

## The distribution, status and habitats of *Dolomedes fimbriatus* (Clerck) and *D. plantarius* (Clerck) in Europe

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### Spiders, *Dolomedes plantarius*, distribution, habitats, Europe

**Abstract.** The status of *Dolomedes fimbriatus* (Clerck) and *D. plantarius* (Clerck) in Europe is discussed based on old and recent records. An assessment is made of the present distribution and habitat preferences of these two species in 18 western and central European countries. *D. fimbriatus* is widespread throughout the area discussed but *D. plantarius* is rare. The only places where *D. plantarius* appears to be locally numerous (though few sites are known) are in northwest Europe. *D. fimbriatus* is shown to have a much wider amplitude of exploitable habitats including places with no open water while *D. plantarius* appears to prefer lowland wetlands with large areas of open water.

### INTRODUCTION

*Dolomedes fimbriatus* and *D. plantarius* are the only representatives of this genus in Europe (Renner, 1987). *D. plantarius* is obviously closely related to its congener and in the past has frequently been regarded as a variety or subspecies of *fimbriatus* (Dahl, 1908; Roemer, 1928; Palmgren, 1939). By careful examination Renner (1987) has confirmed the view held by most arachnologists today that both species are distinct. The epigynes can be readily separated and the males are most easily recognised by the shape of the projection on the palpal tibia which is finely pointed in *fimbriatus* and *truncated* in *plantarius*. The variation in the shape of this projection is well demonstrated by Bonnet (1930) and Renner (1987) and seems to have been the feature used by other authors to create new species which were later synonymised. The tuft of forward-projecting hairs on the ventral side of the palpal tibia is much longer in *plantarius* than in *fimbriatus* (well illustrated in Roberts, 1985; Renner 1987).

Bonnet (1930) and Palmgren (1939) made detailed studies of the behaviour and breeding biology of the two *Dolomedes* species; Bonnet separated them taxonomically while Palmgren regarded *plantarius* as a colour form of *fimbriatus*. These two authors assumed that both species had the same habitat requirements. Bonnet (1930) dealt with two populations, "le Dolomède de Lourdes" and "le Dolomède de Toulouse", the former being *fimbriatus* and the latter *plantarius*. As he lived in Toulouse and had easy access to the canal where he found his specimens it is possible that his comments about habitat refer mainly to *plantarius*. A further difficulty about the Bonnet records and material sent to him from outside France was that he was prepared to name immature specimens. My experience is that there is no accurate method of distinguishing between the two European species when they are immature. Normal specimens of both species with pale yellow or gold lateral bands which may be broad or narrow seem to be identical in both species. There is also a considerable range in body size so this

factor cannot be used in determination. However, a small proportion of the populations of *plantarius* in the UK (11,8% of 127 specimens, Duffey, 1991) were completely brown without any trace of pale bands. In Britain this colour form has not been recorded for *fimbriatus* but in September 1991 immature *Dolomedes* collected from an "étang" in Haute Savoie, France appeared to be completely brown (F. Murphy and P. Merrett, pers. comm.). They were tentatively identified as *plantarius* but the only specimen to reach maturity in 1993 proved to be a female *fimbriatus*. Mrs. Murphy kindly sent this specimen to me and although it may have appeared bandless in the field, when closely examined very faint stripes could be detected. At one of the British *plantarius* sites I have never seen juvenile spiders without pale bands (although unbanded adults occur), which possibly suggests that banding may be lost in some specimens as the spiders grow. However, second and third instar *plantarius* are often very pale and the bands may not be easy to see unless the specimen is caught and examined closely.

### **DOLOMEDES IN SOME EUROPEAN COUNTRIES**

In the following account the available information on the status, distribution and habitat preferences of the two *Dolomedes* species will be summarised.

Unfortunately data are very sparse and it seems strange that two large spider species should not have attracted more attention from arachnologists. The quality of the records may in some cases be doubtful where they are based on immature specimens and there is also evidence of mis-identification in some instances.

