

Systematics, Historical Biogeography and Ecological Phylogenetics in a clade of water striders¹

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Abstract: I hereby review the current knowledge about systematics, historical biogeography and ecological phylogenetics in the three principal northern temperate genera of water striders *Limnoporus* STÅL 1868, *Aquarius* SCHELLENBERG 1800 and *Gerris* FABRICIUS 1794. Most of the discussion is based on comparison of a recently published combined analysis tree involving four genetic markers and a morphological data set with older phylogenetic trees primarily based on manual cladistic optimization of morphological characters.

Key words: DNA-barcodes, Gerrinae, phylogeography, simultaneous analyses.

Introduction

Water striders (Hemiptera-Heteroptera, Gerromorpha, Gerridae) are familiar inhabitants of aquatic habitats throughout the Worlds temperate, subtropical, and tropical regions comprising approximately 640 described species in 72 genera (ANDERSEN & WEIR 2004). Most water striders are found in freshwater habitats, such as rivers, streams, lakes and ponds, but a few genera are found in marine – even oceanic – habitats, and still others have become semi-terrestrial (ANDERSEN 1982). Being Hemipterous insects, water striders use their rostrum to immobilize and suck out prey, which often comprises dead or drowning insects caught in the surface film. Water striders are particularly variable with respect to wing reduction, and often display striking patterns of wing polymorphism (ANDERSEN 1993b, 1997, 2000). Populations often comprise both long-winged (macropterous) and short-winged (brachypterous/micropterous) or wingless (apterous) individuals, but the situation may be even more complicated by macropterous individuals mutilating their wings and/or histolyzing flight muscles, thereby becoming secondarily flightless. Fi-

nally, water striders show great variation in mating strategies, and morphological and behavioral adaptations to accomplish or avoid multiple mating (ANDERSEN 1994, 1996; ARNQVIST 1997). The striking diversity in habitat selection, wing polymorphism and mating strategies – along with the practically two dimensional habitat, has made water striders popular objects in studies of behavior, ecology and evolution (SPENCE & ANDERSEN 1994; ROWE et al. 1994; FAIRBAIRN et al. 2003; ABE et al. 2004; BERTIN & FAIRBAIRN 2005).

The late Dr. Andersen (1940-2004) from the Zoological Museum in Copenhagen, Denmark, was an expert in extant and fossil Gerromorpha, and a pioneer in studies of historical biogeography and ecological phylogenetics (e.g. ANDERSEN 1982, 1998; SPENCE & ANDERSEN 1994; ANDERSEN & WEIR 2004). By mapping different traits in question upon a cladogram, he reconstructed ancestral states and inferred the number and sequence of evolutionary transitions between states. Andersen thereby offered new hypotheses about the evolution of water striders that were not purely speculative but testable, and by dating the events with fossils he furthermore established a

¹ This paper is dedicated to Dr. Ernst Heiss on the occasion of his 70th birthday and in recognition of his considerable contribution to the study of aradids and their allies.

