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Distribution and ecological aspects of four rare wetland spiders, recently reported from Belgium

Kris Decleer and **Robert Bosmans**
State University of Ghent,
Laboratorium voor Ecologie der Dieren,
Zoögeografie en Natuurbehoud,
K.L. Ledeganckstraat 35,
9000 Gent, Belgium

Summary

Four rare wetland spiders were recently recorded in Belgium: *Clubiona juvenis* Simon, *Centromerus incultus* Falconer, *Carorita paludosa* Duffey and *Halorates reprobus* (O. P.-Cambridge). Data are presented on their distribution in Europe and their life cycles and habitats.

Introduction

During the last few years, interest in the study of spiders has increased considerably in Belgium. Both amateur and professional arachnologists have been making species lists of numerous areas. However, until recently, wetland habitats received relatively little attention. During the period 1982-1988 some humid areas were intensively sampled. One result of this was the discovery of several rare or new spider species for the Belgian fauna and the provision of additional information about their life history, habitat and synecology.

Since wetlands are much endangered everywhere, and are of special interest for wildlife conservation, we thought it of interest to compile ecological and biogeographical data of four rare wetland species, which we recently recorded for the first time in our country: *Clubiona juvenis* Simon, *Centromerus incultus* Falconer, *Carorita paludosa* Duffey and *Halorates reprobus* (O. P.-Cambridge). A detailed knowledge of the ecology of each species is indispensable before conservation management can take them into account, along with other animals and plants.

In the following synopsis a survey of literature is given. Data on the distribution in Europe, the life cycle and the habitat of each species are discussed. As the available biogeographical data are probably not complete, the need was again strongly felt for an international monitoring programme of spiders. As a starting-base the distribution maps given below will undoubtedly be of value.

Clubiona juvenis Simon, 1878 (Fam. Clubionidae)

Distribution

C. juvenis is definitely a rare spider. Its range extends from eastern to central and western Europe. As far as we know it does not occur in southern and northern countries (Fig. 1).

Data were available from 12 countries: Switzerland: 1 record before 1910 (de Lessert, 1910; Maurer, 1978); Northern Italy: 1 record (Minelli & Mannucci, 1979); Austria: abundant at 'Neusiedler See' (Nemenz, 1967; Pühringer, 1975); Roumania: 2 records (Roşca, 1939; Fuhn & Oltean, 1970); France: 4 records before 1932 (Simon, 1878, 1932), 1 recent record (Henry, 1981); Great Britain: 4 records (Carter, 1972; Locket, Millidge & Merrett, 1974; E. Duffey, pers. comm.; P. R. Harvey, pers. comm.); Ireland: 2 records (Jackson & Pack-Beresford, 1913; Carter, 1972); Netherlands: 1 record in 1924 (De Jong, 1982); West Germany: 1 record before 1941 (Von Bochmann, 1941; Wiehle, 1965); East Germany: 2 records (Martin & Heimer, 1977); Estonian SSR: 1 record (Vilbaste, 1987); Poland: 1 record (Czajka, 1976).

For Belgium we can add four records: Damme, nature reserve 'Stadswallen van Damme': 3♂, 1♀, 1 juv.♂ using 24 pitfall traps from 16 July-9 Oct. 1982 (Decleer, 1986), 1♀ by hand-collecting on 6 March 1988. Rekem, nature reserve 'Vallei van de Zijpbeek': 3♂, 3♀ by sweep-net sampling and hand-collecting (M. Janssen, pers. comm., leg. P. Poot). Zandvliet, nature reserve 'Groot Buitenschoor': 1♀ by pitfall trapping from 18 April-10 May 1987. Berg, nature reserve 'Torfbroek': 5♂, 9♀, 2 subad., 5 juv. by hand-collecting on 18 March 1988.

Life cycle

From the phenological data summarised in Table 1, it is probable that adults and various juvenile stages can be found throughout the year (Schaefer, 1976: eurychronous type). Most likely *C. juvenis* has a similar life cycle to *C. phragmitis* C. L. Koch which has been described by Nentwig (1982), i.e. two generations separated by only one to three developmental stages. The first generation starts in spring, hibernates as adult and reproduces next spring. They produce a second generation in summer which hibernates in different subadult stages. The latter specimens reproduce next autumn and overwinter as egg or juvenile.

