Thoughts on the Phylogeny of Coleorrhyncha- Heteroptera (Hemiptera)【Review article】

鞘吻群 - 異翅目之系統發育初步見解【綜合論述】

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Abstract

The Psylloidea is selected as the sister group of Coleorrhyncha-Heteroptera. The Dipsocoromorpha, Gerromorpha, and Nepomorpha are determined to be a monophyletic taxon by the possession of a synapomorphy, i.e., the hypopleurites of abdominal segment VIII that evolved to an appendage-like structure. A new formal relationship hypothesis in the Coleorrhyncha-Heteroptera is proposed with the Psylloidea as the sister group: (Coleorrhyncha + Enicocephalomorpha + (Leptopodomorpha + Cimicomorpha + Pentatomomorpha)) + (Dipsocoromorpha + (Gerromorpha + Nepomorpha)).

摘要

選本蝨總科為鞘吻群 - 異翅目之姊妹群。鞭蝽次目、龜蝽次目與蝎蝽次目判定為單系分類群，以其帶有近裔共性 - 第八腹節下側片演進為附肢狀結構。以木蝨總科為姊妹群之新的鞘吻群與異翅目次目間假設關係建議為：（鞘吻群 + 奇蝽次目 +（細蝽次目 + 臭蟲次目 + 蝽次目））+（鞭蝽次目 +（龜蝽次目 + 蝎蝽次目））。

Key words: Coleorrhyncha, Heteroptera, cladistic analysis, phylogeny

關鍵詞: 鞘吻群、異翅目、分歧分析、系統發育

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Preliminary Thoughts on the Phylogeny of Coleorrhyncha-Heteroptera (Hemiptera)

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ABSTRACT

The Psylloidea is selected as the sister group of Coleorrhyncha-Heteroptera. The Dipsocoromorpha, Gerromorpha, and Nepomorpha are determined to be a monophyletic taxon by the possession of a synapomorphy, i.e., the hypopleurites of abdominal segment VIII that evolved to an appendage-like structure. A new formal relationship hypothesis in the Coleorrhyncha-Heteroptera is proposed with the Psylloidea as the sister group: (Coleorrhyncha + Enicocephalomorpha + (Leptopodomorpha + Cimicomorpha + Pentatomomorpha)) + (Dipsocoromorpha + (Gerromorpha + Nepomorpha)).

Key words: Coleorrhyncha, Heteroptera, cladistic analysis, phylogeny

Introduction

The author finds it hard to resist the temptation to study the amazing diversity of external male genitalia among the Heteroptera. After examination of 40 families and 300 species, the evolutionary trends of characters seemingly have emerged. At this time, the phylogenetic tree is much needed for consultation. Unfortunately the current view of phylogenetic relationships of infraorders (Wheeler *et al.*, 1993) appears difficult to use to interpret evolutionary trends. In view of this, the present data were carefully evaluated.

An evaluation was made based only upon the data of the present investigation, and several points impressed me with their importance. 1) The Coleorrhyncha, Enicocephalomorpha, Leptopodomorpha, Cimicomorpha, and Pentatomomoprha form a monophyletic taxon. This monophyletic taxon is determined by the possession of a synapomorphy, i.e., abdominal hypopleurite VIII is prominent; or the epipleurites are fused with the tergite, the hypopleurites are fused with the sternite, and the tergite-sternite is separated; or the tergite-sternite is fused and ring-like. 2) The Disocoromorpha, Gerromorpha, and Nepomorpha form a monophyletic taxon. This monophyletic taxon is determined by the possession of a synapomorphy, i.e., abdominal hypopleurite VIII evolved to appendage-like structure, and a parallel derived