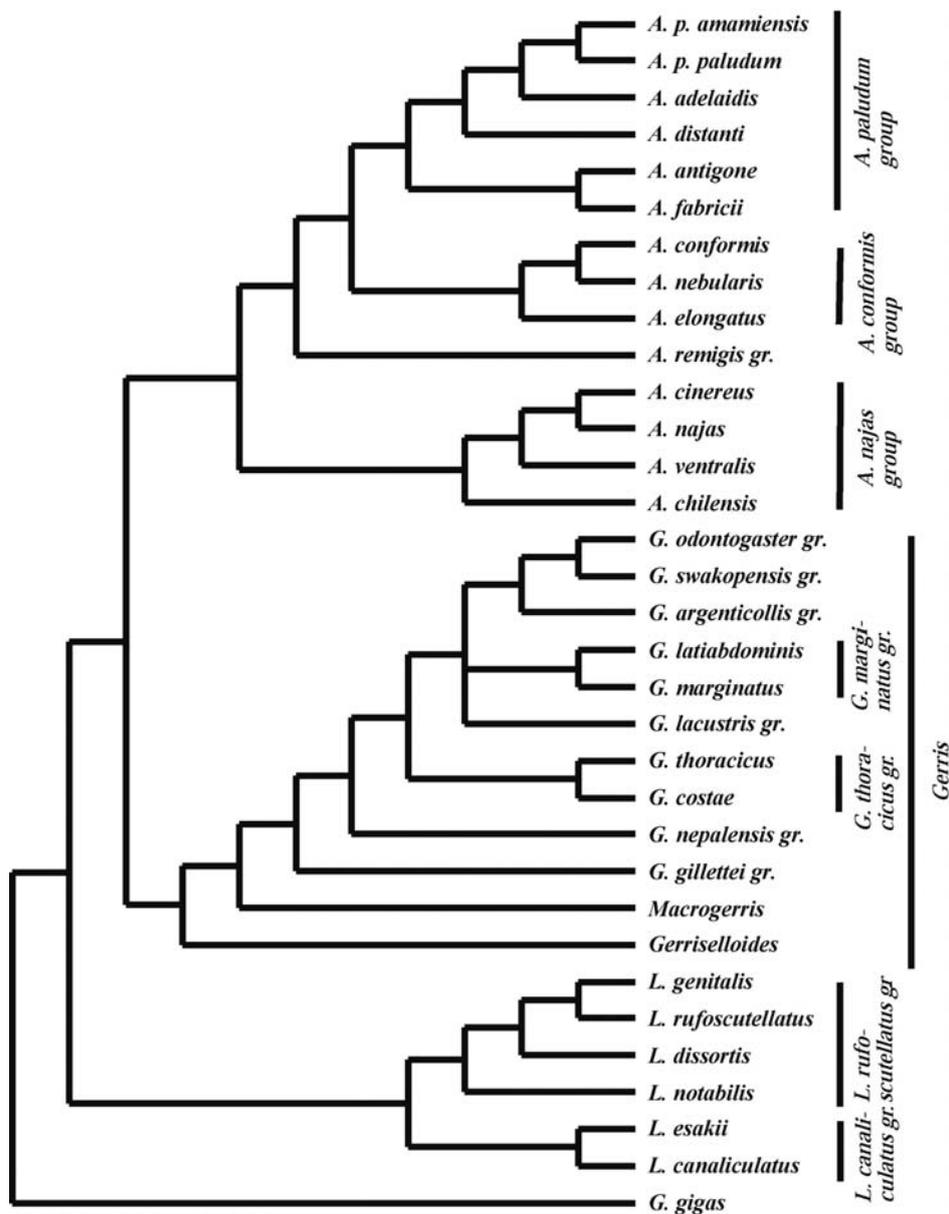


Fig. 1: Phylogenetic relationships among species, species and subgenera of *Limnporus*, *Aquarius* and *Gerris* based on ANDERSEN (1990, 1993b) and ANDERSEN & SPENCE (1992).

time frame for the evolution of such traits. Such hypotheses of course rely heavily on correct observations and a robust phylogenetic reconstruction, and most studies therefore address a clade comprising the three principal northern temperate genera, *Limnporus* STÅL 1868, *Aquarius* SCHELLENBERG 1800 and *Gerris* FABRICIUS 1794. By comparing extant and extinct taxa, Andersen found that members of the three genera exhibited a strong structural stasis in some characters, but abundant convergences in others, probably due to evolutionary and ecological constraints associated with the life on water surfaces, and realized that morphological characters alone would not suffice for providing robust phylogenetic hy-

potheses. As a student of Andersen, I was given the opportunity to participate in studies of the molecular phylogeny of water striders, and after working with the subject for a decade, I find it appropriate to synthesize the results and outline some of the problems that still prevail about the systematics, ecology, behavior, and distribution of this fascinating group of insects.