Habitat

C. juvenis is a so-called 'diplostenoecious species' (Duffey, 1968) as it occurs in seemingly totally opposite

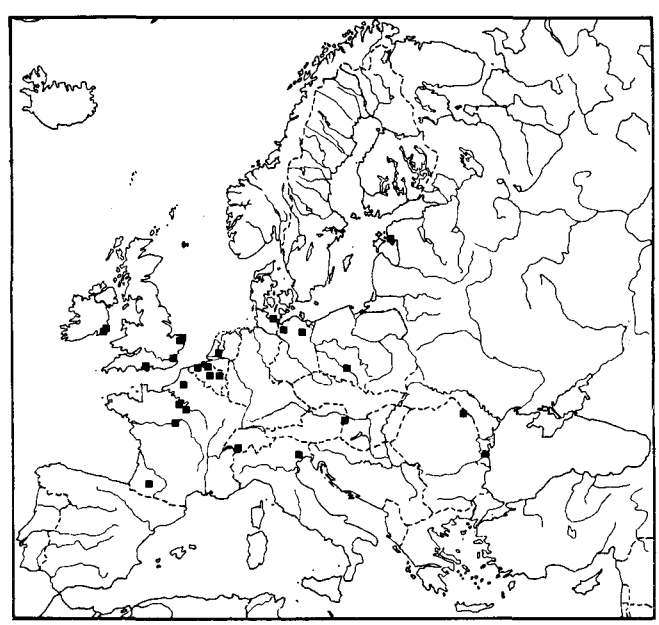

Fig. 1: Distribution map of *Clubiona juvenis*.

	J	F	M	A	M	J	J	A	S	O	N	D	Total
Jackson & Pack-Beresford (1913)						±							3♂ 8♀
Von Bochmann (1941)	.	.	.	×°	.	×°	.	×°	×°	.	.	.	46 ad 40 j
Nemenz (1967)	.	.	.	.	+	±	±	±	±	±	±	±	
Carter (1972)									±				4♂ 5♀
Locket, Millidge & Merrett (1974)							±						
Pühringer (1975)	.	.	.	×°	×	×	×	×	×	×	.	.	
De Jong (1982)						±							2♂ 7♀
E. Duffey (pers. comm.)									+				2♂
P. R. Harvey (pers. comm.)					−				−	−			
Belgium	.	.	±°	−	+	.	+	+	±	+°	.	+	11♂ 15♀ 8j

Table 1: Life cycle data on *C. juvenis*. + = adult male(s); − = adult female(s); × = adult(s) = ad; ° = juvenile(s) = j; . = no sampling.

habitats, here both 'dry' and 'wet'.

In most cases the species has been found in high, dense *Phragmites*-belts or in *Cladium* vegetation. It does not avoid brackish situations (Locket, Millidge & Merrett, 1974) and can be found high in the vegetation (even in flower heads of reed), on bare ground and among the ground vegetation or in the moss layer (e.g. *Sphagnum*: Carter, 1972) of reed beds. Exceptionally, *C. juvenis* was found in Italy in moist *Salix*-groves (Minelli & Mannucci, 1979); the latter was probably the result of natural succession of former reedland which still may be present at the site. Hence, the species can be considered as a typical riparian spider with preference for tall and usually dense vegetation. P. R. Harvey (pers. comm.) mentions the presence of the species in a previously tidal reedmarsh along the Thames, which was cut off from the sea several years ago by new seawall defences.

On the other hand large numbers of *C. juvenis* have been observed on coastal sand dunes in Ireland (Jackson & Pack-Beresford, 1913; Carter, 1972) and West Germany (Von Bochmann, 1941) where it lives in the densest parts of grass tussocks. When disturbed they run rapidly over the sand. During six samplings in April, June, August and September, Von Bochmann (1941) easily captured by hand a total of 46 adults and at least 40 immature specimens at two sites along the German Baltic coast. He found the species not only in the young, more or less mobile sand dune systems nearest to the sea where *Ammophila arenaria* dominated, but also in older, fixed sand dunes where dense *Carex arenaria* was growing along with *Corynephorus canescens* and *Calluna vulgaris*. Carter (1972) supposed that the species has a strong affinity with the dense tussocks where humidity is higher. Moreover, near to the sea the humidity is always relatively high. So far, *C. juvenis* has not been found along the continental coast of western Europe, possibly because microclimatic conditions differ considerably from the situation in North Germany or in the British Isles, owing to much lower production of the vegetation (*Ammophila, Elymus*).

As in the literature, the Belgian habitats of *C. juvenis* can be described as follows:

At Damme captures were made in a rather small (0.3 ha) and isolated reedbelt, bordered by a few willows. This habitat developed spontaneously from an open-water moat, which surrounded the village of Damme in the 17th century as a defensive system. On the bare soil, low plants are nearly absent owing to yearly flooding from November until May. In the past, this reedbelt has regularly been burnt during winter. A litter layer is present only at the borders; sieving during winter, however, yielded no further records. Neither was the species found in the adjacent *Carex paniculata/Thelypteris palustris* vegetation, nor in the *Betula pubescens/Alnus glutinosa* climax. One female was found hibernating in a broken, hollow reed stalk from the previous year. The area is surrounded by polder grasslands in which reeds are only sparsely present along some of the many ditches.

At Rekem the species was found in the small reed borders of two old fishing ponds. Here two adult males were caught in the vegetation, and one adult male and 3 adult females were found overwintering in 'cigar-galls' of reed, caused by the chloropid fly *Lipara*.

