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On the morphological separation of two sibling species: *Pardosa proxima* (*P. vlijmi* syn. nov.) and *P. tenuipes* (Araneae: Lycosidae)

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Abstract. Morphological descriptions of *P. proxima* (C. L. Koch, 1847) (= *P. vlijmi* den Hollander & Dijkstra, 1974, **syn. nov.**) and its sister species *P. tenuipes* L. Koch, 1882 (= *P. proxima* auct.), a pair of species hardly distinguishable on a morphological basis but easily separable through behavioural characters, are given. The identification on an ethological basis allowed us to study the morphology of the males and to point out the morphological characteristics that can be used to discriminate the two species. Moreover, the examination of type material of *Pardosa proxima* and *P. tenuipes*, together with details given in the original descriptions, led us to conclude that *P. vlijmi* is a junior synonym of *P. proxima* and that *P. tenuipes* has been long overlooked. However, females remain hard to distinguish due to high intraspecific variability in the shape of the epigyne, vulva and habitus. According to the examination of material from different parts of Europe, *P. proxima* seems to be quite common in Italy and in the south of the Balkan Peninsula (mainly Greece and Bulgaria) while *P. tenuipes* is more widely distributed in western Europe, reaching central Europe. Contact zones between the two species were found in north-western Italy and France. Far from detailing the precise distribution of the two species, we suggest that material previously identified as "*Pardosa proxima*" should be checked for establishing the occurrence of one or both species in different countries.

Keywords: ethospecies, synonymy, taxonomy, wolf spiders

Zusammenfassung. Zur morphologischen Unterscheidung von zwei Schwesterarten: *Pardosa proxima* (*P. vlijmi* syn. nov.) und *P. tenuipes* (Araneae: Lycosidae). Es werden morphologische Beschreibungen von *P. proxima* (C. L. Koch, 1847) (= *P. vlijmi* den Hollander & Dijkstra, 1974, **syn. nov.**) und ihrer Schwesterart *P. tenuipes* L. Koch, 1882 (= *P. proxima* auct.) präsentiert. Es handelt sich um ein Artenpaar, das morphologisch nur schwer, aber durch ihr Verhalten leicht zu unterscheiden ist. Die Bestimmung auf ethologischer Basis ermöglichte uns die Morphologie der Männchen genauer zu untersuchen und morphologische Merkmale zu finden, die es möglich machen die beiden Arten zu trennen. Weiterhin führte die Untersuchung von Typusmaterial von *Pardosa proxima* und *P. tenuipes*, zusammen mit in den Originalbeschreibungen genannten Details, zu dem Schluss das *P. vlijmi* ein jüngeres Synonym von *P. proxima* ist und dass *P. tenuipes* lange übersehen wurde. Jedoch bleiben die Weibchen, bedingt durch eine hohe intraspezifische Variabilität der Form von Epigyne und Vulva sowie ihrem Habitus, schwer unterscheidbar. Nach Untersuchung von Material aus verschiedenen Teilen Europas scheint *P. proxima* in Italien und dem Süden der Balkanhalbinsel (vor allem in Griechenland und Bulgarien) häufig zu sein, während *P. tenuipes* im westlichen Europa, bis Mitteleuropa, verbreitet ist. Kontaktzonen beider Arten sind aus Nordwest-Italien und Frankreich belegt. Bisherige Nachweise von "*Pardosa proxima*" sollten überprüft werden um die genaue Verbreitung beider Arten in den verschiedenen Ländern zu belegen.

Pardosa C. L. Koch, 1847 is the largest genus within the family Lycosidae with 549 known species and subspecies (WSC 2018) and represents one of the largest spider genera in the world. Most of the species have been placed in informal phenetic species-groups based on similarities in the copulatory organs (Zyuzin 1979, Dondale & Redner 1990, Almquist 2005, Chiarle et al. 2013).

The *proxima*-group includes nine Palaearctic species (Zyuzin 1979): *P. proxima* (C. L. Koch, 1847), *P. hortensis* (Thorell, 1872), *P. morosa* (L. Koch, 1870), *P. tatarica* (Thorell, 1875) [= *P. strigillata* sensu Zyuzin 1979], *P. atomaria* (C. L. Koch, 1847) [= *P. strigillata* sensu Buchar & Thaler 2002], *P. cribrata* Simon, 1876, *P. roscai* (Roewer, 1951), *P. pseudostrigillata* Tongiorgi, 1966 and *P. vlijmi* den Hollander & Dijkstra, 1974. The subspecies *P. proxima poetica* Simon, 1876 was also described from Europe, although Tongiorgi (1966) considered it doubtful since it does not display a well-defined geographical separation from the typical form (see remarks below on *P. proxima poetica*).

Zyuzin (1979) showed clearly outlined characters for the *proxima*-group such as a small, trapezoidal tegular apophysis and, in some cases, a sclerotized lamellar process on the palea in males. Females are characterized by a more or less narrow

anterior part of the septum, which is not connected with the anterior margin of the epigyne, and a broadened posterior part usually characterized by a triangular or anchor-like shape.

Historical background

Carl Ludwig Koch originally described *Pardosa* (sub *Lycosa*) *proxima* on material from unspecified localities in Greece in 1847. According to the original description, specimens were collected by the Bavarian explorer Franz Joseph Schuch (1808-1863). He was a military physician serving in the Bavarian Auxiliary Corps in Greece around 1834-1837. The Corps was stationed in Nauplia (now Nafplio, Ναύπλιο) in the Peloponnese. Supposedly, Dr. Schuch collected the type material of *Pardosa proxima* in the vicinity of Nafplio, as this locality was mentioned for other spiders collected by him and described by C. L. Koch (Koch 1847). The distribution of the species was later considered Euro-Mediterranean (Tongiorgi 1966, Vlijm 1971, den Hollander & Dijkstra 1974), although Dahl (1908) already considered that specimens from south-eastern Europe differed from specimens in south-western Europe. More specifically, Dahl (1908: 507) stated that the south-western specimens showed the same characters that were described by Koch (1882) for *Pardosa tenuipes*, such as the uniform colouration of the male femur of leg I: "Die Exemplare aus Südwesteuropa weichen in ganz bestimmter Weise ab. Beim Männchen von *Lyc. proxima* C. L. Koch sind die Schenkel des ersten Beinpaars stets viel dunkler als die andern, fast einfarbig, bei der südwesteuropäischen Form, welche L. Koch *Pard. tenuipes* genannt hat (vgl. 1881), sind die Vorderschenkel nicht dunkler und meist ähnlich wie die andern geringelt." [The specimens from south-western Eu-

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rope differ in a very specific way. Males of *Lyc. proxima* C. L. Koch have the femora of the first leg pair much darker than the others, almost unicolour, while in the form from south-western Europe, which L. Koch named *Pard. tenuipes* (cf. 1881 [should be 1882]), the first femora are not darker and annulated like the others].

In addition, it is worth noting that in the original description of *P. proxima*, C. L. Koch (1847: 53) mentioned and illustrated the dark femur of leg I of males (see Fig. 24, arrow). The same characteristic was also emphasized by de Lessert (1910: 516, footnote).

Den Hollander et al. (1972) published a paper on the occurrence of wolf spiders of the genus *Pardosa* in southern France. In this work, they observed that specimens previously identified as *P. proxima* showed different courtship behaviour compared to the typical form. They found these “aberrant specimens” in two localities (Pas d’Esculette, near Millau and Le Pin, near Auxerre), occurring together with *P. proxima* auct. and *P. hortensis*. According to den Hollander et al. (1972), the preliminary examination of the external genital structures of the “aberrant specimens” showed intermediate features between *P. proxima* auct. and *P. hortensis*. A few years later, the same material was examined by den Hollander & Dijkstra (1974) who described the “aberrant specimens” as a new ethospecies, *P. vlijmi* den Hollander & Dijkstra, 1974. Ethospecies are defined as pair or complex of species that can be hardly distinguished on a morphological basis, if at all, but are easily separable through behavioural characters (O’Connor et al. 2011, see also Vlijm 1986). The concept of ethospecies was defined by Emerson (1956) to describe species belonging to the genus *Apicotermes* (Isoptera) that could only be distinguished by the different construction of the nests. Among spiders, ethospecies are particularly known in wolf spiders (e. g., Uetz & Denterlein 1979, Cordes & von Helvesen 1990, Töpfer-Hofmann et al. 2000, Roberts & Uetz 2004). Chiarle & Isaia (2013) confirmed that courtship behaviour is a valuable tool to discriminate *P. proxima* auct. from *P. vlijmi*. However, it seems likely that the concept of ethospecies only reflects the inability of the researcher to detect useful morphological features.

The fact that the description of *P. vlijmi* as a new species was only based on courtship behaviour created nomenclature problems (see also Vlijm 1986). In particular, den Hollander & Dijkstra (1974) considered *P. proxima* auct. and *P. vlijmi* “morphologically indistinguishable”, implying that it was not necessary to see any type material of *P. proxima* C. L. Koch, 1847. In their work, they assigned the new name *vlijmi* to the less common species: “It therefore seems plausible that the widespread *P. “proxima”* refers to *Pardosa proxima* (Koch, 1848) [sic!] and that the aberrant specimens belong to a new species”. This kind of conclusion is rather arbitrary, given that there is no evidence that Carl Ludwig Koch had described *P. proxima* on specimens that performs the “normal” or the “aberrant” courtship behaviour observed by den Hollander & Dijkstra (1974). Although the authors provided some preliminary measurements of the body and the external genital structures, the drawings of palps and epigynes are poor and lack details. Moreover, given the apparent lack of documented morphological characters useful to distinguish the new species, it is likely that *P. vlijmi* has been routinely overlooked and often confused with its sibling species, *P. proxima* auct.

