

Distribution, phenology, and conservation status of the larger water striders in Denmark

(Heteroptera: Gerridae)

Jakob Damgaard & Nils Møller Andersen

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This paper presents and discuss the distribution, phenology, and conservational status in Denmark of the three larger water striders *Limnoporus rufoscutellatus*, *Aquarius najas*, and *A. paludum*. *L. rufoscutellatus* is widespread but not very abundant. It often inhabits small water bodies which rarely are surveyed. Populations are univoltine and adults monomorphic long-winged. The species takes readily to flight and seems able to disperse to new and temporary habitats in the early spring and to suitable breeding sites later in the season. The rapid decline in the number of smaller water bodies in many parts of Denmark may be critical. *Aquarius najas* is present in many parts of the great river systems of central Jutland and abundant in several localities. It seems to have disappeared from several marginal localities (especially in northeastern and southern Jutland, Funen, and possibly also in Zealand). Populations are univoltine and monomorphic wingless (long-winged individuals very rare). The limited dispersal capacity of this species agrees well with its preference for the most stable type of habitats, but also make it vulnerable in light of current deterioration of streams and rivers in Denmark. *Aquarius paludum* is extremely local in Denmark, only occurring in two (possibly three) forest ponds in northeastern Zealand. Populations are partially bivoltine in Denmark, overwintering adults being long-winged and adults of the summer generation chiefly short-winged. In spite of the availability of suitable habitats, the species disappeared from one, possibly two of its former localities and its survival in Denmark is possibly in danger. The present study exemplifies the importance of considering differences in habitat use, distribution, and phenology between related species, and to take all these aspects into account when discussing the conservation status.

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Introduction

Water striders or pond skaters (Heteroptera, Gerridae) are familiar inhabitants of the surface film of different types of freshwater bodies in Denmark. Until recently, northern European species were classified in a single genus, *Gerris* Fabricius, with the subgenera *Aquarius* Schellenberg, *Limnoporus* Stål, and *Gerris* s.str. In his comprehensive survey of Danish water bugs, Leth (1943, 1945, 1948) treated these taxa as genera,

using Stål's (1868) names *Hygrotrechus*, *Limnoporus*, and *Limnotrechus*, respectively. In a series of taxonomic revisions, Andersen (1975, 1990, 1993) and Andersen & Spence (1992) reinstated *Aquarius*, *Limnoporus*, and *Gerris* as genera. The subgenus *Gerriselloides* Hungerford & Matsuda was used for a group of *Gerris* species which include *G. lateralis* Schummel (= *G. asper* (Fieber) of Leth, 1943). Kanyukova (1982) broadened the scope of this subgenus to include *G. sphagnetorum* Gaunitz (described from Swe-

den and recorded from Finland, Poland, and Russia, but not yet from Denmark), but this was disputed by Andersen (1993).

In this paper, we focus on the three larger water striders belonging to the genera *Limnoporus* and *Aquarius*. Three species occur in Denmark: *Limnoporus rufoscutellatus* (Latreille) (Fig. 1), *Aquarius najas* (De Geer) (Figs. 3-4), and *Aquarius paludum* (Fabricius) (Fig. 2). The objects of this survey is to compile original observations, data from museum collections, as well as literature data, on the distribution, phenology, and ecology of these species in order to examine their past and current status in Denmark. Particular attention is paid to potential threats against the survival of these conspicuous insects in our fauna. The paper is part of a survey of the Danish fauna of aquatic and semiaquatic bugs carried out by one of the authors (JD). The publication of distributional data for the remaining species is in preparation.

Material and methods

In compiling this survey we have used the extensive material of aquatic bugs deposited in Naturhistorisk Museum, Århus (primarily collected by C.F. Jensen), and the Zoological Museum, University of Copenhagen (especially material collected by K.O. Leth, E.W. Kaiser, and N.M. Andersen). In order to complement label data, we have made use of the diaries and collection files of collectors, especially C.F. Jensen, E.W. Kaiser, and K.O. Leth, the principal investigators of the fauna of aquatic bugs in Denmark. Whenever possible, we have tried to confirm older records (i.e., before 1950) with more recent ones, but this has not always been possible for logistic reasons. Finally, we have used personal information provided by a number of persons acknowledged at the end of this paper.

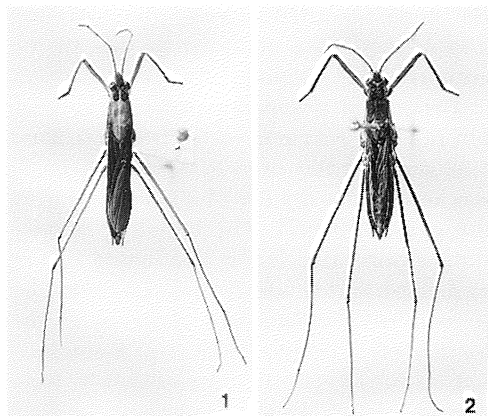
In the text, we have used the following abbreviations: For repositories of material: Natural History Museum, Århus (NM), Zoological Museum, University of Copenhagen (ZMUC). For the faunistic districts

of Denmark (see map, Fig. 11): B, Bornholm; F, Funen; LFM, Lolland, Falster, and Møen; NEJ, northeastern Jutland; NWJ, northwestern Jutland; NEZ, northeastern Zealand; NWZ, northwestern Zealand; SJ, southern Jutland; SZ, southern Zealand; WJ, western Jutland. For wing morphs: apt., apterous; brach., brachypterous; macr., macropterous.

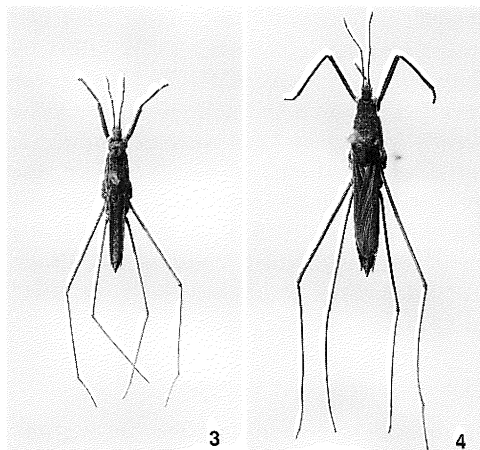
Identification

Adults of the three species dealt with in this publication can be separated from other northern European water striders and from each other by the characters given in the key below. Immature stages (nymphs) can be identified using the keys provided by Vepsäläinen & Krajewski (1986) and Zimmermann (1987).

1. Lateral, posterior corners of abdominal segment 7 produced into connexival spines. Body length more than 12 mm..... 2
- Lateral, posterior corners of abdominal segment 7 at most forming triangular, pointed processes, but not spines. Body length usually less than 11.5 mm.....
..... *Gerris* Fabricius
2. Antenna as long as or longer than half body length; segments 2-3 together longer than segment 1. Pronotum rufous with two black spots anteriorly. Fore wings brownish. Connexiva terminating in long spines, surpassing hind margin of eighth abdominal segment (♂, Fig. 5) or reaching abdominal end (♀, Fig. 6). Length 13-17 mm. Always macropterous (Fig. 1)
..... *Limnoporus rufoscutellatus* (Latreille)
- Antenna shorter than half body length; segments 2-3 together shorter than segment 1. Pronotum entirely dark brown or black with pale median stripe in anterior part. Fore wing (when present) dark brownish (*Aquarius* Schellenberg) 3
3. Connexival spines reaching (♀, Fig. 7) or distinctly surpassing abdominal end (♂, Fig. 8). Pronotum laterally with yellow stripes. Macropterous or brachypterous (wings reaching fifth abdominal tergum). Length 13-16 mm (Fig. 2)
..... *Aquarius paludum* (Fabricius)



Figs. 1-2. 1, *Limnoporus rufoscutellatus*, macropterous ♀ (WJ, Fly, S of Skive, 30.VII.1961, N.M. Andersen); 2, *Aquarius paludum*, brachypterous ♀ (NEZ, Løgsø, Rude Skov, 28.VII.1941, K.O. Leth). Magnification 3.0x (Photos: Geert Brovad, Zoological Museum).