character, abdominal tergite is separated from the remainder. 3) As for the outgroup, in the prevailing view, the Auchenorrhyncha is the sister group of Coelorrhyncha-Heteroptera. However, the data here indicated that (a) the general features in the external male genitalia of the Psylloidea, Coleorrhyncha, and Ochteroidea are similar in every respect: the phallobase is tube-shaped, extremely long, and situated at the base of the aedeagus. (b) abdominal tergite IX is separated from the remainder in the Psylloidea, Dipsocoromorpha, Gerromorpha, and Nepomorpha. (c) the ejaculatory duct is expanded before the anterior opening of abdominal segment IX (foramen sensu Singh-Pruthi, 1925), in the Psylloidea, it is the sperm pump; in the Miridae and Corixoidea it appears after the opening, but it has not been carefully examined and termed yet; in the Pentatomomorpha, it protrudes in the apical half of the aedeagus as the ejaculatory reservoir (defined differently from that of Singh-Pruthi). The relationships of these three forms are difficult to understand. Are these worthy of further exploration? Why did the evolutionary events so frequently in these taxa, as compared to the Auchenorrhyncha?

Furthermore, Wygodzinsky (1966: 31) commented "The male genitalia of most of the Emesinae do not differ in any significant way from those of other reduviids. The structure of the pygophore and parameres has been used by many authors for taxonomic purposes, but the phallus has not been given the necessary attention and has not been analyzed carefully as to its taxonomic significance. As shown in the following discussion and in the systematic part of this paper, the study of the phallus provides characters useful on the specific, generic, and often tribal levels. Its amazing diversity frequently surpasses that of the external visible features of the bug."

If the characters of the external male genitalia actually have high weight as in Wygodznsky's words, the above information can offer a different view of the phylogenetic relationships in the Heteroptera from the prevailing one.

Outgroup selection

According to the prevailing view, Coleorrhyncha is unquestionably the sister group of Heteroptera, but the Psylloidea is not. Why is it selected? The reasons were mentioned in the Introduction. Furthermore, abdominal sternite XI in the Auchenorrhyncha is differentiated into the so-called anal style, while it is undifferentiated in Coleorrhyncha and Heteroptera. This seemingly excludes Heteroptera from having common ancestor with a later line of Auchenorrhyncha.

Character analyses, codes, and state definitions

1. Sperm pump

Sperm pump differentiation is judged to be the advanced character state.

(1) 0 Sperm pump is undifferentiated
1 Sperm pump is already differenttiated

2. Connective (basal plates sensu Singh-Pruthi, 1925; articulatory apparatus sensu Dupuis, 1970)

Yang and Chang (2000: 7) stated "The lower bulb-like growth of the segmental membrane, variable in form, connecting the phallobase, aedeagus or sheath with genital styles." On pape 713, "The connective exposing in genital chamber distributes in Aphidoidea, Coccoidea, Aleyrodoidea, Psylloidea, Cocadoidea, Cercopoidea and Membracoidea. The connective evaginating into body cavity distributes in Membracoidea (part), Fulgoroidea, Coleorrhyncha and Heteroptera." "The connective situating below phallobase distritubes in Aphidoidea,

Coccoidea, Aleyrodoidea, Psylloidea, Cicadoidea, Membracoidea and Fulgoroidea. The connective situating before phallobase distributes in Coleorrhyncha and Heteroptera." According to the phylogenetic tree, evagination into the body cavity and being situated before the phallobase are advaced character states.

(2) 0 The connective is exposed in the genital chamber
1 The connective is evaginated into the body cavity

(3) 0 The connective is situated below the base of the phallobase
1 The connective is situated at the base of the phallobase

3. Support bridge (struts sensu Singh-Pruthi, 1925; ligamentary processes sensu Dupuis, 1970)

Yang and Chang (2000: 7) stated: "The differentiated structure of dorsoanterior upper portion of the phallobase, highy variable in form." On page 709, "The structure is unrecognizable in Stenorrhyncha, Cicadoidea, Cercopoidea and Membracoidea. It is recognizable in Fulgoroidea, Coleorrhyncha and Heteroptera." On page 17, "the structure unrecongizable are judged based on phylogenetic tree undifferentiation."

(4) 0 The support bridge is undifferentiated
1 The support bridge is already differentiated

4. Support tube (basal plates bridge sensu Singh-Pruthi, 1925; ductifer sensu Dupuis, 1970)

Yang and Chang (2000: 9) stated: "The differentiated structure of dorsoanterior lower portion of the phallobase. It is tubular in form, permitting the ejaculatory duct runs through." On page 710, "This structure is unrecognizable in Stenorrhyncha, Cicadoidea, Cercopoidea and Membracoidea." On page 18, "The structure unrecognizable are judged based on phylogenetic tree undifferentiated yet." It is recognizable in the Fulgoroidea, Coleorrhyncha, and Heteroptera.