The results obtained in our previous studies on the courtship behaviour of these two species (Chiarle et al. 2013, Chiarle & Isaia 2013) concur with those reported by den Hollander & Dijkstra (1974). A closer examination of the specimens used for the behavioural analysis, together with the examination of material from different parts of Europe, revealed that the two species were in fact mostly confused in the past, and that a revision of the current nomenclature was needed. Further support for our assumption, linking morphological and ethological traits, is found in the molecular analysis previously conducted (Chiarle 2013), providing evidence for a clear separation of the two species, and justifying our use of morphological characters for species identification.

Here we present the results obtained from the morphological examination, we point out the characters useful for separating the two species and we revise their nomenclatural status.

Material and methods

Samples were photographed using an Olympus E-520 camera attached on an Olympus SZX16 stereomicroscope at the Zoological Museum, University of Turku and a Leica EC3 camera attached on an Leica MS5 stereomicroscope at the Department of Life Sciences and Systems Biology of the University of Torino. Dishes of different size with paraffin at the bottom were used to photograph the specimens in the correct position. Images have been subsequently fixed using “CombineZP” image stacking software. SEM micrographs were taken with a Hitachi S-4300 scanning electron microscope at the Swedish Museum of Natural History in Stockholm. The digital photo (stacked) in Fig. 26 was taken using an InfinityX camera on an Olympus SZX12 stereomicroscope at the Swedish Museum of Natural History in Stockholm.

Part of the examined material (marked with an asterisk*) has been formerly identified on an ethological basis (see Chiarle et al. 2013, Chiarle & Isaia 2013).

For both species, total body length, prosoma length and width, leg I length is reported (minimum and maximum). For males, we also measured palp tibia length and width. Description and measurements of females are based on presumed “pure” populations (i.e. populations where we only found males of one of the two species). All measurements are given in millimetres.

Apart from types, all studied materials are preserved at: Museo Civico di Storia Naturale di Verona, Italy (MSNVR); Museo Civico di Scienze Naturali “E. Caffi” di Bergamo, Italy (MCSNB); Museo Regionale di Scienze Naturali di Torino, Italy (MRSN); Entomology Department of the Royal Belgian Institute of Natural Science in Brussels, Belgium (RBINS); National Museum in Prague, Czech Republic (NMP), Collezione Isaia stored at Dipartimento di Scienze della Vita e Biologia dei Sistemi, University of Torino, Italy (CI), and Swedish Museum of Natural History of Stockholm, Sweden (NHRS).

Taxonomy

Family Lycosidae Sundevall, 1833

Pardosa proxima (C. L. Koch, 1847)

(Figs 1, 2, 5–10, 19, 21, 22, 24–26)

Lycosa proxima C. L. Koch, 1847: 53, figs 1453–1454 (♂♀)

Pardosa proxima (C. L. Koch): Tongiorgi 1966: 306

Pardosa vlijmi den Hollander & Dijkstra, 1974: 58, fig. 1: 1 (♂♀), courtship behaviour; Chiarle & Isaia 2013: courtship behaviour. Chiarle et al. 2013: 119, courtship behaviour. **Syn. nov.**

Brief description of the courtship behaviour. The male quickly raises and lowers the whole body on the spot, with a series of small jumps. The vibration turns into a conspicuous hopping, characterized by up and down movements of the whole body toward the female. At the same time, the male performs some very rapid movements of the opisthosoma, kept parallel to the substrate. During hopping, the palps and opisthosoma scrape on the substrate.

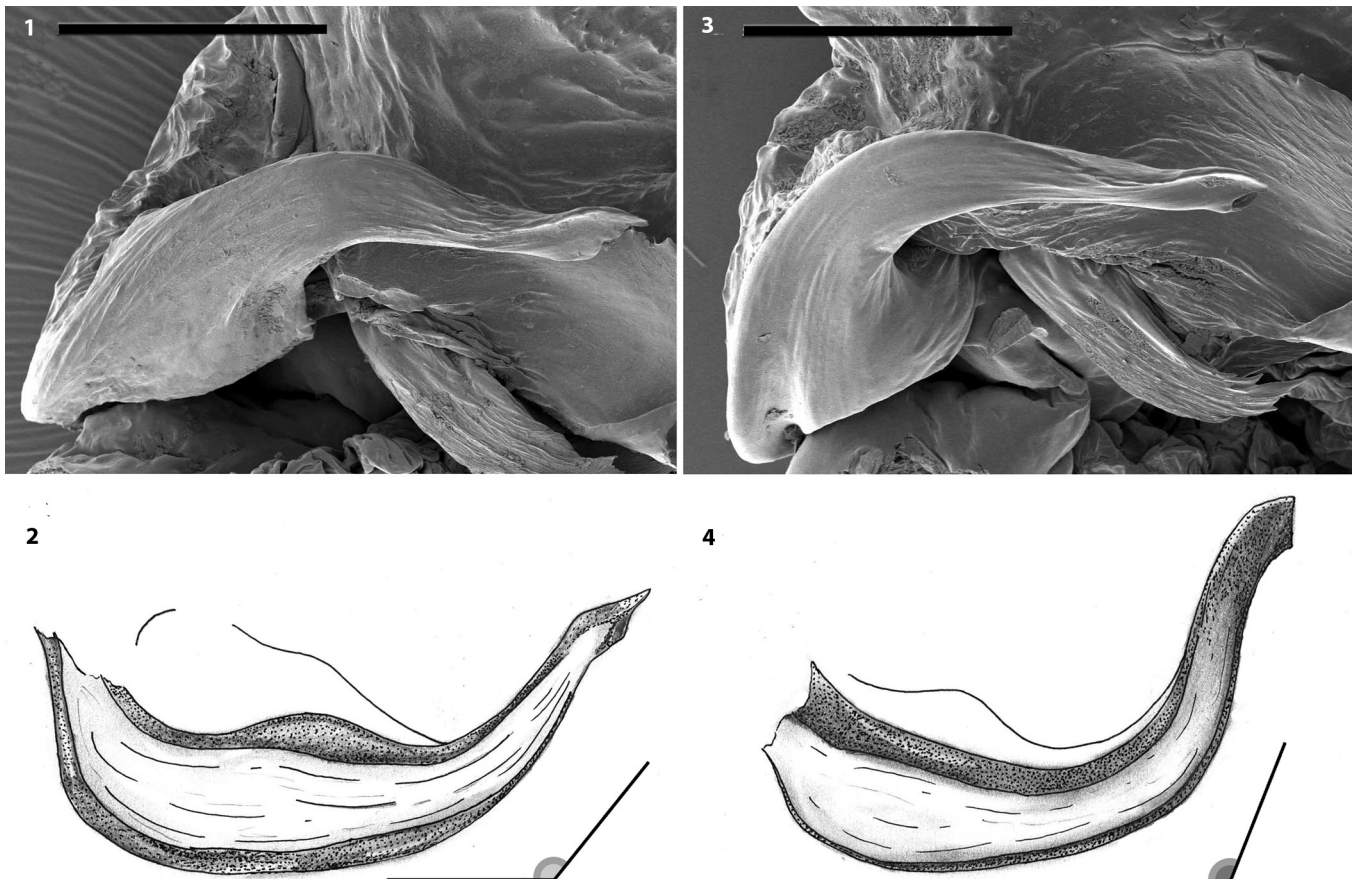
Type material. *Pardosa proxima*: Lectotype ♀ with old labels “*Pardosa proxima*” and “Griechenland Type” in Natural History Museum, London, here examined and designated: GREECE, possibly near Nafplio (cf. “Historical background” above). Another female stored in a separate tube labelled “*Lyc. proxima* type” (not old label) turned out to be *P. hortensis*.

Pardosa vlijmi: Holotype ♂ and allotype ♀ from FRANCE, Lozère, Pas d’Esculette and 2♀ paratypes from FRANCE, Yonne, Le Pin in Naturalis Biodiversity Center, Leiden, examined.

