

A case of dimorphic males in *Troxochrus scabriculus* (Araneae: Linyphiidae), with notes on synonymy

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Abstract. *Troxochrus cirrifrons* (O. Pickard-Cambridge, 1871) is a **junior synonym** of *Troxochrus scabriculus* (Westring, 1851). Moreover, *Troxochrus scabriculus* is a species with dimorphic males, the nominate form is referred to as *T. scabriculus* forma *scabriculus*, and the second morph as *T. scabriculus* forma *cirrifrons*. No significant differences are present in the male palps or any sexual characters of these two forms. Likewise, the accompanying females of different populations exhibit no significant differences in general appearance or genitalia. We provide data on the taxonomic history, national checklists, habitat and distribution, as well as phenology to support the synonymy and to verify male dimorphism in *Troxochrus scabriculus*.

Keywords: Austria, dimorphism, linyphiid spider, Vienna

Zusammenfassung. Ein Fall von dimorphen Männchen bei *Troxochrus scabriculus* (Araneae: Linyphiidae), mit Anmerkungen zur Synonymie. *Troxochrus cirrifrons* (O. Pickard-Cambridge, 1871) ist ein **jüngeres Synonym** von *Troxochrus scabriculus* (Westring, 1851). Zudem handelt es sich bei *T. scabriculus* um eine Species, bei der es zwei männliche Morphen gibt, die Nominatform *T. scabriculus* forma *scabriculus*, und die zweite Form *Troxochrus scabriculus* forma *cirrifrons*. Es gibt keine erkennbaren Unterschiede in den männlichen Palpen zwischen diesen beiden Formen, und auch die Weibchen aus denselben bzw. aus verschiedenen Population weisen keine erkennbaren Unterschiede im allgemeinen Erscheinungsbild oder in den Genitalien auf. Die Synonymie und der Dimorphismus der Männchen von *Troxochrus scabriculus* wird durch Daten zur taxonomischen Erfassungsgeschichte und in nationalen Checklisten, zum Habitat und zur Verbreitung sowie zur Phänologie untermauert.

Taxonomical history

Westring (1851) first described *Troxochrus scabriculus* (sub *Erigone scabricula*) based on male and female specimens from Sweden. A decade later, Pickard-Cambridge (1860) described *Troxochrus scabriculus* sub *Walckenaera aggeris* from southern England and provided the following information with regard to the record date and locality (on page 174): “Adult males and females of this species were discovered by myself in abundance, during the summer of 1859, at the roots of grass and underneath rubbish on dry bank-sides, near Church Town, Southport, Lancashire”. Later, Pickard-Cambridge (1871) described a further new species, sub *Walckenaera cirrifrons*, based on a single male specimen, which clearly came from the same material in which he originally found *T. scabriculus* a decade earlier: “An adult male of this spider was captured, in company with *W. aggeris* (Camb.), at Southport, Lancashire, at the roots of grass &c., in June 1859.” It is important to note that (i) *T. scabriculus* and *T. cirrifrons* came from the same material sampled at the roots of grass in the summer of 1859 near Church Town, Southport, Lancashire; and that (ii) the specimens of *T. scabriculus* were present in abundant numbers, while only one male specimen of *T. cirrifrons* was identified in the same samples.

Simon (1884: 645) established the genus *Troxochrus* and was the first to suspect *Troxochrus scabriculus* of being dimorphic in the males, consisting of the typical form *scabriculus* and the second form *cirrifrons*. Simon stated that: “La forme *cirrifrons* se trouve toujours mêlée au type, mais elle est partout plus rare” [The form *cirrifrons* is always mixed with the type, but it is everywhere rarer].

More than a quarter of a century later, Pickard-Cambridge (1911) reopened the case of *T. scabriculus/cirrifrons* and attempted to negate the statement of Simon (1884) that *T. cirrifrons* is a dimorphic male form of *T. scabriculus*. Although

Pickard-Cambridge (1911) acknowledged that “the two species remarkably differ in the male sex”, he disagreed with the conclusion of Simon (1884), because “Simon relies chiefly, for the identity of *scabriculus* and *cirrifrons*, on the two forms being always found together (i.e., at the same time and place); but this I have by no means myself proved to be the fact”.