At Zandvliet the species occurs in the extensive, brackish reed vegetation along the river Scheldt, forming the transition zone between salt marsh and grassland on the dike. In the highest zone a thick litter layer is present.

At Berg the habitat of *C. juvenis* consists of tall reed vegetation in a calcareous mire. In the reed bordering a pond, and thus regularly subjected to winter inundations, the species was found to be more numerous than in the adjacent reed vegetation on artificially raised, unsubmergeable soil (see Table 2).

In most cases *C. juvenis* is accompanied by the

	A	B
100 broken vertical reed stalks		
C. juvenis	12	2
C. phragmitis	6	6
100 seed panicles of reed		
C. juvenis	2	—
C. phragmitis	2	2
Soil litter samples		
C. juvenis	—	—
C. phragmitis	1	3

Table 2: Number of specimens of *C. juvenis* and *C. phragmitis* found during hibernation in reed vegetation with different structure along a pond margin (A) and on adjacent, higher and unsubmerged soil (B) in the 'Torfbroek' reserve on 18 March 1988.

	A	AB	B
C. juvenis	205	141	36
C. phragmitis	102	124	97

Table 3: Number of specimens of *C. juvenis* and *C. phragmitis* in seed panicles of reed in a transect of reed close to open water with nearly constantly flooded soil (A), monospecific reed in the transition zone with winter and spring inundation (AB) and thin reed on the border zone with irregular spring inundation and *Carex* undergrowth (B) in the 'Neusiedler See' area (data from Pühringer, 1975). Sampling was done from April until October 1970 (number of seed panicles was not specified).

related but much commoner *C. phragmitis*. The latter species, however, can frequently be found in other habitats, e.g. wet meadows, tall sedge vegetation and even under stones along rivers. In reed marshes, habitat partitioning may occur. Data from hibernating specimens at Berg suggest that *C. juvenis* prefers reed on moister soil or closer to open water than does *C. phragmitis* (Table 2). This is in spite of infrequent cutting during winter of parts of the reed along the margin of the pond. Reed plants in open water or in regularly submerged soil produce more and larger seed panicles, grow taller and have thicker stalks than reed from drier places. This hypothesis is supported by the findings of Pühringer (1975) (Table 3). Furthermore it must be noted that, despite considerable efforts, this species could not be found in some of our other study areas: one reedmarsh subjected to desiccation and two reedmarshes originating from abandoned wet, alluvial meadows.

Centromerus incultus Falconer, 1915 (Fam. Linyphiidae)

Distribution

The range of *C. incultus* extends from Scandinavia to the northern parts of western and central Europe (north of the Alps) and as far east as the Urals. From Sweden the species is known as far north as the polar circle (Fig. 2).

Literature data are available from 10 countries: Finland: records from 5 localities (Palmgren, 1975; Lehtinen *et al.*, 1979; Koponen, 1985; S. Koponen, pers. comm.); Sweden: records from 9 localities (Kronestedt, 1968; Westerberg & Granström, 1977; Granström, 1978; Kronestedt, 1983; Almquist, 1984); U.S.S.R.: records from 14 localities (Pachorukov, 1981; Uzenbaev, 1986; Vilbaste, 1964, 1987); Netherlands: records from 2 localities (Van Helsdingen, 1963, 1981); West Germany: records from 5 localities (Schenkel, 1936; Casemir, 1960; Wunderlich, 1973; Löser, Meyer & Thaler, 1982; Nentwig, 1983); East Germany: records from 3 localities (Miller, 1958; Wunderlich, 1971; Martin, 1977; Hiebsch, 1985); Poland: records from 8 localities (Staręga, 1978, 1983, 1988; Dziabaszewski, 1979; Woźny, 1985); Czechoslovakia: records from 4 localities (Miller, 1958); Great Britain: records from 2 localities (Falconer, 1915; Duffey, 1971a); Switzerland: records from 1 locality (Hänggi, 1982; Hänggi & Maurer, 1982).

For Belgium we can add records from two localities: Oostkamp, nature reserve 'Leiemeersen': 16♀ using 24 pitfall traps from 16 July-9 Oct. 1982 (Decleer, 1986), and 3♂ during February 1988, 2♂, 6♀ during March 1984, 2♂, 13♀ during May 1988 by sieving litter. Neerpelt, nature reserve 'Hageven': 1♂ in April using 16 pitfall traps from 5 August 1985-13 August 1986 (Janssen, 1987).

Life cycle

Phenological data (Table 4) suggest that *C. incultus* has a stenochronous annual cycle with a reproduction period in spring and hibernation as adult or subadult. A few females can still be found until the beginning of August. In northern regions, no February or March observations being available, the copulation period seems to have shifted to the summer. In more southern countries juveniles may become adult from the end of September onwards as illustrated by the observations of, e.g., Duffey (1971a), Martin (1977) and Hänggi (1982).