Figs. 3-4. 3, *Aquarius najas*, apterous ♂ (WJ, Løven Å at Ørre, 2.VI.1940, K.O. Leth); 4, *A. najas*, macropterous ♀ (WJ, Sønder Å, Tarm Kær, 25.VIII.1948, Carlo F. Jensen). Magnification 3.0x (Photos: Geert Brovad, Zoological Museum).

- Connexival spines shorter, not reaching abdominal end (Figs. 9-10). Pronotum laterally dark, sometimes with a yellowish dot (the rare macropterous form has a narrow lateral yellow line on pronotum). Usually apterous. Length 12-17 mm (Figs. 3-4) *Aquarius najas* (De Geer)

Limnoporus rufoscutellatus (Latreille, 1807)

Distribution in Denmark

The Danish records are mapped in Fig. 11. The species is so widespread in Denmark that it has not been found necessary to provide a separate list of all localities. The concentration of records from northeastern Zealand, central Jutland, and Bornholm is most certainly due to the more intensive collecting efforts in these areas.

Most Danish records of *L. rufoscutellatus* are of single or at most a couple of individuals taken at the same time in the same locality. The following records are based on larger samples: **NWJ:** Hykjær in Hanstedreservatet (28.VII.1954, 2♂♂ 3♀♀, K.O. Leth, ZMUC); Tved Klitplantage (17.IV.1964,

2♂♂ 3♀♀, N. Kolstrup, ZMUC). **EJ:** Horsens (16.IV.1869, 2♂♂ 2♀♀, O.G. Jensen, ZMUC). **WJ:** Bratbjerg NE of Ringkøbing (30.VII.1942, 2♂♂ 2♀♀, K.O. Leth, ZMUC); Ringkøbing, road to Søndervig (8.VIII.1947, 10♂♂ 6♀♀, K.O. Leth, ZMUC); **F:** Vindinge Å at Vindinge (4.VIII.1941, 4♂♂ 3♀♀, K.O. Leth, ZMUC). **NEZ:** Tikøb Sogn 500 m NE of Jonstrup (14.VII.1947, 6♂♂ 4♀♀, K.O. Leth, ZMUC). **LFM:** Engestofte v. Maribo, small stream or ditch (27.IX.1961, 5♂♂ 3♀♀, B.V. Pedersen, ZMUC). **B:** Blykobbe at Skovly, 2♂♂ 2♀♀, 26.VII.1936, K.O. Leth, ZMUC).

L. rufoscutellatus is known to readily take flight when disturbed and may try to escape by flying from the collecting net (Vepsäläinen, 1974b; NMA, unpublished). In this light a few exceptional findings should be mentioned. An individual was taken at Hg-light on the roof of the power plant Svanemølleværket near Copenhagen, 50-100 m above sea level, 22-23.VIII.1965, N.L. Wolff (ZMUC). One of the authors (JD) found about 25 adults and a few nymphs in small rock pools and water reservoirs on the isolated islands Ertholmene (about 20

km NE of Bornholm) in August 1994 (1♂ and 1 nymph collected, 5.VIII. 1994, J. Damgaard leg., coll. ZMUC). The experienced collector K.O. Leth visited the same islands in August 1945 without finding *L. rufoscutellatus* (Leth, 1945). Therefore, the species must have colonized Ertholmene sometimes after 1945, most likely by flying there from the North coast of Bornholm (recorded from Randkløve by Leth, 1945 and Johnsen, 1946).

Distribution in NW Europe

L. rufoscutellatus is distributed throughout the subarctic region of Eurasia and north-western North America (Andersen & Spence, 1992; Andersen, 1995), and is widely distributed in Northern Europe (Fig. 11) including Finland (Vepsäläinen, 1973), Sweden (Coulianos & Ossianilsson, 1976), and southern Norway (Jastrey, 1981). It is characterized as widely distributed but scarce in the Netherlands (Nieser & Wasscher, 1986). Because of its scarcity in the British Isles, it has been suggested (Leston, 1956; Southwood & Leston, 1959) that *L. rufoscutellatus* regularly fly in from the continent and doesn't breed there. Murray (1986), however, found breeding populations in Ireland.

Habitats

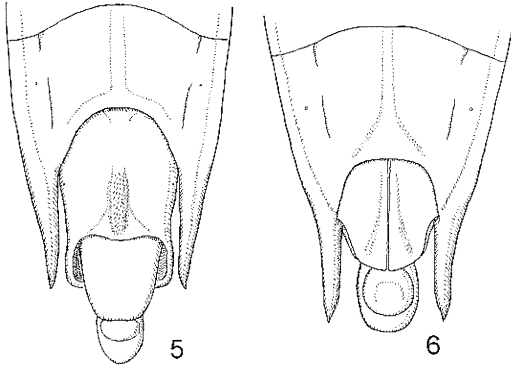
L. rufoscutellatus is found in various types of stagnant waters (including temporary habitats), from fresh to slightly brackish, as well as on quietly flowing streams. Johnsen (1946) observed an adult specimen at Randkløve, Bornholm, in a protected creek of the Baltic Sea (salinity 6.2 per mille). According to Vepsäläinen (1973) nymphal (i.e., breeding) habitats are more restricted, predominantly semipermanent or permanent ponds and lake shores with fairly strong insolation, dense shore vegetation and moderate cover of floating vegetation. The diversity in habitat use is seemingly associated with the strong dispersal ability of the species. It has the habit of showing up in well-investigated places where it has

not been recorded before. The following unpublished data obtained by one of the authors (NMA) illustrate this point.

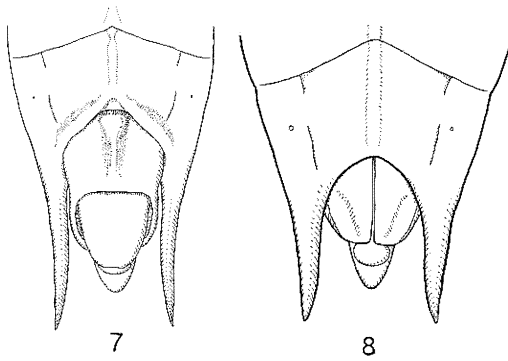
The gerrid populations of a small dug-out pond in Nærum, northeastern Zealand (the study locality used by Andersen, 1973) was kept under regular observations during the period 1969-71. The breeding population of pond skaters was dominated by *Gerris lacustris* and *G. odontogaster*. The first *Limnopus rufoscutellatus* was observed in the locality on 5 August 1969, and a single ♂ was captured (flying spontaneously from the net) on 30 August, same year. In 1970 the following observations were made: 7.V.1970: 1 adult; 27.VI.1970: 1 nymph (fifth instar); 1.IX.1970: 6♂♂ 4♀♀ (several flying spontaneously), most infested by juvenile stages of water mites. Since the resident gerrid population were free of water mites, this may indicate that at least some of the *L. rufoscutellatus* found in the pond were immigrants. Of these adults, 6♂♂ 3♀♀ were marked with a nail-varnish dot on their pronotum. On subsequent dates, marked individuals were recaptured together with unmarked individuals (3.IX.1970: 3♂1♀ marked, 1♂ unmarked; 7.IX.1970: 1♀ marked, 1 unmarked adult; 24.IX.1970: 1♀ marked). *L. rufoscutellatus* was also observed on the locality in early May 1971, before the observations were terminated.

Life cycle and phenology

Adult individuals have been collected throughout the season, from late March to late September, and egg-filled females (with distended abdomen) are recorded from the period May-August. Nymphs are recorded from June and July. In southern Finland, Vepsäläinen (1973, 1974b) found adults from mid May to mid October, egg-filled females from late May onwards, and nymphs from mid June to mid September. On one occasion, second to fifth instar nymphs were still found on 4 October. Thus, in Denmark as well as Finland *L. rufoscutellatus* overwinter in the adult stage and reproduce from late May onwards.