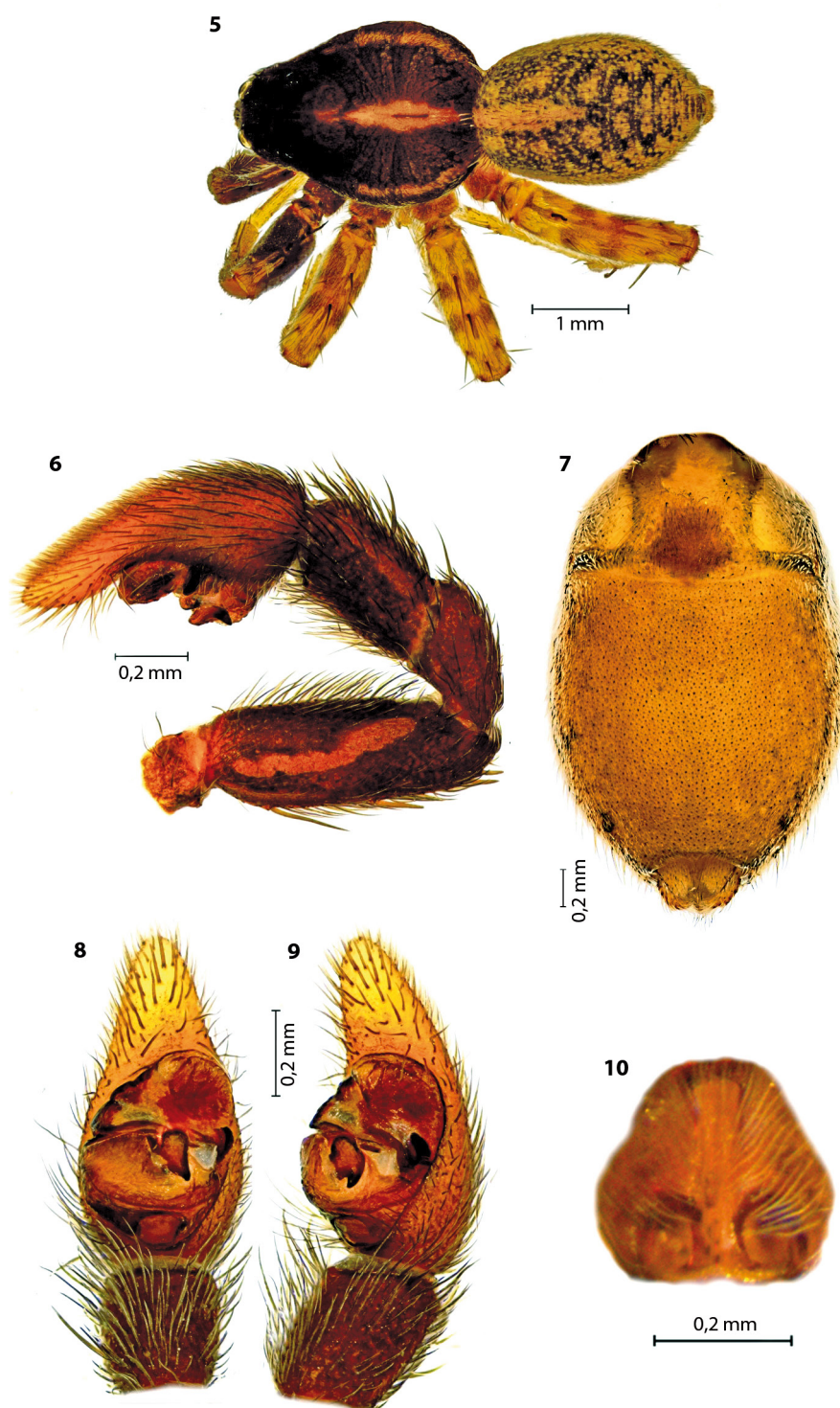
Other material examined. Asterisks (*) indicate specimen used in previous studies for behavioural analysis.

BULGARIA. Blagoevgrad: Sandanski, shore, 20.VI.1963, 16♂ (J. Buchar, NMP). – FRANCE. Corse: Haut-Asco, short grazed grass partly wet from water flow, 24.V.2005, 6♂ 3♀ (T. Kronstedt, NHRS). – GREECE. Eastern Mace-

donia and Thrace: Lake Mitrikou area, 1.IV.1988, 12♂ 17♀ (D. Cordes, NHRS). Crete: La Canea, Vryses, ashore with stones, 24.VI.1999, 4♂ 1♀ (J. Buchar, NMP); Moni Toplou, small basin, 12.V.2010, 1♂ (J. Buchar, NMP); also material in Bosmans et al. (2013). Peloponnese: Nomia, 16.VI.1974, 1♂ (V. Švihla, NMP); Tolo, drain, 20.VI.2000, 3♂ 3♀ (J. Buchar, NMP); Argos, brook, 22.VI.2000, 3♂ 1♀ (J. Buchar, NMP). – ITALY. Calabria: Cosenza, Cecita lake, 6.VIII.1958, 2♂ (F. Papi, coll. P. Tongiorgi); S. Giovanni in Fiore, Lorica, 24.VIII.1999, 1♂ (E. Ferrario, MSNB). Emilia–Romagna: Ravenna, Cervia, inside the city, IV.1991, 1♂ (P. Tongiorgi, MCSNB); Reggio Emilia, Regnano, meadow with *Medicago sativa*, 23.IV.1978, 4♂ 20♀, lake shore, 1♂ 1♀ (P. Tongiorgi, MCSNB); Viano, 275 m, 30.IV.1978, 1♂ 6♀ (P. Tongiorgi, MCSNB). Lazio: Roma, Campaegli, Cervare di Roma, Monti Simbruini, 18.VIII.2010, 11♂ 1♀ (F. La Casella, CI); Palatino hill, 14.III.1965, 1♂ (P. Brignoli, MCSNB). Liguria: LaSpezia, Bozzi, suburbs, 24.III.1957, 2♂ 2♀; Canaletto, ?V.1957, 1♂ (G. Mazza, MCSNB). Lombardia: Bergamo, Bariano, Serio river, 120 m, pitfall trap, uncultivated meadow, 8.III.–8.IV.2002, 1♂; 16.VI.–7.VII.2002, 3♂ (S. Ciocca, MCSNB); Bonate Sotto, Brembo river, 175 m, pitfall trap, dry grassland, 11.II.–23.III.2002, 2♂ (S. Ciocca, MCSNB). Zanica, Serio river, 190 m, pitfall trap, grassland with *Artemisia* sp., 8.III.–8.IV.2002, 2♂ (S. Ciocca, MCSNB); river shore, 1.IV.–13.IV.2003, 1♂ (S. Ciocca, MCSNB); Pavia, 20th naviglio, ?IV.1999, 1♂ (S. Ciocca, MCSNB); Piemonte: Alessandria, Pecetto di Valenza, poplar wood, 06.VII.2006, 1♂ (M. Isaia, CI); Asti, Canelli, vineyard, 4.VII.2009, 3♂ (E. Caprio,



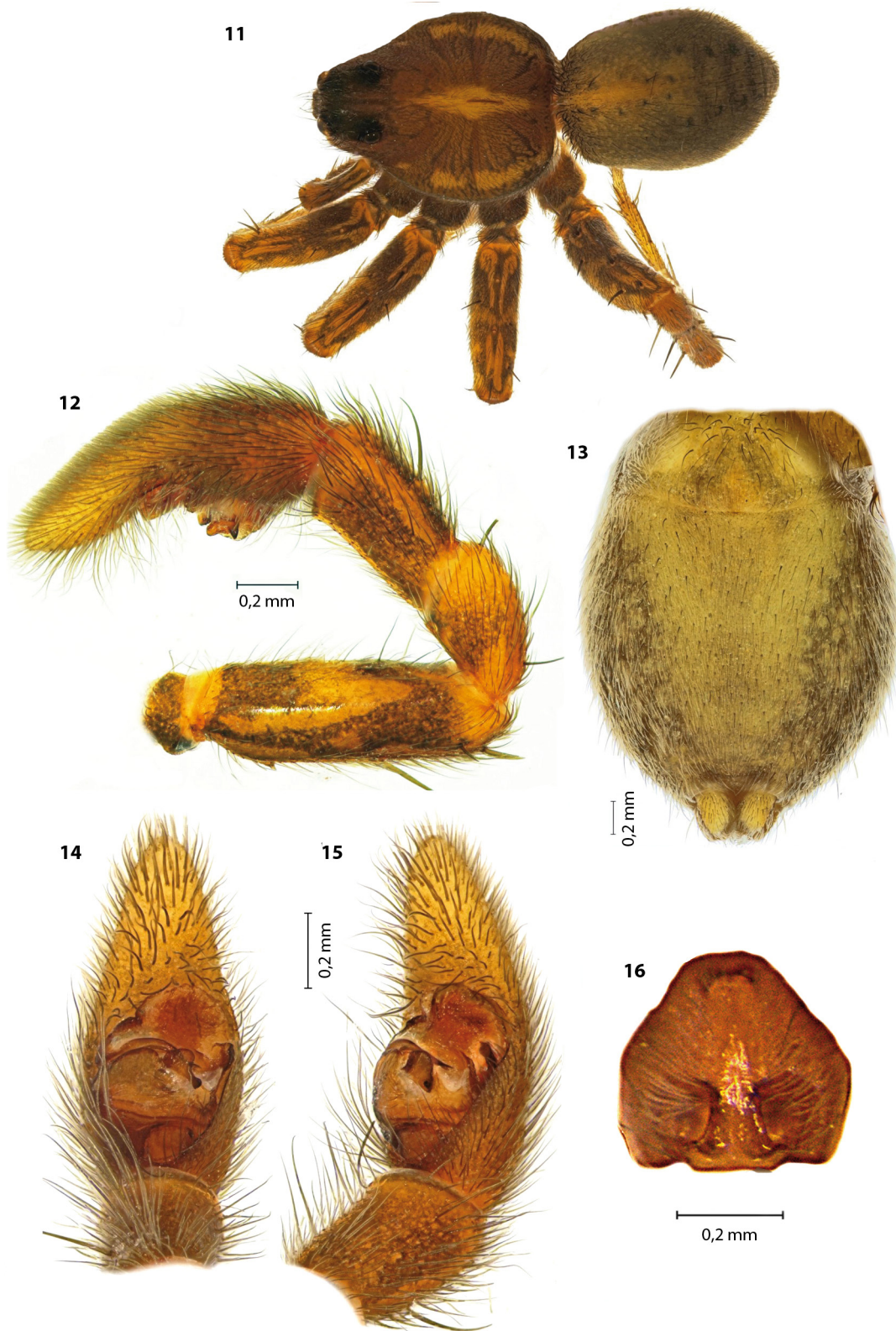
Figs 1-4: 1-2. *Pardosa proxima*, male: 1. SEM picture of the embolus; 2. embolus with inclination angle. 3-4. *P. tenuipes*, male: 3. SEM picture of the embolus; 4. embolus with inclination angle. Scale lines = 100 µm. 1-2. male from Vicoforte Mondovi, Cuneo (IT) 3-4. male from “La Mandria” natural park, Venaria Reale, Torino (IT)



Figs 5-10: *Pardosa proxima*, male: **5.** habitus; **6.** left palp retrolateral view; **7.** abdomen ventral view; **8.** left palp ventral view; **9.** left palp ventrolateral view; **10.** epigyne. **5-9.** male from Caldiero, (Verona, IT). **10.** female from Belfiore (Verona, IT)

CI); Cuneo, Vicoforte Mondovì, wet meadows, 3.III.2007, 2♂ (MRSN); 22.III.2009, 9♂ (A. Chiarle, CI)*; Guarene, meadows, 7.III.2009, 7♂ (A. Chiarle, CI)*; Torino, Ivrea, Meugliano lake, 30.IV.2010, 1♂ (M. Paschetta, CI). Puglia: Taranto, 6 km from S. Basilio, Lato river shore, 1961, 4♂ 20♀ (P. Tongiorgi, MCSNB). Sardegna: Cagliari, Muravera, Costa Rei bay, 24.VI.1987, 15♂ 14♀ (P. Tongiorgi, MCSNB); Nuoro, Belvì, Enazzu, 550 m, pitfall trap, hazel grove, 13.VII.–27.VII.2006, 1♂ 2♀; 21.II.–19.III.2007, 5♂; 19.III.–26.IV.2007, 1♂; 26.IV.–30.V.2007, 1♂ 3♀ (I.S.E., MCSNB). Toscana: Lucca, Pania della Croce, near the Mosceta lodge, 18.IV.1957, 1♂ (P. Tongiorgi, MCSNB); Sillano, Capanne di Sillano, swampy area, 4.VII.1965, 1♂ 1♀ (P. Tongiorgi, MCSNB); S.

