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Phylogenetic Relationships of the Pentatomomorpha (Hemiptera: Heteroptera) Inferred from Nuclear 18*S* rDNA Sequences

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Abstract: Sequences from a region of the nuclear ribosomal 18*S* rDNA gene of approximately 1 912 base pairs (bp) were used to generate a molecular phylogeny for the Pentatomomorpha based on 53 species representing 21 putative families. Phylogenetic analyses using the most parsimony method (MP), maximum likelihood method (ML), and neighbor joining method (NJ) showed strong support that the Pentatomomorpha lineage is a monophyly and the superfamily Aradoidea is a sister group to the remainder of the Pentatomomorpha (Trichophora). The Trichophora could be divided into two clades: one clade consisted of the monophyletic superfamilies Pentatomoidea and Pyrrhocoroidea; the other was mainly the polyphyletic superfamilies Lygaeoidea, Coreoidea and Idiostoloidea. The superfamilies Lygaeoidea and Coreoidea were both polyphyletic. Within Lygaeoidea, Piesmatidae was sister to Berytidae. They formed a clade locating at the basal of the Trichophora and distantly related to the other two families Lygaeidae and Rhyparochromidae. This research suggested that 18S rDNA was a proper marker to reconstruct the phylogeny of Pentatomomorpha that was accordant to morphological studies and the research of Li et al (2005). The Pyrrhocoroidea was further divided from the Coreoidea (*s. lat*). It was suggested that the Piesmatidae might be assigned as a superfamily of Pentatomomorpha rather than a family in Lygaeoidea.

Key words: Molecular phylogeny; Pentatomomorpha; 18*S* rDNA; Trichophora

基于 18*S* rDNA 序列的蝽次目(半翅目:异翅亚目)系统发育关系

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摘要: 利用 18*S* rDNA 分子约 1 912 bp 的序列对蝽次目 21 个科 53 个种进行系统发育分析。运用 MP 法、ML 法和 NJ 法分析后的结果表明: 蝽次目的单系性得到很高的支持; 扁蝽总科成为毛点类的姐妹群; 毛点类基本确定为两大分支: 一支包含蝽总科和红蝽总科; 另一支主要由长蝽总科、缘蝽总科和南蝽总科组成; 长蝽总科和缘蝽总科都是多系; 长蝽总科中, 跷蝽科和皮蝽科的关系最近, 构成姐妹群, 位于整个毛点类的基部; 与长蝽总科中另外两个科长蝽科和地长蝽科的关系很远。说明利用 18*S* rDNA 分子对研究蝽次目的系统发育关系是适合的, 能够重建蝽次目; 扁蝽总科和蝽总科单系性的结果与形态学的研究以及 Li et al (2005)的研究一致; 但较 Li et al (2005) 的研究更进一步把红蝽总科从广义的缘蝽总科中分出来; 并建议皮蝽科作为一个独立的总科更合适。

关键词: 分子系统发育; 蝽次目; 18*S* rDNA; 毛点类
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The Pentatomomorpha is the second largest suborder and one of the most important groups of the Het-

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eroptera, numbering from 12 500 to 15 000 species worldwide. Of the 29 families of Heteroptera (Schuh & Slater, 1995), 20 have been recorded in China. All of the taxa in this infraorder are terrestrial, and most are plant-feeding. They are important in agriculture, as some of them are pests. The Pentatomomorpha has an important phylogenetic position because it is one of the most phylogenetically distal groups in the Heteroptera. Since the twentieth century, many comparative morphology studies have provided strong evidence and important information for the construction of a reasonable classification system for the Heteroptera. Tullgren (1918) established Trichophora based on the abdominal trichobotheia, which was the origin of "Pentatomomorha" in the present classification system. Leston et al (1954) established the infraorder Pentatomomorpha based on the pretarsal structure, male and female genitalia, wing venation, egg morphology, and salivary gland structures. The superfamily Aradoidea (including Araridae and Termitaphididae) and the group Trichophora make up the present Pentatomomorpha (Henry, 1997). Schuh (1979) and Wheeler et al (1993) had proved that Pentatomomorpha was a monophyly using cladistic analysis, and the sister group appeared to be Cimicomorpha.