Limnoporus rufoscutellatus

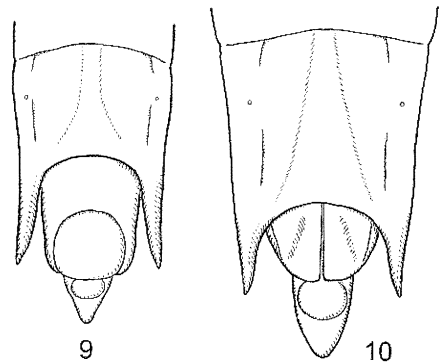


Aquarius paludum

Figs. 5-6. *Limnoporus rufoscutellatus*, abdominal end in ventral view. 5, macropterous ♂; 6, macropterous ♀ (after Andersen & Spence, 1992).

Figs. 7-8. *Aquarius paludum*, abdominal end in ventral view. 7, macropterous ♂; 8, macropterous ♀.

Figs. 9-10. *Aquarius najas*, abdominal end in ventral view. 9, apterous ♂; 10, apterous ♀.



Aquarius najas

L. rufoscutellatus exhibit male territoriality in the breeding season (Vepsäläinen & Nummelin, 1985a). Eggs are laid side-by-side in regular rows on the lower surface of floating leaves of *Potamogeton*, *Nuphar*, and *Nymphaea*. The egg-band illustrated by Wesenberg-Lund (1943: fig. 95) most probably belong to this species. Eggs of *Limnoporus* spp. are known to be heavily infested by a wasp parasitoid, *Tiphodytes Gerriphagus* Marchal (Hymenoptera: Scelionidae) (Spence, 1986; Nummelin et al., 1988). Henriksen (1918-19) recorded this egg parasitoid from eggs of "Gerris", but his description of the way these eggs were deposited indicates that he examined *Limnoporus*-eggs. All eggs in an egg-batch collected in NEZ: Fantasidam, Grib Skov, 16.VIII.1967, N.M. Andersen (ZMUC) were infested by *T. Gerriphagus* (P.N. Buhl det.).

L. rufoscutellatus has only one generation per year from Finland to Austria although there are some indications that a few ♀♀ may oviposit the same season they moult. *L. rufoscutellatus* is always macropterous (Spence & Andersen, 1992) and many adults (males in particular) retain their flight capacity throughout the reproductive period, although a high proportion of females have reduced flight muscles in July (Kaitala & Huldén, 1990).

Aquarius najas (De Geer, 1773)

Distribution in Denmark

The distribution is mapped in Fig. 12. Because *A. najas* usually is found in well defined habitats (rivers and streams) and has a limited dispersal ability (being pre-

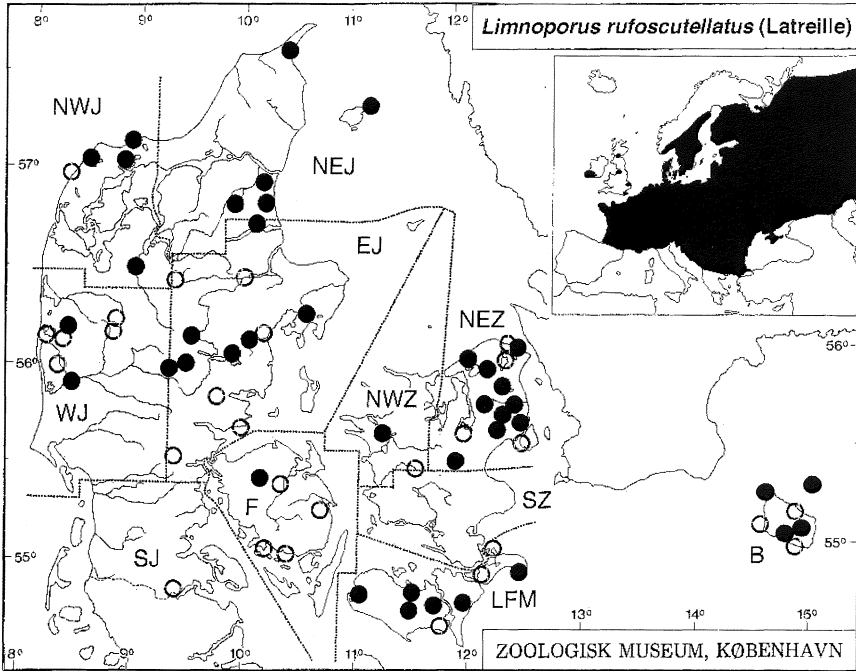


Fig. 11. *Limnopus rufoscutellatus*, distribution in Denmark and Europe (insert map). Records from before 1950 shown as open symbols, records from after 1949 shown as filled symbols.

dominantly wingless), we have chosen to give a complete survey of Danish records below (with comments). The localities are listed from North to South for each faunistic district (*A. najas* has never been recorded from the districts NWJ, SZ, LFM, and B). Material collected by E.W. Kaiser, C.F. Jensen, and K.O. Leth have collection file numbers (in brackets) attached. Adult specimens are apterous (wingless) except when noted.

NEJ: *Bangsbo Å* (4.VIII.1887, 12♂♂ 12♀♀, F. Meinert, ZMUC). *Sæby Å* (8-12.VII.1887, F. Meinert, ZMUC); (20.IX.1889, 6♂♂ 10♀♀, R.W.T. Schlick, ZMUC) (Leth, 1943). The stream runs through Sæbygård Skov W of Sæby, a locality which may be suitable for the species. *Voers Å* (or *Vors Å*), about 2 km upstreams *Vors Kro* in *Rugtved Skov* (15.VII.1938, 3♂♂ 1♀, E.W. Kaiser (41/38), ZMUC (Leth, 1943). There are no recent records, even though the *Voers Å* drainage system has been thoroughly sampled by

Mogens Holmen (personal communication). *Uggerby Å*, at *Uggerby* (4.VI.1964, 2♂♂ 2♀♀ in copula, E.W. Kaiser (26/64), ZMUC) (Kaiser, 1966); (31.VII.1969, 1♂ 1♀ 7 nymphs, H. Heidemann Lassen, NM); this locality, which is a quietly flowing, shaded river with steep banks, was visited by one of the authors in April 1995 without success. Finally, the locality "Jydske Ås, Vendsyssel" (VI.1871; 2♂♂ 1♀, Løvendahl, ZMUC) is situated in the source area of *Voers Å*, *Ryå*, and *Uggerby Å*.

WJ: *Madum Å*, at road no. 16 (24.VIII.1958, 1♀ 1 nymph, C.F. Jensen (58/099), NM). **Storå drainage system:** *Sunds Nørreå*, 100-200 m W of *Sunds Sø* (3.VI.1942, 3♂♂, K.O. Leth (3344), ZMUC); outlet in *Sunds Sø* (3.V.1949, 16♂♂ 20♀♀, K.O. Leth (3581), ZMUC). *Løven Å*, at *Ørre* (2.VI.1940, 4♂♂ 2♀♀, K.O. Leth (1678), ZMUC) (Leth, 1943). **Skjern Å drainage system:** *Skjern Å*, fishponds at *Vester Mølle* between *Rørbæk Sø* and

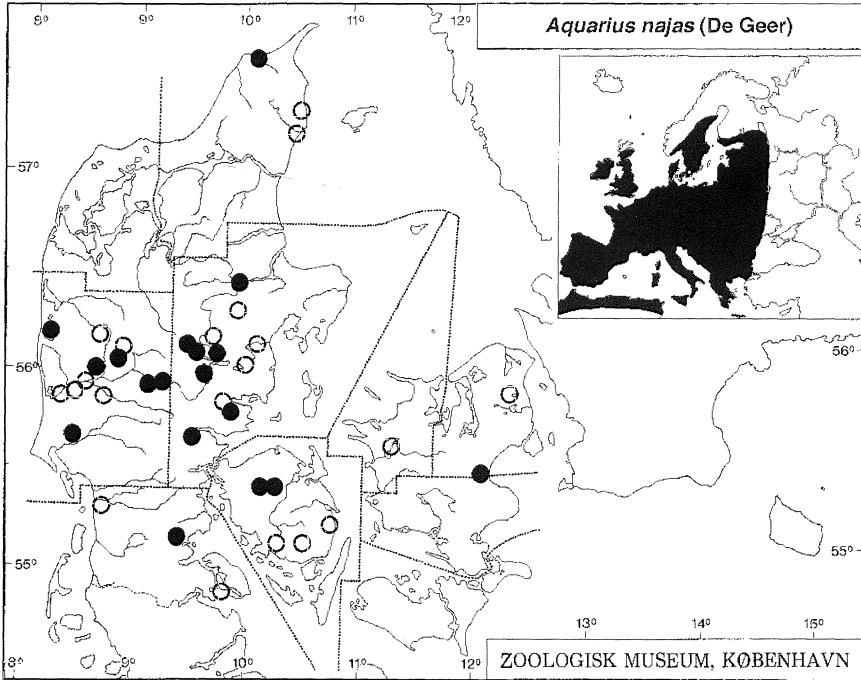


Fig. 12. *Aquarius najas*, distribution in Denmark and Europe (insert map). Records from before 1950 shown as open symbols, records from after 1949 shown as filled symbols.