In the same work, Pickard-Cambridge (1911) described the female of *T. cirrifrons* which he believed to be different from the *T. scabriculus* female by drawing reference to illustrations of the epigynes (*T. scabriculus*, Plate A, Fig. 18 and *T. cirrifrons* Plate A, Fig. 19). Curiously, Pickard-Cambridge (1911) in his description to Plate A, placed a question mark in the figure captions before both species names, perhaps indicating uncertainty about any differences between the females. Nevertheless, Pickard-Cambridge (1911) managed to conclude that “on the whole *T. cirrifrons* still seems to me to be a distinct species from *T. scabriculus*”.

Oddly, Simon (1926), in a work which was completed by Lucien Berland and Jean-Louis Fage two years after Simon's death in 1924, recanted the original opinion of Simon (1884). Thus, in the identification key for the genus *Troxochrus*, *T. scabriculus* and *T. cirrifrons* were treated as different species (Simon 1926: 369). Nevertheless in our opinion, the drawings of the epigynes in Simon (1926) (*T. scabriculus*, Fig. 652, *T. cirrifrons*, Fig. 655) are as inconclusive as those in Pickard-Cambridge (1911).

Although *T. scabriculus* and *T. cirrifrons* were henceforth recognized as different species in World Spider Catalogs (see Roewer 1942, Platnick 1989), many arachnologists continued to infer that *T. cirrifrons* is perhaps a subspecies of the typical form *T. scabriculus* (e.g. Bristowe 1939: 75), or that it is a variety (e.g. Wiehle 1960: 466, Lockett & Millidge 1953: 264), or indeed a dimorphic form (Thaler 1986: 496) or at least a sibling species (Aakra et al. 2016). With regard to the females, Wiehle (1960: 466) stated that female specimens which were found with the two male forms cannot be distinguished from each other, not even with detailed vulva preparation. Consequently, in one of his following works, Wiehle (1961: 183) di-

stinguished between the nominate form *Troxochrus scabriculus* and the form *T. scabriculus cirrifrons*.

Almost three decades later, Roberts (1987) briefly summarized the debate surrounding *T. scabriculus/cirrifrons* and pointed out that the male *Troxochrus scabriculus* forma *cirrifrons* (page 74, Fig. 31b) differed from the typical form *Troxochrus scabriculus* (page 74, Fig. 31a) in the size and shape of the cephalic lobe and by the presence of long bristles lateral to each posterior median eye. According to Roberts (1987) there are, however, no significant differences in the male palps between these two forms, and accompanying females exhibit no significant differences in general appearance or genitalia. Concerning the females, there is only slight but insignificant variation in the epigynum of *T. scabriculus*. Roberts (1987) stated in his book on the spiders of Great Britain and Ireland that *T. cirrifrons* is a dimorphic male form of *T. scabriculus*, and he designated it as *T. scabriculus* f. *cirrifrons*. Nonetheless, he declined to synonymize the two species. Instead, he argued that this case would have to be ultimately resolved by breeding experiments.

Recently, Aakra et al. (2016) found two additional differentiating morphological features between the two forms, which they considered as two species with reference to the World Spider Catalog (2018). First, males of *T. scabriculus* possess an extra set of glandular openings on each side of the field of short hairs above the anterior median eyes (Aakra et al. 2016, Figs. 22A–D), while no such structures are visible in *T. cirrifrons*. Second, considerable differences were noted in the invaginations of the sulci, which are much larger in *T. cirrifrons* than in *T. scabriculus* (Aakra et al. 2016, Fig. 22E).