Habitat

Several authors give brief descriptions of the habitat of *C. incultus*. Some specimens came from different kinds of moist, mostly open woodland: in *Sphagnum* and litter of a pine-forest (Miller, 1958), Alnetum (Schenkel, 1936), *Sphagnum* in a half-shaded situation with young *Alnus* and *Picea* (Wunderlich, 1971). Others were caught in oligotrophic, treeless *Sphagnum* vegetation: peat-moor (Van Helsdingen, 1981; Hänggi & Maurer, 1982; Hiebsch, 1985), heathland bogs choked with *Sphagnum* along their margins (Casemir, 1960). On the other hand specimens have also been found in rather eutrophic conditions, often with tall sedges: *Carex paniculata*-moor (Palmgren, 1975), Caricion elatae with high water-level at 625 m altitude (Löser, Meyer & Thaler, 1982), *Phragmites* vegetation with thick litter layer and *Salix cinerea* islands

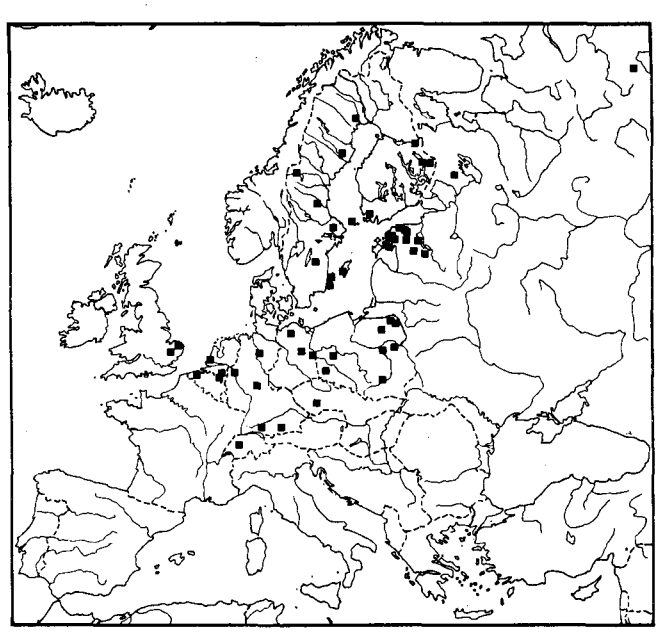

Fig. 2: Distribution map of *Centromerus incultus*.

(Nentwig, 1982), sedge-marsh (Wunderlich, 1973), eutrophic fen dominated by the moss *Scorpidium scorpioides* (Lehtinen *et al.*, 1979), litter layer of *Calamagrostis canescens* and *Thelypteris palustris* growing by the edge of fen waterways, heaps of cut sedge and in moss on waterlogged ground of sedge beds close to thick *Alnus/Salix* carr (Duffey, 1971a). In spite of intensive searches by the last author and his colleagues at the same site, leaf litter on heavily shaded, wet peat under closed canopy of *Alnus/Salix* carr yielded no specimens. Finally three records of *C. incultus* are available from wet meadows (Van Helsdingen, 1963; Martin, 1977; Westerberg & Granström, 1977). Almquist (1984) compared densities of *C. incultus* in four different vegetation types of a complex mire on the island of Öland (Sweden) by taking 335 sieve samples of 0.25 m^2. He found a mean density of 1 individual/m^2 in a narrow, humid meadow with *Molinia caerulea, Carex panicea* and *Filipendula ulmaria* as dominants, against 0.6 ind./m^2 in a *Cladium mariscus* mire with *Calliergon giganteum* moss layer, and 0.3 ind./m^2 in both a *Carex elata* mire with *Lysimachia vulgaris* and *Comarum palustre* and a *Sphagnum* bog. During a detailed survey of a small, variegated peat-moor relict near Bern (Switzerland) Hänggi (1982) recorded the species exclusively in all types of wet vegetation. It was most numerous in a mesotrophic, mixed sedge-alder carr (Carici elongatae — Alnetum glutinosae) with some willows and buckthorns, and also in more oligotrophic *Sphagnum* vegetation (25 × 40 m) and a dense, regularly submerged, monospecific alder carr developed by natural succession of the peat-moor. Finally, in early June, Staręga (pers. comm.) captured several females on high reed and beat 2 females from nearby branches of *Picea abies;* these observations may reflect aeronautic behaviour. As a confirmation of the eury-hygrophilous character of the species we can add the Belgian habitat data:

At Oostkamp the species was found both in swampy meadow vegetation with *Dactylorhiza majalis, Carex disticha, Juncus acutiflorus, Mentha aquatica,* etc.; in Magnocaricion (*Carex acuta*) and in *Phalaris arundinacea* and *Phragmites australis* vegetation with thick litter layer. Under closed canopy of *Alnus* the species could not be found.