Kulsø, (4.VII.1948, 2♂♂ 2♀♀, C.F. Jensen (48/100), NM); below Kulsø (12.V.1950, 2♂♂ 1♀, E.W. Kaiser (42/50), ZMUC); Hasstrup Skov (9.VII.1950, 1♂ 1♀, C.F. Jensen (50/066), NM); above outlet of Holtum Å (27.VIII.1949, 2♂♂ 3♀♀ 3 nymphs, C.F. Jensen (49/153), NM); at Enesøgård (7.IV.1950, 2♂♂ 1♀, C.F. Jensen (50/028), NM). Søby Å, Søby Sø c. 10 km S of Herning (20.IX.1887, 1♀ 10 nymphs, R.W.T. Schlick, ZMUC); above outlet of Hallundbæk (18.IX.1963, 1♂ 3♀♀, C.F. Jensen (63/113), NM). Hallund Bæk, between road and railway S of Kølkaer (24.VIII.1949, 5♂♂ 2♀♀, C.F. Jensen (49/142), NM). Rind Å, Bærslund S of Herning (18.IV.1935, 7♂♂ 2♀♀, K.O. Leth (985), ZMUC); (18.IV.1949, 6♂♂ 8♀♀, C.F. Jensen (49/038), NM); 6.VI.1949, 2♂♂ 4♀♀, C.F. Jensen (49/070), NM; 27.VIII.1949, 3♂♂ 1♀ 1 nymph, C.F. Jensen (49/150), NM); Høgildgård (18.VIII.1935, 2♂♂ 1♀, K.O. Leth (1618), ZMUC; 2.V.1943, 9♂♂ 14♀♀, K.O. Leth

(1984), ZMUC); Kideris (18.VIII.1947, 2♂♂ 5♀♀, K.O. Leth (3316), ZMUC); Arnborg Kirke (6.VI.1949, 2♂♂ 2♀♀, C.F. Jensen (49/069), NM; 18.VI.1949, 1♂ 1♀, K.O. Leth (3609), ZMUC); Birkebæk (22.X.1950, 1♀, C.F. Jensen (50/099), NM); 3.VI.1952, 2♂♂ 2♀♀, C.F. Jensen (52/039), NM). Fjederholt Å, Rind Plantage (26.VIII.1949, 2♂♂, C.F. Jensen (49/148), NM); Skærbæk Bro (18.IV.1964, 1♂ 1♀, C.F. Jensen (64/060), NM); outlet from Skærbæk Dam, 6 km S of Herning (28.III.1943, 14♂♂ 1♀, K.O. Leth (1974), ZMUC; 14.IX.1948, 2♂♂ 2♀♀, K.O. Leth (3427), ZMUC). Karstoft Å, Clasonsborg Park (13.X.1946, 33♂♂ 20♀♀, K.O. Leth (3246), ZMUC; 15.V.1949, 7♂♂ 6♀♀, K.O. Leth (3576), ZMUC). Vondå, Olling, V of Kibæk (13.VI.1949, 2♂♂ 1♀, C.F. Jensen (49/078), NM; 19.VIII.1949, 4 nymphs, C.F. Jensen (49/131), NM). Vorgod Å, W of Trolldhede (23.IV.1950, 2♂♂ 1♀, C.F. Jensen (50/036), NM). Omme Å, at Ørbæk

(24.VI.1942, 1♀, C.F. Jensen (3488), ZMUC) (Leth, 1943). *Sønderå*, in Tarm Kær at Tarm Vestermark (25.VIII.1946, 1♀ macr., C.F. Jensen (46/059), NM). *Styg Bæk*, c. 0.5 km before outlet in Ringkøbing Fjord (13.X.1946, 1♂, C.F. Jensen (3334), ZMUC). *Tarm Møllebæk*, at Teglgårdsbro (24.IX.1950, 1♀, C.F. Jensen (50/084), NM). **Varde Å drainage system:** *Linding Å*, at the bridge on the road Varde-Grindsted (1.VIII.1943, 9♂♂ 7♀♀, K.O. Leth (2025), ZMUC; 13.V.1967, 3♂♂ 3♀♀, C.F. Jensen (67/042), NM); at Nørholm (11.VI.1907, 1♀, A.C. Jensen-Haarup, ZMUC); railway bridge at Nørholm Skov (18.VII.1948, 2♂♂ 2♀♀, C.F. Jensen (48/116), NM); near Thorstrup (7.VI.1959, 1♂ 2♀♀, C.F. Jensen (59/021), NM); Thorstruplund (14.V.1966, 2♂♂ 2♀♀, C.F. Jensen (66/008), NM).

EJ: *Nørreå*, Fussingø W of Fussing Sø (without date, 1♂, A.C. Jensen-Haarup, ZMUC (Leth, 1943)); NW end of Fussing Sø (22.VIII.1964, 1♀, C.F. Jensen (64/150), NM). **Gudenå drainage system:** *Gudenå*, Fladbro at Randers (8.IX.1910, 1♀ macr., O. Jacobsen, ZMUC) (Leth, 1943); Klostermølle (20.IV.1962, 2♂♂ 2♀♀, C.F. Jensen (62/019), NM; 6.V.1963, 2♂♂ 2♀♀, C.F. Jensen (63/027), NM; 25.VIII.1963, 1♂ 3♀♀ 6 nymphs, C.F. Jensen (63/094), NM; 22.IX.1963, 4♂♂ 2♀♀ 1 nymph, C.F. Jensen (63/115), NM; 19.VII.1964, 2♂♂ 2♀♀, C.F. Jensen (64/128), NM; 5.VI.1965, 1♂, C.F. Jensen (65/078), NM; 5.IX.1965, 13♂♂ 7♀♀ 39 nymphs, unknown collector, ZMUC; 27.VII.1966, 1♂ 2♀♀, C.F. Jensen (66/050), NM; 19.VII.1966, 1♂ 1♂, C.F. Jensen (66/041), NM; 27.X.1966, 1♀, C.F. Jensen (66/079), NM; 16.VII.1970, 1♂ 2♀♀ 2 nymphs, F. Jensen a.o., NM; 1.VIII.1970, 8 nymphs, F. Jensen a.o., NM; 27.VIII.1977, 1♂, C.F. Jensen (77/085), NM; 2.V.1980, 1♂, F. Jensen, NM; 6.V.1980, 1♂, F. Jensen, NM; 2.VI.1980, 1♂ 1♀, F. Jensen, NM; 22.IV.1995, 4♂♂ 1♀, J. Damgaard, NM; 30.IV.1995, 4♂♂ 2♀♀, P. Wiberg-Larsen, ZMUC). *Lilleå*, at Laurbjerg (5.V.1910, 2♀♀, O. Jacobsen, ZMUC; 11.VI.1910, 3♂♂ 1♀, H. Ussing, ZMUC; 1.V.1913, 1♀, E.B. Hoffmeyer, ZMUC) (Leth, 1943). *Silkeborg* (per-

