

Cryptic species and behavioural isolation in the *Pardosa lugubris* group (Araneae, Lycosidae), with description of two new species

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Summary

A comparative study of the courtship behaviour of “*Pardosa lugubris*” (Araneae, Lycosidae) from Europe revealed the existence of six closely related cryptic species: *Pardosa lugubris* (Walckenaer, 1802), from northern and central Europe, *P. alacris* (C. L. Koch, 1833) from various localities distributed all over Europe, *P. saltans* Töpfer-Hofmann, new species, from northern, central and south-western Europe, *P. baehrorum* Kronstedt, 1999 from central Europe, *P. pertinax* von Helversen, new species, from Greece, and finally *P. caucasica* Ovtsharenko, 1979 from the Caucasus mountains. These six species should be separated from the *Pardosa amentata* group (*sensu* Wunderlich, 1984).

Cross-mating tests showed that *P. lugubris*, *alacris*, *saltans*, *baehrorum* and *pertinax* are well isolated biospecies. Some of these species have been found syntopically in different species associations, suggesting that courtship behaviour is the main isolating mechanism between these species. The species can be discriminated by having different courtship postures and movement patterns, as well as specific combinations of movements. The courtship display of the five European species is described in detail.

Despite some overlap in the diagnostic characters, an identification key for the males of all known taxa is presented. Females of the different species cannot be distinguished reliably by means of their somatic or genital morphology, but some characters were found that help to characterise at least some of the species. For the revision and the formation of this species-group it was necessary to designate a neotype for *P. lugubris* as the name-bearing taxon of the group. All type material will be deposited in the Senckenberg Museum, Frankfurt.

Introduction

The wolf spider genus *Pardosa* C. L. Koch, 1848 is widespread throughout the Holarctic region and has undergone a great deal of diversification. Some of the groups comprise a large number of taxa with a comparatively high degree of similarity in habitus as well as in the form of their genitalia (for example see Tongiorgi (1966a,b) for the European *Pardosa monticola* group and Holm & Kronstedt (1970) for the *P. pullata* group). This still causes problems in identifying and separating taxa because many of the species are still poorly known.

One such problematic group that has received attention in recent years is the so-called *Pardosa amentata* group (*sensu lato*). For a long time only two European species were listed in this group: *P. amentata* (Clerck, 1757) and *P. lugubris (s.lato)* (see also Zyuzin, 1979). In 1969 Wunderlich described the new species *P. barndti* from one male specimen and later revised collections of the *amentata*-group species in 1984, describing one further new taxon, *P. pseudolugubris* Wunderlich, 1984.

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In the latter study the comparatively large variability in the morphological characters of *P. lugubris (s.lato)* was discussed. Additionally the taxon *P. barndti* (which had never been found since its description) was synonymised with *P. lugubris (s.lato)*, the reason given being that possible teratogenic effects might have been responsible for the aberrant morphology of the single type specimen. Later, Kronstedt (1992) found the name *P. pseudolugubris* to be a synonym of the older name *P. alacris* (C. L. Koch, 1833). In 1979, Ovtsharenko described *P. caucasica* from the Caucasian region, and considered it related to *P. lugubris (s.lato)*.

Problems in discriminating between wolf spider species can often be solved by observation of their courtship displays, as has been shown in several cases by Hollander & Dijkstra (1974) for *Pardosa proxima / vlijmi*, by Kronstedt (1979a, 1990) for *Alopecosa aculeata / taeniata*, by Stratton & Uetz (1981) and Stratton (1991) for the complex *Schizocosa ocreata / rovneri / stridulans*, by Costa & Capocasale (1984) for *Lycosa carbonelli / thorelli*, by Reiskind (1988) and Reiskind & Cushing (1996) for *Lycosa ericeticola / ammophila* and by Cordes & v. Helversen (1990) for *Alopecosa accentuata / barbipes*. In all these cases the courtship display of the males revealed distinct differences between species that were morphologically similar or almost identical. Such species are often called “cryptic species”. The European *Pardosa lugubris* group is such a group of cryptic taxa with almost identical appearance and very similar genital organs. In this paper we report on the courtship displays of the five European species. First, cross-mating experiments were performed to establish their biospecies status. Then we describe the movement pattern of the courtship in detail. The morphological description of all six taxa (including *P. caucasica*) follows, including a revision of collection material. This revisory section is restricted to male specimens.

Nomenclatural note

A preliminary report on this study was published in 1990 (Töpfer-Hofmann & v. Helversen, 1990) following the 12th European Colloquium of Arachnology in Paris. At that time four Central European taxa had been sorted on the basis of their sexual behaviour. The two newly discovered species (*P. baehrorum* and *P. saltans*) were preliminarily described, but the names were explicitly stated to be “nomina nuda”. One of these species (*P. baehrorum*) has recently been described by Kronstedt (1999). *P. saltans* and *P. pertinax*, a further new species from Greece, are formally described here. Following the meeting in 1990 the name *saltans* has been used by several authors referring to the usage of names in Töpfer-Hofmann & v. Helversen (1990). Owing to the different authority in this paper the describing authors of the two new species have also changed (see the respective sections)!

Material and methods

For behavioural analyses all individuals were collected as subadults to ensure that the females used were virgins. The animals were reared to the adult stage in small plastic containers filled with leaf litter from their original habitat. They were moistened daily with a water-spray and fed on *Drosophila*.

The displays of males were recorded on a S-VHS recorder with a Panasonic video-camera F-10. For the observations one male and one female were placed together in a glass terrarium with a diameter of 30 cm. Through the transparent acrylic walls, and using tele-lenses, it was possible to record the courting spiders at a high level of magnification. The pattern and duration of behavioural elements were measured using the "still-image" and "jog-shuttle" modes of the video-recorder. The video-signal of a timer (1/100 s=minimal resolution) was added to the video-signal of the film, marking each individual half frame (1/50 s frame-to-frame interval).

Cross-mating tests: Sequential cross-mating tests were conducted in plastic containers with a diameter of approx. 15 cm that ensured close contact of both sexes during the experiment. To be sure that a female had enough time to evaluate a male, both sexes were kept in contact for at least 15 minutes. A male was judged as *accepted* when the female allowed him to touch her body with his fore-legs and to mount into mating position.

First a heterospecific, then a conspecific male was placed into the testing arena near the female. The decision of the female was noted as (a) "heterospecific accepted", (b) "heterospecific rejected" (=conspecific accepted), or (c) "no decision made". These were defined as follows: (a) when the first heterospecific male was accepted, (b) when the first male was rejected during a testing time of 15 minutes, but then the second conspecific male was accepted, and (c) when neither the heterospecific nor the conspecific male was accepted.

As most of the females were collected in habitats where two or more species lived syntopically, their species identity was not known at the beginning of an experiment. We first had to determine the female's species by observing her decision towards different males. For this, a female was confronted with several males in sequence, until she accepted one. In this case copulation was not allowed but immediately interrupted by touching the pair with a fine paint brush. Only in the final tests were all females allowed to complete copulation.

Abbreviations, collections: CB=Coll. Buchar, Prague; CH=Coll. Hänggi, Basle; CSch=Coll. Schenkel, Museum Basle; CSt=Coll. Stumpf, Würzburg; CSv=Coll. Svaton, Museum Basle (1990); CTH=Coll. Töpfer-Hofmann, Erlangen; CvH=Coll. v. Helversen, Erlangen; MNHNP=Muséum National d'Histoire Naturelle, Paris; NHM=Natural History Museum, London; NHMB=Naturhistorisches Museum, Basle; SMF=Senckenberg Museum, Frankfurt/M; ZMB=Zoologisches Museum, Berlin; ZMP=Zoological Museum, Prague; ZSM=Zoologische Staatssammlung, Munich.