The case of *T. scabriculus/cirrifrons* is not the only taxonomic example within the family Linyphiidae of male morphs having different head forms within one species, without there being differences in genital morphology. Recently, Bosmans & Oger (2018) confirmed *Diplocephalus cristatus* as a dimorphic species, having two male morphs: *cristatus* and *foraminifer*. Other examples are *Diplocephalus conatus/jacksoni* and *Oedothorax gibbosus/tuberosus* (see Roberts 1987). Wunderlich (2008) added further examples of species from the family Linyphiidae, in which the male prosoma has two or more different shapes (i.e. lobes) and/or hairy areas, and he explicitly considered *T. cirrifrons* as a variation (or “form”) of *T. scabriculus* [*Troxochrus scabriculus* (= *cirrifrons*)].

Thus, the phenomenon of dimorphic males in spiders must be considered as an established fact. As a result of these considerations and based on the examination of our own material, we now follow the original assessment of Simon (1884) and conclude that the *cirrifrons* male is a second male morph of *T. scabriculus*. Since there are no differences in the genital morphology between male specimens of *cirrifrons* and *scabriculus*, and since there are no differences in the females of different populations, we consider *Troxochrus cirrifrons* (O. Pickard-Cambridge, 1871) to be a junior synonym of *Troxochrus scabriculus* (Westring, 1851) and consequently, the male morph *cirrifrons* as a second form of the nominal *T. scabriculus*.

We are not the first to arrive at this conclusion. For example, Müller (1984) clearly regarded *T. scabriculus* and *cirrifrons* as not being distinct species since their male genital morphology is identical, and he also did not consider them as sub-species (as suggested by Heimer 1976) due to their sympatric occurrence.

In several checklists *T. scabriculus* and *T. cirrifrons* have been treated as synonyms. Yet in the checklist of spiders of Germany, Platen et al. (1991) listed *T. scabriculus* and *cirrifrons* as two distinct species. In the checklist four years later, Platen et al. (1995: 36) considered *T. cirrifrons* as a synonym of the typical *T. scabriculus*; and again, in Platen et al. (1999: 25) *T. cirrifrons* is defined as a synonym of *T. scabriculus*. Notwithstanding the fact that *T. cirrifrons* was recorded in Berlin (von Broen 1977), Platen & von Broen (2002) no longer listed *T. cirrifrons* in the checklist of the spiders of Berlin.

Likewise, in the checklists of the spiders of Russia, Mikhailov (1996: 99; 1997: 102; 2013: 96) consistently mentioned *T. cirrifrons* (O. Pickard-Cambridge, 1871) as a (junior) synonym of *T. scabriculus* (Westring, 1851). This is also true in the provisional atlas of the British spiders by Harvey et al. (2002). In the caption to the map of records of *Troxochrus scabriculus*, Harvey et al. (2002: 116) commented that any record submitted to the scheme as *T. cirrifrons* (O. Pickard-Cambridge, 1871) under BRC number 15301, is now considered to be a form of male *T. scabriculus*. Thus, we can summarize that *T. cirrifrons* (O. Pickard-Cambridge, 1871) has been repeatedly considered to be a form of male *T. scabriculus* in several national spider checklists.

However, there are spider checklists of other countries or regions where *T. scabriculus* and *T. cirrifrons* are still listed as separate species, e.g. in the departments “Nord” and “Pas-de-Calais” of northern France (Lecigne 2016: 56), in Flanders (Maelfait et al. 1998: 136), Belgium (Bosmans 2009: 52, Bosmans & van Keer 2017), the Netherlands (van Helsdingen 1999: 156, 2016: 111) and Bulgaria (Blagoev et al. 2002–2018); and of course, in the World Spider Catalog (2018) *T. cirrifrons* and *scabriculus* are still considered two separate species (see also Bosmans & Oger 2018: 52).

Material examined

The epigeic spider fauna of six overgrown gardening plots (study sites A–F) on the rooftop of the “Biozentrum Althanstraße” in Vienna, Austria, was examined from 8 April 2016 to 7 April 2017 by means of one pitfall trap per site (Milašowszky & Hepner 2017).

Troxochrus scabriculus/cirrifrons material: AUSTRIA: 100 ♂♂ (95 *scabriculus*, 5 *cirrifrons*), 34 ♀♀, Vienna, Alsergrund, Biocenter Althanstraße, UZA1, rooftop, overgrown gardening plots, ruderal sites, 176 m a.s.l., M. Hepner & N. Milašowszky leg. & det., M. Hepner collection.