At Neerpelt a single specimen was recorded from a heathland area in the transition zone of a disturbed wet area with *Juncus effusus* etc. and a dry sand dune with *Molinia caerulea* and *Corynephorus canescens,* with nearby *Sphagnum* bogs. It was probably a wandering specimen.

In conclusion, we can state that *C. incultus* lives in all kinds of wetlands, especially with peaty soil, being however less frequent in vegetation under closed canopy of woodland and absent in brackish habitats and hypertrophic conditions with e.g. *Glyceria maxima* vegetation or heavily manured grassland. The presence of this species therefore can probably be considered as an indication of good ecological quality of the habitat.

Living in a wetland requires special adaptations to survive regular flooding. At Oostkamp one male was seen walking on a floating mass of litter during a February inundation. Furthermore, in some preliminary laboratory experiments 4 out of 5 specimens of *C. incultus* survived a 20-day flooding period with aerated water at 4°C (Decleer, 1988b).

Carorita paludosa Duffey, 1971 (Fam. Linyphiidae)

Distribution

Described for the first time only 18 years ago, only 10 localities are known, in the British Isles, Belgium and Sweden (Fig. 3). Undoubtedly it is a rare species, but because of its minuscule proportions (total length: 1.4-1.7 mm) it may sometimes have been overlooked.

The following data were available: Great Britain: 3 records (Duffey, 1971b; Merrett, 1975, pers. comm.);

	J	F	M	A	M	J	J	A	S	O	N	D	Total
Vilbaste (1964)	.	.	.	×	×	×		×	×	×	.	.	
Kronestedt (1968)						±	−		−	−			1♂ 10♀
Palmgren (1975)							−						1♀
Lehtinen *et al.* (1979)						−				±			2♂ 8♀
Falconer (1915)							−						1♀
Schenkel (1936)					−								1♀
Miller (1958)				×									
Casemir (1960)					−								2♀
Van Helsdingen (1963)			−										1♀
Wunderlich (1971)						+							1♂
Duffey (1971a)									±				2♂ 6♀
Martin (1977)											−		1♀
Van Helsdingen (1981)			±	−									2♂ 8♀
Nentwig (1983)				+			−						1♂ 1♀
Staręga (1978, pers. comm.)						−			−	±			3♂ 54♀
Hiebsch (1985)						×			×		×		10 ad
Hänggi (1982)	±	±	±	±	+	−	−	−		−	−	±	71♂ 16♀
Belgium	.	±	±	+	±	.	−	−			.	.	7♂ 36♀

Table 4: Life cycle data on *C. incultus*. + = adult male(s); − = adult female(s); × = adult(s) = ad; ^ = peak activity; . = no sampling.

Ireland: 1 record (Duffey, 1971b); Sweden: 1 record (Westerberg & Granström, 1977; Granström, 1978).

Five further localities are known in Belgium: Woumen, nature reserve 'De Blankaart': 2♀ using pitfall traps from 30 June-6 Nov. 1977 (Hublé, 1980), 80♂, 22♀ using 60 pitfall traps from 27 April-15 Sept. 1984 and 4♂ using 24 pitfall traps from 19 April-15 Nov. 1985 (Decleer, 1988a). Also 2♂, 2♀ in enclosures in April and May 1988. Lebbeke, 'Denderbellebroek': 1♂, 2♀ using pitfall traps from 4-20 May 1984 (Bosmans, 1986). Oostkamp, nature reserve 'Leiemeersen': 4♂, 4♀ in March 1984 by sieving litter (Decleer, 1986) and 2♂, 2♀/16♂, 26♀ in February and May 1988 by sieving litter. Meerdonk, nature reserve 'Saleghemkreek': 1♀ on 11 Feb. 1988 by sieving litter. Lokeren, nature reserve 'Molsbroek': 3♂ (pitfall trapping from 1 May-25 Sept. 1984).

Life cycle

The phenological results in Table 5 indicate that the species reproduces in spring and may hibernate both as juvenile or adult. Pitfall trapping in 'De Blankaart' yielded 42♂ and 12♀ during May 1984 (Decleer, 1988a).

Habitat

Since *C. paludosa* seems to be a very rare spider in Europe it is worthwhile to list all information concerning its habitat. It is striking that the species has been found in oligotrophic, mesotrophic and even very eutrophic situations, especially on peaty soil.

From 'The Burren' in Ireland its habitat has been described as "thin layer of moss, growing over the floor of an old peat cutting, being invaded by *Eriophorum*". From the fens of 'The Norfolk Broads' (England) the species was recorded from "*Sphagnum* tussocks of an old *Betula/Alnus* carr in a sedge marsh" and "leaf litter and cut grass and sedge in a long-abandoned grazing marsh, adjacent to a fairly extensive growth of *Cladium mariscus* on one side and *Phragmites australis* on the other" (Duffey, 1971b). At the third British locality, Somerset (Merrett, 1975), the species was found among *Phalaris* litter and moss on moist but not very wet ground, with some old peat cuttings and *Salix, Betula* and *Alnus* nearby (P. Merrett, pers. comm.). In Sweden 27 specimens were found on an alluvial meadow dominated by *Calamagrostis canescens, C. pururea* and *Deschampsia caespitosa* close to the river Vindelälven, well within the boreal region (Westerberg & Granström, 1977; Granström, 1978).