Results

Cross-mating experiments

According to the "Biospecies Concept" (for details see Mayr, 1963) species are defined by having separate gene

♀	x		♂	n	n [tests]	decisions	
	n					hetero	con
<i>P. lugubris</i>	20		<i>P. alacris</i>	25	27	-	22
	10		<i>P. baehrorum</i>	3	13	-	10
	22		<i>P. saltans</i>	27	36	-	30
	4		<i>P. pertinax</i>	8	8	-	8
<i>P. alacris</i>	20		<i>P. lugubris</i>	20	24	-	15
	8		<i>P. baehrorum</i>	3	10	-	9
	10		<i>P. saltans</i>	10	16	-	11
	10		<i>P. pertinax</i>	10	15	-	8
<i>P. saltans</i>	25		<i>P. alacris</i>	25	36	-	24
	8		<i>P. baehrorum</i>	3	10	-	8
	25		<i>P. lugubris</i>	27	48	-	31
	5		<i>P. pertinax</i>	7	7	-	5
<i>P. pertinax</i>	8		<i>P. alacris</i>	10	11	-	8
	8		<i>P. saltans</i>	9	11	-	5
	8		<i>P. lugubris</i>	6	8	-	8

Fig. 1: Results of the cross-mating experiments, showing a behavioural isolation that prevents the *P. lugubris*-group species from cross-breeding. All decisions were made in favour of conspecifics (con), no cross-mating occurred (hetero). All females were used first in heterospecific tests, then checked against a conspecific male. Not all tests resulted in a decision by the respective female, and most females were involved in tests more than once; therefore the number of decisions and the number of females are usually smaller than the number of tests (n [tests]).

pools, and genetic separation is brought about and ensured by isolating mechanisms. As most species are separated by premating isolating mechanisms, we first tested if different forms would mate. For this, virgin females were tested whether they would accept males.

The results of all cross-mating tests are given in Fig. 1; they clearly show that courtship behaviour alone serves as an effective reproductive barrier between all tested species of the *P. lugubris* group; not a single cross-mating occurred. Females usually accepted conspecifics within the first minute. Thus females recognise conspecific mates without error. The term "courtship behaviour" in the sense of this study comprises all sensory modalities that may be involved in communication between the sexual partners (vision, vibration, tactile signals, volatile as well as contact pheromones).

Syntopic occurrence

Neither habitat nor seasonal isolation can be a barrier between species of the *P. lugubris* group. All European species have their mating period in spring (April to May) and combinations of two or even three species can be found syntopically. All species prefer leaf litter in deciduous forests as well as at the forest edges. Figure 2 shows the syntopically observed species combinations for Europe.

Courtship behaviour

The courtship display of *P. lugubris*-group species was studied in the 1960s and 1970s by the research group of L. Vlijm (Amsterdam). They published a comparative study in 1966 (Vlijm & Dijkstra, 1966), dealing with the display of *P. amentata*, *P. hortensis* (Thorell), *P. nigriceps* (Thorell) and *P. lugubris* (*s.lato*). A detailed description of the display of *P. alacris* (under the name

chelata) was given by Hallander in 1967. Recently a study on the courtship of *lugubris*-group species was published by Vlček (1995). This study dealt with *P. alacris*, *P. lugubris* (*s. stricto*) and the new *lugubris*-group species preliminarily published by Töpfer-Hofmann & v. Helversen (1990) under the nomen nudum *P. saltans*.

Both new species (*P. saltans*, *P. pertinax*) were discovered by the analysis of their courtship behaviour, can be characterised by distinct differences in their displays, and now can also be distinguished by morphological differences.

The display

Apart from the main courtship display in the strict sense, two further types of displays can often be observed in the context of courtship, here called “pre-courtship displays”. The courtship display itself (“main display”) can be divided into distinct phases that the male must pass through before being accepted for copulation by a female. The courtship begins with a *start-display* (except in *P. pertinax*), continues with a sequence of two types of palpal presentations (*main display*) and ends with the *approach* to the female and *mounting*.

Note: All figures illustrating the display movements represent the “mean” of a large number of observed behavioural sequences from many individuals. Females have a strong influence on the completion of male display presentations and on the number of repetitions of certain components of the displays. They express this mainly with “leg-waving” behaviour (*sensu* Koomans *et al.*, 1974) or with quick approaches towards the male, which immediately interrupts its display or initiates repetitions of sequences.

To facilitate comparison of the behavioural characteristics of the species’ display, the graphics are grouped according to the behavioural phases. Instead the text explains the whole display of each species from phase II (main display) until mounting (phase IV) for a better understanding of the behavioural pattern. For a comparison of diagnostic differences see the section “Diagnostic characters and behaviour” and the corresponding figures and figure captions.

Pre-courtship displays

Leg-waving (Fig. 3): This display, occurring in the context of courtship, is a “leg-waving” behaviour previously described by Koomans *et al.* (1974), and is also known from other *Pardosa* species. As shown in Fig. 3 the spider lifts the palp and leg I on one side

	<i>lugubris</i>	<i>alacris</i>	<i>saltans</i>	<i>baehrorum</i>	<i>pertinax</i>
<i>lugubris</i>	■	+	+	+	
<i>alacris</i>		■	+		+
<i>saltans</i>			■		
<i>baehrorum</i>				■	
<i>pertinax</i>					■

Fig. 2: Syntopic occurrence of European *P. lugubris*-group species: *P. lugubris*, *alacris* and *saltans* are often syntopic, *P. baehrorum* is syntopic with *P. lugubris*, and *P. pertinax* with *P. alacris*.

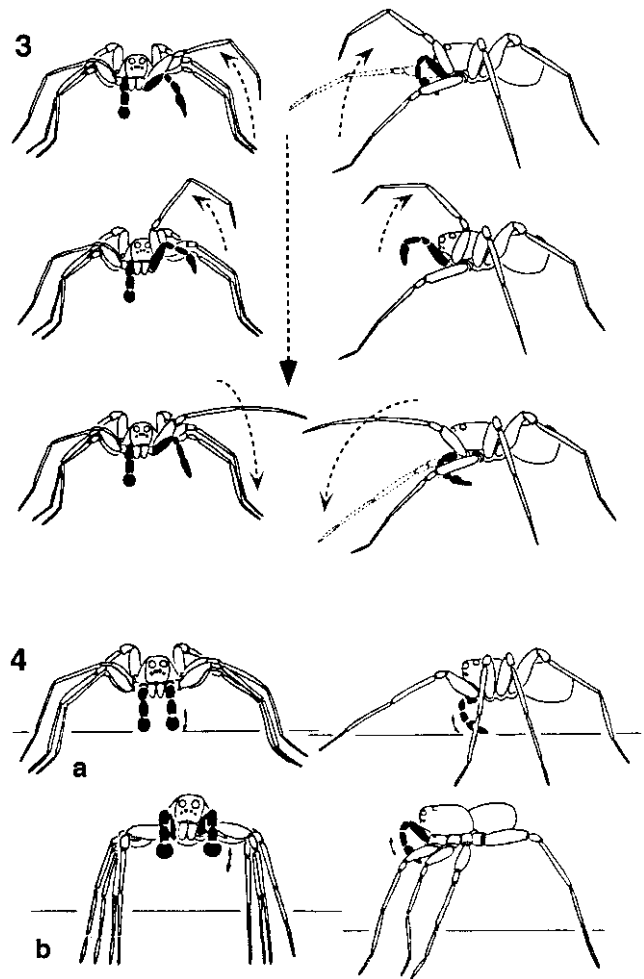


Fig. 3–4: Precourtship displays (left column frontal view, right column lateral view). **3 Leg-waving:** the spider lifts one leg I and palp, then moves them back to the substrate — see arrows; the movements may be repeated several times, changing sides. **4 Search-walk:** the spider moves along while scraping the cymbia over the substrate (a), and during short pauses stands highly elevated on the legs, with vibrating palps (b); shortly afterwards it continues with searching (a).

synchronously and then brings both appendages downwards stepwise to their previous positions. Then the male may use the palp and leg I of the opposite side and repeat this movement. This behaviour can be repeated several times and can also be observed in females.

Search-walk (Fig. 4): Males of the *lugubris*-group species often display a specific searching behaviour in the presence of females. Figure 4 shows the typical posture of males during “search-walk”. Basically the behaviour consists of a swinging movement with the pedipalps while walking slowly with frequent changes of direction. Thereby the cymbia are scraped over the substratum (see arrows, Fig. 4). After several steps the spider stops and raises its body high above the ground before beginning the next searching sequence.

Courtship displays

Phase I: *Start-display* (Figs. 5, 6): This phase of the display can be observed in *P. lugubris*, *alacris*, *saltans* and *baehrorum*, but not in *P. pertinax*. The first part of the male courtship display begins on physical

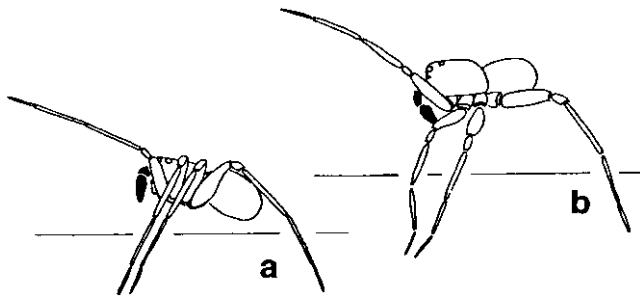


Fig. 5: Body postures during courtship display: **a** Typical posture for *P. lugubris*, *alacris*, *baehrorum* and *pertinax*; **b** Typical posture for *P. saltans*.

contact between the sexes. The male follows the female, attempts to move in front of her, and takes up a specific body posture as shown in Fig. 5a,b. This “courtship-posture” is similar in all species except *P. saltans* which also raises the opisthosoma to an elevated position (Fig. 5b).

