[REVIEW]

Water Mites: Phylogeny and Evolution

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ABSTRACT

Studies on water mite evolution regarding the phylogenetic implication are reviewed. Hydracarina is a large parasitengone mite group. Currently, more than 5,000 species are integrated into 52 families in nine superfamilies. Although there are some conflicts on the origin of water mites, their monophyletic nature is suggested by several cladistic studies. The current taxonomic system of water mites does not reflect monophyletic groupings. Some researches have focused on phylogenetic relationships within Hydracarina, however, reliable hypotheses have not been obtained. Attempts to analyze data in a phylogenetic framework have been made in several ecological and behavioral studies. A comparative method has also been employed in a few studies, however, the real worth of this approach is not appreciated due to the absence of reliable phylogeny. Phylogenetic background estimated by modern cladistic methodology is indispensable for testing hypotheses on water mite evolution.

Key words: biogeography, cladistics, evolution, Hydracarina, phylogeny, taxonomy

In the long history of mite evolution, several lineages have successfully invaded aquatic habitats. According to Walter and Proctor (1999), a large number of families in Prostigmata and several or a few families in Ixodida, Mesostigmata, Oribatida and Astigmata have migrated into aquatic or subaquatic (not completely aquatic) habitats in springs, streams, ponds, lakes and seas. These groups exhibit a large diversity of lifestyle. An uropodid species *Phaulodinychnus mitis* is regularly submerged by tidal flooding on the sea shore (Krantz, 1974). Hydrozetids known as an aquatic Oribatida are found on aquatic plants, wet moss, and floating sphagnum (Grandjean, 1949; Sellnick, 1960). Members of the acaroid family Hyadesidae are encountered in tide pools, algae, barnacle and mussel beds in coastal areas (André, 1931; Fain, 1974a, b; Pugh and King, 1985; Pugh, 1988; Luxton, 1990a, b; Bücking, 1999). Some astigmatid mites characteristically inhabit 'phytotelma' a water-holding cavity formed by a plant (Fashing, 1994, 1998; OConnor, 1994). A few members of prostigmatid mites invaded unusual environments. A marine halacarid *Bathyhalacarus quadricornis* was discovered at a depth more than 5,000m in the Kuril-Kamchatka trench (Sokolov and Yankovskaya, 1968). A thyasid species in Hydriphantoidea *Trichothyas (Lundbladia) japonica* was collected from a hot-spring at a temperature of 40 °C (Uchida and Imamura, 1953). Several species are parasitic on marine vertebrates. Some members of Halarachnidae exist in the nasal passages of seals and walruses (Strandtmann and Wharton,

1958). An *Amblyomma* tick parasites sea snakes that have a completely underwater life (Hoogstraal, 1973).

Aforementioned marvelous biological diversity observed in aquatic mites reflects various evolutionary histories of each lineage. To understand the nature of aquatic mites in an accurate way, evolutionary considerations in phylogenetic framework are indispensable. In this paper, the author reviews some works which are implicated in water mite phylogeny.

In the strict sense of the word, 'water mites' refers to members of the cohort Parasitengona in the suborder Prostigmata. Within aquatic mites, water mites taxonomically referred to as Hydracarina (also as to Hydrachnellae, Hydrachnidia, and Hydrachnida) are the largest group including more than 5,000 species (Viets, 1987). They are obligatorily aquatic and have characteristically complex life cycles with parasitic larva and the predatory post-larval stage. This strict definition of water mites is adopted here.

ORIGIN

The outline of chelicerate phylogeny has recently been reviewed by Weygoldt (1999). By recent cladistic works (Weygoldt and Paulus, 1979a, b; Lindquist, 1984; Beall and Labandeira 1990; Schultz, 1990; Wheeler and Hayashi, 1998) Acari was regarded as a sistergroup of Ricinulei (Fig.1).