After identifying the material of male *scabriculus* and *cirrifrons* available to us, we completed drawings of the prosomas in lateral and frontal views from both morphs (Figs 1a–d). Additionally, we provide drawings of the female genitalia, i.e. the epigynum and vulva (Figs 2a–b). For views of the identical-looking palps of *scabriculus* and *cirrifrons* males see Figs 3a–b.

Habitat and distribution

Platen et al. (1991) listed *T. scabriculus* and *T. cirrifrons* as two distinct species, however, the information provided for both with regard to habitat was identical, i.e., plant formation: subatlantic broom-heathland, sand dry grassland, couch grass-meadows and persistent ruderal areas. Furthermore, both species or forms were characterized as xerophilic inhabitants of the soil-surface with a peak of activity in the summer

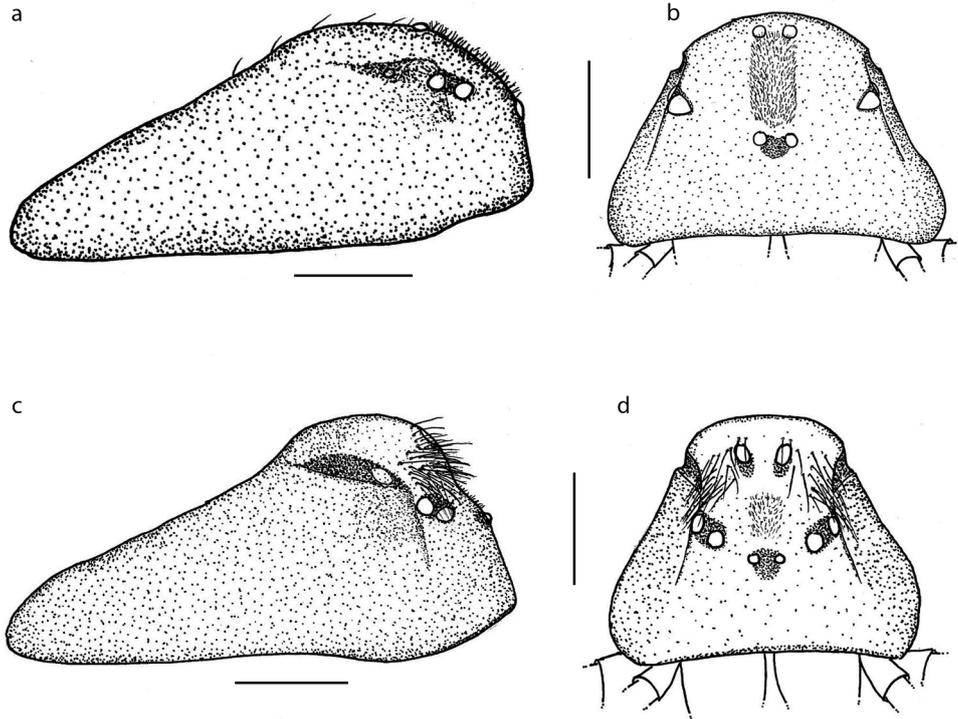


Fig. 1: *Troxochrus scabriculus* (Westring, 1851), male prosoma: **a.** forma *scabriculus*, lateral view, **b.** frontal view, **c.** forma *cirrifrons*, lateral view, **d.** frontal view. Scale bar 0.2 mm