Male and female then stand face to face. Highly elevated on the tips of the legs and keeping legs I stretched out laterally (6.1), the male begins with a quick palpal display that does not take more than a second. Beginning on either side one palp is moved, its tip following the shape of a circle (Fig. 6.2–7) and passing through an elevated position where the palp is held erect (6.5). With movement 6.7 it regains the starting position. This movement is repeated once with the opposite palp (6.8–13). The *start-display* may be repeated depending on the behaviour of the female. If the female moves away or responds with *leg-waving* the male immediately

follows and tries to regain his initial position in front of the female, repeating the *start-display*. After this display sequence the general body posture does not change significantly during the following phases of the display.

Phases II–III: *Main display* (Figs. 5, 7–17):

***Pardosa lugubris*:** This species is characterised by an almost complete lack of further display behaviour in the context of courtship. Only the previously described *start-display* was occasionally observed during aggressive encounters with females. On meeting a female the courtship of *lugubris* consists of chasing, during which the male touches the legs or body of the female, causing her to stop running. This is followed by further tactile communication. In general the courtship behaviour consists of a sequence of such chases with short interruptions and tactile communication, finally ending in copulation.

Pardosa alacris (Figs. 7, 8, 14): The male remains in the body posture of the *start-display* for some seconds and then, if the female remains motionless, begins the second type of display (phase II, Figs. 7, 8). For several seconds he vibrates the cymbia with them held in the position shown in Fig. 7.1; this is referred to as “*palpal trembling*”. Within one second (0.9 ± 0.4 $n=9$ inds./42 obs.) both palps are moved upwards accompanied by vigorous vibrations of the spider’s body (Fig. 7.2–4). The palps are moved alternately in *c.* four short steps each (4 ± 0.9 , $n=9$ inds./42 obs.) until they reach their erect position (Fig. 7.4), and immediately afterwards are moved downwards (Fig. 7.5) in a similar manner; referred to as “*palpal jerk*”. The whole behavioural

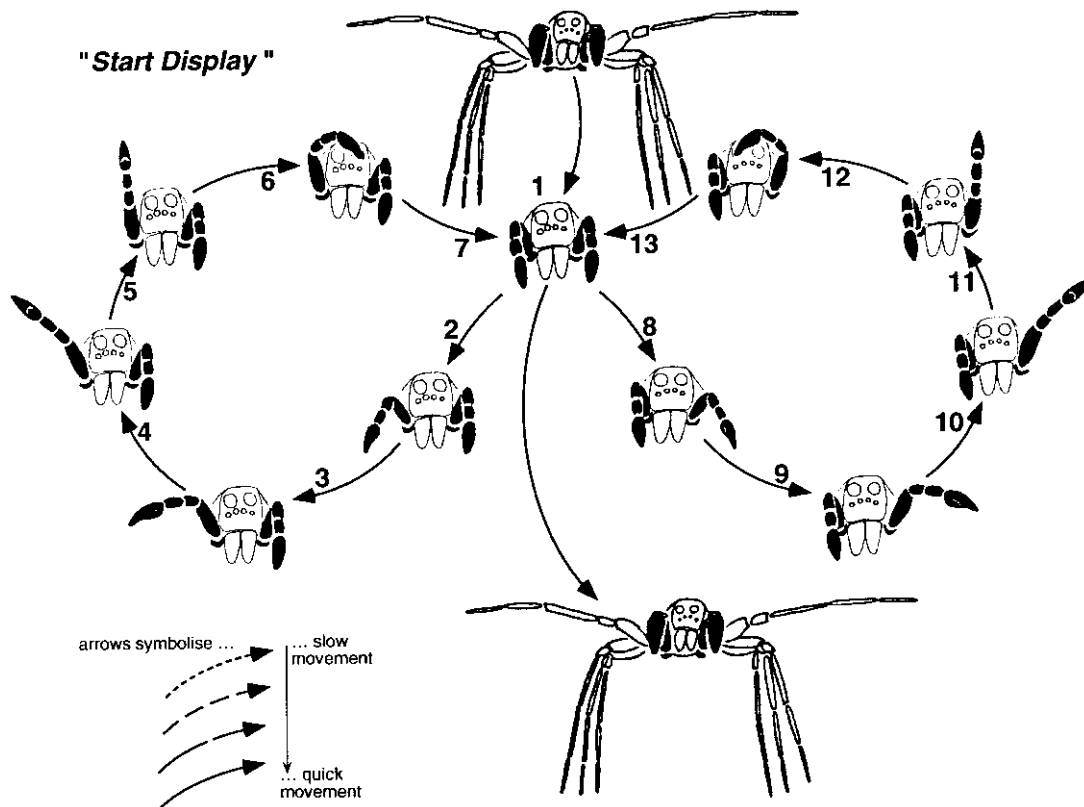
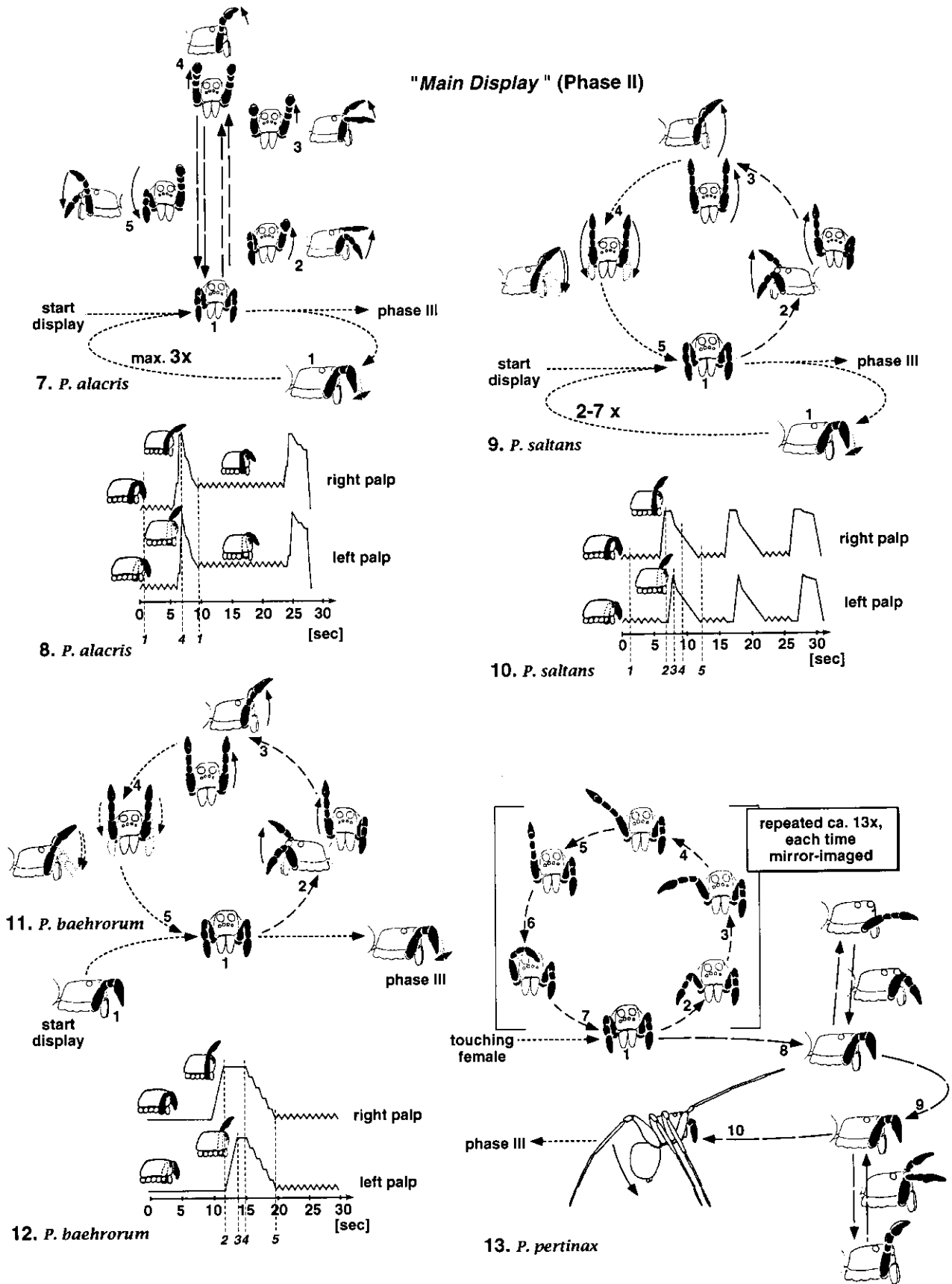
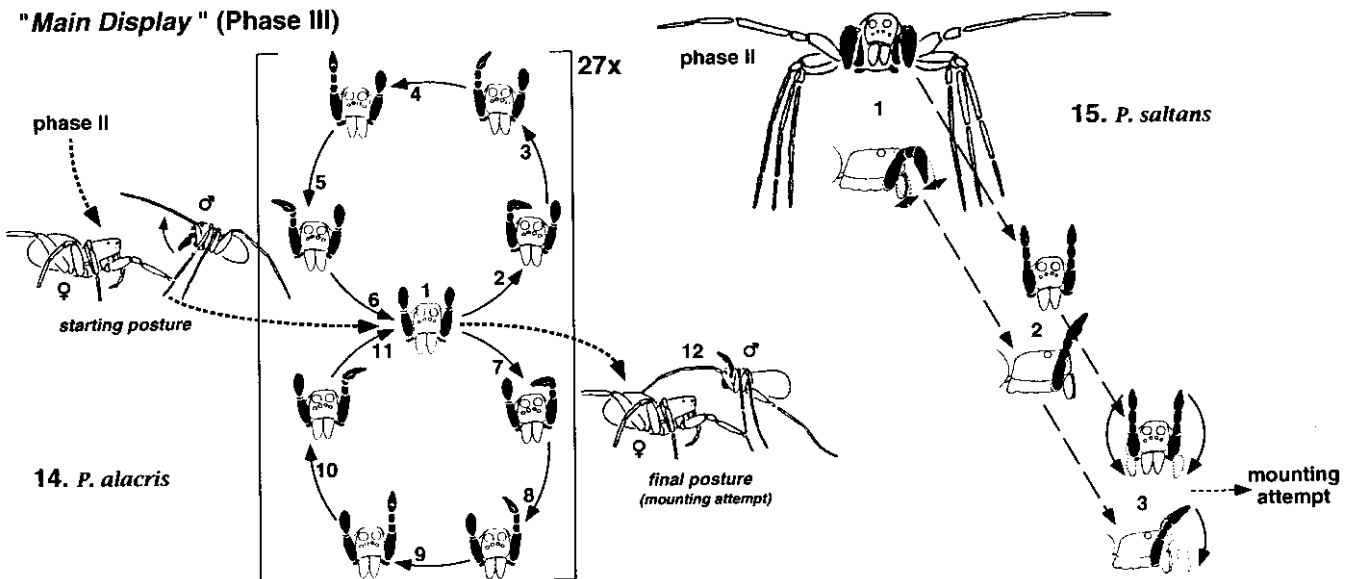