In all the Belgian localities, conditions were very eutrophic and, with the exception of Lokeren, a peaty soil and a thick litter layer were present. At Woumen,

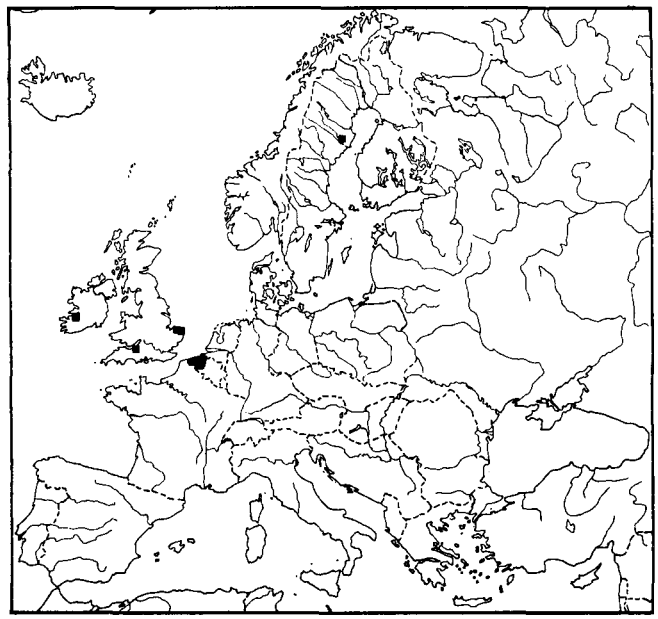

Fig. 3: Distribution map of *Carorita paludosa*.

large numbers came from the litter layer of dense *Phragmites* vegetation, being invaded by *Urtica dioica* and *Calystegia sepium* as a result of a decline in the summer water-level of more than 20 cm during recent years. At Oostkamp *C. paludosa* was sieved from *Phragmites* but also from *Phalaris arundinacea* and *Carex acuta* litter in a former wet meadow, abandoned for 30 years. At Lebbeke the habitat was *Glyceria maxima* vegetation with *Calystegia sepium, Rorippa amphibia, Galium palustre* and *Thalictrum flavum*. At 'Saleghemkreek' the species is known from *Phragmites* vegetation with much litter, originally a trembling bog, but now stuck to the soil and more eutrophic owing to a water-level decline in the area. At Lokeren three specimens were trapped in a small *Phragmites* islet (0.1 ha), annually cut in winter and surrounded by a large wet meadow and grassland area on alluvial clay soil. Here the litter layer was only poorly developed, especially during spring. Despite sampling in neighbouring *Phragmites* vegetation with a thick litter layer, the species was not found. It is therefore possible that the latter records represent accidental, wandering specimens.

The importance of the presence of litter can be illustrated by the large scale investigation of the first author in the reed marshes of the nature reserve 'De Blankaart' (Woumen). The spider fauna of two plots cut in winter, one plot cut both in winter and summer, and seven uncut reference plots was compared by intensive pitfall trapping. The traps in cut plots yielded fewer or far fewer specimens of *C. paludosa* than uncut

	J	F	M	A	M	J	J	A	S	O	N	D	Total
Duffey (1971b)						−			±				1♂ 7♀
P. Merrett (pers. comm.)										±			3♂ 2♀
Belgium	.	±	±	±	±t	±	±		−	−		.	112♂ 70♀

Table 5: Life cycle data on *C. paludosa*. + = adult male(s); − = adult female(s); t = freshly moulted adults; . = no sampling.

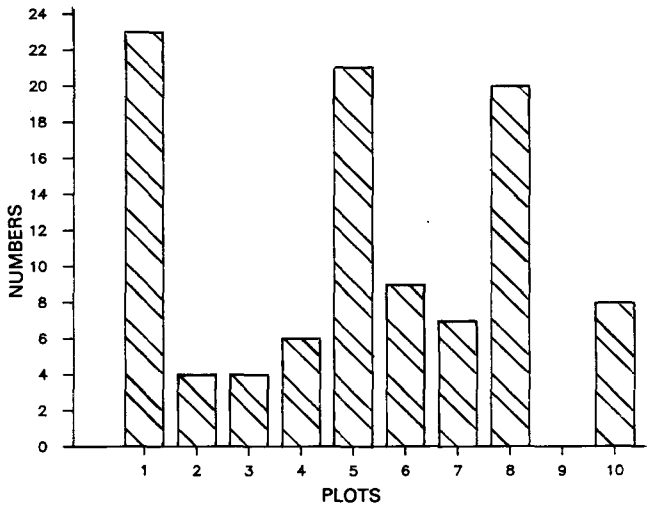

Fig. 4: Numbers of *Carorita paludosa* in 10 plots in the "Blankaart" reed marsh (pitfall trapping from the end of April to mid September 1984). Plot 2 and 9 are cut during winter; plot 3 is cut in July and September. The others are uncut.

plots where the litter layer remained deep and undisturbed (see Fig. 4). It is surprising that with such a habitat preference, the species is not more common in Europe.

