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Morphological Phylogeny of the Water Snake Subfamily Homalopsinae (Serpent: Colubridae)

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Abstract: The morphological phylogeny of the water snake subfamily Homalopsinae, containing 10 genera, of which seven are monotypic, was not reported up until now. Here fourteen morphological characters were selected for the cladistic analysis. Using software Hennig 86, two phylogenetic trees were inferred and the results showed that the subfamily Homalopsinae was divided into two groups. Compared with the molecular phylonenetic tree of Voris et al(2002), the genera *Gerarda* and *Fordonia* are sister groups in both studies; both studies also yielded the same monophyletic lineage, which contained three genera (*Cerberus* + *Erpeton* + *Homalopsis*). However, the position of the genus *Cantoria* is distinctly different with the study of Voris et al(2002).

Key words: Homalopsinae; Cladistic analysis; Morphological characteristic

水蛇亚科形态学特征的支序分析

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摘要: 水蛇亚科属于游蛇科, 包含 10 个属。其中 7 个属为单型属。选取水蛇亚科 14 个形态学特征进行支序分析, 并利用计算机软件 Hennig 86 对水蛇亚科中 8 个属之间的系统发育关系进行初步探讨, 结果显示水蛇亚科分为两支: *Gerarda* 和 *Fordonia* 两个属构成姊妹群, *Cerberus*、*Erpeton* 和 *Homalopsis* 三个属也构成单系群, 与 Voris et al(2002)的分子系统树相同, 但 *Cantoria* 属的地位则与 Voris et al(2002)的明显不同。

关键词: 水蛇亚科; 支序分析; 形态学特征
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The Homalopsinae species are all rear-fanged aquatic snakes, widely distributed in South and Southeast Asia. Guenther (1864) firstly named the water snake family Homalopsidae, which was regarded as a subfamily of Colubridae by Boulenger (1890). Smith (1943) partly revised the systematics of Homalopsinae, such as moving *Hypsirhina* into *Enhydris*, and *Hipistes* into *Biotia*, and finally recognized 10 genera in Homalopsinae.

According to morphological criteria, Gyi (1970) performed a detailed taxonomic revision about this subfamily, in which 10 genera and 34 species were recognized, but did not attempt a phylogenetic analysis. Based on partial sequences of three mitochondrial genes, Voris et al (2002) presented a molecular phylogenetic study of the subfamily and their results showed not only a moderate support to the monophyly of Homalosinae, but also relationships among eight of the 10 genera. Kraus & Brown (1998) and Lawson et al (2005) also showed the validity of the Homalopsine lineage. However, they studied only a few species of this subfamily.

Although the monophyly of Homalopsinae was supported (Kraus & Brown, 1998; Voris et al, 2003;

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Lawson et al, 2005), there were still no attempts to analyze the morphological phylogeny of this subfamily and the morphological phylogenetic relationships among genera of this subfamily were still poorly understood.

From the middle of last century, almost all of the zoological taxonomists have been using cladistic principles (Hennig, 1966) for animal classification and systematic study. Furthermore Sokal & Sneath (1963) set up the numerical taxonomy method, which reduced empiricism or individualism and made the zoological classification more objective. Here the morphological phylogeny of Homalopsinae was also analyzed with cladistic principles (Hennig, 1966; Wiley, 1981) to compare with the results of Voris et al (2002).

1 Materials and Methods

1.1 Materials

We examined all characters of genera and species that Boulenger (1896), Bourret (1936), Smith (1943), Taylor (1922, 1966), Pope (1935), Deuve (1970) and Zhao et al (1998) reported in their works. We also observed all specimens of water snakes conserved in Kunming Institute of Zoology, the Chinese Academy of Science. Unfortunately, our work did not include *Myron* in Australia and *Heurnia* in New Guinea, because we did not have enough information about the characteristics of their maxillary bone and palatine.

1.2 Selection of outgroup

So far the phylogeny of Colubridae has not been clear and the relationship of homalopsine snakes to other colubroid lineages was also not well understood. Actually studies clearly showed that subfamily Homalospinae is monophyletic and is very closely related with the subfamily Natricinae (Siegel et al, 1987; Kraus & Brown, 1998; Voris et al, 2003; Lawson et al, 2005). This study focuses on the phylogenetic relationships among genera rather than the monophyly of Homalopsinae. Here we selected genus *Amphiesma*, a typical and common genus of subfamily Natricinae, as the single outgroup, to assess the polarities of the morphological characters.

1.3 Polarities of characters

Fourteen characters were selected for the phylogenetic analysis, and each character has two or more states: "0" indicates the primitive state that occurred in the outgroup (*Amphiesma*) and other genera of Homalopsinae, which have the same morphological characteristics; "1" or "2" indicates a derived state of the others (Maddison et al, 1984).

CH1 (abbreviation for character 1, the same abbreviation follows): Eyes moderate and with round pupil are defined as code "0"; eyes smaller and with vertically elliptic pupil, as "1".

CH2: Maxillary teeth more than 20, followed by a pair of enlarged denticles, as "0"; maxillary teeth less than 20, followed by a pair of enlarged grooved fangs, as "1".

CH3: Upper face of head with normal shields, as "0"; upper face of head with unusually large shields, as "1".

CH4: Nasals separated from each other as "0"; nasals in contact with one another, as "1".

CH5: Internasal insert between nasals, as "0"; internasal behind nasals, as "1".

CH6: Maxillary bone extending forward of the palatine, as "0"; maxillary bone not extending as far forwards as the palatine, or projecting beyond the palatine, as "1".

CH7: Nasal completely divided as the front nasal and the behind nasal, as "0"; nasal semi-divided by a cleft, as "1", or nasal entire as "2".