Fig. 6: Courtship displays (phase I), *start-display* (all species except *P. pertinax*): a quick display that begins when the male arrives in front of the female. The palps are moved in sequence (right, 2–7) and mirror-imaged (left, 8–13). The small numbers in all diagrams stand for movement-numbers (when near arrows) or for posture-numbers (when near spider-icons). The numbers refer to explanations in the text.



Figs. 7–13: Courtship display (phase II), *main display*: the main behavioural element of this phase is palpal vibration interrupted by jerky, stepwise movements of the palps (upwards and downwards) in *P. alacris* (7, 8), and by more smoothly moving the palps upwards and downwards in *P. saltans* (9, 10). *P. baehrorum* (11, 12) raises the palps smoothly and takes them down stepwise only once, then continues with palpal vibrations, whereas *P. pertinax* (13) immediately starts a repetitive palpal turning movement which is finished by flicking the palps and bending the opisthosoma. Figs. 8, 10 and 12 show a quantitative example taken from a video sequence. The curve depicts height of the cymbium tip relative to height of the posterior median eyes. Numbers in italics near vertical lines indicate the same body postures indicated by those numbers in Figs. 7, 9 and 11.



Figs. 14–15: Courtship display (phase III), *main display*. **14** *P. alacris* performs a stereotyped and simple-shaped cymbial turning sequence which is repeated while the male bends his body towards and over the female, ending in mounting attempts; **15** *P. saltans* uses a very short and jerky palpal movement after standing for a long time with vibrating cymbia. After the palpal jerks the spider tries to mount.

unit—*palpal trembling* and *palpal jerk*—may be repeated up to three times (twice in Fig. 8). The whole sequence has an average duration of about 22 s (22 ± 8.8 , $n=9$ inds./27 obs.), depending on the number of repeated units. Figure 8 shows the whole sequence plotted along the time axis. It can be seen that most of the time is spent with *palpal trembling*. The palps may be held at a slightly different height (relative to the eyes) during the trembling phases (8.1).

Having finished the last sequence of *palpal jerks*, the male switches to the next display mode (phase III, Fig. 14). The basic body posture does not change during the next few seconds when the male, with legs I held high, begins to turn his palps alternately. The movements begin with the palps held slightly higher than the level of the cephalic part of the prosoma. One cymbium is turned from the position, cymbium tip pointing ahead (Fig. 14.1), in an arch (first inwards, then outwards) as shown in Fig. 14.2–6. This movement is performed with both cymbia alternately (Figs. 14.2–6 to 14.7–11); referred to as "*cymbial circling*". While repeating these movements the male bends his body towards the female in a stepwise manner (with each *circling* unit). Legs I are lowered more and more with each such step and eventually are brought together to touch the female on her opisthosoma (final posture, Fig. 14.12). At this time legs II are switched to a position parallel to legs I and now also touch the female's opisthosoma (phase IV, *mounting attempt*, Fig. 18). The palpal display is completed and the male mounts. On average the cymbia are circled 27 times (27 ± 11 , $n=9$ inds./39 obs.) during this display sequence and the overall duration is about 24 s (24 ± 7 , $n=9$ inds./40 obs.).

Pardosa saltans (Figs. 9, 10, 15): After the start-display the male remains in the same position and vibrates the cymbia (Fig. 9.1) and the whole body. At intervals he raises both palps, one after the other, to an erect position (9.2–3), taking them down together after a

few seconds (9.4–5). These palpal movements are repeated 2–7 times (3 ± 1.8 , $n=5$ inds./13 obs.). The whole sequence takes about 30 s (30 ± 14 , $n=5$ inds./12 obs.). Figure 10 shows the rather slow and smooth movements of the palps that take more than 4 s to be moved down.

The basic body posture remains unchanged and the male now begins the third display sequence (phase III, Fig. 15): slow movements with the chelicerae (Fig. 15.1), together with palpal trembling and the whole body moving up and down. This display sequence ends with a quick movement of the palps which are quickly thrown upwards together to the erect position (15.2) with the body of the spider vibrating vigorously, then taken down together, the whole movement occurring within about 0.1 s (15.3). Then, while keeping legs I stretched out he approaches the female (phase IV, *mounting attempt*) with several jerky steps and tries to mount

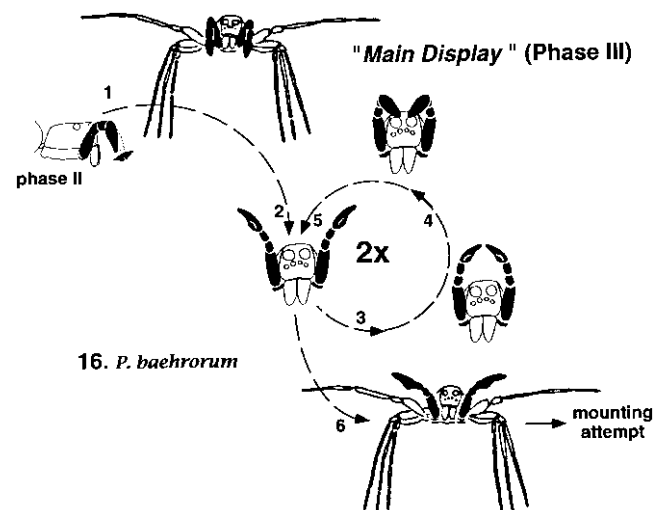


Fig. 16: Courtship display (phase III), *main display*: *P. baehrorum* finishes the courtship display with a short and unique palpal turning movement (2–5).

(Fig. 18). Phase III lasts about 22 s (22 ± 4.7 , $n=4$ inds./14 obs.).