Up to now, the phylogenetic hypothesis (Aradoidea + (Pentatomoidea + the remainder of Trichophora)) of this infraorder has been supported by Leston (1958) and Henry (1997), and accepted by most researchers. Within the Pentatomomorpha, the relationships of superfamilies are uncertain. Only the Aradoidea and Pentatomoidea are consistently recognized as monophyletic within these schemes (Henry, 1997). Studies have recognized four (Schaefer, 1964), five (Štys, 1961, 1967; Schaefer, 1993; Schuh & Slater, 1995), six (Carver et al, 1991; Henry, 1997), or seven (Schuh, 1986; Henry & Froeschner, 1988; Li & Zheng, 1994) superfamilies. No consensus exists for the relative position of the Piesmatidae and Idiostolidae. The other superfamilies Coreoidea, Lygaeoidea, and Pyrrhocoroidea have been defined with some difference. More recently, Henry (1997) brought together all the variable morphological character information found in the literature to analyze it cladistically, and recognized six superfamilies (Aradoidea, Pentatomoidea, Coreoidea, Pyrrhocoroidea, Idiostoloidea, Lygaeoidea). The Piesmatoidea was placed into the Lygaeoidea. Until now, it was showed that the relationships among the superfamilies in Pentatomomorpha and the families within the superfamilies were still uncertain.

With further research into insect molecular phylogenetics, great progress has been made using molecular markers. The genes of rDNA and mtDNA are the two most widely used markers. Thus far, little attempt has been made to incorporate molecular data into phylogenetic analyses of the Pentatomomorpha. Xie et al (2005) used 18*S* rDNA to recover phylogeny for the main lineages (Pentatomoidea, Coreoidea, Pyrrhocoroidea, and Lygaeoidea) of Trichophora with Bayesian analysis, using Pentatomoidea as an outgroup. The results showed that the relationship of Coreoidea, Pyrrhocoroidea, and Lygaeoidea was Pyrrhocoroidea + (Coreoidea + Lygaeoidea), which differed to the hypothesis of Henry (1997) and Leston (1958) that was (Coreoidea + Pyrrhocoroidea). Li et al (2005) were the first to analyze the whole Pentatomomorpha phylogeny using 18*S* rDNA and the mitochondrial *COX1* gene based on 40 species representing 17 putative families. The phylogenies were mostly congruent with morphological studies. Results strongly supported the monophyly of Pentatomomorpha, and the placement of Aradoidea as sister to Trichophora. The monophyletic Trichophora was grouped into two major lineages: one being the monophyletic Pentatomoidea, and the other comprising Lygaeoidea, Coreoidea, and Pyrrhocoroidea. The phylogeny of the whole Pentatomomorpha was: Aradoidea + (Pentatomoidea + ((Pyrrhocoroidea + Coreoidea + Lygaeoidea))). Thus the results supported that the morphological characteristic abdominal trichobothria was a synapomorphy of Trichophora. This is significant to determining the polarities of morphological characteristics in phylogenetic studies of Pentatomomorpha. Li et al (2005) suggested that 18*S* rDNA may be an optimal molecular marker for the phylogeny of Pentatomomorpha; on the contrary, the *COX1* segment might not be. The position of Piesmatidae, and the relationships among Pyrrhocoroidea, Coreoidea, and Lygaeoidea will require further sampling and more complete studies to resolve.

The 18*S* rDNA gene is one of the most widely used markers in studies of insect phylogeny. Nowadays, many sequences of Pentatomomorpha 18*S* rDNA have been accumulated in GenBank. According to the research of Li et al (2005), we chose 18*S* rDNA gene to generate the phylogeny of Pentatomomorpha. The study included additional superfamilies and families, which were *Trisecus pictus* (Idiostoloidea), Canopidae, Cydnidae, and Hyocephalidae, based on 53 species representing 21 putative families and six superfamilies.

The most parsimony (MP), maximum likelihood (ML), and neighbor joining (NJ) methods were used to reconstruct the relationships among superfamilies in the Pentatomomorpha lineage. The position of Piesmatidae is also discussed.

1 Materials and Methods

1.1 Taxa

Fifty three taxa representing six superfamilies and 21 putative families were analyzed to study the relationship at the high level of Pentatomomorpha. The specimens used and their current taxonomy are shown in Tab. 1.

We collected 25 species in Guangdong Province during 2003 and sequenced their 18*S* rDNA. The nucleotide sequence data has been deposited in GenBank and their accession numbers are listed in Tab. 1. Other sequences were collected directly from GenBank. Three other species (*Emesaya brevipennis*, *Lygus hesperus* and *Campyloneura virgula*) were used as outgroups belonging to Cimicomorpha. Accession numbers of these sequences are also listed in Tab. 1.

1.2 Total genomic DNA isolation

Total genomic DNA was extracted from frozen, ethanol-preserved (95% ethanol) specimens and from pinned-dried specimens, usually obtained from thoracic muscles. Heads, abdomens and legs were stored in 70% alcohol as voucher specimens. The method of DNA extraction is referred to Wen & He (2003), and was revised. The protocol was as follows: each specimen was softly ground in 100 μL buffer (10 mmol/L Tris, 1 mmol/L EDTA, 0.1 mol/L NaCl, pH 8.0). After adding Proteinase K (200 μg /mL), the homogenate was incubated at 56 ℃ for 1 – 2 hours, 95 ℃ for 45 seconds, and then centrifuged for 5 minutes. The supernatant was collected as the template for the PCR. DNA from some specimens, especially a few pinned-dried specimens, was extracted with EaZy Nucleic Acid Isolation Kit (Omega Bio-tek).