haps one of the following localities) (13.IV.1913, 6♂♂ 2♀♀, A.C. Jensen-Haarup, ZMUC). *Lysbro* (1915, 1♂ 1♀, A.C. Jensen-Haarup, ZMUC; 5.VI.1943, 32♂♂ 27♀♀, K.O. Leth (1992), ZMUC). *Slåen Sø* (5.VI.1935, 2♂♂ 2♀♀, K.O. Leth (1046), ZMUC; 7.VII.1955, 7♂♂ 7♀♀, K.O. Leth (3964), ZMUC; 25.IV.1964, 7♂♂ 6♀♀, 3 pairs in copula, E.W. Kaiser (10/64), ZMUC) (all Kaiser, 1966); S end of Slåen Sø (25.IV.1964, 1♂ 1♀, C.F. Jensen (64/070), NM; 13.VIII.1966, 1♂ 2♀♀ 3 nymphs, C.F. Jensen (66/063), NM). *Almind Sø*, N end of Almind Sø (18.IV.1962, 3♂♂, C.F. Jensen (62/006), NM); at public bath and Vesterskov (28.X.1994, 1 adult, and 1.VIII.1995, 2 adults, Bioconsult). *Fårbæk*, between Almind Sø and Vejlsø (3.VI.1962, 1♂ 1♀, C.F. Jensen (62/104), NM; 13.VIII.1966, 3♂♂ 1♀ 5 nymphs, C.F. Jensen (66/060), NM). *Borresø*, canal at the sawmill (6.VI.1943, 3♂♂ 3♀♀, K.O. Leth (1996) ZMUC). *Ry* (3♂♂ 3♀♀, J.C. Schiødte, ZMUC (Leth, 1943)). *Knud Å*, at Knud Bro (14.V.1962, 1♂ 1♀, C.F. Jensen (62/065), NM). *Ravn Sø*, outlet (12.VI.1967, 1♂ 1♀, E.W. Kaiser (40/67), ZMUC; 30.VIII.1979, 1♂ 4♀♀ 7 nymphs, F. Jensen, NM). *Bryrup Å*, near Bryrup Langsø (12.VIII.1975, 3♂♂ 1♀, M. Holmen, ZMUC). *Gjern Å*, at Søbyvad (8.XII.1921, 1♀, E.B. Hoffmeyer, ZMUC (Leth, 1943)). *Borum Å* (Leth, 1943; without further reference. Possibly the same as the following locality or a stream with outlet in Lyngbygårds Å). *Lyngbygårds Å* (2.X.1912, 3♂♂ 8♀♀, E.B. Hoffmeyer, ZMUC). *Århus Å*, W of Brabrand Sø (20.VI.1913, 1♀, E.B. Hoffmeyer, ZMUC); Møllehuset at Århus (20.V.1918, 1♂, A.C. Thomsen, ZMUC) (Leth, 1943); below Pinds Mølle (17.VI.1943, 12♂♂ 9♀♀, E.W. Kaiser (76/43), ZMUC). *Jeksen Bæk*, above Århus Å (17.VI.1943, 1♂, E.W. Kaiser (78/43), ZMUC). **Bygholm Å drainage system:** *Bygholm Å*, inlet E of Hatting near Nedermølle (19.VIII.1941, 2♀♀, E.W. Kaiser (90/41), ZMUC). *Ølsted Bæk*, at Nedermølle near Hatting (3.VI.1943, 10♂♂ 10♀♀, E.W. Kaiser (59/43), NM). *Horsens* (perhaps one of the following localities)

(23.04.1869, 4♂♂ 4♀♀, O.G. Jensen, ZMUC) (Leth, 1943). **Store Hanstedå drainage system:** *Lille Hanstedå*, in Hansted Skov (15.V.1943, 32♂♂ 31♀♀, E.W. Kaiser, (38/43), NM). *Klokkedal Bæk*, at E.W. Kaisers house (9.IV.1949, 1♂ 1♀ in copula, E.W. Kaiser, (30/49), ZMUC; 9.VI.1963, 1♂ 1♀ in copula, N.M. Andersen, ZMUC). *Højen Å*, st. 2b (perhaps one of the following localities) (5.V.1976, 4♂♂ 2♀♀, C.F. Jensen (76/153), NM); c. 1.5 km above Stokbro, S of Vejle (9.VIII.1940, 8♂♂ 4♀♀ 72 nymphs, E.W. Kaiser (70/40), NM); above Ny Højen (9.VIII.1940, 7♂♂ 17♀♀ 25 nymphs, E.W. Kaiser (67/40), ZMUC (Leth, 1943)); Højen (14.IX.1974, 2 nymphs, P. Aagaard Jensen, NM); S of Søndermarksgård (15.X.1974, 4♂♂, A. Lindebo, NM); Stokbro 2 km S of Vejle (30.IX.1975, 3♂♂ 2♀♀ 1 nymph, C.F. Jensen (75/097), NM).

SJ: *Ribe* (without date (probably before 1869), 1♂, E. Hansen, ZMUC). *Vedbøl Bæk*, outlet of Vedbøl Sø (3.VII.1977, 1♂ 1♀, A. Lindebo, NM). Leth (1943) records Sønderborg from which there are 2♂♂ in the Wüstnei collection (ZMUC), but Wüstnei (1891) does not mention this record. Schiødte (1869: 196) states that *A. najas* (as "*Hydrometra aptera*") was found at Ribe by "Stud. zool. Emil Hansen". There is a single male in ZMUC labelled "Ribe, E. Hansen" (coll. R.W. Schlick), but without further details. Thus, the only reliable record of this species from southern Jutland is the one from Vedbøl Bæk.

F: *Nordfyn* (exact locality not known, 1♂, R.W.T. Schlick leg., ZMUC). *Stavis Å* (12.VI.1943, 3 adults, nymphs and eggs, E.W. Kaiser (68/43), NM); st.4 (unknown locality) (23.VIII.1967, 1 nymph, E.W. Kaiser, ZMUC); at Langesø (11.VI.1871, 9♂♂ 1♀, R.W.T. Schlick, ZMUC; 13.VI.1871, 5♂♂ 3♀♀, R.W.T. Schlick, ZMUC; VI.1871, 6♂♂ 2♀♀, R.W.T. Schlick, ZMUC; 15.VIII.1942, 3♂♂ 3♀♀, E.W. Kaiser (19/42), NM); Sjøvbro (13.IX.1951, 1♂ 3♀♀ 5 nymphs, E.W. Kaiser (23/51), ZMUC; 12.VII.1952, 7 nymphs, E.W. Kaiser (39/52), ZMUC); bridge above Lænkehus (13.IX.1951, 9♂♂

9♀♀ 1 nymphs, E.W. Kaiser (24/51), ZMUC; 12.VII.1952, 6 nymphs, E.W. Kaiser, (40/52), ZMUC; 10.VII.1953, 18 nymphs, E.W. Kaiser, (39-40/53), ZMUC); in Langesø Skov downstream Lænkehus and outlet from Rue Dairy (13.IX.1951, 2♂♂ 2♀♀ 1 nymph, E.W. Kaiser (25/51), ZMUC); at Frostens Bro on Langesøvejen (16.IV.1995, 1♂ 1♀, P. Wiberg-Larsen, ZMUC); Morud Skov (29.V.1943, 3♂♂ 3♀♀, E.W. Kaiser (55/43), ZMUC); (12.VI.1943, 32♂♂ 31♀♀, E.W. Kaiser (68/43), ZMUC); (2.VII.1943, 2 adults 59 nymphs, E.W. Kaiser (83/43), NM); (25.IV.1947, 1♂ 2♀♀, E.W. Kaiser (13/47), ZMUC); (27.IV.1995, 1♂ 2♀♀, J. Damgaard, NM); (11.IX.1996, 10 eks., J. Damgaard, ZMUC); bridge in Næsby (13.IX.1951, 3♂♂ 1♀, E.W. Kaiser (26/51), ZMUC). *Vejstrup Å* (21.IV.1878, 2♂♂ 2♀♀, collector unknown, ZMUC). *Vindinge Å*, at Vindinge (4.VII.1941, 4♂♂ 3♀♀, K.O. Leth (1832), ZMUC) (Leth, 1943)). Leth (1943) also records this species from the outlets of *Brændegård Sø* and *Arreskov Sø*, but no further reference can be found in Leth's files. These lakes are interconnected and further connected to both Odense Å and Kongshøj Å. The Odense Å drainage system has been thoroughly investigated on several occasions without records of the species.