Pardosa baehrorum (Figs. 11, 12, 16): Males of this species begin courtship phase II (*palpal jerks*, Figs. 11, 12) with the body remaining motionless in the posture of the start-display. After about 27 s (27 ± 11 , $n=3$ inds./12 obs.) the male smoothly lifts both palps one after the other to an erect position (Fig. 11.1–3), and then takes them down again in successive alternate steps (11.4–5). The lowering of the palps usually occurs in 5–8 steps ($n=3$ inds./12 obs.) and takes, as shown in Fig. 12, about 4–5 s. When this sequence is finished after 21 s (21 ± 12.5 , $n=3$ inds./12 obs.), and after several seconds of *palpal trembling*, the male goes on to the next display sequence; the *palpal jerks* are never repeated.

The male remains motionless with trembling cymbia (Fig. 16.1) and after a few seconds (phase III) raises his palps synchronously with a rotation of the joints such that the dorsal surfaces of the cymbia face each other (16.2). This position is followed by a second rotation of the palps which brings the bulbs face to face (16.3). After this the cymbia are bent ventrally with their tips converging and pointing downwards (16.4), and finally are returned to the initial position (16.5). This sequence (16.2–5) is repeated once and ends in the body posture (16.6) that is characterised by the palps pointing laterally. Finally (phase IV, mounting attempt) the male vibrates the palps and legs I and quickly approaches the female (Fig. 18).

Pardosa pertinax (Figs. 13, 17): This species lacks the *start-display* in its strict sense; instead, after orienting

itself towards the female, the male starts directly with phase II, beginning with a palpal display that resembles the palpal movements of the *start-display*, but presented in a very slow manner. Thereby, while standing in close contact with the female (Fig. 13) — the tips of legs I are stretched out over the female's back — one palp is moved, the tip following the shape of a circle (13.2–7) and coming back to the initial posture (13.1). On average this sequence is repeated 13 times (13 ± 5 , $n=6$ inds./6 obs.). This *palpal turning* is displayed each time mirror-imaged to the preceding sequence and performed with increasing speed. Phase II ends with two *palpal jerks*; first both palps are synchronously flicked forwards (13.8), then upwards (13.9) accompanied by vigorous vibrations of the opisthosoma. Immediately afterwards there follows a movement of the opisthosoma which is bent strongly downwards to the substrate (13.10) at an angle of *c.* 90° accompanied by vigorous movements of the spinnerets. The whole phase II lasts about 13 s (12.8 ± 9.2 , $n=7$ inds./20 obs.) with an additional 5 s (5 ± 2.72 , $n=7$ inds./20 obs.) duration for the opisthosoma bending behaviour.

Phase III (Fig. 17) of the display has considerable similarities to phase II, but is separated from it by a short pause. Legs I remain stretched out over the back of the female. Phase III begins with *palpal turning*, as in phase II (Fig. 17). The male begins to turn his palps around (Fig. 17.2–7, 9–14), one after the other, but now each palp only once. Then both palps are flicked forwards (17.15) and taken back together, then thrown up synchronously and taken back again (17.16) into the

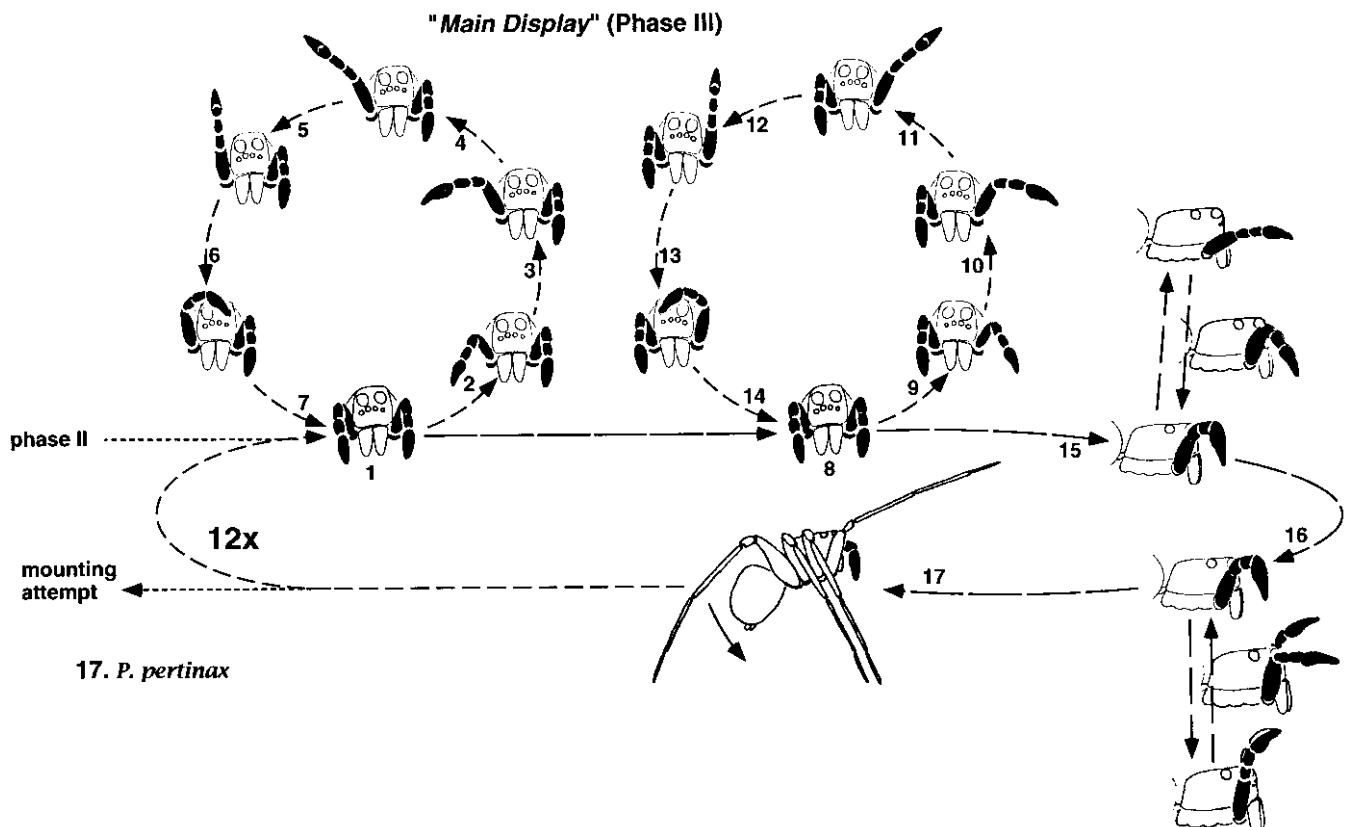


Fig. 17: Courtship display (phase III), *main display*: *P. pertinax* starts a long-lasting display with continuous (*c.* 12) stereotypic repetitions of a complex sequence of palpal turning movements (2–7 and 9–14), palpal flicks (15–16) and opisthosomal movements (17).

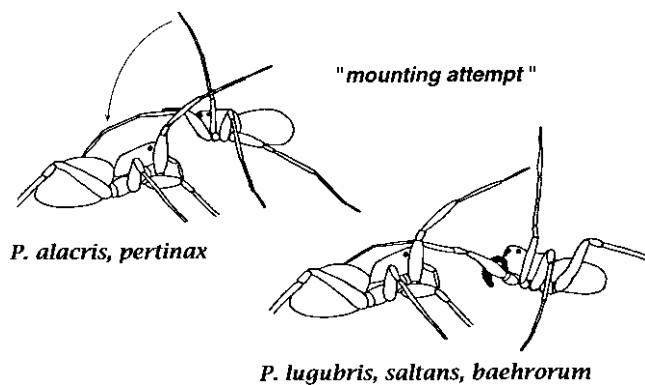


Fig. 18: Courtship display (phase IV), *mounting attempt*: in *P. alacris* and *P. pertinax* the display phase III continues with mounting attempts, whereas in the other three species the male finishes his display, then approaches the female and tries to mount.

flexed position. One such behavioural cycle ends with a short bending movement of the opisthosoma at an angle of 30–45° (17.17). One such element can be seen as a modified version of the phase II display and is repeated about 12 times (11.7 ± 6 , $n=6$ inds./15 obs.), lasting about 45 s (45.3 ± 23.5 , $n=7$ inds./15 obs.).

Phase IV: *Mounting* (Fig. 18): Mounting differs depending on the type of courtship. *P. alacris* and *P. pertinax* approach the female while stimulating her with intense courtship displays, while the other species (*P. lugubris*, *P. saltans*, *P. baehrorum*) stop the display (*lugubris*: chasing the female) and run towards the female; as a consequence the posture of these two groups of males is different when mounting (Fig. 18). The species that use the continuous approach (*alacris* and *pertinax*) hold their body high on their legs and bend over the female while starting to mount. The species which approach the female (running or jumping) after finishing their display (*saltans* and *baehrorum*, also *lugubris*) keep the body near the ground and try to climb over her back.