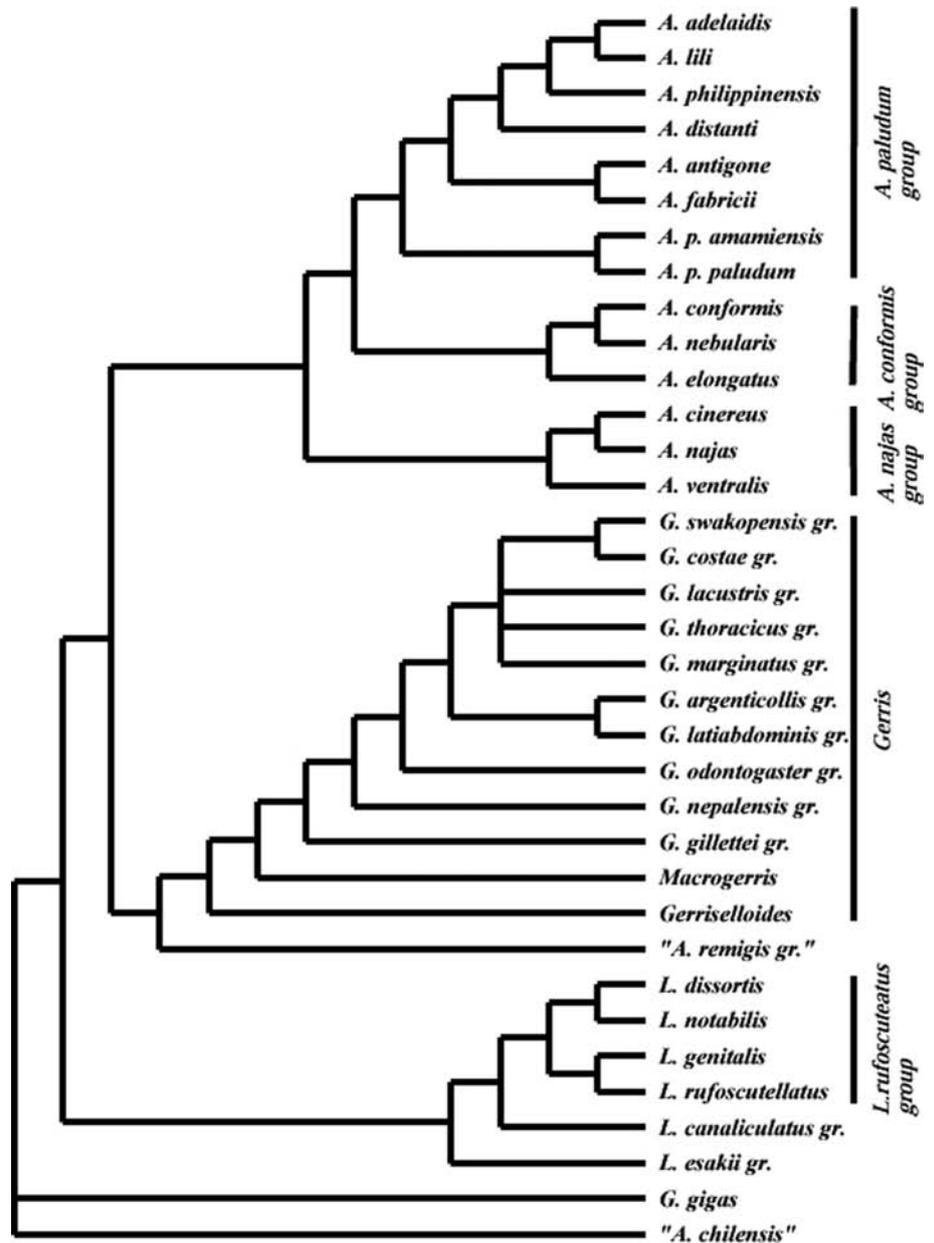
Phylogeny

Until quite recently, *Limnporus*, *Aquarius* and *Gerris* were treated as subgenera of *Gerris*, but in a series of papers, ANDERSEN (1975, 1990, 1993b) and ANDERSEN & SPENCE (1992) re-established their generic ranks, and organized their members into presumed monophyletic subgenera and species groups. In his most recent checklist of gerrine water striders, ANDERSEN (1995) listed six species of *Limnporus*, 15 species and two subspecies of *Aquarius*, and three subgenera, 42 species and five subspecies of *Gerris*. Today, four new species can be added to this assemblage: *Aquarius lili* POLHEMUS & POLHEMUS 1994, *A. remigoides* GALLANT & FAIRBAIRN 1996, *A. philippinensis* ZETTEL & RUIZ 2003, and *Gerris kobaishanus* LINNAVUORI 1998, and there are furthermore indications of several yet undescribed species (ANDERSEN 1990, 1993b; ZIMMERMANN & SCHOLL 1993; MURAJI 2001; DAMGAARD 2005). Andersen never published a global phylogenetic analysis for the three genera, but his most exhaustive analysis (ANDERSEN 1993b), includes 63 morphological characters scored for two species of *Limnporus*, seven species of *Aquarius*, and 19 species of *Gerris*. His preferred topology from this analysis (ANDERSEN 1993b: Fig. 23), however, was a manual correction of a strict consensus of two equally parsimonious trees obtained by a successive approximation weighting of 102 trees. Later he manually expanded and corrected this phylogenetic reconstruction (e.g. ANDERSEN 1994: Fig. 2, 1997: Fig. 4) for inferring evolutionary trends, but the cladograms were never based on computer-based parsimony analyses. In order to summarize Andersen's hypotheses of the phylogenetic relationships within and between the three genera, the results from ANDERSEN (1990) and SPENCE

& ANDERSEN (1992) are therefore inferred onto his preferred tree (Fig. 1).

The phylogenetic hypotheses outlined above have been tested repeatedly in simultaneous analyses of genetic and morphological characters (SPERLING et al. 1997; DAMGAARD et al. 2000; DAMGAARD & SPERLING 2001; DAMGAARD & COGNATO 2003), and recently DAMGAARD & COGNATO (2005) summarized these studies in a study of 53 species and five subspecies comprising all species of *Limnopus* and *Aquarius* and a dense taxon sampling of *Gerris* including representatives of all subgenera and species groups. The character matrix comprised 66 morphological characters and DNA sequence data from the mitochondrial protein coding genes for *cytochrome c oxidase subunit I+II* (COI+II 1349 characters); the ribosomal gene encoding the *large mitochondrial ribosomal subunit* (16S rRNA 426 characters), and the nuclear protein coding gene for *elongation factor 1 alpha* (EF-1 α 515 characters), adding to a total of 2356 characters. A parsimony analysis of this data set gave 8 equally parsimonious trees, and Fig. 2 shows a reduced version of the strict consensus tree (DAMGAARD & COGNATO 2005: Fig. 2).