It is an ongoing debate whether the Acari is monophyletic (e.g. Weygoldt and Paulus, 1979a; Schultz, 1989, 1990) or polyphyletic (occasionally, diphyletic of Anactinotrichida and Actinotrichida in which water mites are contained) (e.g. Zachvatkin, 1952; Woolley, 1961; Van der Hammen, 1972, 1977, 1989; Alberti, 1979, 1980a, b, c, 1983, 1984, 1991, 1995). Lindquist (1984) debated that authors recognizing polyphyletic origin have not applied the methodology in a reliable manner. At present, it appears that there is no

Fig. 1. Extant chelicerate phylogeny. Modified from the summary cladogram in Wheeler and Hayashi (1998).

convincing evidence of a polyphyletic origin for the Acari. A detailed treatment of this problem is beyond the scope of this paper, and several additional texts will provide a reference for this subject: Krantz (1978), Woolley (1988), Evance (1992) and Walter and Proctor (1999).

The fossil record of larval specimen from Tertiary deposits provided little insight on the origin of water mites (Cook, 1957; Poinar, 1985). Consequently, significant clues for the evolutionary history must be indirectly obtained by examining extant taxa. Water mites are presumed to have evolved from terrestrial parasitengone stock. In some early literature, the water mites were regarded as ecological assemblage and of polyphyletic origin (André and Lamy, 1937; Sokolov, 1954; Bader, 1954, 1967, 1977; Mitchell, 1957, 1962; Woolley, 1961). Pieczynski (1962) reviewed some of these studies. The ancestral water mites are supposed to resemble extant, weakly-sclerotized Thyadinae (Mitchell, 1957; Cook, 1974). Barr (1972) proposed a monophyletic origin of Hydracarina except for Hydrovolzioidea indicating the structural uniformity of ejaculatory complex (cf. Barr, 1972, 1973) in all groups other than *Hydrovolzia*. Smith and Oliver (1976, 1986) speculated that members of Hydryphantoidea retained many plesiomorphic characteristics of the earliest water mites and this superfamily might represent the sister-group of water mites except for Hydrovolzioidea. On the other hand, Prasad and Cook (1972) postulated additional ancestral lineages including sperconid-like stock. Smith and Cook (1991) proposed that Hydracarina excluding the Stygothrombidoidea and Hydrovolzioidea was a monophyletic group derived from hydriphantoid-like ancestors. Although these polyphyletic hypotheses are induced on the basis of precise observation of biological attributes, they are apt to fall into narrative works.

A cladistic analysis of the cohort Parasitengona on the basis of larval morphology by Welbourn (1991) revealed a branching pattern among three subcohorts: (Erythraeina, (Hydracarina, Trombidiina)). Erythraeina consists of Erythraeoidea and Calyptostomatoidea. Trombidiina includes Trombidoidea, Trombiculoidea, Chyzeroidea and Tanaupodoidea. According to this scheme, Hydracarina constructs a sister-group with a clade of Trombidiina, and is characterized by four autapomorphies: 1) supracoxal seta ϵ absent, 2) companion seta associated with ψ and ω on leg I absent, 3) companion seta associated with dorsal eupathid on tarsus I absent, and 4) two setae on palpal genu. Within the terrestrial Parasitengona, the Tanaupodoidea retaining primitive larval condition is placed in the closest group of Hydracarina (Welbourn 1991). In contrast, Witte (1991, 1995) made a morphology-based cladistic analysis and reached another result (Hydracarina (Trombidoidea (Calyptostomatoidea, Erythraeoidea))). According to his opinion, Hydracarina is supported by six autapomorphies: 1) sclerite in larva with one pair of setae, 2) anal pore in larva and adults surrounded by single sclerite, 3) median eye dorsal, 4) glandularia present, 5) acrosome filament of sperm cell reduced, and 6) posterior rami of proximal-arm sclerite of ejaculatory complex distally form an apex projecting into the atrium. In his cladogram, Hydracarina is recognized as a sister-taxa to Trombidia which includes Trombidoidea, Calyptostomatoidea and Erythraeoidea. Although it is not clear whether Witte (1991) included enigmatic water mite Stygothrombidoidea in the analysis, these modern cladistic works suggest a monophyletic nature of Hydracarina.