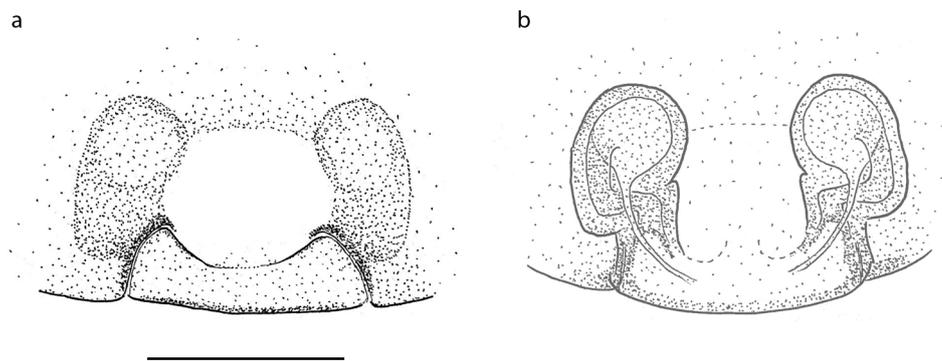


Fig. 2: *Troxochrus scabriculus* (Westring, 1851), female genitalia: **a.** epigynum, ventral view, **b.** vulva, dorsal view. Scale bar 0.1 mm



Fig. 3: *Troxochrus scabriculus* (Westring, 1851), male palps: **a.** forma *scabriculus*, lateral view, **b.** forma *cirrifrons*, lateral view (photos taken from Oger 2018)