1.3 18*S* rDNA sequence cloning and sequencing

The primers are listed in Tab. 2. Primers were derived from Loxdale & Lushai (1998). PCRs were conducted in 25 μL volume containing 2 – 6 μL of DNA, 0.5 U *Taq* polymerase (Takara, Dalian), 1.5 μL 10 μmol/L primers, 2.0 μL 2.5 mmol/L dNTPs (Takara), and 2.5 μL 10 × buffer. Amplification conditions were 95 ℃ for 5 min; 35 cycles of 95 ℃ for 30 s, 50 ℃ for 40 s, 72 ℃ for 2 min; 72 ℃ for 8 min. Target products from the PCR were purified with Agarose Gel DNA Purification Kit (Takara) and sequenced directly. DNA sequencing was performed in a PE/ABI 377 automated sequencer.

1.4 Sequence alignment and phylogenetic analyses

The sequences were aligned using default parameters of Clustal X (Thompson et al, 1997) with further adjustments by eyes and reference to two predicted secondary structure models for SSU rRNA; the generalized eukaryotic SSU rRNA model (Peer et al, 2000) and the peloridiid 18*S* RNA model (Ouvrard et al, 2000). Some highly variable regions, which were not able to be aligned unambiguously across all taxa, even considering the secondary structure, were excluded from further analyses. The aligned data are available from the author or may be downloaded from the following web site: http://life.zsu.edu.cn/insect_18*S*/.

Phylogenetic analyses were done by PAUP * 4.0b10 (Swofford, 2002) and MEGA 2.0 (Kumar et al, 2001). The method of constructing trees were NJ, MP, and ML. Unweighted parsimony analyses of various datasets were performed without considering gaps. As the number of taxa and the size of the data matrix often precluded more thorough searches, heuristic searches were performed with 100 random-taxon-addition replicates, and TBR (tree bisection-reconnection) branch swapping. When maximum parsimony tree was not the only tree used, either the strict consensus tree or 50% majority-rule consensus tree would be calculated. Clade stability was evaluated using two different parameters: bootstrap (Felsenstein, 1985) and branch support (Bremer, 1994). Bootstrap values were generated in PAUP* from 1 000 replicates, each with ten random-addition heuristic searches. Branch support values (a.k.a. Decay indices) were estimated with the program Autodecay V5.0 (Eriksson, 2001). We used the computer program MrModeltest 2.0 (Nylander, 2004) to identify the most appropriate substitution model for the ML analysis. Based on the result from the program, the ML tree was reconstructed using PAUP*.

2 Results

2.1 Sequences variation

The length of the collected fragments ranged from 942 base pairs (bp) in *Maevius indecorus* to 1 925 bp in *Megacopta cribraria*. The aligned region used in analyses comprised 1 910 bp, of which 793 (41.52%) sites were variable and 519 (21.17%) sites were parsimony informative. The mean nucleotide composition was T 23.8%, C 23.8%, A 25.1%, G 27.3%. No significant bias in base composition among taxa were found.