HIGHER CLASSIFICATION

The most widely accepted, traditional classification was provided by Viets and Viets (1960). Thereafter, Cook (1974) reviewed the classification and recognized seven superfamilies and 44 families. Since then, the families have been conservatively integrated into eight superfamilies (Smith and Cook 1991). Recently, Harvey (1998) erected a superfamily Sperchontoidea for a single family Sperchontidae which was formerly placed in Lebertioidea. He newly recognized Zelandothyadidae in Hydryphantoidea, and Frontipodopsidae and Wettinidae in Hygrobatoidea from which Limnesiidae removed into Lebertioidea. Gerecke et al. (1999) recently established a family Apheviderulicidae in Eylaoidea. Consequently, nine superfamilies and 52 families are recognized in the current classification (Table 1).

As mentioned before, the monophyly of the traditional Hydracarina may not always be acceptable. Some researchers have placed Hydrovolzioidea outside of Hydracarina (Barr, 1972; Schwoerbel, 1986). Schwoerbel (1986) proposed that Hydrovolziidae should be incorporated into Halacaroida. In addition, the monophyly of the higher category, especially superfamilies, has not been warranted (Smith and Cook, 1991). At least, Hydryphantoidea, Lebertioidea, and Hygrobatoidea are each paraphyletic taxon (Smith, 1983a; Smith and Cook, 1991; Witte, 1991). For the future, the current taxonomic system must be revised into an assemblage reflecting monophyletic clades based on detailed phylogenetic analysis.

Table 1. Superfamilies and families of Hydracarina, mostly based on Harvey (1998).

Superfamily	Family	Superfamily	Family
STYGOTHROMBIOIDEA	Stygotrombiidae		Ferradasiidae
HYDROVOLZIOIDEA	Hydrovoziidae		Frontipodopsidae
HYDRYPHANTOIDEA	Ctenothyadidae		Hygrobatidae
	Hydrodromidae		Omartacaridae
	Hydryphantidae		Pionidae
	Rhynchohydracaridae		Pontarachnidae
	Teratothyadidae		Unionicolidae
	Thermacaridae		Wettinidae
	Zelandothyadidae	ARRENUROIDEA	Acalyptonotidae
EYLAOIDEA	Apheviderulicidae		Amoenacaridae
	Eylaidae		Arenohydracaridae
	Limnocharidae		Arrenuridae
	Piersigiidae		Athienemanniidae
HYDRACHNOIDEA	Hydrachnidae		Bogatiidae
SPERCHONTOIDEA	Sperchontidae		Chappuisiidae
LEBERTIOIDEA	Anisitsiellidae		Harpagopalpidae
	Lebertiidae		Hungarohydracaridae
	Limnesiidae		Kantacaridae
	Oxidae		Krendowskiidae
	Rutripalpidae		Laversiidae
	Stygotoniidae		Mideidae
	Teutoniidae		Mideopsidae
	Torrenticolidae		Momoniidae
HYGROBATOIDEA	Astacocrotonidae		Neoacaridae
	Aturidae		Nipponacaridae
	Feltriidae		Nudomideopsidae

PHYLOGENY

Very few phylogenetic hypotheses within water mites have been presented in a testable manner. The first phylogenetic relationship for Hydracarina in a cladistic procedure was demonstrated by Witte (1991). Witte (1991) reconstructed fully resolved cladistic relationships among 15 genera mainly on the basis of morphological characters. He assigned some characters relating to sperm-transfer on the cladogram to discuss evolution of reproductive mechanisms. As Harvey (1998) pointed out, however, the character matrix for the analysis is not presented and the cladistic handling is obscure. Furthermore, a limited number of terminal taxa which are not all representatives of currently recognized families is used in the analysis. Recently, Witte and Döring (1999) presented a somewhat revised cladogram of Witte (1991). Despite several defects, Witte (1991) and Witte and Döring (1999) offer new insights on water mite systematics. According to their hypotheses (Fig. 2), Hydrovolzioidea is proposed as a sister-group of Eylaoidea, and the paraphyly of the traditional three superfamilies (Hydryphantoidea, Lebertioidea and Hygrobatoidae) is implied.