All known localities on Funen, as well as a few new potential, were shortly surveyed by one of the authors (JD) 13.IX. 1996. The only locality still found to inhabit *A. najas* was Stavis Å (see above). A few stations along the stream were surveyed but all had dried up during the dry summer except for the station in Morud Skov, where the stream was reduced to a chain of isolated, shallow, stagnant puddles containing about 150 adults and a few nymphs. Vejstrup Å was visited downstream Lillemølle near the road Svendborg-Nyborg with no new records. However, it can not be ruled out that the species still exists in upper parts of the stream. Vindinge Å was surveyed at several stations near Vindinge, and the streams Ørbæk and Ladegårds Å, both connected to Vindinge Å, were visited without results on the following stations: Ladegårds Å

upstream the road to the village Ørbæk; Ørbæk at Lillefølle near Sulkendrup; and Ørbæk near Lykkesholm. The outlets from Brændegård Sø and Arreskov Sø were shortly surveyed with no new records. The outlet from Brændegård Sø was a shallow and linear ditch, while the outlet from Arreskov Sø was a broader ditch filled with algal bloom. Based on the survey it seems like Stavis Å is the only stream on Funen inhabiting *A. najas*. Most of the other earlier localities have suffered from destruction of habitats by damming, drainage and regulation. However, a thorough search for the species on other potential localities, as well as an survey of the entire Stavis Å drainage system, especially during spring when the stream has its maximal waterlevel, should be carried out.

NEZ: *Køge Å* (3.VI.1898, 1♂ 1♀, C. Larsen, ZMUC); in Lellinge Skov (21.IV.1889, 1♂, O. Jacobsen, ZMUC; 25.V.1941, 1♂, T. Wolff leg., ZMUC; 25.V.1941, 2♂♂ 1♀, Ammentorp, ZMUC; 25.V.1941, 25♂♂ 16♀♀, E.W. Kaiser, (50/41), ZMUC) (all Leth, 1943); same locality (17.III.1967, 1♂, N.M. Andersen, ZMUC; 24.VIII.1968, 1♀ macr. (1 macr. adult escaped) more than 50 apt. adults, N.M. Andersen, ZMUC; 25.V.1994, 2♂♂, J. Damgaard, ZMUC; 30.VIII.1994, 11♂♂ 7♀♀ 1 nymph, N.M. Andersen & J. Damgaard, ZMUC). *Donse* (12.VI.1898, C.C.R. Larsen, ZMUC 1♀ / NM 2 adults) (Leth, 1943). One of the authors (NMA) has searched for *A. najas* in a small stream at Donse Dam but without finding this species.

NWZ: Leth (1943) records Halleby Å in western Zealand (near Tissø), but we have neither been able to locate specimens from this locality in NM and ZMUC nor found any further reference in Leth's locality files. Søren Birkholm (personal communication) reports to have seen "large waterstriders" near the outlet of Halleby Å in Tissø, but Mogens Holmen (personal communication) did not find *A. najas* at this locality or in Åmose Å south of Holmstrup during a visit in the spring of 1995. An inspection of Halleby Å by the authors in August 1995 was also negative although the stream at

Strids Mølle seems to be a typical locality for *A. najas*.

Distribution in NW Europe

A. najas is widely distributed in Europe (see map, Fig. 12) including the northwestern part of Russia (Andersen, 1990, 1995). In Scandinavia, the species is found in the southern parts of Finland (Vepsäläinen, 1973), in Sweden as far north as Lapland (Coulianos & Ossiannilsson, 1976). There are only four records from southern Norway (Jastrey, 1981), of which only one is of more recent date (SE Norway, Geving, Tvedestrand; a small creek outlet into the sea, where the water in periods were brackish). Nieser & Wasscher (1986) compared the present distribution of *A. najas* in The Netherlands with an earlier survey (Higler, 1967) reporting a dramatic decline in the number of localities occupied by this species. Finally, *A. najas* is widespread, but rare in the British Isles (Savage, 1989).

Habitats

A. najas favours quieter parts of relatively shallow rivers and streams, especially where these are running through forests (e.g., Stavis Å in Langesø and Mørud Skov; Gudenaå at Klostermølle; Linding Å in Nørholm Skov; Køge Å in Yderholme Skov, Lellinge). Although this species displays food-based, female territoriality (Vepsäläinen, 1985; Vepsäläinen & Nummelin, 1985b), adults are often gathering in large schools near overhanging banks or near bridges. The species is also known from a few localities with stagnant water: Slåen Sø near Silkeborg (Kaiser, 1966) and Almind Sø (Jens Skriver, personal communication). In the British Isles, the species is recorded from Lake Windermere (Brinkhurst, 1966).

Life cycle and phenology

Copulating pairs of *A. najas* have been observed as early as April 9th and by the end of April most individuals are in copula

at daytime. This species displays extended postcopulatory mate guarding and the female may carry the smaller male around for hours, days, or even weeks (Vepsäläinen & Nummelin, 1986b; Sattler, 1957). The maturing eggs cause the female abdomen to swell so that the pale membranes between the mediotergites and laterotergites are distinctly visible. Such egg-filled females are recorded from the months May–July. The eggs are laid in ovate batches below the water, on stones or submerged logs or twigs (Sattler, 1957). First instar nymphs appear around mid June and nymphs are recorded until late September. By the end of August, there are large numbers of newly moulted (teneral) adults and in the second half of September most individuals have completed their final moult. Thus, in Denmark *A. najas* overwinters in the adult stage and probably only completes one generation per year. These observations agree with those of Mitis (1937) for Austria, Brinkhurst (1959, 1966) for England, Nieser & Wasscher (1986) for The Netherlands, and Murray & Giller (1990) in Ireland. Since small numbers of first instar larvae may appear relatively late in the season, Murray & Giller (1990) suggested that some populations of this otherwise univoltine species may have a partial second generation.

A. najas is usually apterous (wingless) and therefore unable to disperse by flight. Only four macropterous (long-winged) adults are known from Denmark, but it is uncertain how frequent this form may be in large populations. One of the authors (NMA) found only two macropters among more than 50 apterous individuals from Køge Å near Lellinge. So far, macropters have not been recorded from Sweden (Lundblad, 1923), Finland (Vepsäläinen, 1974b), Norway (Jastrey, 1981), and The Netherlands (Nieser & Wasscher, 1986). A few long-winged *A. najas* have been observed at Lake Windermere, England (Brinkhurst, 1959, 1966). Moreover, those examined had undeveloped indirect flight muscles (Brinkhurst, 1966). Macropters are

more frequently found in southern France (Poisson, 1957) and in Portugal (Nieser, 1983).

Aquarius paludum paludum
(Fabricius, 1794)

Distribution in Denmark

NEZ: This species has a very restricted distribution in Denmark (Fig. 13) and the only stable populations are found in Rude Skov near Holte, northeastern Zealand. The first Danish record of *A. paludum* is from “Ruderhegn ved Holte” and was published by Jensen-Haarup (1912) in a postscript to his volume in “Danmarks Fauna: Tæger” (p. 298). The record was credited Oluf Jacobsen, one of the most devoted collectors of bugs in the early part of the century. From the diaries of Jacobsen and J.P. Kryger (who frequently made joint collecting trips in northeastern Zealand), it is clearly indicated that the exact locality for the new gerrid was Løgsø (or Løjesø) in Rude Skov (or Ruderhegn) (see map, Fig. 13). The following material from “Ruderhegn” is found in ZMUC: 1♂ 9♀♀ macr., 28.IV.1912; 9♀ macr., 26.V.1912; 6♂♂ 8♀♀ macr. and 2♂♂ 8♀♀ brach., 29.IX.1912. These specimens originate from the collections of O. Jacobsen as well as Chr. Engelhardt, A.C. Jensen-Haarup, and Emil Olsen, collectors with whom Jacobsen exchanged material. However, Oluf Jacobsen was not the first to collect this species in Denmark. The record from 1912 is predated by 7♂4♀ macr. collected by Carl C.R. Larsen in “Ruderhegn”, 11.IX.1911 (NM).