Romano, Orecchiella wildlife reserve, 1200 m, 14.V.1967, 7♂ 22♀ (P. Tongiorgi, MCSNB); Galliciano hill, road to Monterpoli, 3.V.1968, 17♂ 30♀ (P. Tongiorgi, MCSNB); Pisa, humid meadow near the pool, 2.IV.1957, 2♂ (P. Tongiorgi, MCSNB); Caprona, Arno river banks, ?1962, 11♂ 7♀ (P. Tongiorgi, MCSNB); S. Rossore, field and scrub, 4.IV.1960, 1♂ 4♀ (P. Tongiorgi, MCSNB); meadow near the swampy area, 11.IV.1960, 5♂ 10♀ (P. Tongiorgi, MCSNB); meadows with salted pools, 19.IV.1963, 1♂ 9♀ (P. Tongiorgi, MCSNB); Ponte dei Biacchi, 3.III.1963, 4♂ 2♀ (P. Tongiorgi, MCSNB). Val d'Aosta: Pont-Saint-Martin, Holay, 4.VII.–28.VII.2011, 4♂ (M. Paschetta & D. Giuliano, CI). Veneto: Padova, Vò, Zovon, pitfall trap, 20.X.2010, 5♂ 2♀ (M. Zotti, MSNVR);



Figs 11-16: *Pardosa tenuipes*, male: **11.** habitus; **12.** left palp retrolateral view; **13.** abdomen ventral view; **14.** left palp ventral view; **15.** left palp ventrolateral view; **16.** epigyne. **11-15.** male from Bariano (Bergamo, IT). **16.** female from "La Mandria" Natural Park, Venaria Reale (Torino, IT)

Padova, Colli Euganei, pitfall trap, 10.VII.2010, 30♂ 20♀ (M. G. Paoletti, MSNVR); Verona, Natural History Museum inner court, 1♂ (Boscolo & Zaupa, MSNVR); Belfiore, Porto, uncultivated meadow, 22.III.2008, 3♂ 3♀ (F. Ballarin, MSNVR); Caldiero, Ca' Tantini, pitfall trap, uncultivated meadow, 15.VI.–5.VII.2008, 1♂ (F. Ballarin & D. Fattori, MSNVR); Cologna Veneta, 19.III.1967, 1♂ (Gioco, MSNVR). – MOROCCO. Agadir, lawn in the city, 9.XII.1998, 3♂ (T. Kronestedt, NHRS). – SPAIN. Tenerife: Aguamansa, 1000 m a.s.l., grassland at edge of conifer forest, 11.XII.1999, 10♂ 3♀ (T.

Kronestedt, NHRS); Puerto de la Cruz, lawn, 8.XII.1999, 16♂ 4♀ (T. Kronestedt, NHRS). – TURKEY. Mediterranean Region: Side, wet meadows, 1.VI.2002, 14 ♂ (J. Buchar & V. Céza, NMP).

Description. The general description is based on specimens for which we observed courtship behaviour (marked with an asterisk on the material section). Specimens from other localities were considered for comparison.

Male. Total length: 4.50–5.05. Prosoma: 2.18–2.6 long, 1.75–1.92 wide.

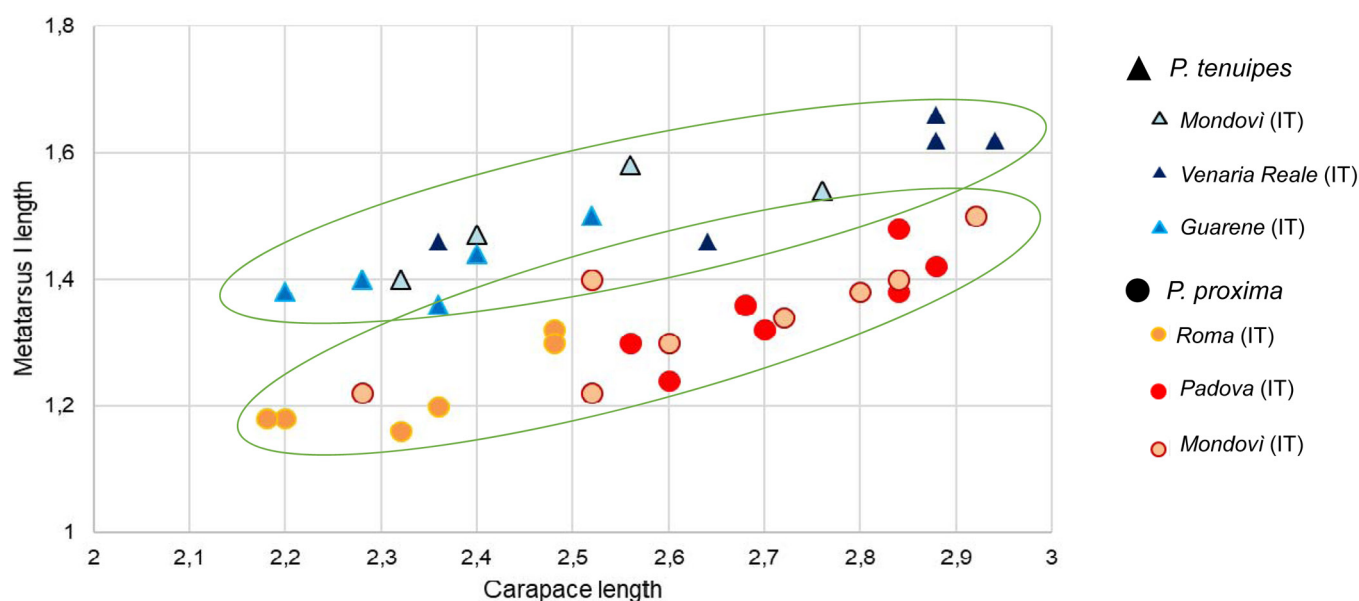


Fig. 17: Clustering of *Pardosa proxima* and *P. tenuipes* based on the carapace (x-axis) and leg I metatarsus length (y-axis).

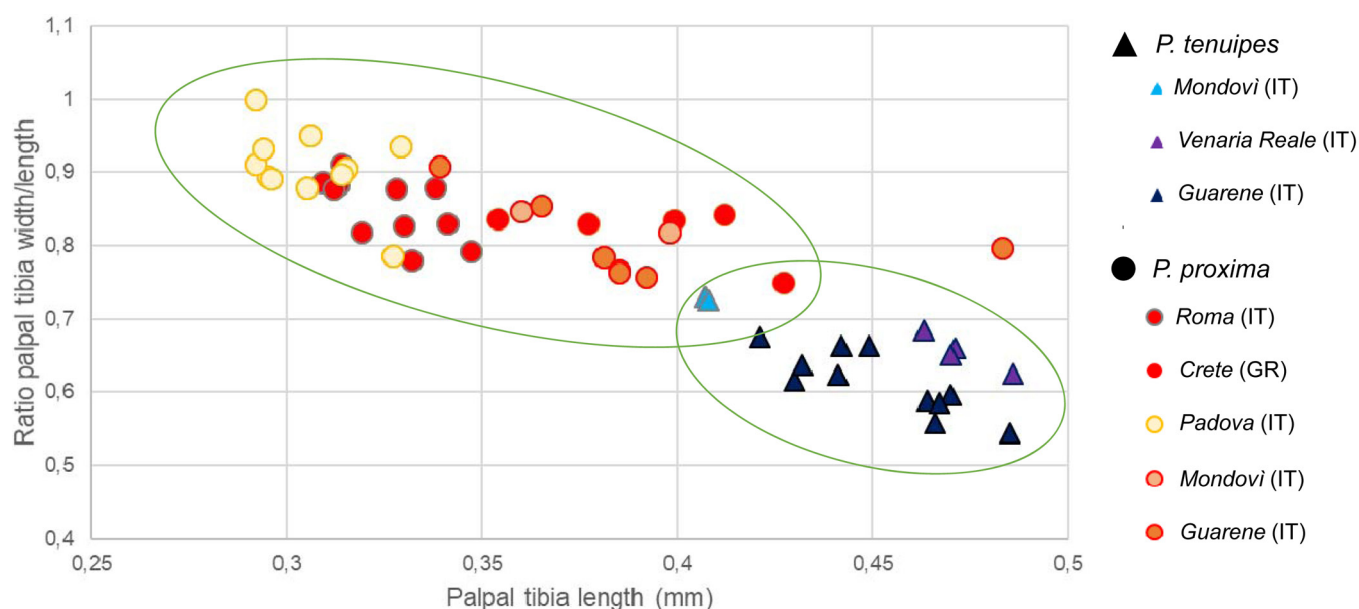


Fig. 18: Clustering of *Pardosa proxima* and *P. tenuipes* based on palpal tibia length (x-axis) and the palpal tibia width/length ratio (y-axis).