Tab. 1 Taxa used in this study

Current family classification	Taxa	Accession No. (GenBank)	Length (base pairs)
Aradoidea Aradidae	*Mezira granulata*	AY252221[a]	1 021
	Mezira sayi	AY252222[a]	991
Pentatomoidea			
Scutelleridae	*Dysodius lunatus*	AY252138[a]	1 058
	Coleotichus costatus	AY252274[a]	1 879
	Poecilocoris latus (Dallas)	AY627311	1 866
	Cantao ocellatus (Thunberg)	AY627316	1 838
Tessaratomidae	*Tessaratoma papillosa* (Drury)	AY627312	1 923
Plataspidae	*Megacopta cribraria* (Fabricius)	AY627313	1 925
	Aponsila montana (Distant)	AY627314	1 924
Pentatomidae	*Erthesina fullo* (Thunberg)	AY627315	1 835
	Austrotechus rugosus	AY252273[a]	1 883
	Graphosoma lineatum	U88339[c]	1 886
	Rhaphigaster nebulosa	X89495[d]	1 924
	Elasmostethus sp. WCW-2003	AY252322[a]	1 859
Acanthosomatidae	*Stauralia compuncta*	AY252269[a]	1 877
	Canopus sp. WCW-2003	AY252269[a]	1 885
Canopidae	*Allocoris* sp. WCW-2003	AY252269[a]	1 863
Cydnidae	*Megymenum* sp. WCW-2003	AY252224[a]	1 865
Dinidoridae	*Urostylis westwoodi*	AY252207[a]	1 104
Urostylidae			
Coreoidea Coreidae	*Notobitus meleagris* (Fabricius)	AY627321	1 774
	Mictis fuscipes (Hsiao)	AY627317	1 804
	Cletus punctiger (Dallas)	AY627323	1 802
	Anoplocnemis binorara (Distant)	AY627329	1 813
	Cletus trigonus (Thunberg)	AY742883	1 848
	Homoeocerus unipunctatus (Thunberg)	AY742886	1 859
	Cletus sp. WCW-2003	AY252261[a]	1 094
	Leptoglossus occidentalis	AY252225[a]	1 875
Alydidae	*Leptocorisa* sp.	AY627320	1 865
	Leptocorisa acuta (Thunberg)	AY627320	1 865
	Riptortus linearis (Fabricius)	AY627320	1 865
	Riptortus sp. WCW-2003	AY252161[a]	1 016
Hyocephalidae	*Maevius indecorus*	AY252214[a]	942
Rhopalidae	*Harmostes* sp. WCW-2003	AY252226[a]	1 889
	Serinthea sp. WCW-2003a	AY252162[a]	1 014
Lygaeoidea Lygaeidae	*Spilostethus hospes* (Fabricius)	AY627319	1 831
	Spilostethus hospes (Fabricius)	AY627325	1 865
	Nysius sp. (Dallas)	AY627326	1 823
	Graptostethus sp.	AY742885	1 848
	Neacoryphus sp. WCW-2003	AY252411[a]	1 894
Rhyparochromidae	*Pseudopachybrachius guttus* (Dallas)	AY627327	1 844
	Paraeucosmetus pallicornis (Dallas)	AY627328	988
	Paromius piratodes (Costa)	AY742881	1 857
	Udeocoris nigroaeneus	AY252262[a]	1 879
Berytidae	*Neoneides muticus*	AY252412[a]	1 890
	Jalysus spinosus	AY252125[a]	1 048
Piesmatidae	*Mcateella* sp. WCW-2003a	AY252164[a]	1 010
	Mcateella sp. WCW-2003b	AY252260[a]	1 101
Pyrrhocoroidea Largidae	*Largus* sp. WCW-2003	AY252227[a]	1 502
	Physopelta quadriguttata (Bergroth)	AY742882	1 835
	Physopelta gutta (Burmeister)	AY742884	1 846
Pyrrhocoridae	*Dysdercus* sp. WCW-2003a	AY252197[a]	1 100
	Dysdercus poecilus (Herrich-Schaeffer)	AY627318	1 829
Idiostoloidea	*Trisecus pictus*	AY252213	1 038
Cimicomorpha; Reduviidae	*Emesaya brevipennis*	AY252321[a]	1 865
Miridae	*Lygus hesperus*	U06476[b]	1 922
	Campyloneura virgula	AY252317[a]	1 880

Classification follows Henry (1997). [a] Direct submission to NCBI GenBank database by Wheeler & Schuh (2004). [b] Campbell et al, 1994. [c] Aleshin et al, 1995. [d] Direct submission to NCBI GenBank database by Chalwatzis & Zimmermann (1996).

Distance values among superfamilies and within superfamilies were determined by discarding positions with gaps in pairwise comparisons using the Kimura (1980) two- parameter model (Tab. 3).

Tab. 2　Primers for amplification and sequencing

Primer name	Direction	Primer sequence
F	Forward	5′-TCCCTGGTTGATCCTGCCAGTA-3′
R	Reverse	5′-TAATGATCCTTCCGCAGG TTCA-3′
2F	Forward	5′-GGGAGGTAGTGACAAAAAATAACG-3′
2R	Reverse	5′-CCTGTTATTGCTCAATCTCGTG-3′
3F	Forward	5′-GGTGAAATTCTTGGA TCGTC-3′
3R	Reverse	5′-ACATACTTGGCAAATGCTTTCGC-3′
4R	Reverse	5′-GTTAGAACTAGGGCGGTA TCTG-3′

Tab. 3　Sequence divergence using Kimura two-parameter model

	Pentatomoidea	Coreoidea	Pyrrhocoroidea	Lygaeoidea
Variable range in superfamilies(%)	0.4 – 3.4	0.1 – 4.5	0.7 – 7.7	0.4 – 10.9
Mean value between in-group species 4.6%		Variable range between in-group species 0.3% – 12.7%		Variable range between superfamilies 0.3% – 7.8%

2.2　Phylogenetic relationships

The phylogeny of Pentatomomorpha was reconstructed using 18*S* rDNA. Trees recovered by MP, ML and NJ methods were mainly congruent (Fig. 1, 2, and 3).