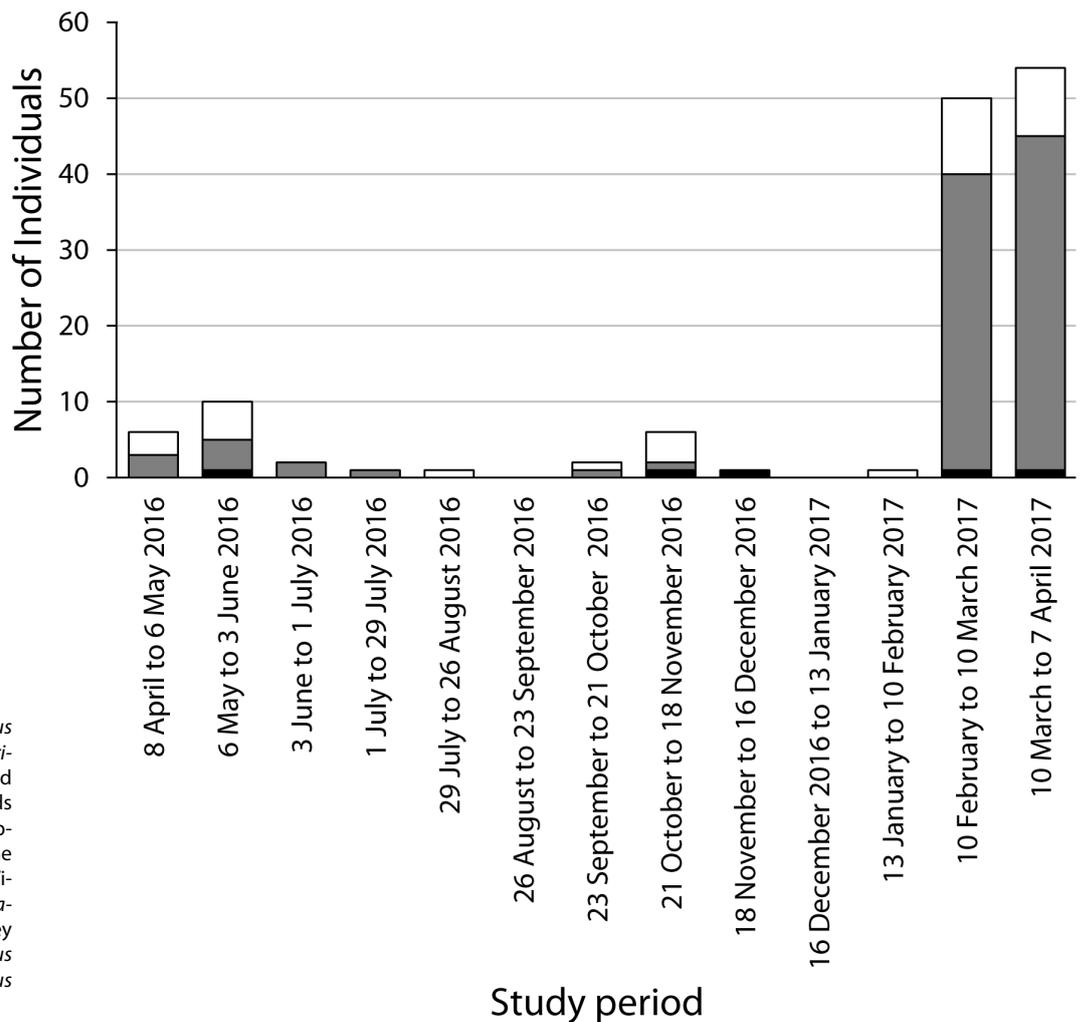


Fig. 4: Phenology of *Troxochrus scabriculus* males (forma *scabriculus* and forma *cirrifrons*) and females in 13 study periods between 8 April 2016 and 7 April 2017 on the rooftop of the “Biozentrum Althanstraße” in Vienna (Austria). Black bars: *T. scabriculus* f. *cirrifrons* males; Grey bars: *T. scabriculus* f. *scabriculus* males; White bars: *T. scabriculus* females.

months (mid-June to mid-September). Müller & Schenkel (1895) reported *T. scabriculus* and *T. scabriculus cirrifrons* adult male forms under the taxon *T. scabriculus*; both forms were collected from October to December in an alder forest along a meadow riverbank in Switzerland. Also, Thaler (1986) documented that both forms occurred together in a black alder forest near Vienna (Austria), where, 69 males of the form *scabriculus* and two males of the form *cirrifrons* were collected. Steinberger & Thaler (1990) collected one *cirrifrons* male in a small relictual floodplain forest strip on the left riverbank of the river Inn in Tyrol (Austria). Interestingly, *T. scabriculus* males were present in the same area, but not in the same study sites, in contrast to Thaler (1999), who considered the records in the two study sites as evidence of sympatric occurrence.

In Denmark, Larsen & Bøggild (1970) noted sympatric occurrences of *T. scabriculus* and *T. cirrifrons* from sand dunes and marram grass. Wiehle (1960) related that one male of the form *cirrifrons* was on the southern slope of the “Kyffhäuser” mountains in Germany, 4 October 1958, and another male in a salt meadow (*Salicornietum*) near Hecklingen-Anhalt, 12 June 1958. Von Broen (1977) reported *T. scabriculus/cirrifrons* from a “Ligusterhecke” [privet hedge] in Berlin, Germany. In the “Niederrhein”-Lowland, Otrembnik (1978) secured one *T. scabriculus* f. *cirrifrons* male and one female in a riparian grassland and seven *T. scabriculus* f. *cirrifrons* males and one female in a fertilized nutrient-rich meadow; however, no records were made of the typical male form. In Aldenhoven,

Germany, Esser (1997) collected two *cirrifrons* males together with 64 *T. scabriculus* specimens (probably mostly males) in a small ryegrass-plantain field margin strip (300 m length, 3 m width) situated between an arable field and an asphalt road. In Renkum, a town in the eastern Netherlands near Arnhem, van Helsdingen & IJland (2008) discovered a single male in a former arable grassland field between 1 April and 31 October 2008. Dekkers-Scheutjens (2010) obtained 31 *T. scabriculus* males in a study site within a nature reserve southwest of Tilburg, together with three *cirrifrons* forms.

According to Harvey et al. (2002), *T. scabriculus* is restricted to dry habitats in the British Isles, such as calcareous grassland, quarries, river shingle, haystacks and bare ground. The spider is a typical inhabitant of sand dunes where it prefers dense clumps of marram grass; in gardens the species can be encountered on gravel paths (Harvey et al. 2002). Mikhailov & Trishina (2013) observed one *T. cirrifrons* male form co-occurring with one male and two females of *T. scabriculus* in a birch and lime tree plantation in the vicinity of Pushta (Mordovian Republic, Russia) on 19 August 2011. In Norway, *T. cirrifrons* inhabited the same type of habitat as *T. scabriculus*, i.e. open sand and shingle (= gravel) dominated localities near rivers, streams and the seashore (Aakra et al. 2016). Entling et al. (2007) compared 224 Central European spider communities along two major environmental gradients, i.e. shading and moisture. Within the shading gradient from open habitats to forests, *T. scabriculus* and *T. cirrifrons* had very similar

average niche positions in open habitats (Entling et al. 2007, Appendix S2), while within the moisture gradient their niche positions slightly differed; *T. scabriculus* could thus be considered as an inhabitant of mesic moist habitats, while *T. cirrifrons* as one of mesic dry habitats. However, niche width values indicate a wide niche range in both species/forms, i.e. a great niche overlap within the moisture gradient.