Diagnostic characters and behaviour

As a general rule, the later phases of the courtship display differ more between species than the earlier phases.

The courtship display in the *P. lugubris* group can be divided into distinct phases, and from phase II onwards contains species-typical sets of behavioural sequences (*P. lugubris* without visual display). All species except *P. pertinax* regularly exhibit a “*start-display*” (*P. lugubris* only sporadically) on contacting a female. During phase II (*palpal trembling* and *palpal jerks*) further differences between the species can be observed: *P. lugubris* does not exhibit visual displays, but instead chases the female; *P. alacris* and *P. saltans* are similar in that they perform the palpal jerks more than once (*alacris*: 1–3×, *saltans*: 2–7×) whereas *P. baehrorum* never repeats this behaviour. *P. alacris* lifts its palps in up to six successive steps, whereas *P. saltans* and *P. baehrorum* smoothly raise their palps to an erect position; *P. baehrorum* and *P. saltans* lift both palps one after the other, whereas *P. alacris* lifts them together in an alternate-stepwise manner. At the end of this phase *saltans* moves its palps

smoothly back to the flexed posture, whereas *baehrorum* takes them back in many steps and *alacris* in a smaller number of steps. *P. pertinax* is different from all the other *lugubris*-group species in that it exhibits elements similar to those of the *start-display* in phase II followed by flicking movements of the palps, and ends the display with strong opisthosomal movements.

Phase III of the display is characterised by large differences in the type of display movements as well as in the general character of the behaviour. *P. alacris* and *P. pertinax* begin a long-lasting palpal display while approaching the female, and come so close to the female’s body that they touch it with their legs I and try to mount from this position. Both species differ greatly in the complexity of their repertoire shown during this phase. *P. alacris* performs a very rigid and simple *circling* of its cymbia, mirror-imaged and in alternation, while *pertinax* again turns its palps in a way that can be considered a repetition of the phase II display. Thus *pertinax* uses only one set of display movements during the whole courtship. The other two species, *P. saltans* and *P. baehrorum*, perform a short and jerky palpal display and immediately afterwards run towards the female and try to mount. The palpal movements are quite complicated in *baehrorum*, which displays a kind of waving movement with the whole palp that allows the tips of the cymbia to point towards and away from each other. The distinctive feature of the *saltans* courtship is a very short *palpal jerk* in phase III. Immediately afterwards the male runs towards the female with jerky skips.

Synonymy based on behavioural data

Pardosa lugubris (Walckenaer, 1802)

Pardosa lugubris: Vlijm & Dijkstra, 1996: 51–55; Vlček, 1995: 174–183.

Pardosa alacris (C. L. Koch, 1833)

Lycosa chelata: Hallander, 1967: 145–150.

Pardosa alacris: Vlček, 1995: 174–183.

Pardosa saltans Töpfer-Hofmann, new species

Lycosa lugubris: Bristowe, 1929: 324; Skinner, Thompson & Cooke, 1967.

Pardosa lugubris: Vlijm & Dijkstra, 1966: 51–55.

Pardosa saltans: Vlček, 1995: 174–183.

Key to the species

Males

- Femora of all legs pale yellow with indications of dark annulations; carapace dark with variable coverage of dense white and yellow hairs, white median band distinct, and small white-haired spots laterally; carapace length ≤ 2.4 mm (Fig. 19); male bulb as in Figs. 28, 29. Only known from riparian forests near Vienna (Austria) and Munich (Germany).....*P. baehrorum*
- All femora dark brown, more distal segments pale yellow, appearing transparent; carapace dark brown covered with black hairs, with contrasting white-haired median band, no lateral markings; carapace length > 2.4 mm (Fig. 19).....2

2. Carapace length >3 mm (Fig. 19); tegular apophysis comparatively broad and strong (Fig. 32); cymbium tip wide in lateral view (Fig. 33). Only known from Caucasus region *P. caucasica*
- Carapace length ≤3 mm (Fig. 19); tegular apophysis thinner (Figs. 20, 24, 26, 30); cymbium tip narrower in lateral view (Figs. 21, 25, 27, 31). Species found in Europe.....3
3. Carapace length 2.8–3.0 mm (Fig. 19); anterior branch of tegular apophysis strongly curved, together with lateral branch forming shape of sickle (Fig. 30). Only known from montane beech forests in Greece *P. pertinax* von Helversen, new species
- Carapace length <2.8 mm (Fig. 19); anterior branch of tegular apophysis only slightly curved (Figs. 20, 26) or straight (Fig. 24). Species widespread in Europe4
4. Cymbium proximally with large dorsal brownish-red patch (in preserved material becoming pale yellow); cymbium distally narrow in lateral view, slightly concave dorsally (Fig. 25); anterior branch of tegular apophysis almost straight (Fig. 24) *P. alacris*
- Cymbium uniformly dark, or dark at least proximally; cymbium distally straight or convex in lateral view (Figs. 21, 27); anterior branch of tegular apophysis slightly curved (Figs. 20, 26)5
5. Dorsal surface of cymbium strongly convex in lateral view (Fig. 21); cymbial tip short, ratio tip-length to cymbium-length ≈0.32–0.37 (Fig. 34); cymbium tip with strong claw (Fig. 21); palpal tibia and cymbium with sparse dark bristles; proximal half of cymbium dark, more distally brownish *P. lugubris*
- Cymbium in lateral view almost straight (Fig. 27); cymbial tip long, ratio tip-length to cymbium-length ≈0.36–0.43 (Figs. 34, 35); cymbial claw indistinct, hidden among bristles; tibia and cymbium densely covered with dark bristles; cymbium completely dark *P. saltans* Töpfer-Hofmann, new species

Description of taxa

***Pardosa lugubris* (Walckenaer, 1802)** (Figs. 19–21, 34; 22, 23 (*P. barndti*))

Aranea chelata Müller, 1764: 94.

Aranea dorsalis Fabricius, 1775: 373.

Aranea lugubris Walckenaer, 1802: 239 [types lost].

Lycosa lugubris: Walckenaer, 1805: 13; 1837: 329.

Lycosa silvicola Sundevall, 1833: 176; Menge, 1879: 553.

Pardosa lugubris: Simon, 1876: 337; 1937: 1065, 1082, 1130; Holm, 1947: 33, fig. 12a, pl. 6, 10; Bonnet, 1958: 3381; Wunderlich, 1984 (in part): 11; Tanaka, 1993: 261–318; Roberts, 1998: 233–234; Kronstedt, 1999: figs. 1c, 3f–k, 5b,c, 6b, 8b, 9.

Pardosa barndti Wunderlich, 1969: 384, figs. 10, 11 [holotype (SMF 24437) examined].

Remarks on synonymy: Synonyms for the name *lugubris* exist in large numbers. Two species, which could be conspecific with *P. lugubris*, are *Aranea chelata* Müller, 1764 and *Aranea dorsalis* Fabricius, 1775, but both descriptions have not been accepted by most arachnologists. Only the name *lugubris*, given by Walckenaer in 1802, has been regarded as valid. Dahl (1908) argued in his revision on German lycosids that the description of Müller was as precise as the one Walckenaer had given and decided that the earlier name *chelata* should be used. Following Simon (1937) the name *lugubris* was introduced again and has been taken as the valid name for the taxon. Bonnet (1958) argued that the name *lugubris* was more frequently used by taxonomists and the description of the species was inadequate in both earlier studies.