Unweighted parsimony analyses yielded 24 equally parsimonious trees of 1 830 steps (CI = 0.560, RI = 0.624); the strict consensus tree is presented in Fig. 1. The monophyly of infraorder Pentatomomorpha was strongly supported. The monophyletic Aradoidea (*Mezira granulata*, *Mezira sayi* and *Dysodius lunatus*) was recovered by three methods. It was a sister group to the remainder of the Pentatomomorpha (Trichophora), which was at a basal position of the tree topology. The monophyletic Trichophora was subgrouped into two major lineages. One of the two major lineages uncovered by 18*S* rDNA analysis comprised superfamily Pentatomoidea and Pyrrhocoroidea. Pentatomoidea was found to be monophyletic with strong support, which formed a sister relationship to Pyrrhocoroidea, except in the NJ tree (Pyrrhocoroidea being polyphyletic). However, the family relationships of Pentatomoidea in three tree topologies were incongruent. The other major lineage recovered comprised Lygaeoidea, Coreoidea, and Idiostoloidea. The superfamilies Lygaeoidea and Coreoidea were both polyphyletic. In Lygaeoidea, four families (Piesmatidae, Berytidae, Lygaeidae and Rhyparochromidae) were analyzed, grouping into two clades. One clade was Lygaeidae and Rhyparochromidae, which recovered as a sister group with strong bootstrap value. However, the two families, Piesmatidae and Berytidae appeared to have a sister relationship and were at a basal position of Trichophora lineages, distant to the clade of Lygaeidae and Rhyparochromidae. The superfamily Coreoidea received low branch support in all trees, and is polyphyletic. The superfamily Idiostoloidea, represented by one spcies *Trisecus pictus*, seemed more related to the family Rhopalidae (superfamily Coreoidea).

3　Discussion

3.1　18*S* rDNA marker

Our sequence based on phylogenetic analysis confirmed the monophyly of Pentatomomorpha, Aradoidea, and Pentatomoidea. This was congruent with morphological studies (Schuh, 1979; Wheeler et al, 1993; Henry, 1997) and the research of Li et al (2005). The Pyrrhocoroidea was further divided from the Coreoidea (*s.lat*) in this research, concordant with the results of Xie et al (2005). Therefore we suggest that 18*S* rDNA was a proper marker to reconstruct the phylogeny of Pentatomomorpha. The placement of the Aradoidea within Pentatomomorpha was strongly supported by ML, MP, and NJ analysis, which was the sister group to Trichophora. In morphological studies, this is supported by the presence of pulvilli in some members (Tullgren, 1918), tubular salivary glands (Southwood, 1955), egg structure, and trichophoran-type spermathecae (Pendergrast, 1957). The important implication of our analysis with respect to the higher taxonomy of Pentatomomorpha, was that Pentatomoidea was monophyletic and thus in accord with cladistic analysis of morpholog-