By comparison, the tree based on earlier, morphological studies (Fig. 1) and the combined analysis tree (Fig. 2) give somewhat different conclusions about the phylogenetic relationships within and among the three genera. The most notable differences are (1) *Aquarius* is monophyletic in Fig. 1 but polyphyletic in Fig. 2 because the *A. remigis* group is sister group to *Gerris*, and *A. chilensis* (BERG 1881) is placed unresolved at the basis of the tree; (2) the *Limnopus canaliculatus*-group from Fig. 1 is paraphyletic in Fig. 2 because *L. canaliculatus* (SAY 1832) is sister species to the *L. rufoscutellatus*-group and not to *L. esakii* (MIYAMOTO 1958); and (3) within *Gerris*, both the "*G. marginatus*-" and "*G. thoracicus*-" groups from Fig. 1 are polyphyletic in Fig. 2, and the *G. odontogaster*-group is nested more basal within *Gerris* s.str.

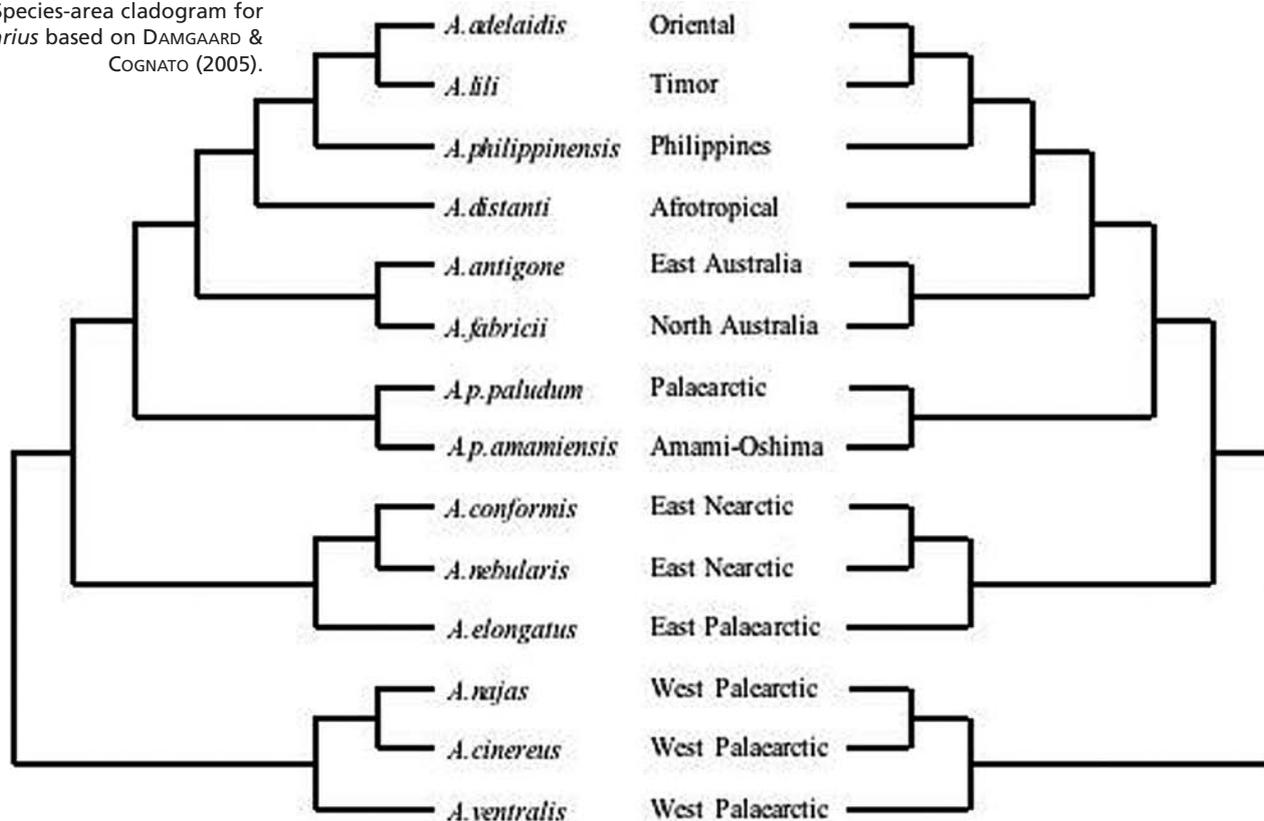


Morphological versus molecular characters

Despite the more exhaustive taxon sampling in DAMGAARD & COGNATO (2005) compared to earlier studies, all additional species are nested within species groups already represented, and therefore probably do not contribute much to the overall phylogenetic resolution. What matter instead is the addition of molecular characters comprising almost 95 % of the total Partition Branch Support (PBS) (BAKER & DESALLE 1997), which summarizes nodal support from each data partition on the simultaneous analysis tree. Because the morphological