Being a typical wetland spider, *C. paludosa* is well adapted to survive temporary flooding (Decleer, 1988b). In the laboratory, out of 10 specimens, 7 survived submersion for 20 days at 4°C. After a high, month-long February flooding in 'De Blankaart' reed marsh, four specimens were captured in six hermetically covered enclosures of 40 × 40 cm. They probably survived in hollow *Phragmites* stems in the litter layer. However, after an extreme flooding period from the middle of September 1984 to the beginning of April 1985 in the same study area, pitfalls yielded 12 times fewer specimens (i.e. 47 individuals in 1984 versus 4 individuals in 1985 in four sites and for the same sampling periods). This shows that mortality may nevertheless be very high due to exceptional inundation.

***Halorates reprobus* (O. P.-Cambridge, 1879)** (Fam. Linyphiidae)

Distribution

Being regarded sometimes as a 'semi-marine' spider, this species occurs only along the north and west European coastline, mostly on rocky shores. It can be found far above the polar circle and consequently on coasts where the sea water may be frozen during winter. The centre of its distribution area seems to be the British Isles (Fig. 5). It may yet be found along the coasts of the Netherlands, Denmark, the Faroe Islands, Greenland and perhaps also deeper into the Baltic Sea. The occurrence along the Russian coast of the Barents Sea is uncertain (Palmgren, 1975).

Literature data are available from 7 countries: Iceland: records from 6 localities (Braendegård, 1958); Norway: records from 7 localities (Tambs-Lyche, 1964; Klausen, 1972; Palmgren, 1975; Ashmole & Planterose, 1979; E. Hauge, pers. comm.); Sweden: records from 3 localities (Kauri, 1965; Backlund, 1945); West Germany: 1 record (Wiehle, 1960); British Isles: widespread but infrequent along the coasts (Bristowe, 1923, 1929, 1930, 1935a, b, 1939; Locket & Millidge, 1953; Cooke, 1967; Mackie, 1973; Locket, Millidge & Merrett, 1974; Merrett, 1975, pers. comm.; P. R. Harvey, pers. comm.); France: records from 4 localities (Berland, 1924; Simon, 1926; Denis, 1939).

Recently the species has been found in Belgium: Nieuwpoort, nature reserve 'De IJzermonding', 1♂, 3♀ on 5 July 1983, using 29 pitfall traps for 3 days (Bosmans, 1986).

Life cycle

Only a few data on the life cycle were found (Table 6). Adults seem limited to the period April-October, but not all British records could be included here. Locket & Millidge (1953) state that adults can be found during most of the year. Possibly the spider hibernates as egg or juvenile.

Habitat

Descriptions of the habitat of this remarkable spider can be found in the work of Bristowe (1923, 1929, 1930, 1935a, b, 1939, 1958), also discussed by Tambs-Lyche (1964). Bristowe found the species in abundance in somewhat aberrant coastal habitats such as Shags' (*Phalacrocorax aristotelis*) nests, in "caves where the sea washes through but does not reach the roof", in "deep and dark fissures of cliffs where the sea extends at high tide" and even below the high-tide level. Usually, however, *H. reprobus* is found under or among stones and seaweed (e.g. *Fucus vesiculosus*) in the high-tide zone. It also occurs under crusts of desiccated seaweed in the high-water mark zone (Denis, 1939). Only Locket & Millidge (1953) mention also salt flats and salt marshes as a suitable habitat. The fact that *H. reprobus* must be adapted to regular flooding of its

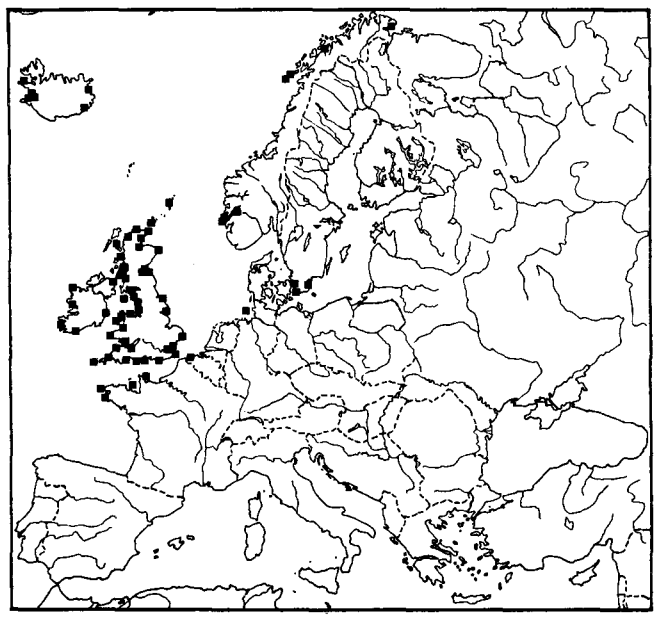

Fig. 5: Distribution map of *Halorates reprobus*.