Bonnet (1956) records *fimbriatus* as widespread all over continental Europe, extending as far east as Siberia. He says that *plantarius* has a similar distribution but is much less frequent. We do not know whether Bonnet based his comment on reliable determinations but the situation today seems to be very different, especially in the case of *plantarius* for which relatively few records exist (Fig. 1). In the following account I summarise available information for some western and central European countries. One hopes that arachnologists will be stimulated to provide more comprehensive and accurate data as it seems likely that both species are under-recorded. Most of the information presented is from correspondence with European arachnologists together with available publications.

#### **Britain and Ireland**

*D. fimbriatus* is widespread in Britain and Ireland, although records are not numerous (Locket et al., 1974; P. Merret, pers. comm.). It is associated with oligotrophic wetland such as bogs with *Sphagnum* spp., *Erica tetralix*, *Calluna* and sedges. In the north and west most sites are open, perhaps with dwarf shrubs. Further south the sites may be quite small, shaded by bushes or trees and *Myrica gale*. In most cases the area of open water is small or the ground may be only waterlogged. Only one locality has been reported recently in East Anglia, perhaps because oligotrophic marshes are scarce, but there are two old records.

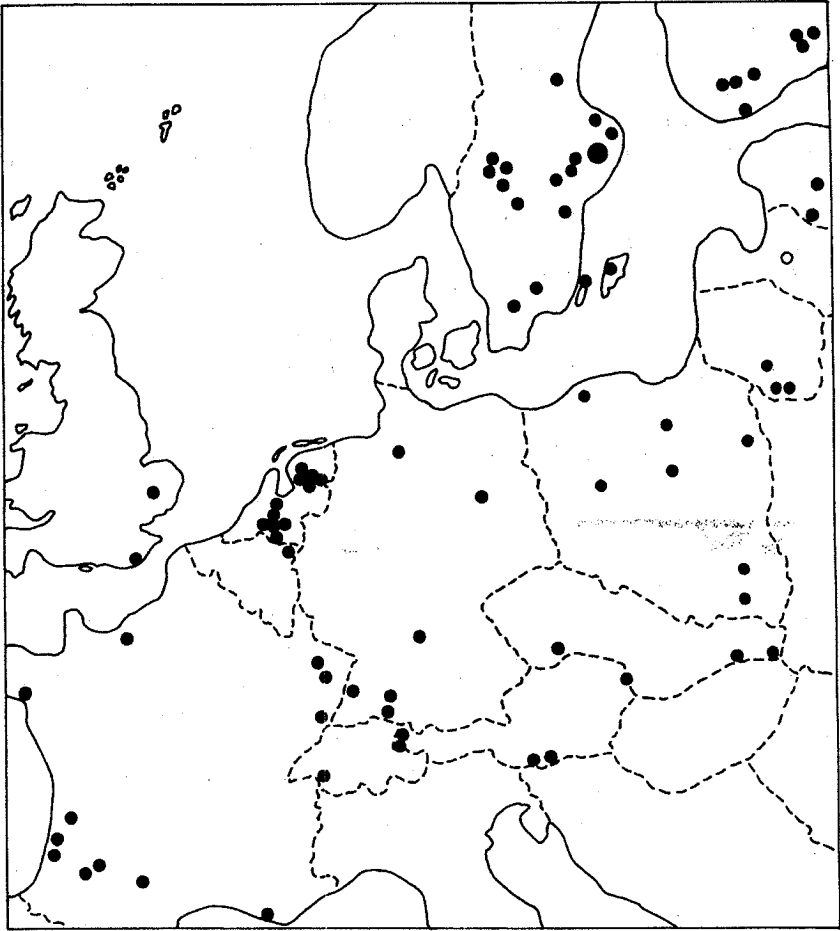


Fig. 1. The distribution of recent records (●) of *Dolomedes plantarius* in Western Europe. ○ Locality unspecified; ● Five records in vicinity of Stockholm.