A. paludum was recovered in a small waterhole (which dries out in the summer) in Rude Skov by E.W. Kaiser on 29.IV.1933 (2♀♀ macr.) and again by Kaiser and K.O. Leth on 28.VII.1941. Leth (1943: 405, translation) specifies that it was found “...in Løgsø in Rude Skov as well as in a waterhole and a ditch connecting it with the lake.” On this date, there was “in Løgsø many hundreds of adults, including many females with eggs, as well as many large lar-

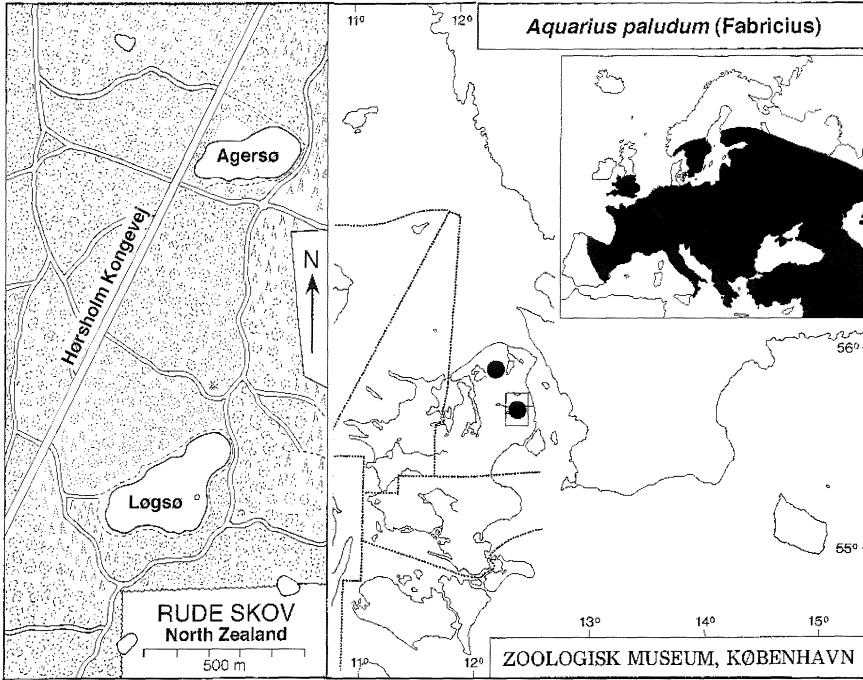


Fig. 13. *Aquarius paludum*, distribution in eastern Denmark (right), Rude Skov, Zealand (left), and Europe (insert map).

vae". The material (in ZMUC) is composed of 12♂♂ 13♀♀ macr., 6♂♂ 14♀♀ brach., and 7 nymphs (fifth instar).

One of the authors (NMA) recovered this species in Løgsø on 18.VI.1967 (1♂1♀ macr. and 1♂ brach.) and again on 8.IX.1968 (2♂5♀♀ macr., 1♂ brach., and 4 fifth instar nymphs). The species was abundant in Løgsø, 22.VIII.1970. On 8.IX.1968, *A. paludum* was for the first time found in Agersø (1♂ and a single fifth instar nymph), a lake which is smaller than Løgsø and situated about 800 m to the North in Rude Skov (Fig. 13). The only record in Rude Skov isolated from the above mentioned lakes, is from a small forest pond c. 400 m SE of Løgsø, close to Hørsholm Kongevej (8.V.1975, 1♂ macr., P. Wiberg-Larsen, ZMUC).

Outside Rude Skov, the only record of this species is based on a single 5th instar nymph collected in Store Gribsø, Gribskov, 16.VIII.1970, N.M. Andersen (ZMUC),

which is located about 22 km northwest of Rude Skov. No adults were observed and subsequent visits to Store Gribsø by the authors have failed to reveal additional specimens.

The populations of *A. paludum* in Agersø and Løgsø have been surveyed regularly



Fig. 14. *Aquarius paludum*, population of adults and larger nymphs in Løgsø, Rude Skov, September 1982 (Photo N.M. Andersen).

Dates	Agersø	Løgsø
3-4.IX.1982	?	many hundreds of adults + nymphs
18.VIII.1984	?	a few macr. adults
21.VI.1987	none	1 adult
21.VIII.1988	2 ♀♀ macr.	1♀ macr., 1♂ 1♀ brach. + nymphs
26.VIII.1989	many adults	3-4 adults
6.VI.1993	4 adults	none
14.VIII.1993	5-6 adults + nymphs	none
4.IX.1994	many adults + nymphs	none
30.IV.1995	more than 10 ad.	none
19.VIII.1995	many adults + nymphs	none

during the 1980s and early 1990s. The results are listed above.

Thus, the population of *A. paludum* in Løgsø seems to have declined during the late 80s and the species disappeared from the lake sometimes between 1989 and 1993. The population in Agersø was sizeable in 1994 and 1995 but has not approached the same magnitude as observed by one of the authors (NMA) in Løgsø in 1982 where there were many hundreds of adults and large nymphs in the western part of the lake (Fig. 14), either on the water surface or resting upon floating leaves of *Nuphar*.

Distribution in NW Europe

A. paludum is found throughout most of Europe (Fig. 13) and across Siberia to China and Japan (Andersen, 1990, 1995). In Scandinavia the species is found in the southern parts of Norway (Jastrey, 1981; Andersen, 1990), Sweden (Coulianos & Ossiannilsson, 1976), and Finland (Vepsäläinen, 1973). The species was earlier considered to be rare in The Netherlands, but has seemingly expanded westward in recent time (Nieser & Wasscher, 1986). In the British Isles the species is confined to the southern parts of England (Savage, 1989).

Habitats

Both Agersø and Løgsø are relatively large ponds (Fig. 13) with moderate shore vegetation and much free water surface. They are surrounded by relatively tall forest. Rude Skov is dominated by tall beeches and some conifer stands and is situated in an undulating landscape with many ponds and bogs. This was one of the reasons King Christian IV during the 17th century established several fish ponds connected by ditches. Most of these ponds are now overgrown and cannot be recognized.

The species is in northwestern Europe known to inhabit larger ponds and lakes with open water free from vegetation and surrounded by marginal vegetation, trees and bushes that provide shelter (Vepsäläinen, 1973). The species does not seem to be restricted in relation to the trophic conditions of the water (Nieser & Wasscher, 1986). From the British Isles the species is recorded not to show the gregarious behaviour found in *A. najas* (Southwood & Leston, 1959), but this observation cannot be confirmed from Denmark, where the species often is seen in large schools in late summer in Agersø (and previously also in Løgsø, Fig. 14). In other parts of its distributional area, *A. paludum* use a wider range of habitats, including relatively small ponds, quiet rivers, and canals (Vepsäläinen, 1974a). Nieser & Wasscher (1986) record this species from recreative fish ponds and assign the expansion of the species in the southern part of The Netherlands to the recent increase in numbers of such ponds. The parallel increase of recreative fish ponds in northeastern Zealand in recent years may forecast a similar expansion and should be carefully monitored.

Life cycle and phenology

In Danish populations, egg-filled females (with distended abdomen) have been found in July and nymphs are recorded from July, August, and September. Thus, adults overwinter and reproduce in the spring. The eggs are laid beneath the water,

the female carrying the male beneath the surface with her. Oviposition extends over a considerable period, and nymphs continue to occur late in the year (Brinkhurst, 1959; Vepsäläinen, 1974b).

A. paludum is dimorphic with respect to wing development. Along with the normal macropterous form (wings reaching or surpassing tergum 7), there is a brachypterous adult form (wings reaching tergum 5 or 6). The fractions of macropterous and brachypterous adult specimens of *A. paludum* collected in various months are (pooled data from all samples from Agersø and Løgsø):

Month	IV	V	VI	VII	VIII	IX
Macropterous	1	1	.67	.56	.20	.75
Brachypterous	0	0	.33	.44	.80	.25
Nos of specimens	12	12	3	45	5	44

Thus, brachypterous adults are found in all months except April and May which probably indicate that the overwintering population only contains macropterous adults in Denmark as in England (Brinkhurst, 1959), Finland (Vepsäläinen, 1974b), and The Netherlands (Nieser & Wasscher, 1986). The presence of brachypterous adults during the period June-September indicates that there is a partial second generation in Denmark as in England (Brinkhurst, 1959), Central Europe (Mitis, 1937; Nieser, 1981; Vepsäläinen, 1974a). In The Netherlands available data point to the same phenology (Nieser & Wasscher, 1986).