CH8: Two internasals, as "0"; a single internasal, as "1".

CH9: Frontal fragmented as "0"; frontal fragmented as one large scale and several small scales, as "1".

CH10: Subocular absent, as "0"; subocular present, as "1".

CH11: Last upper labial complete, as "0"; some last upper labials horizontally divided, as "1".

CH12: Rostral appendages absent, as "0"; two rostral appendages present, as "1".

CH13: Genials longitudinally arranged, as "0"; genials in a transverse row, as "1".

CH14: Oviparous as "0"; ovoviviparous as "1".

The character states of the genera of Homalopsinae are listed in Tab. 1.

2 Results

Using the data matrix of Tab. 1, we analyzed the phylogenetic relationships among the genera of Homalopsinae through the software Hennig 86. Two identical most parsimonious trees were generated (Fig. 1: A, B), which have the same number of steps. In both trees, the eight genera formed a monophyletic clade with two large branches: the first branch was formed by the genera *Cantoria*, *Biotia*, *Fordonia* and *Gerarda*; the second branch formed by the genera *Homalopsis*, *Cerberus*, *Erpeton* and *Enhydris*. The slight difference

Tab. 1　Summary of character states of genera of Homalopsinae

	CH 1*	CH 2	CH 3	CH 4	CH 5	CH 6	CH 7	CH 8	CH 9	CH 10	CH 11	CH 12	CH 13	CH 14
Amphiesma (outgroup)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Biotia	1	1	1	0	0	1	0	1	0	1	0	0	0	1
Cantoria	1	1	1	0	0	1	1	1	0	1	0	0	0	1
Enhydris	1	1	1	1	1	0	1	0	0	0	0	0	0	1
Homalopsis	1	1	1	1	1	0	1	0	1	1	1	0	1	1
Cerberus	1	1	1	1	1	0	1	0	1	1	1	0	0	1
Fordonia	1	1	1	0	0	1	2	1	0	0	0	0	0	1
Gerarda	1	1	1	0	0	1	2	1	0	0	1	0	0	1
Erpeton	1	1	1	1	1	1	0	0	1	1	1	1	0	1

* CH1: Character 1, the same abbreviations are used for others.

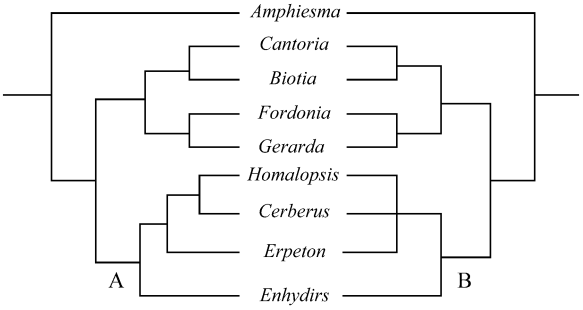

Fig. 1　Phylogenetic relationships among genera of Homalopsinae with *Amphiesma* as outgroup

was that the four genera *Homalopsis*, *Cerberus*, *Erpeton* and *Enhydris* were clustered together in Tree A, while in Tree B the genera *Homalopsis*, *Cerberus* and *Eerpeton* formed a trichotomy branch, that was a sister group of the genus *Enhydris*.

In the phylogenetic trees, CH1, 2, 3 and 14 are derived in all the genera of ingroups, which formed the monophyly of Homalopsinae. *Biotia* and *Cantoria* were different only in CH7, *Homalopsis* and *Cerberus* different only in CH13 and *Fordonia* and *Gerarda* only different in CH11, respectively.

3　Discussion

Snakes of Homalopsinae are distributed in the large area from Pakistan's Indus River delta across India, Burma, Indochina-Malaya Peninsula, South China, Indonesia and eastward to New Guinea and Australia (Murphy & Voris, 1994). It is very difficult to check representatives of each genus and to find enough valuable and informative characteristics from literature either. Although we only used 14 characteristics in this study, the phylogenetic trees produced by Hennig 86 were still valuable. It was clearly shown that the subfamily Homalopsinae is monophyletic and could be classified into two sub-groups.

There are some congruous results between Voris et al (2002) and this study. Forming the same clade in both studies, genera *Gerarda* and *Fordonia* are monotypic and allopatric, which suggests a vicariance event. Both studies also yielded the same monophyletic lineage, which contained three genera (*Cerberus* + *Erpeton* + *Homalopsis*). However, intergeneric relationships of this lineage were not clear. Although having the closest phylogenetic relationships, these three genera exhibit distinctive differences in morphology and ecology, which shows that the evolutionary rate of morphology is faster than that of mitochondrial DNA molecules.

The greatest difference between the results of Voris et al (2002) and ours is the position of genus Cantoria. Our results showed that genus *Cantoria* firstly formed a sister group to *Biotia*, then they formed a monophyletic lineage with the genera (*Gerarda* + *Fordonia*). However, the results of Voris et al (2002) showed that the genus *Cantoria* was the basal branch to all other homalopsine genera. Considering that all species of the four genera are estuarial or marine snakes, and the species of *Cantoria* and *Biotia* feed on fishes, while *Gerarda* and *Fordonia* feed on crabs (Voris & Murphy, 2002), the morphological relationships among them reveal their eco-morphs adapted to estuarial or marine habitat. The difference of evolutionary rate between external morphology and mitochondrial DNA may be due to the different effects of natural selection.

The polyphyletic relationship of the largest genus *Enhydris* (Voris et al, 2002) indicated that there is still much to do in the future. Further morphological studies may focus on the phylogeny at species level, and select more characteristics, not only from the external morphology, but also from the skeletal and muscular

morphology.

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