*D. plantarius* is only known from two widely separated localities in southern England. The original site on the Suffolk/Norfolk border (Redgrave and Lopham Fens) was first discovered in 1956 (Duffey, 1958, 1960) and is a spring-fed sedge fen which today consists mainly of *Cladium mariscus* with *Carex* spp., *Calamagrostis canescens*,

*Juncus* spp., *Phragmites australis* and a little *Schoenus nigricans*. In 1956, when the fen was much wetter, part of the western section known as Little Fen was more open and dominated by *Schoenus*, *Sphagnum* hummocks, *Drosera* spp., *E. tetralix* and *Genista anglica*, although there is no record of *D. plantarius* being seen there at that time. This vegetation has virtually disappeared today due to the falling water table. *Plantarius* is found in the broad expanses of *Cladium* fen on pools, most of which are 2 to 4 m<sup>2</sup> in area, and originate from ancient peat cuttings. New pools have been dug in recent years by machinery to preserve the habitat of this species. Most pools favoured by *plantarius* are where there are no shading bushes. During the last 30 years the numbers and distribution of this species have sharply declined as water levels have fallen due to abstraction for a public water supply by a Water Authority borehole on the boundary.

The second British locality for *plantarius* is 125 km further south, on the Pevensey Levels not far from the Sussex coast. The habitat consist of water-filled dykes draining a vast reclaimed marsh. The land between the dykes is mainly sown pastures used for cattle-grazing. The only habitat suitable for *plantarius* is the fringing vegetation of the waterways and aquatic macrophytes with floating leaves. The marginal plants consist of grasses, sedges, *Juncus* spp., *Rumex hydrolapathum* and umbellifers such as *Sium latifolium* and *Oenanthe fluviatilis*. In the water are *Hydrocotyle vulgaris*, *Potamogeton* spp., *Sparganium erectum*, *Sagittaria sagittifolia* and (locally) *Stratiotes aloides*.

Unlike the site on the Suffolk/Norfolk border, the Pevensey Levels have a constant, good-quality water supply, although there is a drawdown in dry summers. Some of the dykes are cleaned out and deepened periodically so that only a proportion have the full range of aquatic plants favoured by this species. The habitat for *plantarius* is diversified by cattle trampling the margins of the dykes. When not excessive this produces a mosaic of water-filled hoof prints and grass and sedge tussocks; an environment which the spiders seem to favour (Evan Jones, pers. comm.).

The Pevensey Levels National Nature Reserve and the surrounding area (Site of Special Scientific Interest) cover 3501 ha and have 110 km of dykes and ditches, while Redgrave and Lopham Fens NNR is much smaller, only 125 ha, of which about a quarter to a third is at present suitable for *D. plantarius*. The water quality of each site does not differ very much but Redgrave and Lopham is significantly more acid (Table 1).

The Pevensey Levels is too large an area to census accurately but the population is probably of the order of several thousands, while the 1993 count for Redgrave and Lopham Fens (Smith, 1993) was a maximum of 59 spiders (adults and immatures) in the area where most pools still retain water. The latter population is clearly at risk while the water table is continually lowered by pumping from the adjacent borehole. Plans to close it are being made.

## Netherlands

There was much confusion over the identification of these two species by earlier authors. Helsdingen (1993) has checked all the old records and as a result of extensive fieldwork has been able to eliminate misleading or erroneous records and produce

**Table 1.** The water quality of Pevensey Levels NNR and Redgrave and Lopham Fens NNR. Data from Duffey (1991) and M. J. Emery (pers. comm.). Ranges in parenthesis. BOD = Biochemical Oxygen Remand, a measure of the amount of organic pollution in water calculated as the amount of oxygen taken up from a sample containing a known amount of oxygen kept at 20°C for 5 days. A high BOD value means much pollution. The figures quoted in this table show that all these areas are not polluted.

|                      | No. of samples | pH mean          | BOD mean          |
|----------------------|----------------|------------------|-------------------|
| Pevensey Levels      | 52             | 7.6<br>(6.8–8.4) | 2.23<br>(1.0–3.7) |
| Redgrave/Lopham Fens |                |                  |                   |
| Little Fen           | 28             | 5.7<br>(2.4–7.0) | 1.0<br>(0–3.5)    |
| Middle Fen           | 29             | 5.6<br>(2.3–6.0) | 2.9<br>(1.1–3.1)  |

up-to-date distribution maps. The range of both species has contracted and there is virtually no overlap in their distributions. *D. fimbriatus* is largely restricted to marshes and waterbodies in the higher ground of the eastern and southern fringes of the Netherlands while *plantarius* only appears to occur in the central lowland marshes. Several of the *plantarius* sites have large populations and all the best areas are now confined to nature reserves (P. J. van Helsdingen, pers. comm.). He recently recorded it from a water course with *Stratiotes aloides* in an abandoned peat cutting.