In the distribution maps of the “Nord” and “Pas-de-Calais” departments of northern France, six records exist of *T. cirrifrons* that overlap with the records of *T. scabriculus* to 100 % (Lecigne 2016). Of interest here is that fact that 26 of the overall 33 records of *T. scabriculus* were located on the coast (Lecigne 2016: 212). Furthermore, in Bulgaria, where *T. scabriculus* also occur, the first record of *T. cirrifrons* was made by Deltshev (2004) in a pine forest near Sandansky, where he uncovered three *cirrifrons* and no *scabriculus* males. Perhaps this exclusive occurrence of the form *cirrifrons* is the reason for its entry in the spider checklist of Bulgaria. Deltshev (2004) commented that the locality in Bulgaria is at the southeastern border of its range. However, Mikhailov (1996, 1997) previously documented *T. cirrifrons* [as a junior synonym of *T. scabriculus*] from Russia (e.g. Russian Plains, Urals, and Middle Siberia) and the Ukraine. Mikhailov & Trishina (2013) noticed one *T. cirrifrons* male form co-occurring with one male and two females of *T. scabriculus* in a birch and lime tree plantation in the vicinity of Pushta (Mordovian Republic, Russia) on 19 August 2011. According to Roberts (1987), *T. scabriculus* and *T. scabriculus* f. *cirrifrons* have a similar distribution throughout the British Isles. However, both forms do not always occur together, rather they are locally common in dry habitats. Thus, *T. scabriculus* and its form *cirrifrons* have a widespread but patchy distribution in much of Britain. In summary, both forms are extensive in western and central Europe, and their distribution range extends east to Russia and the Far East.

Phenology

Simon (1884) stated that the form *cirrifrons* is “commun au premier printemps dans les détritus humides” [common in early spring in moist litter]. Wiehle (1960) reported one male of the form *cirrifrons* from Germany, 4 October 1958, and another male, 12 June 1958. Larsen & Bøggild (1970) registered *T. scabriculus* males in June, July, August and October, and *T. cirrifrons* in June and August. Females were present in April, May, June, July, August and October. Thaler (1986) recorded one *cirrifrons* male in the period from 24 April to 5 May, and one *cirrifrons* male in the period from 5 to 19 May. Von Broen (1977) reported *T. scabriculus/cirrifrons* from urban ruderal areas in Berlin, Germany, and presented the phenology data of both forms over one calendar year. According to this data, *T. scabriculus* males occurred from the beginning of March until the end of November. Nine specimens of *T. cirrifrons* were collected in April, May and June. According to von Broen (1977), the activity peak of adult males was in April. Since the species could be found nearly all year round, von Broen characterized it as eurychronus. Adult females may be present throughout the year but there is a peak in recorded number of adults of both sexes in late spring and early summer, and again in the autumn (Harvey et al. 2002). Mikhailov & Trishina (2013) discovered one *T. cirrifrons* male form co-occurring with one male and two females of *T. scabriculus* on

19 August 2011. In our study, we noted that the highest peak of activity of *T. scabriculus* was in the months February and March (Fig. 3), which is about a month earlier than in the study from Berlin where the maximum lies between March and April (von Broen 1977). According to the phenology figure in Harvey et al. (2002), the activity peak in the United Kingdom seems to be in May.