Prosoma dark brown with darker eye region, with a narrow yellowish median band, lateral bands of the same colour, broken into three distinct parts (Fig. 5). Eye region with short hairs. Clypeus brownish, chelicerae brown with yellow internal side. Sternum brown. Opisthosoma dorsally dark brown with a distinct lighter cardiac mark surrounded and followed by a couple of spots of the same colour, spots fused near the spinnerets (Fig. 5). Ventral side of the opisthosoma yellowish with short, stumpy dark hairs (Figs 7, 19, 21–22). Legs uniformly yellowish, femora with brown annulations (Fig. 5). Leg I with femur brown (Fig. 5) and with only few long hairs on tibia and metatarsus. Leg I length: Femur 1.5, Patella 0.70, Tibia 1.17, Metatarsus 1.30, Tarsus 0.91. Palp as in Figs 6, 8, 9 dark brown, cymbium brown with yellow distal part. Embolus as in Figs 1–2.

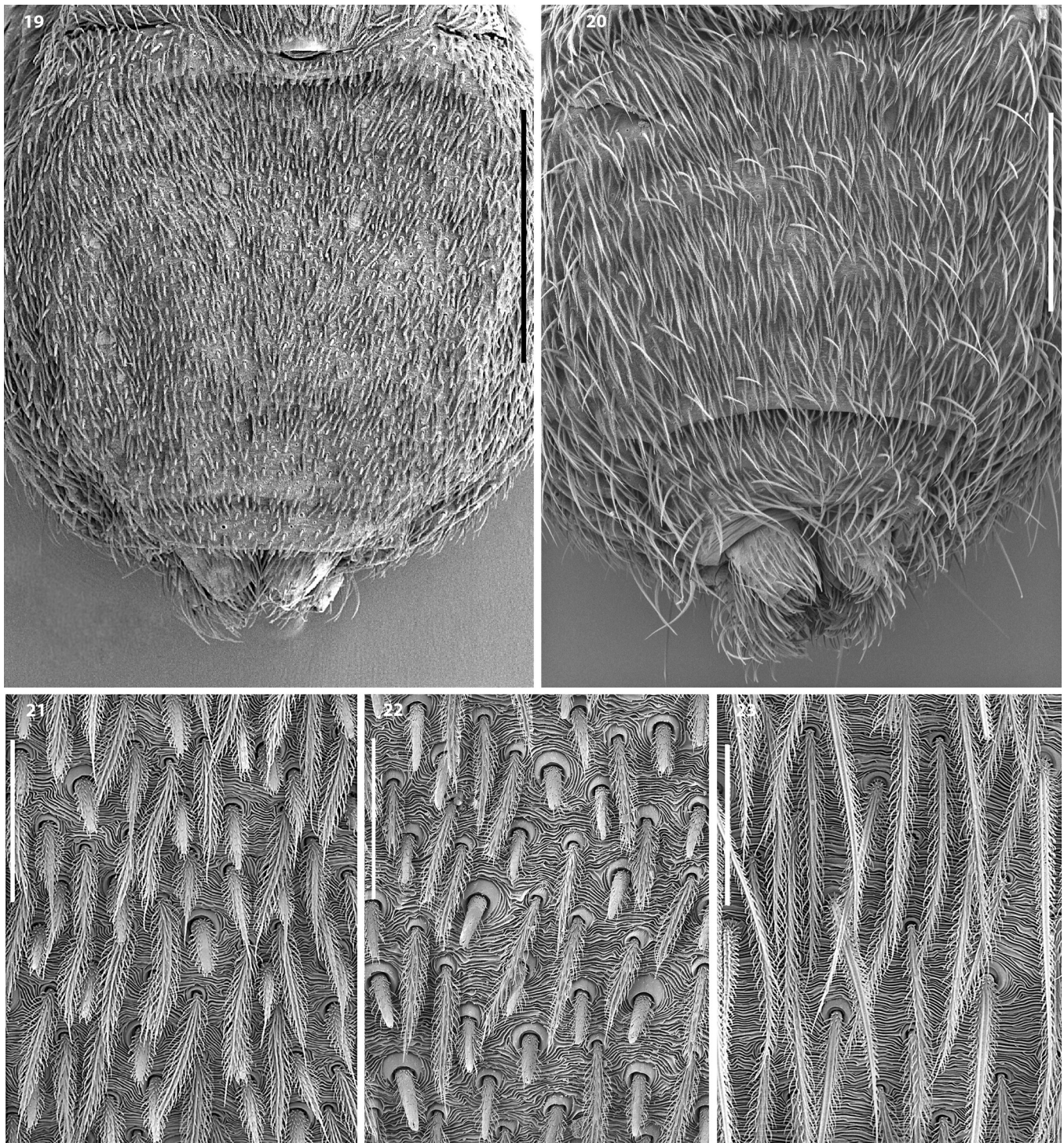
Female. Total length: 5.41–6.25. Prosoma: 2.16–2.40 long, 1.56–1.74 wide.

Prosoma dark brown with darker eye field. Median band yellowish, lateral bands broken into three distinct spots, same

colour as median band. Rarely, the lateral bands are unbroken. Clypeus and cephalic flanks yellow-brownish, chelicerae of the same colour. Sternum brownish sometimes with a lighter central area. Dorsal side of the opisthosoma dark brown with a distinct narrow cardiac mark, flanked and followed by 4–5 couples of yellow-brownish spots, which are fused near the spinnerets. The whole pattern is quite variable and, in some specimens, it is faint and not clearly visible. Ventral side of the opisthosoma light brown with two lighter V shaped strips. Legs uniformly yellowish brown with few faint brownish marks on femora and patella. Leg I length: Femur 1.54, Patella 0.76, Tibia 1.22, Metatarsus 1.24, Tarsus 0.89. Epigyne as in Fig. 10.

Habitat. Similar to *P. tenuipes*. The two species may co-occur in the same habitat.

Remarks. The stumpy (peg-like) dark hairs on the venter of the male opisthosoma show some variation in density, being somewhat less dense in males from Morocco and Tenerife in



Figs 19-23: SEM pictures of male abdomens (ventral side): **19.** *Pardosa proxima* showing short (light) and modified (dark) hairs; **20.** *Pardosa tenuipes* showing numerous long and thin (light) hairs, scattered with more erect (dark) hairs; **21.** *P. proxima*, close-up of abdominal hairs; **22.** as in Fig. 21 (note the shabbier modified (dark) hairs); **23.** *P. tenuipes*, close-up of abdominal hairs. Scale line = 500 μ m (19, 20), 50 μ m (21-23). **19, 22.** male from Campaegli (Roma, IT); **20, 23:** male from "La Mandria" natural Park, Venaria Reale (Torino, IT). **21.** male from Padova (IT)

comparison with males from e.g., Greece, and being slightly longer in some males from Tenerife.

***Pardosa tenuipes* L. Koch, 1882** (Figs 3, 4, 11-16, 20, 23)

Pardosa tenuipes L. Koch, 1882: 649, fig. 24 (δ).

Lycosa proxima tenuipes Dahl 1908: 425, fig. 81 (δ ♀). Dahl & Dahl 1927: 33, figs 81-82 (δ ♀).

Pardosa proxima tenuipes Lessert 1910: 515.

Lycosa proxima Locket & Millidge 1951: 267, fig. 130C-D, G (δ ♀).

Pardosa proxima den Hollander et al. 1972: 79, fig. 1 (δ ♀).

Pardosa proxima Loksa 1972: 17, fig. 12F-J, 25A, 26C-D (δ ♀, S).

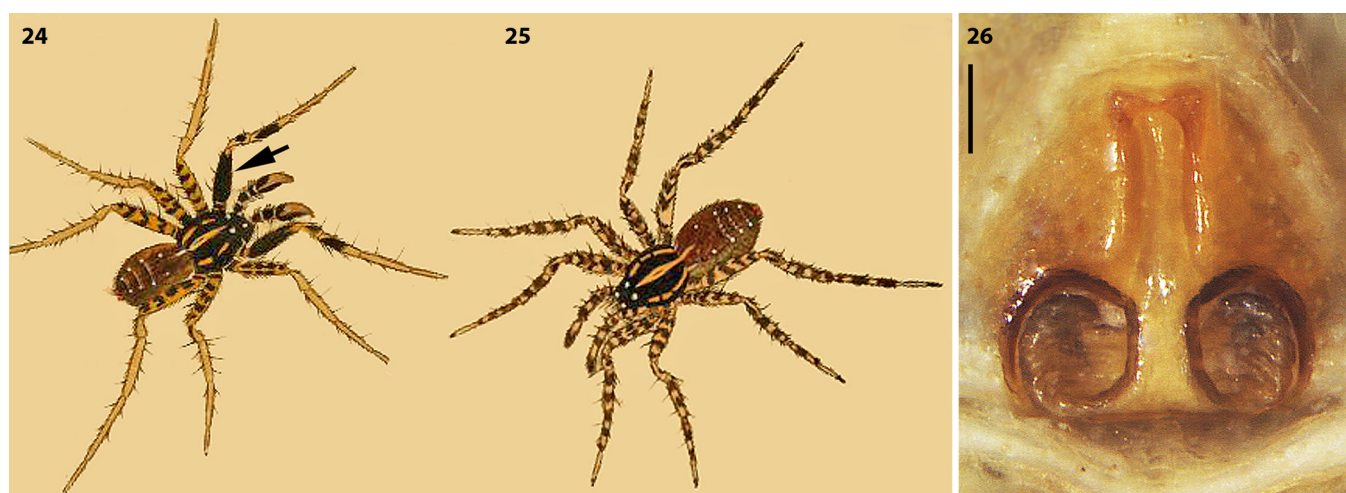
Pardosa proxima den Hollander & Dijkstra 1974: 57, fig. 1.2a-b (δ ♀).