### Belgium

*D. fimbriatus* is known from about ten sites, mostly in the Ardennes and the northeast. It occurs in wet heathland and oligotrophic permanently wet grasslands (J.-P. Maelfait, pers. comm.). *D. plantarius* is recorded from only one restricted area in Limburg close to the Dutch border. The spider was collected along the narrow, sometimes steep, sides of a large artificial fishpond about 5 ha in area, the vegetation consisting mainly of *Carex acutiformis*, *Typha angustifolia* and *T. latifolia*, *Juncus effusus*, *Rumex hydrolapathum*, *Calamagrostis canescens* and other field-layer plants. In the open water is a patch of tall sedges where this spider had been caught in the past (Marc Janssen, pers. comm.).

In the same type of countryside, but over 1 km distant, a population of *D. fimbriatus* occurred around a small open pool (also artificial) surrounded by trees but not shaded. As the water level was low there was a wide margin of moss and very short vegetation but no *Dolomedes* were found there. However, females with egg sacs were collected 2–3 m away in taller patchy grass about 20 cm in height. The general vegetation in the *fimbriatus* area was similar to that recorded where *plantarius* was found. Both sites are fed from the same stream, but the *plantarius* locality is a fairly large lake which always maintains a good depth of water while the small *fimbriatus* pool dries out during the summer.

## France

*D. fimbriatus* is widely distributed in France, especially in the east (Bonnet, 1930). It is most probably under-recorded as a recent publication (Rollard, 1990) lists nine records for northeast France. Data on the habitat of this species in France are scarce. Simon (1914) mentions marshes, wet ditches, wet grasslands and peat diggings and also a river margin. In September 1991 immature specimens were found in a small marsh surrounded by trees in Haute Savoie (F. Murphy and P. Merrett, pers. comm.). The site was formerly a fishpond. I visited this area in June 1993 and found that open water had virtually disappeared, the vegetation consisted of *P. australis*, *Juncus* spp., grasses and other tall herbs. There was no trace of *Dolomedes*. In the same month I found several specimens of *fimbriatus* in a small mesotrophic fen occupying a narrow valley with forested sides, in the Vosges near Corniment. The vegetation was dominated by *Juncus* spp. and tall *Carex* spp. with grass in the drier areas. The water was shallow and the specimens were found around the bases of the stems of *Juncus* and *Carex*.

Bonnet (1930) listed six records of *plantarius* in the south of France and one in the north. Denis (1937) recorded a further specimen from Bouches-du-Rhône, Etang de Berre near St Chamas. In July 1979 I found a female with newly hatched young in the extensive marshes of the Parc Naturel Régional de Brière in Normandy. It occurred in the regrowth of grass and sedge (after earlier mowing) not far from the margin of a dyke. Further specimens were taken in 1993 (Murphy, 1994). Bonnet (1930) described the habitat of *Dolomedes* which we assume here to have been mainly *plantarius*. He collected them along the margins of the Canal du Midi in a rich vegetation of grasses and aquatic plants whose leaves extended over the surface of the water. He adds that the waterway habitat for *Dolomedes* should not have steep sides, the water must be clean and the locality fully exposed to sunlight. When I visited this canal with Dr. Bonnet in 1968 the water was dirty, there was little marginal vegetation and he said that *Dolomedes* (presumably *plantarius*) had long disappeared.

## Switzerland

*D. fimbriatus* is widespread in peat-bogs as well as in fen areas with *Cladium mariscus* and *P. australis* such as along the margins of Lake Neuchatel (C. Neet, pers. comm.). Maurer & Hänggi (1990) record this species from 13 out of 25 cantons. There are no records for the typical alpine areas.