Since long-winged Gerrids normally are able to fly during spring, adults from the isolated Danish populations of *A. paludum* should have the potential to disperse when they emerge from their overwintering sites.

Discussion

There are noticeable differences in the distribution of the three larger water striders in Denmark. *Limnoporus rufoscutellatus* is the most widely distributed species and the localities mapped (Fig. 11) are probably more a reflection of the very uneven col-

lecting activity in different parts of Denmark than an expression of the actual distribution of this species. Its relative abundance is probably also underestimated since it often inhabits small water bodies which rarely are surveyed. Of the three larger water striders, *L. rufoscutellatus* extends farthest to the North, e.g., in Finland and Russia (Fig. 11), but its distribution in Denmark does not seem to reflect any preference for a more continental climate. The species is quite vagile and cannot be expected to return to the same locality year after year. In summary, *L. rufoscutellatus* is in Denmark a widespread but not very constant or abundant species.

Aquarius najas has a very uneven distribution in Denmark (Fig. 12), but seems to be constantly present in several parts of the river systems of central Jutland and abundant in several localities. Because of the lack of suitable habitats, *A. najas* is not expected to be found in the districts LFM and B. It is surprising, however, that the species is only found in one locality on Zealand (Køge Å), despite the presence of several suitable localities (e.g., Halleby Å and Suså). The species seems to have disappeared from the Sæby Å and Voers Å drainage systems in northeastern Jutland where it apparently was common in the 1880s. The species still occurs in the Stavis Å system in the northeastern part of Funen, but has not in recent years been recovered from the localities in southern Funen. Thus, *A. najas* is a rather local species, but constant and usually abundant where it occurs.

Aquarius paludum is extremely local in Denmark since it only occurs in two (possibly three) forest ponds in northeastern Zealand (Fig. 13). However, despite of its size and habit of skating far from the shore it cannot be ruled out that it is overlooked by casual collectors. There seems to be several suitable localities for the species (e.g., Skodborgdam and Bøllemosen) where the species should be searched for. It is also interesting to see if the species is able to invade the numerous recreational fish ponds which have been established in

northeastern Zealand. Although the Danish populations of *A. paludum* are close to the northern limits of the species total distribution (Fig. 13) and is characterized as rare in the other Nordic countries, the very restricted occurrence of the species in our country is difficult to explain.

The three larger water strider species have widely different phenologies and life history strategies associated with their habitat use. *Limnoporus rufoscutellatus* is univoltine and adults are monomorphic long-winged and able to disperse to new and temporary habitats in the early spring and to suitable breeding sites later in the season. The vagility of this species has been associated with the high mortality imposed by hymenopterous egg parasitoids. By colonizing new habitats, the water strider may be able to escape the parasitoid, at least temporarily. Other water strider species which lay their eggs at some depth in the water seems less infested by egg parasitoids (Spence, 1986; Nummelin et al., 1988). In general, *L. rufoscutellatus* uses habitats that are less stable than the two other large water striders.

Aquarius paludum is probably partially bivoltine in Denmark like in other parts of northwestern Europe. Adults are seasonally dimorphic, overwintering generation being monomorphic long-winged, and the summer generation at least partly short-winged. The kind of habitats occupied by this species (large forest ponds) appear to be rather stable, but variation in salient features within the habitat (exposure to wind, insolation, etc.) may limit the suitability of a particular locality as breeding site. Finally, *A. najas* is univoltine and adults are monomorphic wingless (long-winged individuals rare). This species inhabits the most stable type of habitats, that is running water.

Following Vepsäläinen (1978), the three species can be arranged in a sequence after the decreasing stability and predictability of their habitats, *A. najas* – *A. paludum* – *L. rufoscutellatus*. We suggest that habitat use, phenology, and life history strategy are some of the most important factors to be

considered when discussing the status of these species in Denmark and the need for conservational measures. Pollution and eutrophication are usually pictured as the greatest threats against aquatic organisms, but so far there is no evidence of any direct effect of water pollution on the distribution of water striders. Obviously, the number of suitable habitats may be critical. *Limnoporus rufoscutellatus* seems to be widespread in Denmark, but the rapid decline in the number of smaller water bodies in many parts of the country may be critical to this species. Although it may disperse readily by flight, the distance between suitable breeding sites may be too large for the species.

Aquarius najas may be threatened by the regulation of rivers and streams in Denmark which was common policy a few decades ago. More indirectly, lowering the groundwater level as an effect of increased use of water for industry, cities, and agriculture is a serious threat to the diversity of organisms inhabiting rivers and streams. Although being a protected locality, the water level in Køge Å has been reduced by the establishment of Regnemærksværket which supply water for the city of Copenhagen. Although *A. najas* may be able to survive for shorter drought periods without free water (by estivation; see Wilcox & Maier, 1991), the very limited dispersal capacity of this primarily flightless species requires that a sufficient number of suitable breeding sites are maintained within a river system.

Of the three species, *Aquarius paludum* appears to be most vulnerable because of its very local occurrence in Denmark. This is illustrated by the recent disappearance of this species from one locality (Løgsø in Rude Skov) where it was abundant about ten years ago. So far, no explanation can be offered for this development. Algal bloom during warm summers, increased predation by fish or water birds, or disturbance by increased traffic along the shores (Kirby, 1992) are some possible causes (all boat traffic on the pond is banned). The frequent mild winters during the past ten

years may have affected the winter mortality of the species since higher temperatures may increase the risk of predation or infections by fungi. However, the population in Agersø, only 800 m north of Løgsø, seems to have increased during the same period. In order to prevent *A. paludum* from going extinct in Denmark, it is crucial to protect Agersø from any source of pollution, e.g., oilspills from the main road running close to the pond. It is also important to prevent treecutting in the surrounding forest since this may open up for winds preventing the species from cruising on open water where it probably gets much of its food.

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Dansk sammendrag

I artiklen præsenteres udbredelse, livscyklus samt status i Danmark for de 3 største arter af danske skøjtølbertæger (Heteroptera, Gerridae): *Limnoporus rufoscutellatus*, *Aquarius najas* og *A. paludum*. *L. rufoscutellatus* er den mest udbredte art i Danmark og lever i mindre vandsamlinger. Arten har én årlig generation, og er samtidigt den art, der har den største spredningsevne, idet den altid er langvinget og ofte ses flyvende. Det er en art, der pludselig kan dukke op på velundersøgte lokaliteter, hvorfra den ikke før

har været kendt. At arten er knyttet til mindre vandsamlinger, gør den udsat for dræning, opfyldning og tilgroning af disse. *A. najas* er vidt udbredt i de store midtjyske vandsystemer, men findes kun få steder uden for disse. Arten er næsten udelukkende knyttet til vandløb, især lavvandede slyngninger igennem skovbeplantninger. Arten har én årlig generation og findes næsten udelukkende som vingeløs, hvorfor dens spredningsevne er begrænset til de vandløbssystemer, hvori den allerede er etableret. Arten er sårbar over for forringelser af levestedet i form af reguleringer og udtørring som følge af bl.a. grundvands-sænkninger, og er tilsyneladende forsvundet fra perifere dele af det tidligere udbredelsesområde. *A. paludum* er meget lokal og findes idag kun med sikkerhed på én dansk lokalitet, Agersø i Rude Skov i det nordøstlige Sjælland. Arten er normalt fuldvinget, men har ofte en partiel sommergeneration, som overvejende udgøres af kortvingede individer. På trods af mange potentielle levesteder i Nordøstsjælland synes arten ikke at sprede sig, og er endda forsvundet fra et, muligvis to, tidligere lokaliteter. Indtil ca. 1990 fandtes arten også i Løgsø i Rude Skov, ca. 800 m nord for Agersø, hvor arten i begyndelsen af 1980'erne var særdeles talrig. *A. paludum* er den eneste af de tre store arter af skøjtølbertæger, som for alvor er truet i Danmark. Artiklen viser hvor stor forskel der kan være i udbredelse, habitatvalg og livscyklus hos enddog nært beslægtede arter, og viser, vigtigheden af at kende disse aspekter hos arter, hvis status skal vurderes.