Recently, Gil (1996) did a cladistic analysis of 12 European genera in addition to *Hydrovolzia* as an out-group. She examined 20 morphological characters and depicted only one of 15 most parsimonious cladograms in which relationships between *Arrenulus* and some hygrobatoid genera varied from one to another. Each lineage was supported by no or

Fig. 2. Phylogenetic relationships of higher taxa in Hydracarina. Modified from Witte (1991), Witte and Döring (1999) and Witte and Olmski (1999).

Fig. 3. Provisional superfamily relationships in Hydracarina. Modified from Harvey (1998).

only a few apomorphic characters, i.e. most of the characters appeared more than once on the cladogram, so that the monophyly of each lineage was weakly supported. In her conjecture, however, the paraphyly of Hydryphantoidea is possibly confirmed.

Regarding the current superfamilies of each monophyletic group, Harvey (1998) inferred a tentative phylogeny of nine superfamilies (Fig. 3) on the basis of characters mainly provided by Mitchell (1957), Witte (1984, 1991), Smith and Cook (1991) and Gil (1996). Although Harvey (1998) summarized identifiable autapomorphies of each superfamily, the cladistic methodology and data matrix were not provided.

Phylogenetic investigations concerning a limited group of Hydracarina have been actively carried out. Morphocline of external characters was estimated in several families (Sparing, 1959; Besch, 1963, 1964a; Bader, 1985). Larval morphology sometimes provided useful information concerning phylogeny. Smith (1976) carried out a comprehensive cladistic analysis of Pionidae on the basis of larval characters. Thereafter, he gave phylogenetic inferences to some taxa mainly on the basis of larval characters (e.g. Smith and Oliver, 1976, 1986; Smith 1977, 1978, 1982, 1983a, b, c, 1984, 1991; Simmons and Smith, 1984). Proctor (1992b) presented cladistic relationships within Unionicolidae in a testable manner using 28 morphological and behavioral characters. Phylogenetic considerations are sometimes made in some revisional works (Vidrine, 1986; Bertrand, 1990). Although cladistic terminology is frequently employed in extensive literature, cladistic relationships have seldom actually been depicted.

Unfortunately, no satisfactory hypothesis concerning water mite phylogeny currently exists. Morphology-based analysis has its methodological limitation mainly caused by the difficulty of homological character search. The application of some molecular techniques is also recommended for reconstructing a phylogenetic relationship on which evolutionary hypotheses can be tested.

EVOLUTION IN PHYLOGENETIC IMPLICATIONS

Several attempts for analyzing data on water mites from an evolutionary point of view have been made. Morphology-based character evolution has occasionally been discussed. Mitchell (1962) made a comparative study of mouth part morphology in water mites and presented evolutionary implications on the structure and function. Barr (1979) made a cluster analysis of the morphology of the male reproductive organ, i.e. ejaculatory complex, in water mites by using the phenetic method (Sneath and Sokal, 1973). Proctor (1992a, 1998) and Proctor and Smith (1994) suggested that mating behavior and spermatophore morphology provided clues about phylogenetic relationships within water mites. Olomski (1991) and Witte and Olomski (1999) inferred evolutionary transformations of the male reproductive system and the osmoregulatory system on the basis of phylogenetic relationships within Trombidia and Hydracarina.