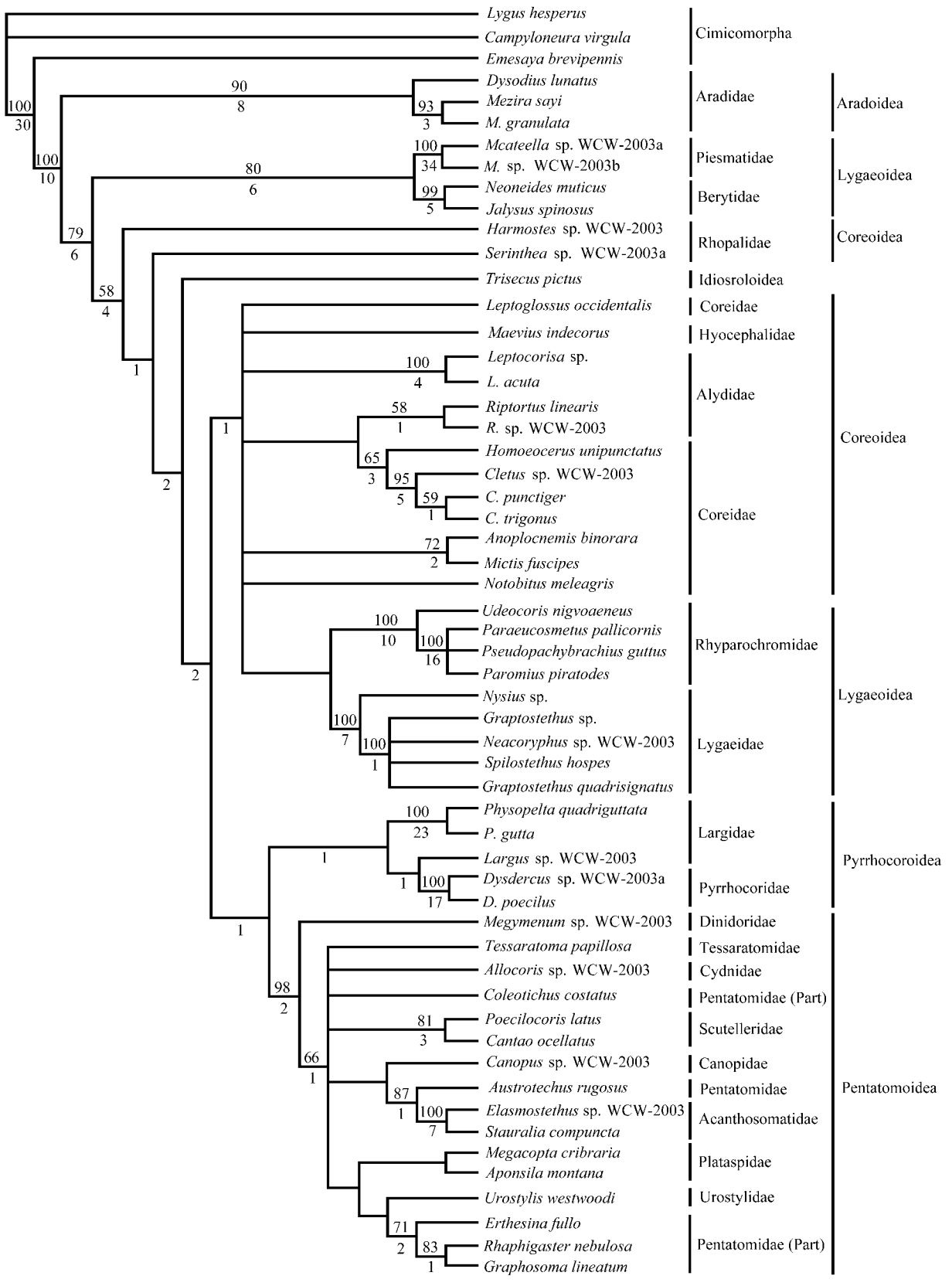

Fig. 1 The phylogenetic trees using the Minimum parsimony (MP) method according to 18*S* rDNA sequences of Pentatomomorpha with 21 families and 53 species

Bootstrap values are shown above nodes. Decay indices are shown below nodes. Current superfamily and family taxa following Henry (1997) are indicated on the right.