Pardosa proxima Roberts 1985: 134, fig. 59d (δ ♀).

Pardosa proxima Roberts 1995: 220, fig. (δ ♀).

Pardosa proxima Roberts 1998: 235, fig. (δ ♀).

Pardosa proxima Chiarle et al. 2013: 119, courtship behaviour.



Figs 24-26: *Pardosa proxima*. **24-25.** after Koch (1847): male (24) and female (25); **26.** epigyne (lectotype). Scale line = 0.1 mm

Brief description of the courtship behaviour. The male moves one step forward with legs I raised, moving the palps up and down and vibrating the opisthosoma. Afterwards, he moves toward the female with hops, hitting the legs and rubbing the cymbia on the substrate.

Type material. *Pardosa tenuipes*: Holotype ♂ from SPAIN, Majorca, Ses Prat de San Jordi, May (Schaufuss) in Museum für Naturkunde, Berlin (ZMB 7921), examined. The male lacks both palps, but one palp and the legs on the right side are mounted on a microslide (ZMB 7921a). The illustration of the palp in Koch (1882: Fig. 24 also Bosmans & Van Keer 2012: Fig. 21) is misleading.

Other material examined. Asterisks (*) indicate specimen identified on ethological basis and used in previous studies (Chiarle & Isaia 2013, Chiarle et al. 2013) for behavioural analysis.

BELGIUM. Flandre: Brabant, Tienen, sugar factory, sandy substrate, 52 m a.s.l., 20.V.2009, 5♂ 13♀ (A. Chiarle, F. Hendrickx & J. Pétillon, RBINS); Antwerpen, 15.V.2009, 5♂ 8♀ (F. Hendrickx, RBINS); Laarne, Damvallei, 30.IV.2009, 1♂ (F. Hendrickx, RBINS). – **FRANCE.** Languedoc-Roussillon: Pyrénées-Orientales, Mas Larrieu, sandy sea shore among debris of *Arundo donax*, 7.V.2007, 5♂ 10♀ (T. Kronestedt, NHRS). Midi-Pyrénées: Ariège, Fougax-et-Barrineuf, grassland, 1.V.2006, 7♂ 9♀ (T. Kronestedt, NHRS), Lac Mondély, glade with litter and herbs close to lake, 25.IV.2006, 4♂ 2♀ (T. Kronestedt, NHRS), Lac de Montbel, clayey shore with low vegetation, 2.V.2006, 4♂ 4♀ (T. Kronestedt, NHRS). – **GREAT BRITAIN.** “England (Cambridge)”, 1♂ 1♀ (Collectio Thorell No. 246/1546, NHRS). – **ITALY,** Emilia-Romagna: Reggio Emilia, Viano, Casola Querciola, 30.IV.1978, 1♂ (P. Tongiorgi, MCSNB). Liguria: Imperia, stream Prino slopes, 40 m a.s.l., 3.VI.2006, 1♂ (R. Fabbri, MCSNB). Lombardia: Bergamo, Bariano, Serio river, uncultivated meadows, pitfall trap, 120 m a.s.l., 8.III.–8.IV.2002, 4♂; 16.VI.–7.VII.2002, 6♂; 24.VII.–10.VIII.2002, 11♂; 31.I.–14.III.2003, 1♂, river shore 7.VII.–24.VIII.2002, 1♂ (S. Ciocca, MCSNB, MSNVR); Bonate Sotto, Brembo river, pitfall trap, 175 m a.s.l., 11.II.–23.III.2002, 2♂ (S. Ciocca, MCSNB); Zanica, Serio river, grassland with *Artemisia* sp., pitfall trap, 190 m a.s.l., 8.III.–8.IV.2002, 48♂; 7.VII.–24.VIII.2002, 5♂, 14.IX.–1.XI.2002, 2♂, 14.III.–1.IV.2003, 1♂; grassland with bushes, 14.III.–23.IV.2003, 1♂ (S. Ciocca, MCSNB). Piemonte: Cuneo, Guarene, meadow, 155 m a.s.l., 7.III.2009,

15♂ (A. Chiarle, CI)*; Torino, Venaria, La Mandria natural park, meadow, 09.IV.2010, 9♂ 4♀, (A. Chiarle, MRSN)*; Leini, 10.VII.1967, 1♂ (G. Osella, MSNVR), Ivrea, Meugliano lake, 30.IV.2010, 1♂ (M. Paschetta, CI), Porte, Chisone river pebbly shore, 600 m a.s.l., 06.IV.2008, 2♂ 1♀ (M. Isaia, CI), Verbano-Cusio-Ossola, Fondotoce, meadow, 9.VI.–8.VII.2009, 2♂ 1♀ (M. Paschetta, CI). – **PORTUGAL.** Algarve: Patá, small river, ashore, 4.VII.2001, 4♂ 4♀; Roja Pé, brook, 1.VII.2001, 2♂ 3♀ (J. Buchar, NMP). – **SPAIN.** Andalusia: Ardales, ashore, 13.VI.1997, 3♂ 3♀; Campo de Golf between Malaga and Torremolinos, 15.V.1977, 13♂ 5♀ (T. Kronestedt, NHRS); San Pedro de Alcántara, among grass at small stream, 12.V.1977, 6♂ 6♀ (T. Kronestedt, NHRS). Majorca: Platja de Muro, Estany d'en Mama, grassland at lake and canal, 21.–23.IV.2013, 3♂ 17♀ (T. Kronestedt, NHRS).

Description. The general description is based on specimens in which we observed courtship behaviour (marked with an asterisk in the material section). Specimens from other localities were considered for comparison.

Male. Total length: 4.32–5.70. Prosoma: 2.20–2.97 long, 1.86–2.32 wide.

Prosoma dark brown, blackish in eye region, with narrow yellowish brown median band, and lateral light brown bands broken into three spots (Fig. 11). Eye region with long hairs. Clypeus yellowish, chelicerae brown with a light longitudinal strip on the internal side. Sternum dark brown. Opisthosoma dorsally grey-brownish with a remarkable brownish cardiac mark followed by 4–5 faint spots of the same colour (Fig. 11). Ventral side greyish with a wide yellow central area covered with hairs, normally developed (Figs 13, 20, 23). Leg I and all other legs uniformly yellow, femora with dark markings (Fig. 11). Leg I with numerous scattered long hairs on tibia and metatarsus. Leg I length: Femur 1.98, Patella 0.94, Tibia 1.61, Metatarsus 1.94, Tarsus 1.23. Palp as in Figs 12, 14, 15, brown with some yellowish areas on patella and femur, cymbium brown with lighter distal part. Embolus bent at approximately 90°, with the distal part almost equal in length to the proximal one (Figs 3–4).

Female. Total length: 5.28–5.91. Prosoma: 2.56–2.76 long, 2.02–2.12 wide.

Prosoma dark brown with darker eye region. Median band light brown, lateral bands of the same colour broken into three different parts, sometimes wide and unbroken with few

small brownish marks. Clypeus, cephalic flanks and chelicerae yellow-brownish. Sternum uniformly light brown. Opisthosoma dorsally dark brown with a distinct lighter cardiac mark usually bordered by black dots. Pairs of light brown spots, often fused, follow the cardiac mark until the spinnerets. Ventral side of the opisthosoma uniformly light brown, sometimes a lighter V shaped strip is present. Legs uniformly yellowish brown with brownish marks clearly visible on femora. Leg I length: Femur 1.74, Patella 0.78, Tibia 1.48, Metatarsus 1.40, Tarsus 0.92. Epigyne as in Fig. 16.

Habitat. Meadows, wet meadows, cultivated fields, swampy areas, edge of ponds and lakes.

Comparative remarks

Males of *P. proxima* and *P. tenuipes* show differences in the shape of the embolus (Figs 1–4), yet other morphological features permit a clear separation of the two species (Tab.1). In addition, the two species can be also well clustered comparing leg I metatarsus length with prosoma length (Fig. 17) and comparing palpal tibia width/length ratio with palpal tibia length (Fig. 18). However, the easiest way to discriminate males of the two species is looking at the hairiness ventrally on the opisthosoma (with numerous short modified hairs in *P. proxima* and normally developed in *P. tenuipes*, Figs 19 and 20, respectively) and at femur of leg I (same as other legs in *P. tenuipes* and darker in *P. proxima*; Figs 5 and 11, respectively). Photos with SEM (Figs 19–23) highlight striking differences in the length and the shape of the ventral hairs. As previously observed (Kronestedt 1996, 2005, Chiarle et al. 2013), modified hairs ventrally on the opisthosoma are found in other lycosid species in which the opisthosoma hits the substrate during courtship. Thus, the modified hairs present in *P. proxima* may be associated with a similar behaviour in this species.

On the other hand, females remain hard to distinguish on a morphological basis due to the high intraspecific variability and high overlap with respect to the shape of epigyne and vulva. Although some slight differences in shape and in the proportion between length and width of the epigyne could be considered, we argue that females of the two species cannot be distinguished on a morphological basis.