*D. plantarius* is at present only known from one locality. In June 1971 I found specimens in the mesotrophic marsh of Gros Brassat nature reserve where the River Rhône enters Lake Léman. The marsh was a large open area dominated by tussocks of *Carex* spp. and grasses. My specimens were found on the shallow water between the tussocks and also in the vegetation. A second visit in June a few years later failed to find the spider as the water was too deep. Neet & Delarze (1992) refound *plantarius* in the same area and record that the Gros Brassat occurrence is the first for Switzerland since the beginning of the century.

## Germany

*D. fimbriatus* is widespread and common in all types of wetlands. F. Renner (pers. comm.) has recorded it in wet meadows far away from open water and also in water-filled cuttings in a raised bog. Renner (1987) records five localities for *D. plantarius* but a sixth has recently been discovered (F. Renner, pers. comm.). Four of the six are in southern Germany and habitat details are available for three—(1) in a Nature Protection Area in Baden-Württemberg where specimens were found on the bank of a eutrophic drainage ditch in a stand of *Phalaris arundinacea*; (2) from the margin of a small lake near Kisslegg (Renner, 1987) where a female was found sitting on a floating leaf of *Nymphaea alba*; (3) a specimen was caught in *Phalaris arundinacea* by a small pond near Offenburg in the valley of the Rhine (F. Renner, pers. comm.).

## Austria

Bonnet (1956) includes four publications referring to *fimbriatus* localities but none later than 1898. Thaler (1981) mentions several other records between 1967 and 1979 and comments that it is found boggy wetlands. *D. fimbriatus* would appear to be widespread, occurring up to 1200 m altitude, but there are relatively few records. Renner (1987) records a male from a lake side at Lunzer See in the calcareous Alps of Lower Austria at 600 m a.s.l.

Bonnet (1930) refers to an 1852 record of *plantarius* from the region of Vienna and in the museum of that city he found specimens collected in two other lowland areas. Steinberger (1985) records a male from Moosburger Teich in Carinthia and a male from Vorarlberg, Reinspitz. K. Thaler (pers. comm.) received an adult female from Faak am See, also in Carinthia, in 1988. He comments that all these localities are warm lowland lakes, characteristically mesotrophic-oligotrophic. These records suggest that *plantarius* is essentially a lowland species while *fimbriatus* can exploit suitable habitats at higher altitudes.

## Poland

Both species of *Dolomedes* are recorded for Poland (Staręga, 1971) including seven localities for *D. plantarius*, all widely scattered through the country. *D. fimbriatus* is widespread, having been recorded in 15 out of 26 districts and sub-districts all over Poland (Prószyński & Staręga, 1971).

## Czech Republic and Slovakia

Prof. J. Buchar (pers. comm.) has made an up-to-date assessment of the records for *Dolomedes* in these countries. *D. fimbriatus* is widespread though most of the records are from the Czech Republic. Data are available for 27 records but a few from the 19th century and those based on immature specimens cannot be verified. Where the habitat was recorded, six are from peat bogs, seven from margins of ponds, one from a lake margin, one from a brook margin, two from sweeping in wet meadows, and one from alder carr.

*D. plantarius* appears to be rare, as Prof. Buchar lists four occurrences, of which only one can be verified. Of the other three, two are from the 19th century (1857, 1891) and recorded by Bonnet (1930) and the third was a juvenile specimen without

pale bands taken on the marshy margins of the River Tisa. Adult specimens are needed before this record can be accepted. The verified occurrence is for a male taken in 1980 by the margin of a pond in a mesotrophic wetland in south Bohemia (Igt. V. Růžička).

### Italy

Bonnet (1956) lists numerous publications referring to *D. fimbriatus* in Italy, ranging from 1790 to 1936. Renner (1987) quotes four fairly recent records between 1966 and 1969 for localities in northern Italy. He also shows that *D. italicus* Thorell 1875 is a synonym of *D. fimbriatus*.

Bonnet (1956) quotes four 19th century publications for *D. plantarius* and others for 1902 and 1936. No further information is available.