Fig. 2: Phylogenetic relationships among species, species and subgenera of *Limnopus*, *Aquarius* and *Gerris* based on DAMGAARD & COGNATO (2005).

Fig. 3: Species-area cladogram for *Aquarius* based on DAMGAARD & COGNATO (2005).



data comprise less than 3 % of the total number of characters, it could look as if the morphological characters are simply “swamped” by the molecular data, but when morphological characters were optimized upon the combined analysis tree *a posteriori* (DAMGAARD & COGNATO 2005: Fig. 3) it became evident that many synapomorphies suggested by earlier studies were still diagnostic. An inspection of the homoplastic characters revealed that several of these were poorly defined, or even incorrectly scored. As examples are characters in the shape of the male ventral segments 7 and 8 in *Aquarius* which ANDERSEN (1990) used for assigning *A. paludum* (FABRICIUS 1794) and *A. adelaidis* (DOHRN 1860) as sister species, and *A. distanti* (HORVÁTH 1899) as sister species to this clade but, as pointed out by DAMGAARD & ZETTEL (2003), these characters are difficult to score and probably functionally related. The color of the pronotal disc is another poorly defined character, which ANDERSEN (1993b) gave only two states, but which DAMGAARD & COGNATO (2005) found should either be ignored or broken up into several new states.

With the new phylogenetic relationships several clades are left without convincing morphological synapomorphies. This is most problematic for clades that have been given formal names, such as the genus *Aquarius* and the subgenus *Macrogerris* (ANDERSEN 1993a) even though both clades may be diagnosed on basis of unique combinations of homoplasious characters. ANDERSEN (1993b) used the relative length of the antennal segments as his character 3 and gave it two states: (1) antennal segments 2+3 longer than antennal segment 1 and (2) shorter than antennal segment 1. He used the relatively long segment 1 to diagnose *Aquarius*, even though MATSUDA (1960) stated that in *A. remigis* (SAY 1832) and related species, this segment was subequal to the remaining antennal segments. By using the current, incorrect character states, *Aquarius* is left without synapomorphies but, by giving a third character state for the *A. remigis*-group (antennal segments 2+3 subequal to 1), DAMGAARD & COGNATO (2005) gave new diagnostic states for both *Aquarius* and for the *A. remigis*-group. Whether diagnostic morphological characters can be

found for the remaining clades still need to be investigated. Unique nucleotide substitutions of a <1kb strand of COI, a.k.a. "DNA-barcodes", have been used successfully to diagnose clades in other groups of organisms (e.g. HEBERT et al. 2003). Also DAMGAARD & ZETTEL (2003) found that species of the *A. paludum*-group were monophyletic in their mitochondrial DNA, and that they each could be diagnosed by unique substitutions. However, in the much denser population sampling of the two sibling species *Aquarius najas* (DEGEER 1773) and *A. cinereus* (PUTON 1869), DAMGAARD (2005) showed that these two species were not reciprocally monophyletic in their mitochondrial DNA (Fig. 4) Whether this is due to cryptic species, hybridization, incomplete lineage sorting, or something else, still needs to be worked out, but it calls for caution when trying to identify species via a tree-building algorithm, especially when based on a single character system.

The conclusion is that molecular characters have provided abundant information, thus leading to new and better supported phylogenetic hypotheses of water strider relationships, and that simultaneous analyses of molecular and morphological characters have offered far better phylogenetic estimates than analyses of individual data sets. However, there are major problems also in using molecular data sets. First of all it is very difficult to obtain DNA sequences from museum material that is more than a few years old, unless it has been preserved in strong (96-100 %) ethanol. This is even more so for single copy nuclear genes, such as EF-1 α , which only exists in two copies per cell, compared to mitochondrial and/or ribosomal genes, which exists in hundreds or perhaps thousands of copies per cell. Although museum material of many species were available due to the earlier studies, it has taken long time and involved numerous collaborators all over the World to get the taxon sampling used in DAMGAARD & COGNATO (2005), and additional work is needed in order to obtain fresh material of the *Geris* species that have not yet been sequenced. Even though molecular systematics is a highly promising discipline, it is still in a premature phase in terms of output, quality, and homologizing of the data, and in inter-