	J	F	M	A	M	J	J	A	S	O	N	D	Total
Wiehle (1960)				±									1♂ 25♀
Tambs-Lyche (1964)						–							2♀
Kauri (1965)							×	×					
Klausen (1972)					–					±			8♂ 4♀
Mackie (1973)						+							
Palmgren (1975)								±					1♂ 2♀
E. Hauge (pers. comm.)						±							
Bristowe (1929)							±						
P. R. Harvey (pers. comm.)					±°	–	–	±		+			
P. Merrett (pers. comm.)					+								
Belgium							±						1♂ 3♀

Table 6: Life cycle data on *H. reprobus*. + = adult male(s); – = adult female(s); × = adult(s); ° = subadult males.

habitat had already been noticed by Bristowe (1923) and Berland (1924). They observed how shelter was found in crannies or cracks under stones, and elsewhere among seaweed or pebbles where air is trapped. Consequently activity must be limited to the low-tide period, an adaptation also shown by other epilittoral, semi-marine invertebrates such as the beetle *Aepus robini* and the bug *Aepophilus bonnairei*.

In Belgium *H. reprobus* was recently found in the lower zone of a saltmarsh at the mouth of the river IJzer. For an impression of the exact habitat characteristics, places where the species was found are indicated on a transect through the saltmarsh (see Fig. 6), being: (1) vegetation with dominance of *Limonium vulgare* with 30% bare mud; (2) vegetation with dominance of *Puccinellia maritima* with some *Aster tripolium*, giving 100% cover; and (3) *Elymus athericus* vegetation with developed litter layer, also giving 100% soil cover.

Most striking is the fact that the saltmarsh of 'De IJzermonding' had been sampled intensively in the past for almost 9 years (within the framework of a field course in terrestrial ecology for students of the State University of Ghent), but never was one specimen of *H. reprobus* caught. So there is a high probability that this species is only a very recent invader of the saltmarsh. The presence of this spider on several small and large islands, sometimes far away from the continent, suggests a considerable dispersal capacity, probably as a passenger on drifting seaweed. It is most likely that one or more egg cocoons attached to seaweed give the best chances for a successful colonisation. After washing ashore the eggs may hatch and in a suitable habitat a small population may consequently arise. As for the presence of *H. reprobus* in cormorants' nests on rocks far above sea level, this may be the consequence of the use of seaweed by these birds as nesting material.

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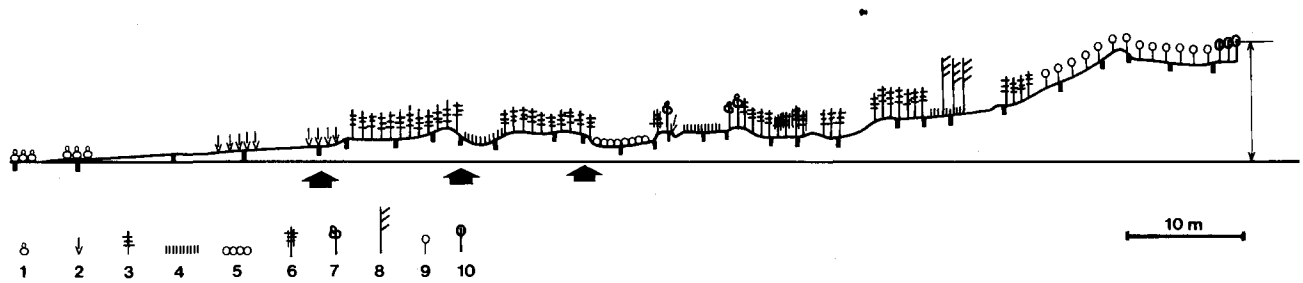

Fig. 6: Transect through the saltmarsh at the mouth of the river "IJzer", showing the positions of the pitfall traps (black squares) and the places where *Halorates reprobus* was captured (black arrows).
1 = *Spartina townsendii*; 2 = *Limonium vulgare*; 3 = *Elymus athericus*; 4 = *Puccinellia maritima*; 5 = rubbish washed ashore; 6 = *Halimione portulacoides*; 7 = *Aster tripolium*; 8 = *Phragmites australis*; 9 = *Lolium perenne* and *Arrhenatherum elatius* (dike); 10 = *Hordeum distichon* (field).

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