Remarks on *Pardosa proxima poetica*. Simon (1876) described *Pardosa proxima poetica* as a small sized (‘minima’) variety of *P. tenuipes* (sub *P. proxima*). According to the origi-

nal description, this variety was characterized i.a. by having very clear unbroken lateral bands on the carapace, and the male palp yellowish brown with the cymbium distally of bulb much shorter than the bulb. A sample with material fitting Simon’s description was available from Spain, Andalusia, Fuengirola, ruderal ground, 18.V.1977 (T. Kronestedt, NHRS), 4♂ 5♀, together with 1♂ and 2♀ of *P. tenuipes*.

We think that the characteristics mentioned by Simon (1876) for *P. proxima poetica* should be further investigated, and we have therefore not placed *Pardosa poetica* as a senior synonym of *P. tenuipes*. It should be mentioned that Simon (1937) regarded *P. proxima poetica* as an “espèce dominante” in Spain and Portugal. Regrettably, a loan of the type material of *P. proxima poetica*, probably present in the Muséum national d’Histoire naturelle in Paris, was not possible.

Remarks on WSC entries for *P. proxima*. In an attempt to assign the correct names to each of the WSC entries referring to *P. proxima*, several cases remained doubtful (Tab. 2). Despite the fact that, in a few cases, descriptions were matching some of the diagnostic features of *P. tenuipes* or *P. proxima*, we could not objectively establish whether they were just reporting Koch’s original description or whether they were referring to multiple specimens from different countries.

Distribution

According to our data, *P. proxima* seems to be quite common in Italy and in the south of the Balkan Peninsula (including Macedonia: Komnenov pers. comm.). In Greece, only *P. proxima* has been found (e.g. Bosmans et al. 2013, Bosmans pers. comm.). Contact zones with *P. tenuipes* are found in north-western Italy and in France (original records by den Hollander & Dijkstra 1974). The countries in which the presence of *P. proxima* is certain are: Greece, Macedonia, France, Bulgaria, Italy, Morocco, Turkey, Canary Islands.

Although *P. tenuipes* is considered widespread in Europe, we examined only a few specimens from Western Europe and the Iberian Peninsula. According to our data, *P. tenuipes* occurs in Spain, Belgium, Great Britain, France, Italy and Portugal.

It seems likely that *P. tenuipes* occurs mostly in western Europe, while *P. proxima* seems more common in southern and eastern Europe.

Most illustrations and or descriptions available in literature do not allow a clear understanding about how names were used by previous authors (see Tab. 2). Far from detailing the precise distribution, we suggest that material previously identified as “*Pardosa proxima*” should be checked for establishing the occurrence of one or both species in different countries.

With a certain degree of uncertainty, illustrations and descriptions available in literature seems to confirm the occurrence of *P. proxima* in France (Simon 1876, Tongiorgi 1966), former Yugoslavia, Italy, Macedonia, Albania, Greece and Austria (Tongiorgi 1966).

Concerning *P. tenuipes*, illustrations and descriptions available in literature seems to confirm its occurrence in Germany, Austria, Italy and Spain (Becker 1882), Hungary (Loksa 1972, Dahl 1908, Dahl & Dahl 1927), Switzerland (Lessert 1910, Dahl & Dahl 1927), Great Britain (Dahl & Dahl 1927, Locket & Millidge 1951, Roberts 1985, 1995, 1998), Belgium (Becker 1882, Dahl & Dahl 1927, Roberts 1998), Netherlands (Becker 1882, Roberts 1998) and France (Becker 1882, Dahl & Dahl 1927).

Tab. 1. Morphological characteristics for separating *Pardosa proxima* and *P. tenuipes* males

	<i>Pardosa proxima</i>	<i>Pardosa tenuipes</i>
Prosoma	Eye region with short hairs	Eye region with long hairs
Opisthosoma	Venter covered with short modified (peg-like) dark hairs among short normal white hairs (Figs 7, 19, 21, 22)	Venter covered with recumbent white hairs and scattered more erect dark hairs (Figs 13, 20, 23)
Leg I	Few long hairs on tibia and metatarsus. Femur mostly brown	Numerous scattered long hairs on tibia and metatarsus. Femur yellowish brown with dark markings
Palp	Tibia short and more stumpy, dorsally covered with tuft of thicker hairs	Tibia long and slender

Tab. 2. List of the WSC entries (WSC 2018) for *Pardosa proxima* for which the objective assignment to *P. proxima* or *P. tenuipes* is regarded doubtful.

WSC entry	Comments about the species attribution
<i>Lycosa proxima</i> O. Pickard-Cambridge 1878: 125, pl. 11, f. 6 (♂♀).	Uncertain attribution.
<i>Pardosa furtadoi</i> Simon 1883: 263 (D♂♀).	Only female described. Synonymized by Berland (1932). The description of the female does not allow discrimination between <i>P. tenuipes</i> and <i>P. proxima</i> . On the other hand, when describing <i>P. furtadoi</i> from the Açores, Simon (1883) also mentioned <i>P. proxima</i> , thus keeping the species apart. Later, Wunderlich (1992: 32–33) removed <i>furtadoi</i> from being a synonym of <i>proxima</i> , but still a synonym to <i>P. acorensis</i> , which he regarded as the only species of <i>Pardosa</i> on the Açores.
<i>Lycosa proxima</i> Chyzer & Kulczyński 1891: 57, pl. 2, fig. 24 (♂♀).	Descriptions and drawings does not allow discrimination between <i>P. tenuipes</i> and <i>P. proxima</i>
<i>Lycosa proxima</i> Bösenberg 1902: 383, pl. 36, fig. 561 (♂♀).	Uncertain attribution.
<i>Lycosa proxima</i> Nosek 1905: 140, fig. 19 (♀).	Uncertain attribution.
<i>Lycosa proxima</i> Smith 1907: 26, pl. 3, f. 14.	Smith (1907: 27) reports that “...in the male the femora of the first pair are dark, the remaining femora being irregularly annulated”. This actually fits <i>P. proxima</i> but the description could equally refer to material from other countries or simply refer to Koch’s original illustration.
<i>Pardosa proxima</i> Simon 1937: 1068, 1085, 1129, fig. 1657, 1688–1689 (♂♀). (in part?)	Possibly Simon had both species in his collection. There is no way to understand which species was illustrated. Descriptions and drawings does not allow discrimination between <i>P. tenuipes</i> and <i>P. proxima</i>
<i>Pardosa proxima</i> Fuhn & Niculescu-Burlacu 1971: 122, fig. 55a–e (♂♀, S of <i>P. proxima tenuipes</i>).	Uncertain attribution.
<i>Pardosa proxima</i> Tyschchenko 1971: 175, fig. 509 (♀).	Uncertain attribution.
<i>Pardosa proxima</i> Miller 1971: 159, pl. XXV, fig. 14 (♀).	Uncertain attribution.
<i>Pardosa esperanzae</i> Schmidt 1975: 505, fig. 3 (D♂♀).	Described on a single female. Synonymized with <i>proxima</i> by Wunderlich (1992).
<i>Pardosa proxima</i> Zyuzin 1979: 435, fig. 48 (♂).	Uncertain attribution.
<i>Pardosa canariensis</i> Schmidt 1982: 405, fig. 8–11 (D♂♀).	Synonymized with <i>proxima</i> by Wunderlich (1992).
<i>Pardosa pseudoproxima</i> Wunderlich 1987: 235, fig. 629 (D♂).	Synonymized with <i>proxima</i> by Wunderlich 1992.
<i>Pardosa proxima</i> Hu & Wu 1989: 224, fig. 188.3–4 (♀).	Uncertain attribution.
<i>Pardosa proxima</i> Heimer & Nentwig 1991: 332, fig. 1405 (♂♀).	Descriptions and drawings does not allow discrimination between <i>P. tenuipes</i> and <i>P. proxima</i>
<i>Pardosa proxima</i> Wunderlich 1992: 258, 466 (S).	In comparing <i>P. proxima</i> and <i>P. acorensis</i> from Macaronesia, Wunderlich (1992: 465) mentions that the male of <i>proxima</i> should have few to numerous small bristles ventrally on the opisthosoma “♂-Opisthosoma ventral einige bis zahlreiche Börstchen”.
<i>Pardosa proxima</i> Hepner & Paulus 2009: 342, fig. 17–19 (♂♀).	The authors report about the males having: “legs brownish with unclear annulations”. This feature is common in <i>P. tenuipes</i> but could as well refer to <i>P. proxima</i> (not all specimens have distinctly dark femora).