Walckenaer's descriptions (1802, 1805, 1837) of the species he called *Aranea* (later *Lycosa*) *lugubris* characterise the species only from its habitus. This species plays a major role as name-bearer of the *P. lugubris*

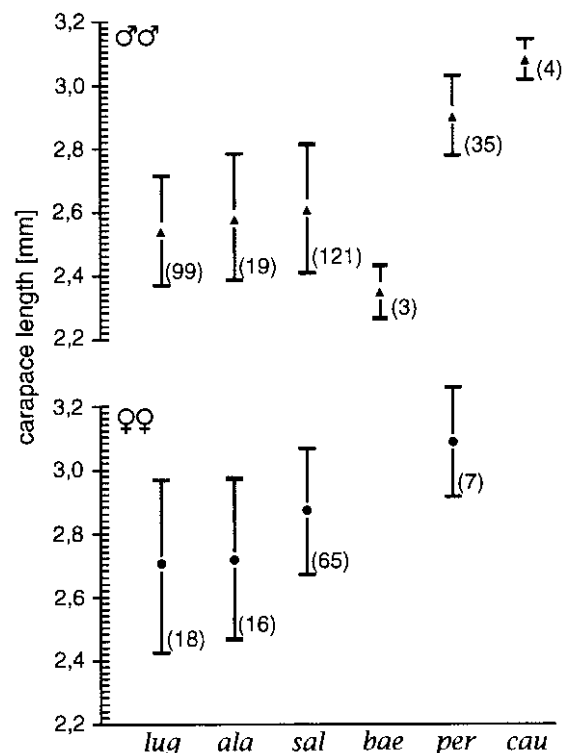


Fig. 19: Carapace length of *P. lugubris*-group species: carapace length of *P. lugubris* (lug), *P. alacris* (ala), *P. saltans* (sal), *P. baehrurum* (bae), *P. pertinax* (per) and *P. caucasica* (cau) is shown with standard deviation (\pm SD). The number of measured specimens is indicated in brackets. In males two groups may be distinguished: the smaller (central/northern European) and the larger (Greek, Caucasian) species. The graph showing the females indicates that *P. saltans* females on average are slightly larger than *P. lugubris* and *P. alacris* females. The females measured were identified by their decisions in the cross-mating tests.

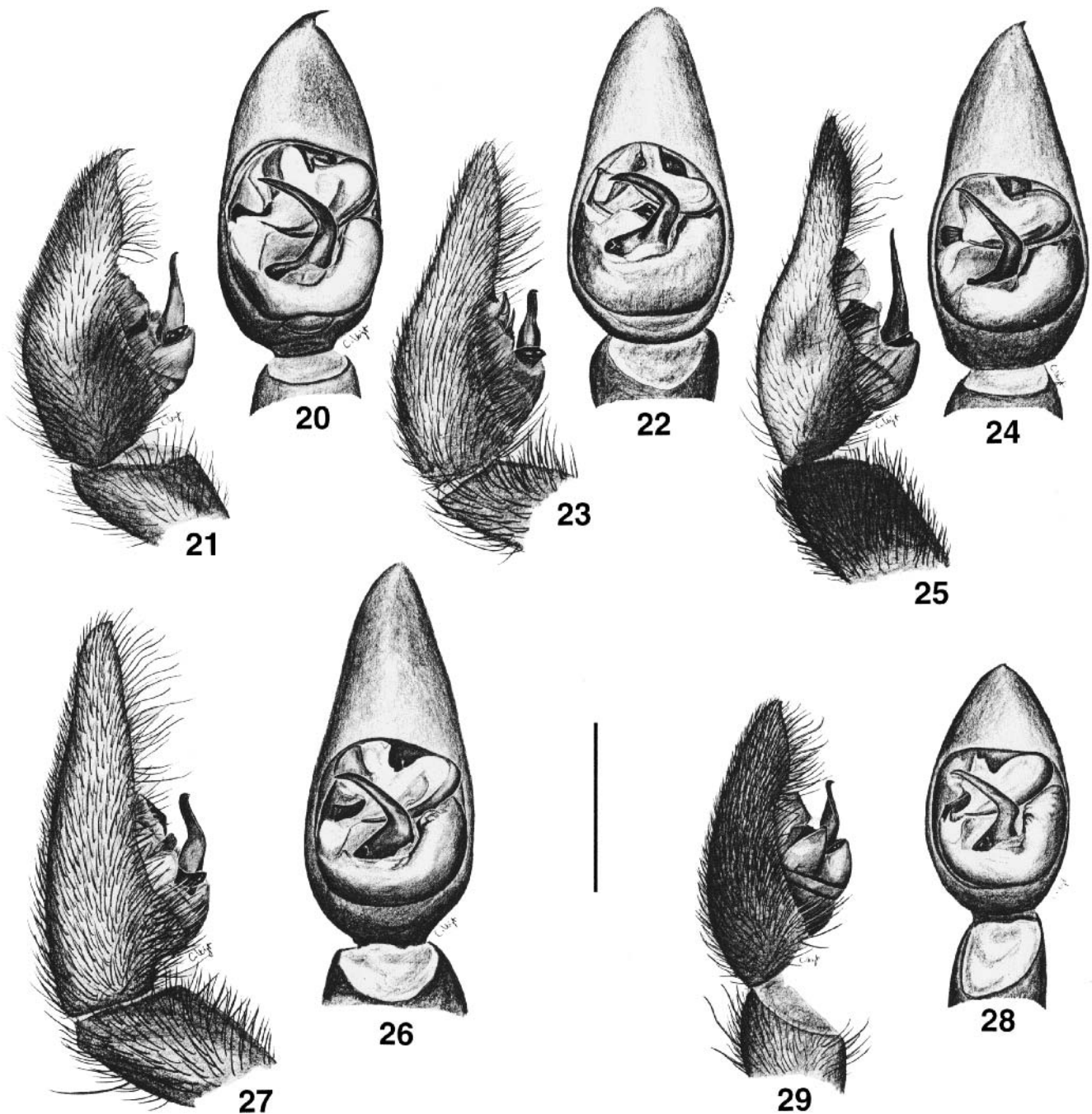
species-group. In the following a neotype is selected and described and will provide a renewed definition of the taxon, because no type material from Walckenaer survives (see Tongiorgi, 1966a). Walckenaer's description does not fulfil any criteria to select one of the taxa. A recent collection in the surroundings of Paris by the first author provides material for neotype selection. The locality comes as close as possible to the type locality indicated by Walckenaer as: "... dans les environs de Paris ...". The new definition is based on characteristics of the courtship display.

Pardosa barndti Wunderlich, 1969 was described based on one male from Berlin (Germany). Our analysis of the type specimen does not exclude the possibility that the taxon might still be valid. Definite evidence for teratogenic effects responsible for the aberrant morphology of the palpal bulb could not be found as both palps have exactly the same morphology. Therefore we include new drawings of the palp of the *P. barndti* holotype for comparison with the other taxa (Figs. 22, 23).

Type material: Neotype ♂ of *Pardosa lugubris* (to be deposited in SMF), Abbaye de Chalis, near Paris, France, deciduous woodland, 26 April 1992 (T.-Hofmann leg.). Holotype ♂ of *Pardosa barndti* (SMF 24437) from Berlin (Wunderlich leg.), examined.

Other material examined: C. L. & L. Koch Coll. (NHM), 5 tubes, labelled "*Lycosa lugubris*", two of them containing *lugubris*: [3♂, "Galizien"] [4♂, without data], several females not identified! JAPAN: Hokkaido, Aizankei, 20♂ 3♀, July 1971 (Tanaka leg., CTH). AUSTRIA: *Vorarlberg*: Latenser Tal, wet forest, 1♂ (SMF 11990); Rheinspitz, deciduous forest, 1♂, 1960 (SMF 12023, Braun leg.). *Steiermark*: Leoben, 600–800 m, 2♂, 1966 (SMF 30497, Hohorst leg.). *Northern Tirol*: near Innsbruck, Stanis, 1♂, April/May 1974 (SMF 36314, Thaler leg.); Innsbruck, Achenkirch, 4♂, May 1976 (SMF 36284, Thaler leg.). BALKANS: Ipek, 3♂, 1984 (SMF 34512). CZECH REPUBLIC: Bohemian mountains, Trautenau, 1♂, 1949 (Spacek leg., ex CSch); south of Prague, *Quercus* forest, pitfall trap, 2♂ 1♀, 24 July 1968 (leg. Buchar, CTH); České Budějovice, *Quercus* forest, pitfall trap, 2♂, spring 1984 (leg. Buchar, CTH). *Biele Karpaty*: Krniroklatska Tiesnava, 1♂, 25 September 1990 (Devon leg., CSv);

Strosovsky Mociar, 2♂, 4 October 1990 (Svaton leg., CSv). ESTONIA: Matsalu, ♂♂, 1983 (SMF 31917, Vilbaste leg.). FRANCE: MNHN Nos. B2202– (351 c.st.), B2197; same data as neotype, 1♂ 1♀ (T.-Hofmann leg., CTH). GERMANY: *Baden-Württemberg*: southern "Black Forest", Wutach-Gorge, slope (beech forest) north of "Schattenmühle" near Göschweiler, 1♂, 16 April 1966 (v. Helversen leg., CvH). *Bavaria*: river Saale (Franken) near Münnerstadt, 1♂ 1♀, 22 May 1967 (Pieper & Wasserthal leg., CvH); Munich, English Garden, 1♂ 1♀, May 1968 (v. Helversen leg., CvH); Murnauer Moos, 9♂, 1977–78, 1983 (SMF 33054, Löser leg.); Isar valley and riparian forest, "Sammerner Heide", 1♂ 1♀, 1 May 1987 (v. Helversen leg., CvH); Rhön near Burkhardroth (350 m), deciduous forest, 1♂, 16 May 1987 (v. Helversen leg., CvH); Stetten, oak wood, 23♂ 4♀, 10 April 1989 (T.-Hofmann leg., CTH); Herbststadt, oak wood, 3♂, 11 April 1989 (T.-Hofmann leg., CTH); Poppenholz, oak