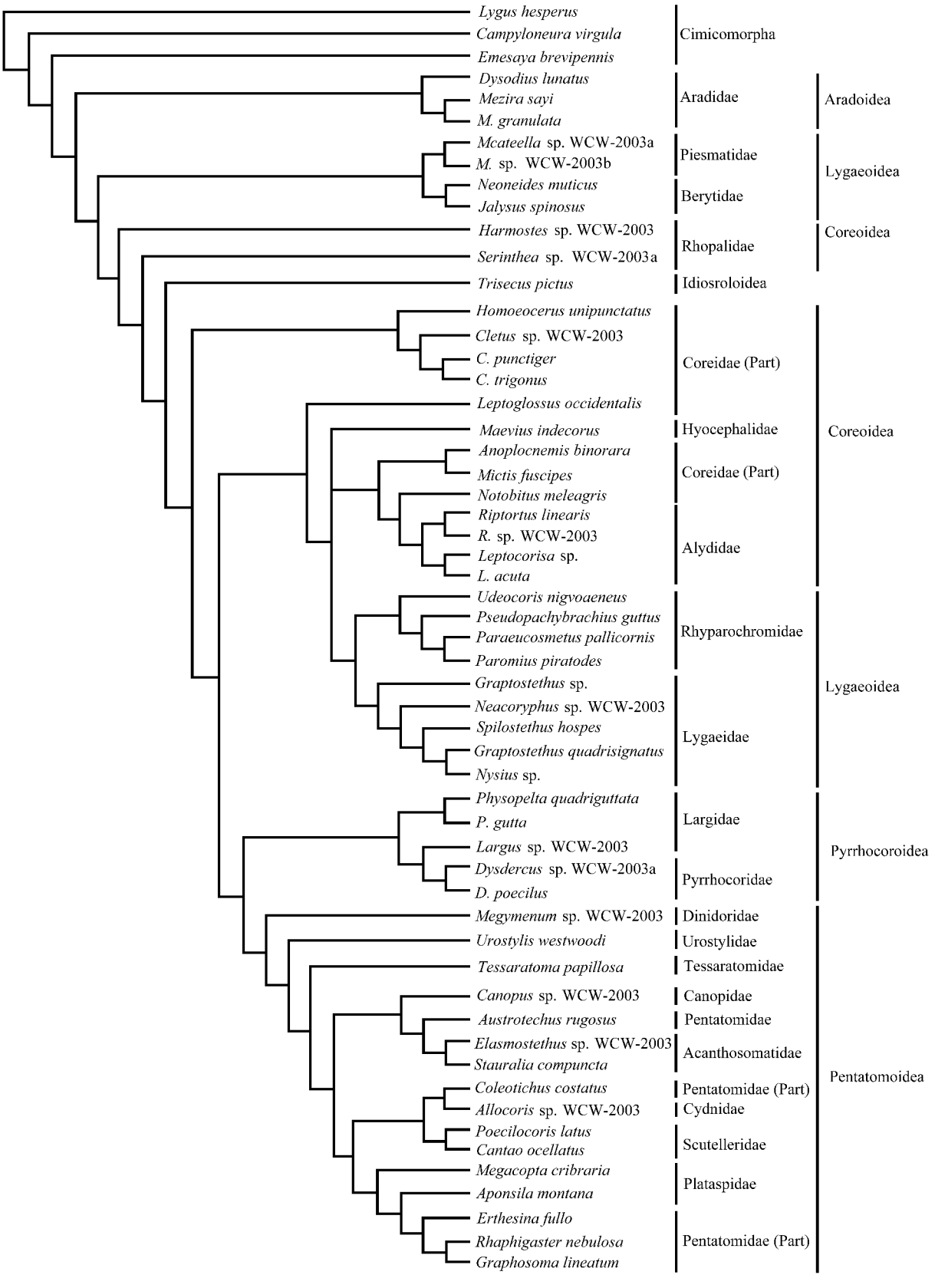

Fig. 2　The phylogenetic trees using the ML method

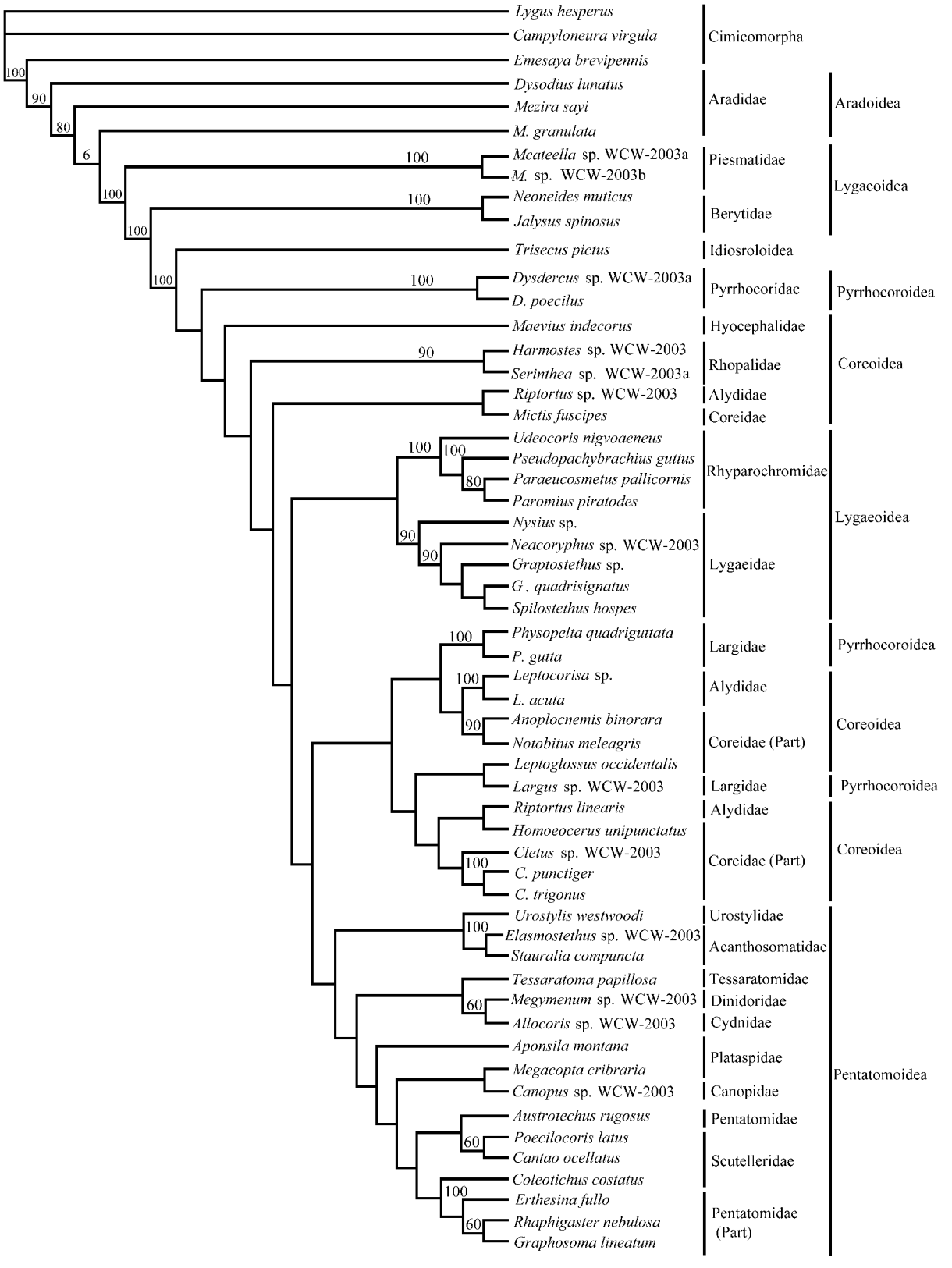

Fig. 3 The phylogenetic trees using the NJ method

ical data (Henry, 1997). Morphologically, monophyletic Pentatomoidea differs from the three superfamilies Pyrrhocoroidea, Lygaeoidea, and Coreoidea of Trichophora in many ways. These include the number of trichobothria, fusion and loss of parts of the plate-like ovipositor, an extra antennal segment, and a characteristic swelling of the spermathecal duct (Schaefer, 1993). However, based on the tree topologies the relationships among families of Pentatomoidea were much less ordered, which was consistent with the morphological studies (Štys & Kerzhner, 1975). Thus 18*S* rDNA did not provide sufficient information to separate families inside this superfamily, suggesting requirement of more sequence data in phylogentic studies.

3.2 Position of Piesmatidae and Berytidae

Piesmatidae is firmly placed in the Pentatomomorpha based on male genitalia, abdominal trichobothria, and pretarsal pulvilli (Drake & Davis, 1958), however its position in the suborder is inconsistent. It has been assigned as one superfamily, Piesmatoidea of Pentatomomorpha (Štys, 1964, 1967; Štys & Kerzhner, 1975; Schuh, 1986; Henry & Froeschner, 1988; Li & Zheng, 1994). Piesmatids have generally been placed in the Lygaeoidea (Schaefer, 1972, 1975, 1993; Schuh & Slater, 1995; Henry, 1997; Xie et al, 2005). Henry (1997) grouped the Piesmatidae to superfamily Lygaeoidea by carinate pronotum, punctate hemelytra, the loss of inner laterotergites, and the barrel-shaped antennal segment Ⅰ. However, these characters are not synapomorphous. Firstly, the barrel-shaped antennal segment Ⅰ is also present in Aradoidea and in some species of Lygaeoidea. Secondly, Aradoidea, Pentatomoidea, and many species of Coreoidea and Lygaeoidea have carinate pronotum. Thirdly the loss of inner laterotergites is quite homoplasious, indicating a more detailed interpretation of their evolution (Henry, 1997). The Piesmatidae are unique in having uniformly punctate hemelytral areoles, and two tarsomeres on each tarsus (also in Aradoidea and family Acanthosomatidae) while Lygaeoidea have three-segmented tarsi. Most significant is