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References

- Almquist S 2005 Swedish Araneae, part 1: families Atypidae to Hahnidae (Linyphiidae excluded) – Insect Systematics & Evolution, Supplement 62: 1–284
- Becker L 1882 Les Arachnides de Belgique I. – Annales du Musée Royal d’Histoire Naturelle de Belgique 10: 1–246 – doi: [10.5962/bhl.title.48721](https://doi.org/10.5962/bhl.title.48721)
- Berland L 1932 Voyage de MM. L. Chopard et A. Méquignon aux Açores (août-septembre 1930). II; Araignées. – Annales de la Société Entomologique de France 101: 69–84
- Bösenberg W 1902 Die Spinnen Deutschlands. II–IV. – Zoologica (Stuttgart) 14(2–4): 97–384, Pl. 9–36 – doi: [10.5962/bhl.title.6508](https://doi.org/10.5962/bhl.title.6508)

- Bosmans R & Van Keer J 2012 On the spider species described by L. Koch in 1882 from the Balearic Islands (Araneae). – *Arachnologische Mitteilungen* 43: 5–16 – doi: [10.5431/aramit4306](https://doi.org/10.5431/aramit4306)
- Bosmans R, Van Keer J, Russell-Smith A, Kronstedt T, Alderweireldt M, Bosselaers J & De Koninck H 2013 Spiders of Crete (Araneae). A catalogue of all currently known species from the Greek island of Crete. – *Nieuwsbrief van de Belgische Arachnologische Vereniging* 28, Supplement 1: 1–147
- Chiarle A & Isaia M 2013 Signal complexity and modular organization of the courtship behaviours of two sibling species of wolf spiders (Araneae: Lycosidae). – *Behavioural Processes* 97: 33–40 – doi: [10.1016/j.beproc.2013.04.004](https://doi.org/10.1016/j.beproc.2013.04.004)
- Chiarle A, Kronstedt T & Isaia M 2013 Courtship behavior in European species of the genus *Pardosa* (Araneae, Lycosidae). – *Journal of Arachnology* 41: 108–125 – doi: [10.1636/Hi12-09.1](https://doi.org/10.1636/Hi12-09.1)
- Chiarle A 2013 The genus *Pardosa* (Araneae, Lycosidae): an integrative approach. PhD Thesis, University of Torino. 137 pp.
- Chyzer C & Kulczyński W 1891 Araneae Hungariae. Tomus I. Academia Scientiarum Hungaricae, Budapest. 170 pp., 4 Pls
- Cordes D & Helsen O von 1990 Indications for the existence of *Alopecosa barbipes* as a sibling species to *Alopecosa accentuata*. – *Bulletin de la Société européenne d'Arachnologie* 1: 70–74
- Dahl F 1908 Die Lycosiden oder Wolfspinnen Deutschlands und ihre Stellung im Haushalte der Natur. Nach statistischen Untersuchungen dargestellt. – *Nova Acta, Abhandlungen der Kaiserlich Leopoldinisch-Carolinischen Deutschen Akademie der Naturforscher* 88: 175–678
- Dahl F & Dahl M 1927 Spinnentiere oder Arachnoidea. Lycosidae s. lat. (Wolfspinnen im weiteren Sinne). – *Die Tierwelt Deutschlands* 5: 1–80
- Dondale CD & Redner JH 1990 The insects and arachnids of Canada. Part 17. The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska (Araneae: Lycosidae, Pisauridae, and Oxyopidae). Biosystematics Research Centre, Ottawa, Ontario. 383 pp.
- Emerson AE 1956 Regenerative behavior and social homeostasis of termites. – *Ecology* 37: 248–258 – doi: [10.2307/1933137](https://doi.org/10.2307/1933137)
- Fuhn IE & Niculescu-Burlacu F 1971 Fam. Lycosidae. – *Fauna Republicii Socialiste România (Arachnida)* 5(3): 1–253
- Heimer S & Nentwig W 1991 Spinnen Mitteleuropas: Ein Bestimmungsbuch. Paul Parey, Berlin. 543 pp.
- Hepner M & Paulus HF 2009 Contributions on the wolf spider fauna (Araneae, Lycosidae) of Gran Canaria (Spain). – *Bulletin of the British arachnological Society* 14: 339–346 – doi: [10.13156/arac.2009.14.8.339](https://doi.org/10.13156/arac.2009.14.8.339)
- Hollander J den & Dijkstra H 1974 *Pardosa vlijmi* sp. nov., a new ethospecies sibling *Pardosa proxima* (C. L. Koch, 1948), from France, with description of courtship display (Araneae, Lycosidae). – *Beaufortia* 22: 57–65
- Hollander J den, Vlijm L, Dijkstra H & Verhoef SC 1972 Further notes on the occurrence of the wolfspider genus *Pardosa* C. L. Koch, 1848 (Araneae, Lycosidae) in southern France. – *Beaufortia* 20: 77–84
- Hu JL & Wu WG 1989 Spiders from agricultural regions of Xinjiang Uygur Autonomous Region, China. Shandong University Publishing House, Jinan. 435 pp.
- Koch CL 1847 Die Arachniden 15. JL Lotzbeck, Nürnberg. 136 pp.
- Koch L 1882 Zoologische Ergebnisse von Excursionen auf den Balearen. II: Arachniden und Myriapoden. – *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 31: 625–678
- Kronstedt T 1996 Vibratory communication in the wolf spider *Hygrolycosa rubrofasciata* (Araneae, Lycosidae). – *Revue suisse de Zoologie*, hors série 1: 341–354
- Kronstedt T 2005 *Pardosa schenkeli* – en för Sverige ny vargspindelart [*Pardosa schenkeli* Lessert (Araneae, Lycosidae), a wolf spider new to Sweden]. – *Fauna och Flora* 100(4): 36–41 [in Swedish with English summary]
- Lessert R de 1910 Catalogue des invertébrés de la Suisse. Fasc. 3, Araignées. Musée d'Histoire naturelle de Genève. 635 pp.
- Lockett GH & Millidge AF 1951 British spiders. Vol. I. Ray Society, London. 310 pp.
- Loksa I 1972 Araneae II. – *Fauna Hungariae* 109: 1–112
- Miller F 1971 Pavouci-Araneida. – *Klíč zvířeny ČSSR* 4: 51–306
- Nosek A 1905 Araneiden, Opilionen und Chernetiden. In: Penther A & Zederbauer E (eds.) *Ergebnisse einer naturwissenschaftlichen Reise zum Erdschias-Dagh (Kleinasien)*. – *Annalen des Kaiserlich-Königlichen Naturhistorischen Hofmuseums in Wien* 20: 114–154
- O'Connor T, Starr CK & Cameron SA 2011 The neotropical social wasp *Mischocyttarus "alfkenii"* Ducke (Hymenoptera: Vespidae) is a pair of ethospecies. – *Systematic Entomology* 36: 446–452 – doi: [10.1111/j.1365-3113.2011.00575.x](https://doi.org/10.1111/j.1365-3113.2011.00575.x)
- Pickard-Cambridge O 1878 Notes on British spiders with descriptions of new species. – *Annals and Magazine of Natural History* (5) 1: 105–128
- Roberts JA & Uetz GW 2004 Chemical signalling in a wolf spider: a test of ethospecies discrimination. – *Journal of Chemical Ecology* 30: 1271–1284 – doi: [10.1023/B:JOEC.0000030277.27514.92](https://doi.org/10.1023/B:JOEC.0000030277.27514.92)
- Roberts MJ 1985 The spiders of Great Britain and Ireland, Vol. 1: Atypidae to Theridiosomatidae. Harley Books, Colchester. 229 pp.
- Roberts MJ 1995 Collins Field Guide: Spiders of Britain & Northern Europe. HarperCollins, London. 383 pp.
- Roberts MJ 1998 Spinnengids. Tirion Natuur, Baarn. 397 pp.
- Schmidt G 1975 Spinnen von Teneriffa. – *Zoologische Beiträge (N.F.)* 21: 501–515
- Schmidt G 1982 Zur Spinnenfauna von La Palma. – *Zoologische Beiträge (N.F.)* 27: 393–414
- Simon E 1876 Les Arachnides de France. Tome troisième. Roret, Paris. 364 pp.
- Simon E 1883 Études arachnologiques. 14e Mémoire. XXI. Matériaux pour servir à la faune arachnologique des îles de l'Océan Atlantique (Açores, Madère, Salvages, Canaries, Cap Vert, Sainte-Hélène et Bermudes). – *Annales de la Société Entomologique de France* (6) 3: 259–314
- Simon E 1937 Les arachnides de France. Synopsis générale et catalogue des espèces françaises de l'ordre des Araneae. Tome VI. 5e et dernière partie. Roret, Paris. pp. 979–1298
- Smith FP 1907 The British spiders of the genus *Lycosa*. – *Journal of the Quekett Microscopical Club* (2) 10: 9–30
- Tongiorgi P 1966 Italian wolf spiders of the genus *Pardosa* (Araneae: Lycosidae). – *Bulletin of the Museum of Comparative Zoology* 134: 275–334
- Töpfer-Hofmann G, Cordes D & Helsen O von 2000 Cryptic species and behavioural isolation in the *Pardosa lugubris* group (Araneae, Lycosidae), with description of two new species. – *Bulletin of the British arachnological Society* 11: 257–274.
- Tyschenko VP 1971 Opredelitel' paukov evropejskoj casti SSSR. Leningrad. 281 pp.
- Uetz GW & Denterlein G 1979 Courtship behavior, habitat, and reproductive isolation in *Schizocosa roveri* Uetz, Dondale (Araneae: Lycosidae). – *Journal of Arachnology* 7: 121–128
- Vlijm L 1971 Some notes on the occurrence of the genus *Pardosa* (Lycosidae, Araneae) in southern France, Spain and Corsica. – *Zoologische Mededelingen* 45: 281–287
- Vlijm L 1986 [Seminario de Etología] Ethospecies. Behavioral patterns as an interspecific barrier. – *Actas X Congreso internacional de Aracnologia*, Jaca 2: 41–45
- WSC 2018 World Spider Catalog. Version 19.0. Natural History Museum Bern. – Internet: <http://wsc.nmbe.ch> (5.IV.2018). – doi: [10.24436/2](https://doi.org/10.24436/2)
- Wunderlich J 1987 Die Spinnen der Kanarischen Inseln und Madeiras: Adaptive Radiation, Biogeographie, Revisionen und Neubeschreibungen. Triops, Langen. 435 pp.
- Wunderlich J 1992 Die Spinnen-Fauna der Makaronesischen Inseln. Taxonomie, Ökologie, Biogeographie und Evolution. – *Beiträge zur Araneologie* 1: 1–619
- Zyuzin AA 1979 A taxonomic study of Palaearctic spiders of the genus *Pardosa* (Aranei, Lycosidae), Part I. Taxonomic structure of the genus. – *Entomologicheskoe Obozrenie* 58: 431–447 [in Russian with English summary]