### Sweden

*D. fimbriatus* is found throughout the country and has a wide habitat amplitude, being found in wet areas by lake margins and other waterways as well as in bogs and fens, preferably with open water. Young stages of *fimbriatus* can also be found in rather dry areas away from wetlands (T. Kronestedt, pers. comm.). *D. plantarius* is scarce but known from a number of sites in south and central Sweden, where it has been found in marshy vegetation such as the shores of lakes. Specimens have been collected recently (T. Kronestedt, pers. comm.) in *Carex* spp. and *Phragmites* vegetation in five localities around Stockholm (Fig. 1).

### Norway

Hauge (1989) in his list of Norwegian spiders records *D. fimbriatus* from south, central and northern Norway as far as Finmark. Collett (1875) describes *D. fimbriatus* as occurring "in humid places, frequent in moss and Carices at least north to Nordland" (65°).

Collet (1875) also records a female *D. plantarius* taken in the vicinity of Oslo but E. Hauge (pers. comm.) thinks it may be a mis-identification. There is no other information about this species in Norway.

### Finland

Palmgren (1943) described *D. fimbriatus* as widespread in Finland. His distribution map shows that there are many more records for the southern half of the country. Nevertheless it reaches Russian Karelia and the southern Kola peninsula. Palmgren (1943) did not distinguish between the two species but his drawing of the "*plantarius* type" of *fimbriatus* shows it to be uniform brown and he says that there are intermediate forms between this and the normal one with lateral bands.

The "*plantarius*" type was, according to Palmgren (1939), a quarter as numerous as *fimbriatus* and both forms were said to occupy similar habitats. Palmgren describes the habitat as peat bogs with a well-developed vegetation of grass, reed and herbs. Open water is not necessary but preferable. Bogs with a uniform ericaceous shrub vegetation are not favoured. This description is probably biased in favour of *fimbriatus* because this species was more numerous in the area where Palmgren worked. The Palmgren

*Dolomedes* collection cannot be found in Helsinki museum (S. Koponen, pers. comm.), but the museum has provided five recent records from three localities of *D. plantarius* in Finland (Tino Pajunen, pers. comm.)—Juva one female 1973 in old boat, Sulkava one female 1980 (no habitat data), Siuntio one female 1993 sandy lake shore with grassy vegetation (Fig. 1). Terhivuo (1933) records captures of *plantarius* at Hauho in 1986, 1987 and 1989 but no habitat details are provided apart from “it appears to occupy (lake) shores”.

### Lithuania, Latvia and Estonia

*D. fimbriatus* appears to be well established in these Baltic countries though information is sparse. *D. plantarius* is recorded from two localities in Estonia (Vilbaste, 1987) and one in Latvia (M. Šternbergs, pers. comm.). The vast marsh in which *plantarius* has found in Latvia suggests that there could be a large population (M. Šternbergs, pers. comm.). *D. plantarius* was discovered in Lithuania in 1985 and since then has been found in two other localities (1986 and 1993) (V. Relys, pers. comm.). No details are available yet on the type of habitat. (Please note that these are the only three records for Lithuania.)

### Denmark

*D. fimbriatus* appears to be well established (Bonnet, 1956) although no references later than 1932 are quoted. *D. plantarius* was formerly recorded but is now believed to be extinct (S. Toft, pers. comm.).

### Spain and Portugal

Bonnet (1956) quotes an 1890 record of *fimbriatus* for Spain but none for *plantarius*. Neither species appears to have been recorded for Portugal.

## CONCLUDING COMMENTS

This brief survey shows that information on the distribution and habitat preferences of both *Dolomedes* species in Europe is very sparse, especially for *D. plantarius*. A number of points emerge from the survey.

1. Both species are probably under-recorded and some of the available records are either too old to be verified or doubtful as they are based on immature specimens. There has also been taxonomic confusion between the two species.

2. During the last 50 years the destruction of freshwater wetlands for land reclamation, the increasing isolation of those which survive, and the modification of waterways by canalisation and pollution, may be responsible for range contraction and fall in numbers.