(5) 0 The support tube is undifferentiated
1 The support tube is already differentiated

5. Genital plates (subgenital plates sensu Singh-Pruthi, 1925)

Yang and Chang (2000: 7) stated: "The pair of plates at posterior margin of abdominal sternite nine." On page 707, "Genital plates present only in Cercopoidea and Membracoidea." The above distribution record is wrong. In *Pantinia darwini* China (Coleorrhyncha), the so-called longitudinal ridge should be the modified genital plates; in most Heteroptera they are recognizable, except in a few cases in which they are difficult to recognize. They are not found in the Psylloidea, so it is judged to be undifferentiated.

(6) 0 The genital plates are undifferentiated
1 The genital plates already are differentiated

6. Abdominal segment eight (VIII)

Sweet (1996: 120) in comparing the external morphology of the pregenital abdomen of the Hemiptera stated: "The pregenital abdomen includes secondary segments 1-8." On page 133, "Psyllomorpha ….. there is a single series of spiracle-bearing lateral pleurites on segments 1-8." On page 139, "Coleorrhyncha ….. There is a single series of large ventral hypopleurites bearing spiracles 3-8." In the Heteroptera, Sweet judged that there are a double set of pleurites: the dorsal epipleurites and the ventral spiracle-bearing hypopleurites. As to the later evolutionary event on VIII, the epipleurites fused with the tergite, and the hypopleurites fused with the sternite.

Schuh and Slater (1996) considered that the paired respiratory processes of the Belostomatidae and Nepidae are modified "abdominal tergum 8." Herein they are judged to be the hypopleurites. The appendage-like structure is judged to

Table 1. Rearrangment data matrix

	Psy	Col	Eni	Lep	Cim	Pen	Dip	Ger	Nep
1	1	0	0	0	0	0	0	0	0
2	0	1	1	1	1	1	1	1	1
3	0	1	1	1	1	1	1	1	1
4	0	1	1	1	1	1	1	1	1
5	0	1	1	1	1	1	1	1	1
6	0	1	1	1	1	1	1	1	1
8	0	1	1	1	1	1	0	0	0
10	0	0	0	0	0	0	1	1	1
9	0	0	0	1	1	1	0	0	0
15	0	0	0	1	1	1	0	0	0
13	0	0	0	0	0	0	0	1	1
7	0	0	1	1	1	1	1	1	1
11	1	0	0	0	0	0	1	1	1
12	1	0	0	0	0	0	0	1	1
14	0	0	0	1	1	1	0	0	1

Psy – Psylloidea
Col – Coleorrhyncha
Eni – Enicocephalomorpha
Lep – Leptopodomorpha
Cim - Cimicomorpha
Pen – Pentatomomorpha
Dip – Dipsocoromorpha
Ger – Gerromorpha
Nep – Nepomorpha

be reduced as the later evolutionary event.

In the Enicocephalomorpha: *Oncylocotis basalis* Westwood (Enicocephalidae) (Sweet, 1996: 127, figs.12-13): The hypopleurites are prominent.

In the Leptopodomorpha:

Aepophilidae: *Aepophilius bonnairei* (Sing.) (Sweet, 1996: 129, fig.22): The hypopleurites are prominent.

Saldidae: *Pentacora ligata* (Say) (Sweet, 1996: 129, figs. 23-24): The hypopleurites are prominent.

Leptopodidae: *Leptopodus hispanus* Ramb. (Sweet, 1996: 129): The hypopleurites are prominent.

In the Cimicomorpha:

Reduviidae: The VIII tergite-sternite is fused and tube-shaped.

Miridae, Nabidae, and Cimicidae: The tergite-sternite is separated.

In the Pentatomomorpha: The tergite-sternite is fused and tube-shaped.

In the Dipsocoromorpha:

Ceratocombidae: The hypoleurites are appendage-like.