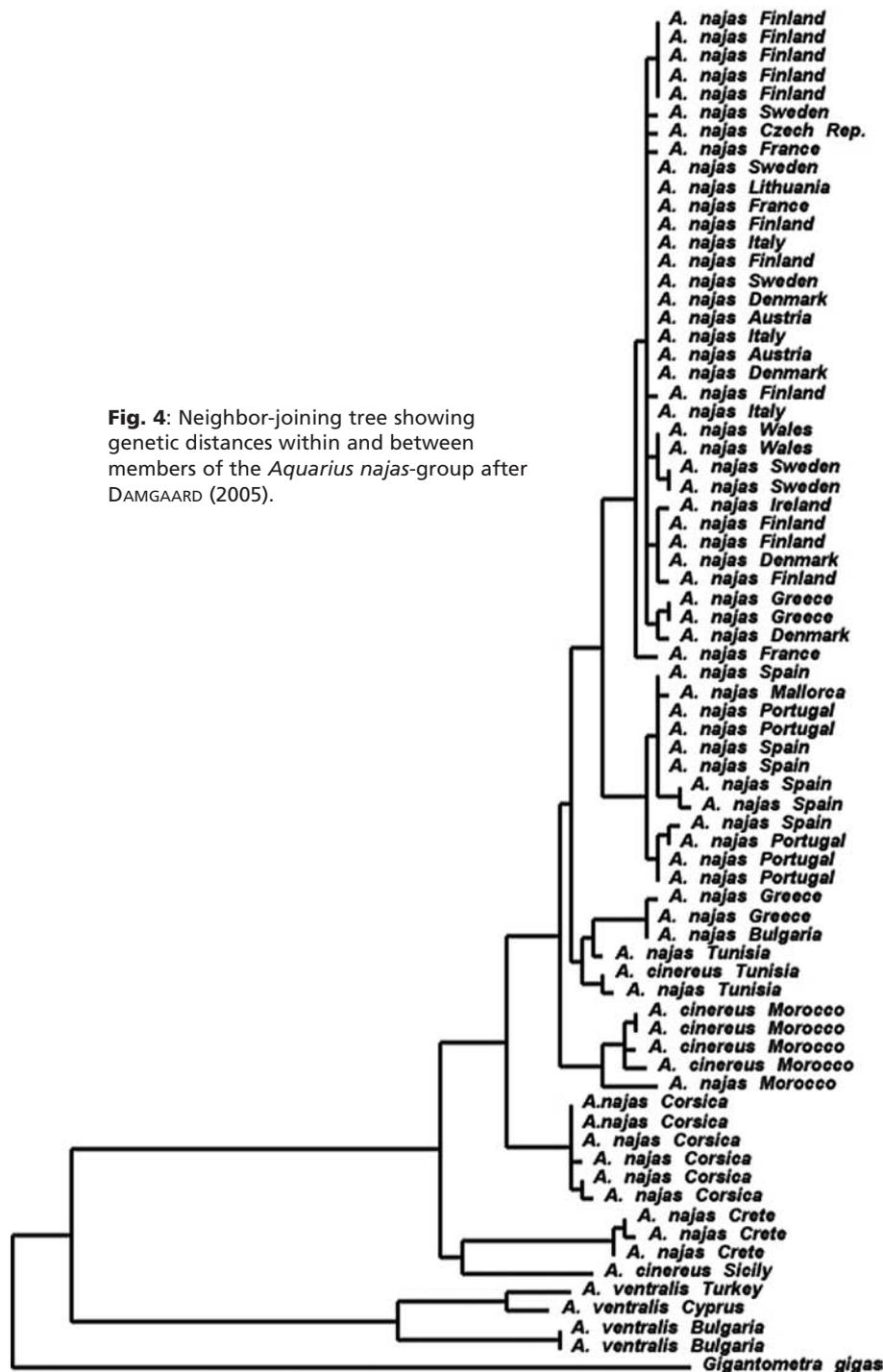


Fig. 4: Neighbor-joining tree showing genetic distances within and between members of the *Aquarius najas*-group after DAMGAARD (2005).

preting the results. It is therefore important to keep a close collaboration with foremost the traditional morphologically based taxonomy, in order to evaluate results from molecular studies.