Ecology and behavior discussed in the phylogenetic context are interesting subjects. Wohltmann et al. (1999) examined evolutionary change in the life history patterns in hygrobiontic parasitengone genera by correlation of the phylogenetic transformation of characters with the environmental conditions. Smith (1999) examined three types of convergently evolved parasitic associations of larval water mites with insect hosts: aquatic larva, preparasitic attendance and extended association. These life-history patterns were reflected in the distribution pattern of mites within host populations. By using a comparative approach, Proctor (1991) determined that copulation evolved 91 times in the 343 water mite genera, and independent evolution of copulation was associated with swimming hairs. Proctor (1992b) made a cladistic test of a behavioral hypothesis of Unionicolidae by mapping male courtship and female predatory behaviors on the reconstructed cladogram. She concluded that male courtship behavior evolved concomitantly with or after female predatory behavior and the sensory exploitation hypothesis (cf. Andersson, 1990; Ryan et al., 1990) was applied to the evolution of male courtship behavior in unionicolid mites. Thereafter, Proctor et al. (1995) made a comparative test of the female-choice hypothesis (cf. Eberhard, 1985) and concluded that the rock-and-key hypothesis did not explain the distribution of spermatophore complexity among water mite taxa. Recently, Witte and Döring (1999) reviewed reproductive behavior of water mites and stated that the mode of sperm transfer evolved in canalization of structural and functional constraints. The comparative method using phylogeny is a useful method to test hypotheses, especially for detection of adaptive clues (Ridley, 1983; Harvey and Pagel, 1991). In spite of its advantages, only a few studies (Proctor, 1991; Proctor et al., 1995) employed this method.

Biogeographical considerations have been added in many descriptive studies of limited taxa or regional fauna (e.g. Angelier, 1953a, b, c; Besch, 1964b, 1969; Smith, 1992a, b; Cramer and Smith, 1993; Smith and Cook, 1994; Gerecke, 1994; Gerecke and Di Sabatino, 1996). Cook (1969) and Schwoerbel (1967) made geographic investigations of interstitial water mites, and inferred that psammobiontic mites were of polyphyletic origin. Recently, Smith and Cook (1999) examined the global distribution pattern of water mites and speculated that distributions of family-group taxa appear to reflect an early vicarious event due to plate tectonics. Unfortunately, these implications of historical biogeography have not been based on reliable phylogenetic framework and have not been analyzed in an accurate way.

PROBLEMS

Many researchers have tried to examine biological phenomena in an evolutionary context. Although the comparative method is a strong approach to test various evolutionary hypotheses, a convincing phylogenetic hypothesis is prerequisite for a successful analysis. Reliable hypotheses on water mite phylogeny, however, are almost unknown in the present circumstances. Phylogenetic background estimated by modern cladistic methodology is indispensable for discussing water mite evolution.

For studying geographical or biological associations, e.g. host-parasite or area relationships, the phylogenetic approach using a statistical method is strongly recommended to test hypotheses (e.g. Brooks, 1990; Brooks and McLennan, 1991; Bremer, 1992; Page, 1994; Ronquist, 1997). Unfortunately, there is no biogeographical or ecological study of water mites analyzed using recent phylogeographical methodology. Instead of traditional methods, the introduction of the mathematical approach is desirable to make further progress in modern acarology.

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摘 要

ミズダニ類：系統と進化 安倍 弘(日本大学・生物資源科学部)

ミズダニ類(Hydracarina)を対象とする多くの研究の中で、特に系統と進化に関わる話題について現在まで得られている知見をまとめた。ミズダニ類はケダニ団に属する分類群で、現在5,000種以上が9上科52科にまとめられている。近年の分岐学的研究はミズダニ類の単系統性を支持しているが、現行の分類体系はそれぞれの単系統群を反映した構成にはなっていない。また、ミズダニ類内部の系統関係については従来から様々な仮説が立てられているが、未だに信頼できる系統仮説は得られていない。近年では生態学や行動学の分野でも系統関係を考慮するようになり、ミズダニ類でも比較法によるデータ解析などが行われている。今後、ミズダニ類の進化に関わる知見を得るためには、様々な現象を系統的側面からテストするための信頼性の高い系統仮説を得る必要があるだろう。