the presence of an m-chromosome (Jacobs, 1989) found only in the Coreoidea and most Lygaeoidea, however lost in a few taxa, e.g. Piesmatidae and Berytidae. Piesmatidae only has one pair of trichobothria on the abdomen 5 – 6, and has lost it on the abdomen 4 – 5 (the same to some species of Berytidae). Li et al (2005) failed to reject that Piesmatidae is a family of Lygaeoidea. However, based on the combined analysis of 18*S* rDNA and *COX1*, the MP and ML tree showed that Piesmatidae and Berytidae were distant to Lygaeidae and Rhyparochromidae (Li et al, 2005). Combining our molecular analysis, Piesmatidae was distantly related to other members of the Lygaeoidea; and according to morphological analysis, we suggest that the piesmatids should be assigned as a superfamily of Pentatomomorpha rather than a family in Lygaeoidea. Morphologically, Berytidae have been placed in Lygaeoidea, along with the Clolbathristidae, Lygaeidae, Malcidae, and sometimes Idiostolidae (Štys, 1961) and Piesmatidae (Schaefer, 1993; Henry, 1997). However, the results of this study showed that Berytidae never merged with the other families of Lygaeoidea and had a sister relationship to Piesmatidae instead. The reconstruction of their relationship will require further studies with other genes and more taxa samples.

3.3 Polyphyletic Coreoidea and Coreidae

With regard to the phylogeny of Coreoidea, there are many arguments in the morphological research. Henry (1997) and Li (1996) described the monophyletic Coreoidea with morphological data, whereas our analysis and result, derived from Xie et al (2005) and Li et al (2005), failed to describe the Coreoidea as monophyletic. This reflects the incongruence between morphology and molecular data. For the family Coreidae, which is a large worldwide family, traditional classification is primarily based on the concepts of "synthetic systematics" (Hsiao et al, 1977; Schuh & Slater, 1995). The lack of morphological synapomorphies suggests that this family is polyphyletic. Although without strong support, the tree topologies of our results also rendered this conclusion. The molecular data and morphological data both indicate that taxonomy of this family should be revised subsequently.

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