Taxonomic consequences

Based on the results from DAMGAARD & COGNATO (2005) *Aquarius* obviously needs to be redescribed and restricted to the *A. paludum*- and *A. conformis*-groups and western Palaearctic members of the *A. najas*-group. In such a revision it will be important to determine if *A. nebularis* (DRAKE & HOTTES 1925) should be synonymized with *A. conformis* (UHLER 1878), since the two species are very much alike both in terms of morphology and molecules (ANDERSEN 1990; DAMGAARD et al. 2000), and whether *A. najas* and *A. cinereus* have unrecognized sibling species in the Mediterranean as indicated by ZIMMERMANN & SCHOLL (1993) and DAMGAARD (2005). The *A. remigis* group probably needs to be erected to a new generic level and diagnosed on basis of the unique male genitalia and in the relative length of antennal segments as compared to *Aquarius* and *Gerris*. Also the four species currently assigned to this clade need to be revised because their taxonomy and exact distributions are poorly known (ANDERSEN 1990; GALLANT & FAIRBAIRN 1996; DAMGAARD unpublished). Finally, the enigmatic “*A. chilensis*“ shows a mixture of characters that on one side points to the *A. najas*-group, and on the other side to more basal members of Gerrinae as originally discussed by ANDERSEN (1990). *Aquarius chilensis* probably needs to be erected to a new, monotypic genus, but is left unresolved until an investigation of gerrine water striders have been carried out following the guidelines laid out by MURAJI & TACHIKAWA (2000) and DAMGAARD et al. (2005) for the superfamily Gerroidea.

Historical biogeography

Even though *Limnoporus*, *Aquarius* and *Gerris* are the dominant water strider genera in northern temperate regions, only *Limnoporus* is strictly Holarctic, while the *Gerris swakopensis*-group is found throughout the Afrotropical region (incl. Madagascar), and *Aquarius* was – until the possible exclusion of *A. chilensis* – considered the only cosmopolitan genus of water striders (ANDERSEN 1982, 1990, 1993b, 1995, DAMGAARD & COGNATO 2005). When comparing the distribution of subgenera, species groups and

species, it is evident that the majority of taxa is confined to the Palaearctic Region, and that only a few species groups are restricted to the Nearctic Region, or are shared between the Palaearctic and Nearctic Regions. However, the relatively species poor genus *Aquarius* deserves special attention because it – according to the new phylogenetic relationships – is represented by geographically highly disjunct species in the Palaearctic, eastern Nearctic, Afrotropical, Oriental, and Australian regions, including several island endemics, such as *A. lili* from Timor, *A. philippinensis* from the Philippines, and *A. paludum amamiensis* from Amami-Oshima and the Ryukyu Islands south of Japan (Fig. 3). Only a single fossil, *A. lunapolaensis* (LIN 1981) from Miocene Tibet, has been assigned to *Aquarius* with any certainty, and was even placed in the *A. najas*-group on basis of striking similarities (ANDERSEN 1998). If this is true then the present distribution of the *A. najas* group in the western Palaearctic region is likely to be relictual. The distribution of the three extant species with *A. cinereus* in the western Mediterranean, *A. ventralis* (FIEBER 1861) in the eastern Mediterranean, and *A. najas* throughout the western Palaearctic Region (ANDERSEN 1990: Fig. 73) could indicate speciation in situ, perhaps following isolation in different refugia during the Pleistocene glaciations, but this view is contradicted by the deep molecular divergence between *A. ventralis* and *A. najas* + *A. cinereus*, which suggests a basal divergence well before the onset of the glaciations (DAMGAARD 2005) (Fig. 4). The disjunct geographical relationship between the eastern Palaearctic *A. elongatus* (UHLER 1896) and the eastern Nearctic *A. conformis*/*A. nebularis* likewise points to a characteristic pattern following habitat fragmentation and isolation of populations following orogeny and climatic changes on the northern Hemisphere during the late Miocene (DAMGAARD & ZETTEL 2003). However, such palaeoclimatic events probably can not solely be used to explain the distribution of the geographically disjunct species in the *A. paludum*-group, since sister species relationships here often are found among geographically highly disjunct species. POLHEMUS & POLHEMUS (1994) were the first to suggest

much older divergences since the newly described Timorese *A. lili* was not sister species to the geographically proximate *A. fabricii* ANDERSEN 1990 from northern Australia, but instead to the widespread Oriental *A. adelaidis*, even though no geographically intermediate populations are known from the region. DAMGAARD & ZETTEL (2003) and DAMGAARD & COGNATO (2005) confirmed the close relationship between *A. lili*, *A. adelaidis* and the newly described *A. philippinensis* from ancient crater lakes in the Philippines (ZETTEL & RUIZ 2003), and found that the Afrotropical *A. distanti* was sister species to this clade instead of the trans-Palaeartic *A. paludum* suggested by ANDERSEN (1990). The relatively small genetic divergences between *A. lili*, *A. philippinensis* and *A. adelaidis* seem to contradict an ancient diversification of this clade, while the sister group relationship with *A. distanti* support an ancient vicariance event, probably following the break-up sequence of the southern super-continent Gondwana.