Male morph ratio within populations

Simon (1884: 645) stated: “La forme *cirrifrons* se trouve toujours mêlée au type, mais elle est partout plus rare” [the form *cirrifrons* is always mixed with the type, but it is everywhere rarer]. Based on their findings, von Broen & Moritz (1965) arrived at the same conclusion that the variety *T. scabriculus cirrifrons* occurs in all populations of *T. scabriculus*. In general, this is true, although there are many exceptions (e.g. see the *T. scabriculus/cirrifrons* maps of Lecigne 2016). Roberts (1987) summarized the up-to-date data and concluded that *T. scabriculus* f. *cirrifrons* was rather less common than the typical form *T. scabriculus*. In general, this is true, but there are exceptions or even populations of *T. scabriculus* that consist purely of *cirrifrons* males. To give an example, Deltshev (2004) documented three *cirrifrons* males in a pine forest in Bulgaria without any *scabriculus* morphs.

Pickard-Cambridge (1860, 1871) was the first to quantify the ratio between the male form of *T. scabriculus* and *cirrifrons* as “abundant” to “one”. In our data set we obtained a ratio of 95:5 = 19:1. Thaler (1986) documented 69 males of the form *scabriculus* and two males of the form *cirrifrons* in a floodplain area near Vienna, Austria; hence, the ratio between the typical form and “*cirrifrons*” was about 35:1. Interestingly, in two relictual floodplain forests along the Inn River in Tyrol, Austria, Steinberger & Thaler (1990) counted about 45 *T. scabriculus* males in the study site “Kufstein” (large floodplain forest on the right river bank) and one “*cirrifrons*” male in the study site “Langkampfen” (small floodplain forest strip on the left river bank), i.e. both forms seemed co-occur in the same study area, but not in the same study sites. In Aldenhoven, Germany, Esser (1997) identified two *cirrifrons* males together with 64 *T. scabriculus* specimens (probably mostly males) in a small ryegrass-plantain field margin strip (300 m length, 3 m width) situated between an arable field and an asphalt road; hence the ratio of *scabriculus* and *cirrifrons* was at a maximum of 32:1, but probably a little lower due to the unknown number of females. Von Broen (1977) accounted for both *T. scabriculus* and *cirrifrons* from three urban ruderal areas in Berlin, Germany, (i) a “Ligusterhecke” [privet hedge], (ii) an “Erdbeerbeet” [strawberry patch] and (iii) a “Holzmehlfläche zwischen Ziegelbau und Holzschuppen” [an area covered with saw dust between a brick building and a woodshed]. In the privet hedge, the ratio between *T. scabriculus* and *T. cirrifrons* males was about 14:1 (164 *T. scabriculus*, 12 *T. cirrifrons*), while in the strawberry patch and the sawdust site only *T. scabriculus* specimens were captured. Von Broen (1977) also provided unpublished data on the ratio of the two forms from Greifswald, where he captured 10 *T. scabriculus* males and two *T. cirrifrons* males; hence, there the ratio was 5:1. Dekkers-Scheutjens (2010) collected 31 *T. scabriculus* males in a study site within a nature reserve southwest of Tilburg (Netherlands) together with three *cirrifrons* forms, i.e. the ratio was about 10:1.

Conclusion

It is evident that the synonymy of *T. scabriculus/cirrifrons* is not a taxonomically problematic case to resolve. Since both males and females from populations with co-occurring male forms are identical in their genital morphology, it is highly plausible that the different male morphs must represent two forms of the same species. It is also apparent that *Troxochrus scabriculus* (Westring 1851) is the typical form, while the later described form *cirrifrons* is a second male morph that must be designated *Troxochrus scabriculus* forma *cirrifrons* (O. Pickard-Cambridge, 1871). Based on further evidence from distribution maps, habitat preferences, phenology and appearance in populations (see above), it is obvious that Simon (1884) made the correct judgement from the very start.

Although breeding experiments would be desirable to clarify the status of the two forms of the male spider, as once recommended, we consider the taxonomic case of the dimorphic males in *T. scabriculus* to be closed and quote the famous fictional figure Sherlock Holmes: “We must fall back upon the old axiom that when all other contingencies fail, whatever remains, however improbable, must be the truth” (Doyle 1908).

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