Dipsocoridae: The hypopleurite (right) is appendage-like (Shuh and Slater, 1995: 78).

Schizopteridae: The hypopleurites are reduced.

Stemmocryptidae: The hypopleurites are appendage-like (Schuh and Slater, 1995: 83).

In the Gerromopha: The VIII tergite-sternite is fused and tube-formed.

In the Nepomorpha:

Nepoidea: The hypopleurites are appendage-like.

Ochteroidea and Corixoidae: The VIII are appendage-like.

(7) 0 Pleurites of VIII are single, consisting of hypopleurites.
1 Pleurites of VIII are double, consisting of epipleurites and

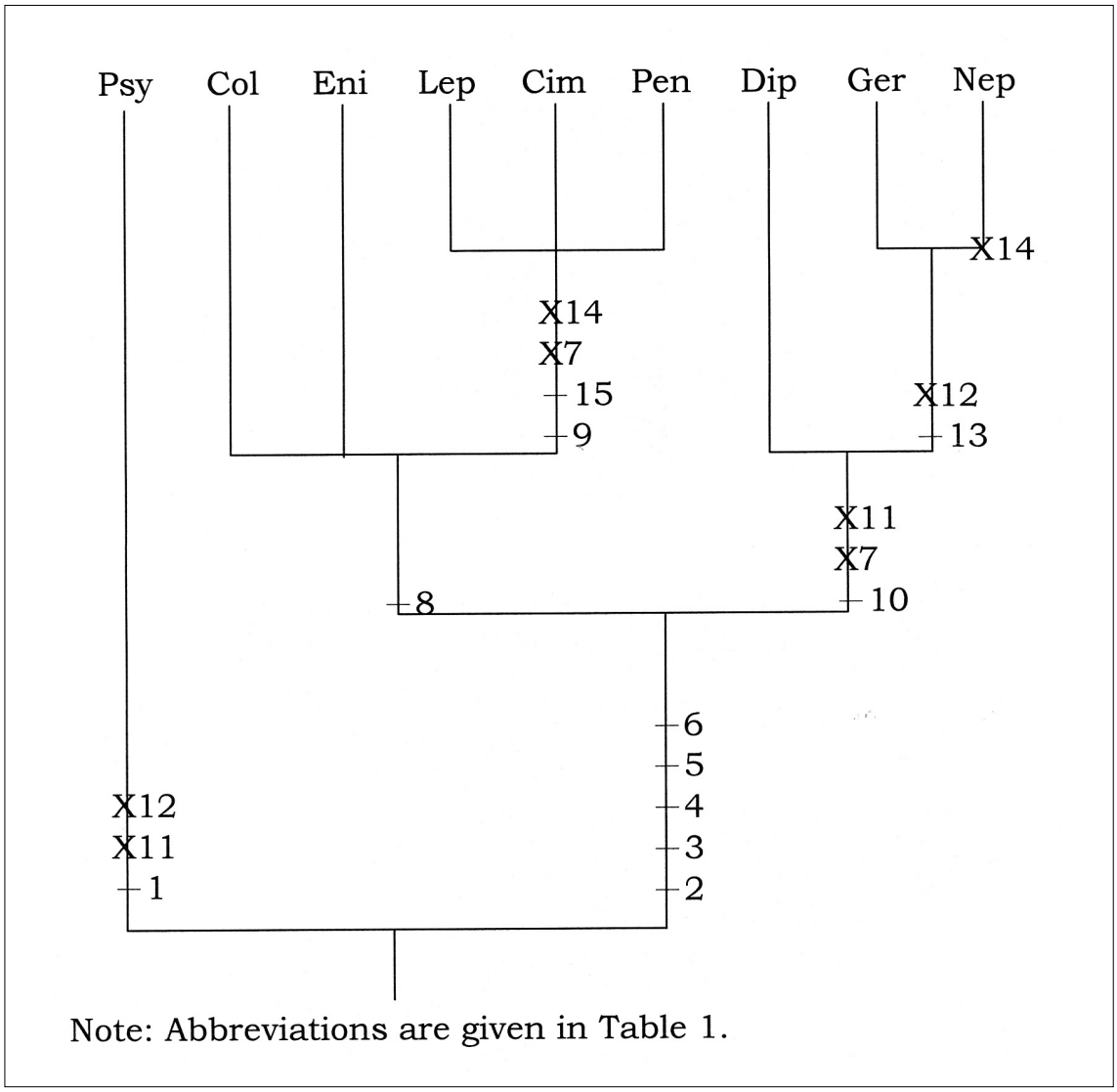

Fig. 1. Cladogram of the Coleorrhyncha-Heteroptera.

hypopleurites.