3. *Dolomedes* species are not able to survive longer than a few days without drinking (Bonnet, 1930) so that dispersal to other areas when an isolated wetland dries out may lead to extinction. Nevertheless, the wide geographic range of *D. fimbriatus* and its ability to colonise man-made water bodies suggests that it has an efficient dispersal mechanism although nothing is known about this. The juveniles of *fimbriatus* have been collected from the foliage of bushes adjacent to wetlands and from relatively dry

areas but there are no records of similar behaviour for *plantarius*. There is no evidence that either species disperses by ballooning.

4. In Britain the habitat preferences of the two species appear distinct although this is based on only two sites for *plantarius*. The preference of *fimbriatus* for oligotrophic wetlands in Britain such as peat-bogs is confirmed by several correspondents on the continent of Europe. Similarly, there is general agreement that *plantarius* is a species of mesotrophic/eutrophic wetlands. This suggests that *plantarius* avoids water bodies with a low pH but this was not the case at Redgrave and Lopham Fens (Table 1), where pools with pH values between 2.4 and 4.0 were occupied.

5. The structure and nature of the vegetation may be more important than pH or even water quality. At Redgrave and Lopham Fen pools stained with iron hydroxides and the oily breakdown of decomposing vegetation were not necessarily avoided but there may have been no better-quality accessible water nearby. Nevertheless, there is a widely held view, including Bonnet (1930) and some of my correspondents, that polluted water discourages *Dolomedes*.

6. Although *fimbriatus* is associated with peat-bogs in Britain and elsewhere in Europe, it also occurs in mesotrophic wetlands where the vegetation consists mainly of grasses, sedges and rushes, e.g. in Belgium and France. There is also evidence from correspondents that *fimbriatus* is frequently found by small water bodies often in open wooded areas, or may be found in marshy ground without open water surfaces.

7. On the other hand, *plantarius* is often associated with larger water bodies or marsh areas with standing water, e.g. Rhône valley in Switzerland, La Grande Brière and (formerly) Canal du Midi, France, lake shores in Scandinavia and the vast marshland with many kilometres of dykes and drains at Pevensy Levels, Britain. At Redgrave and Lopham Fens, Britain, *plantarius* occurs on small pools but these are numerous and situated in a relatively large open marsh area.

8. *D. fimbriatus* ranges up to 1200 m (Austria) but *plantarius* is a lowland species almost everywhere.

9. There is no firm evidence, so far, that *fimbriatus* and *plantarius* coexist anywhere in Europe, although much more information is needed on the habitats of these two species. Carico (1973) shows that seven *Dolomedes* species in the USA often have "fairly well-defined habitats, especially where several species are found in the same stream systems", and that there are frequent invasions of microhabitats by other species. He shows that in the case of three common *Dolomedes* one prefers emergent vegetation in ponds, lakes and slow-moving streams, another is found by moderately swift streams with rocks and boulders, while the third occurs along small streams where most of the sunlight is shut out by tall woody vegetation. *D. fimbriatus* and *D. plantarius* may be separated by similar small variations in the wetland environment. Where *fimbriatus* occurs in a vegetation type usually associated with *plantarius* the sites are small wetlands, sometimes in open forested land which the latter species appears to avoid.

10. The available information on the distribution and habitats of the two *Dolomedes* species suggests that *fimbriatus* is more successful in adapting to a wide range of environmental situations, from lowland to montane regions, has a greater range in latitudinal distribution and a greater ability to utilise both small and large wetlands

whether or not there is open water. *D. plantarius* seems to be more restricted in its capacity to exploit these environmental parameters, preferring permanent open water, large expanses of marsh, and is intolerant of shading.

11. The two species are obviously closely related and it is tempting to speculate how one became widespread and common while the other remained generally rare. If they had a common ancestor which was formerly distributed throughout Europe, the upland and lowland populations of this ancient species may have become isolated from each other perhaps due to changing environmental conditions. The former may have evolved as *fimbriatus* and the latter as *plantarius*. When man changed the natural landscape by agriculture, forest clearance and marsh reclamation it was the upland population (*fimbriatus*) which was best able to adapt to the new conditions and expand its range while the lowland population (*plantarius*), inhabiting larger, more permanent wetlands, was not subjected to the same environmental pressures.

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