Ecological phylogenetics

ANDERSEN (1993b) hypothesized that the ancestor of the three genera was a wing dimorphic species, which lived in relatively stable, lentic water bodies with a high degree of seasonal predictability, and that from this ancestral type of ecology, evolution went in two directions: (1) species of some lineages adapted themselves to lotic habitats, and (2) species of other lineages became adapted to increasingly unstable lentic habitats (temporary ponds, water-filled ditches, etc.). Examples of the first category were the primarily wingless species belonging to the *Aquarius najas* and *A. remigis* groups, and examples of the second category were species belonging to the *Limnopus rufoscutellatus*-, *Gerris thoracicus*-, *G. lacustris*-, *G. marginatus*-, and *G. odontogaster*-groups. These species are either permanently or seasonally wing-dimorphic or monomorphic long-winged, and the most versatile species were the larger *Limnopus* species and *Gerris thoracicus* SCHUMMEL 1832 Andersen further inferred, that there were two kinds of short-winged gerrids, probably as the result of different mechanisms of morph determination (genetic versus environmental). The

loss of flight ability and maintenance of wing polymorphism is undoubtedly a consequence of adaptation through natural selection as first proposed by DARWIN (1872), and is probably somehow linked to the “flight-oogenesis“ syndrome (JOHNSON 1969) whereby the female divert energy normally used in wing and wing muscle development to the production of more eggs, which would increase the female’s fitness more than the advantages associated with the ability to fly. Even though a growing amount of studies is becoming available, our knowledge of the frequency and determination of wing morphs in many species is still highly insufficient. VEPSÄLÄINEN (1974) suggested that *A. najas* probably has genetically determined wing-dimorphism, and long-winged specimens are certainly rare in most northern areas, but may be more common in southern latitudes. However, AHLROTH et al. (1999) were able to induce a high frequency of the long winged morph from several apparently monomorphic wingless Finnish populations by rearing nymphs under high temperature and short day-length, thereby simulating more southern latitudes. It was further noticed that populations from southern Finland gave a higher frequency of the long-winged morph than northern populations, but also that no long-winged specimens survived during winter. Another particularly well-studied species is the likewise eastern Palaeartic *Gerris thoracicus*, which has two long-winged adult morphs differing in their ability to fly during the reproductive period: “non-flyers“ (with flight muscles histolyzed) that live in the most permanent habitats and “flyers“ (with functional flight muscles) that are able to colonize new and temporary habitats during the breeding season (KAITALA 1988, 1991).

This altogether indicates that the interplay between genes, development of flight muscles and wings, and environment is considerably more complicated than previously believed, and calls for more attention before any general evolutionary trends can be revealed.

In water striders, the most common mating system is “scramble competition polygyny (SPENCE & ANDERSEN 1994; “Type I matings“ of ARNQVIST 1997) where the

male simply lunge at any female within his reach, grasps her thorax with his fore legs, and attempts to insert his phallus into her genital opening. After the copulation proper has terminated, males usually exhibit post-copulatory guarding, staying in close contact with the female. Members of the *Aquarius remigis*-group are unique among northern temperate water striders in that they stay in genital contact with the female after the actual mating has taken place. In other species the male simply rides the females back after copulation, and this post-copulatory guarding may last from several hours to days in *Aquarius najas* (ARNQVIST 1997). Because superfluous mating is costly to females (e.g. in terms of increased energetic expenditure, reduced mobility, and increased predation risk), females usually respond to males by vigorous struggling and often succeed in dislodging him. Such a sexually antagonistic co-evolution has resulted in the evolution of morphological adaptations in males that increase their ability to grasp females efficiently and distinct morphological adaptations in females that increase the efficiency with which females dislodge males during these struggles (ARNQVIST & ROWE 2002a, b; ROWE & ARNQVIST 2002).

Even though the phylogeny of *Limnoporus*, *Aquarius* and *Gerris* – and therefore the interpretation of their evolutionary trends – has changed considerably with the inclusion of new molecular data, Andersen and others certainly deserves credits for synthesizing a broad range of individual observations into testable hypotheses. Whether these hypotheses still hold or not will, however, have to await both more studies of ecology, ontogeny, adaptation and selection, as well as a more robust resolution of gerrine water strider relationships as mentioned above.

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Zusammenfassung

Die Arbeit gibt einen Überblick über den aktuellen Kenntnisstand der Systematik, historischen Biogeographie und ökologischen Phylogenetik der drei nordtemperaten Wasserläufergattungen *Limnoporus* STÅL 1868, *Aquarius* SCHELLENBERG 1800 und *Gerris* FABRICIUS 1794. In der Diskussion wird ein aktuell publizierter kombinierter Stammbaum aus vier genetischen Markern und einem morphologischen Datenset mit älteren, kladistischen Stammbäumen morphologischer Merkmale verglichen.

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