(8) 0 Pleurites of VIII are single; or double, hypoleurites evolved to an appendage-like structure; or appendage-like structure is reduced, tergite-sternite is fused; or tergite-sternite completely fused, tube-formed.
1 Hypopleurites are prominent; or epipleurites are fused with the tergite and hypopleurites are fused with the sternite, the tergite-sternite is separted; or tergite sternite fused, ring-like.

(9) 0 Pleurites of VIII single; or double, hypopleurites evolved to an appendage-like structure; or the appendage-like structure is reduced, the tergite-sternite is separated; or tergite-sternite incompletely fused; or tergite-sternite completely fused, tube-formed; or hypopleurites are prominent.

1 Epipleurites are fused with the tergite, and hypopleurites are fused with the sternite, the tergite-sternite is separated; or tergite-sternite fused, ring-like.

(10) 0 Pleurites of VIII are single; or double, hypopleurites are prominent; or epipleurites are fused with the tergite and hypopleurites are fused with the sternite, the tergite-sternite is separated; or tergite- sternite fused, ring-like.

1 Hypopleurites evolved to an appandage-like structure; or appendage-like structure is reduced, tergite-sternite separated; or tergite-sternite incompletely fused; or tergite-sternite completely fused, tube-formed.

7. Abdominal segment nine (IX) (pygophore sensu Schuh and Slateer, 1995)

In Psylloidea: Yang and Chang (2000: 59) stated: "Abdominal segment IX with tergite separated from the remainder and tergite fused with the X."

In Coleorrhyncha, Enicocephalomorpha, Leptopodomorpha, Cimicomorpha and Pentatomomorpha: Ix is ring-like and the tergite is not separated from the remainder.

In Dipsocoromorpha:

Ceratocombidae and Schizoptera: The tergite is separated from the remainder, and each side has a process dirceted mesad. The tergite is not fused with X.

In Gerromorpha:

Mesoveliidae, Hydrometridae, Veliidae, and Gerridae: The tergite of IX is separated from the remainder and is fused with X.

In Nepomorpha:

Nepoidea: The tergite of IX is separated from the remainder and is fused with X.

Ochteroidea, Coroxoidea, Naucoridae, and Notonectoidea: The tergire of IX is seemingly not separated from the remainder, but this is doubtful in some Notonectidae. If Nepomorpha is truly a monophyletic taxon, the tergite not been separated from the remainder is reasonably the reversal.

(11) 0 IX is ring-shaped.

1 Abdominal tergite nine (IXt) is separated from the remainder and is not fused with X; or IXt is separated from the remainder and is fused with X; or the IXt is not separated from the remainder and is not fused with with X, ring-formed.

(12) 0 IX is ring-shaped; or IXt it separated from the remainder and is not fused with X.

1 IXt is separated from the remainder and is fused with X; or IXt is not separated from the remainder and is not fused with X, ring-formed.

8. Extension IX

The base of IX protruding cephalad into the body cavity for various length, is termed the extension of IX.

This character is found in the Psylloidea and many families of the Fulgoroidea: some species of Flatidae, Nogodinidae, Issidae, Acanaloniidae, Fulgoridae, Dictyopharidae, Meenoplidae, and Achilidae. But it is never overly developed as in Gerromorpha or Nepomorpha.

The extension is difficult to judge in some taxa in the Nepomorpha, but it easily assessed in Gerromorpha. In Gerromorpha, it is always rather transparent, without setae. In Nepomorpha, it is easily judged in *Paraplea indistinguenda* Matsumura (Pleidae). When other taxa are compared with the Pleidae, one can roughly take the anterior margin of X as the borderline of IX. This is the way I herein judged the extension of IX.

The extension of IX is unrecognizable, or it is more or less recognizable in the Notonectidae, are judged to be the

reversal.

In Psylloidea: It is more or less recognizable.

In Coleorrhyncha, Enicocephalomorpha, Leptopodomorpha, Cimicomorpha, Pentatomomorpha, Dipsocoromorpha: it is unrecognizable.

In Gerromorpha:

Mesoveliidae: It is subquadrate, higher than long, and slightly shorter than the length of IX.

Hydrometridae: It is subquadrte, longer than high, and distinctly longer than the length of IX.

Veliidae: It is subquadrate, as high as long, and slightly shorter than the length of IX.

Gerridae: It is subquadrate, as high as long, and slightly shorter than the length of IX.

In Nepomorpha:

Nepoidea: It is slender and longer than high.

Ochteroidea: It is triangular, narrowed dorsally, and distinctly shorter than the length of IX.

Corixoidea: According to the above standard of judgment the real IX should be very small, and most part of the so-called IX should be the extension.

Notonectidae: It is more or less recognizable in some species, but unrecognizable in others. It should be the reversal.

Pleidae and Helotrephidae: It is nearly as long as the length of IX.

(13) 0 The extension of IX is unrecognizable; or more or less recognizable.
1 The extension of IX is overly developed; or reduced.

9. Forewings

Schuh and Slater (1995: 43) stated: "The forewing may be either of uniform texture (tegminal) – as in the phylogenetically more promitive group – or in the form of Hemelytra, that is, divided into a distinctly coriaceous anterior portion and a membranous posterior portion."

(14) 0 Forewings have a uniform texture.
1 Forewings are in the form of hemelytra.

10. Capitate processes

Yang and Chang (2000: 7) stated: "capitate processes – the processes of the support bridge." This is a new-born structure.

(15) 0 The capitate processes are undifferentiated.
1 The capitate processes are already differentiated.

Cladistic analysis

Character 1 and the combination of characters 2, 3, 4, 5, and 6 as borne by the largest number of taxa are selected as the basal branch. Here the Psylloidea is determined to be a monophyletic taxon by the possession of a synapomorphy, i.e., character 1. Coleorrhyncha and Heteroptera are determined to be a monophyletic taxon by the possession of synapomorphies, i.e., characters 2-6.

The combination of character, 8 and 10 as borne by the second largest number of taxa is selected as the second branch. Here Coleorrhyncha, Enicocephalomorpha, Leptopodomorpha, Cimicomorpha, and Pentatomomorpha are determined to be a monophyletic taxon by the possession of a synapomorphy, i.e., character 8; and Dipsocoromorpha, Gerromorpha and Nepomorpha are determined to be a monophyletic taxon by the possession of a synapomorphy, i.e., character 10.

Character, 9 and 15 as borne by the third largest number of taxa are selected as the third branch. Here Leptopodomorpha, Cimicomorpha, and Pentatomomorpha are determined to be a monophyletic taxon by the possession of synapomorphies, i.e., characters 9 and 15.

Character 13 as borne by the fourth largest number of taxa is selected as the fourth branch. Here Gerromorpha and

Nepomorpha are determined to be a monophyletic taxon by the possession of a synapomorpha, i.e., character 13.

Finally, characters 7, 11, 12, and 14 of parallel evolution are added.

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鞘吻群－異翅目之系統發育初步見解

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摘　要

選本蝨總科爲鞘吻群－異翅目之姊妹群。鞭蝽次目、龜蝽次目與蝎蝽次目判定爲單系分類群，以其帶有近裔共性－第八腹節下側片演進爲附肢狀結構。以木蝨總科爲姊妹群之新的鞘吻群與異翅目次目間假設關係建議爲：（鞘吻群＋奇蝽次目＋（細蝽次目＋臭蟲次目＋蝽次目））＋（鞭蝽次目＋（龜蝽次目＋蝎蝽次目））。

關鍵詞：鞘吻群、異翅目、分歧分析、系統發育