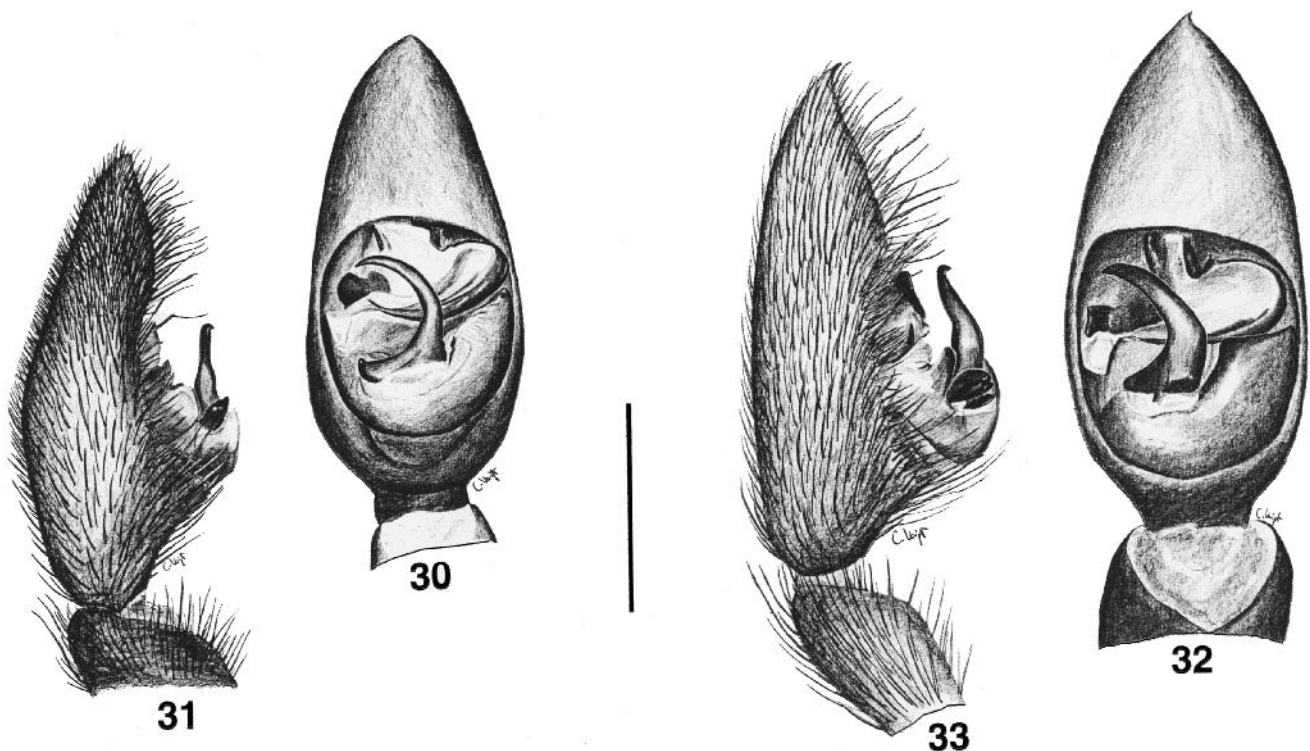
Figs. 20–29: Right male palps (ventral and prolateral views). 20, 21 *P. lugubris*, neotype from Abbaye de Chalis, France (SMF); 22, 23 *P. barndti*, holotype from Berlin (SMF 24437); 24, 25 *P. alacris*, from Steinbach, northern Bavaria (CTH, 1990); 26, 27 *P. saltans*, paratype from Steinbach, northern Bavaria (CTH, 1989); 28, 29 *P. baehrorum*, from Isar valley north of Munich, Bavaria (CTH, 1989). Scale line=0.5 mm. Drawings by Ch. Voigt.

wood, 5♂ 8♀, 11 April 1989 (T.-Hofmann leg., CTH); Puppliger Au, riparian forest, 46♂ 9♀, 21 April 1989, 11 April 1991 (T.-Hofmann leg., CTH); Steinbach, old vineyard and beech wood, 7♂ 2♀, 25 April 1989 (T.-Hofmann leg., CTH); Marktredwitz, Fichtelgebirge, oak and pine trees, 1♂, 24 March 1990 (T.-Hofmann leg., CTH); Deggendorf, Ranzinger Berg, beech wood, 4♂ 3♀, 25 April 1991 (T.-Hofmann leg., CTH); Greding, oak wood, 5♂, 27 April 1991 (T.-Hofmann leg., CTH). *Hessen*: Brandoberndorf, dry slope, 4♂ (SMF 31990, Müller leg.); Taunus, Altkönig, 1♂, 1948 (SMF 5724, Zilch leg.); Spessart, Jossa, 1♂, 1949 (SMF 10007); Darmstadt, "Griesheimer Sand", solitary pine trees, pitfall trap, 1♂, 16 May–12 July 1969 (v. Helversen leg., CvH); between Wetzlar and Weidenhausen, pine forest, 2♂, 1983 (SMF 31993, Müller leg.); same data, 2♂ (SMF 31994, Müller leg.); Hohenahr, deciduous forest, 2♂, 1987 (SMF 36738, Allspach leg.). *Niedersachsen*: Osterholtz-Scharmbeck/Hellingst., oak and pine forest on dune heathland, 1♂, 1 April 1990 (leg. Cordes, CTH). *ITALY*: Northern Italy, P.v. Lucca, near Lucca, montane (1000 m) deciduous woodland, clearing, 1♂, May 1992 (leg. Cordes, CTH). *FORMER JUGOSLAVIA*: Slovenisch Brod, between Zagreb and Belgrade, wet riparian oak wood in valley of Save river, 1♂, 19 April 1968 (v. Helversen leg., CvH); 200 km east of Zagreb, meadows near highway, 1♂, 17 May 1986 (v. Helversen leg., CvH). *POLAND*: Kartuzy, Ciche Lake, Melico-Fagetum, 2♂, 1980 (SMF 35829, Staręga leg.). *SLOVAKIA*: Tatra, 1♂ (SMF 30581, Roewer leg.). *SWEDEN*: Swedish Lappland, near Torneträsk, 9♂, 1976 (SMF 31911, Holm leg.). *SWITZERLAND*: near Basel, 1♂ (Schenkel leg., NHMB); near Vierwaldstätter Lake, 2♂ (Müller & Burckhardt leg.). *Jura*: Chevenez Crengenat, forest edge, 2♂, 1988 (Hänggi leg., CH); Chevenez, Tron du Crengenat, 1♂, 1988 (Hänggi leg., CH); Tschafoué, Combe Ronde, 1♀, 1988 (Hänggi leg., CH). Züricher Oberland, 1♂, 25 April 1991 (Heller leg., CTH).

Male (neotype): Carapace length 2.5 mm, width 1.9 mm, total length 4.6 mm. Leg I (right): Fe 2.2 mm, Pt 0.8 mm, Ti 2.2 mm, Mt 2.2 mm, Ta 1.4 mm. Prosoma dark brown covered with dense black hairs and with a broad white-haired median band; no lateral markings

visible. Margin of carapace bordered by white hairs. Chelicerae brown with darker stripes and some dark bristles and hairs. Sternum light brown with some darker stripes and covered with white hairs. Opisthosoma light brown dorsally with indistinct lanceolate stripe, laterally grey-striped merging into grey spots on venter. Anterior spinnerets in Netherlands populations dark brown, often black (Roberts, 1998); not observed in Bavarian populations. Legs: dorsal parts of coxae and trochanters black with white hairs. Proximal parts of femora black, distal parts and remaining segments light yellow. Palps: femur, patella and tibia brown, cymbium with distinct claw. Cymbium (Figs. 20, 21) proximally dark, more distally where densely covered with chemosensitive hairs greyish-brown (in preserved individuals yellowish-brown). Tibia with some strong bristles especially in prolateral part. Dorsal surface of cymbium convex, tip comparatively short in comparison to length of cymbium (see Fig. 34).

Female: Carapace length 2.6 mm, width 2.2 mm, total length 4.8 mm. Leg I (right): Fe 2.1 mm, Pt 0.9 mm, Ti 1.9 mm, Mt 1.7 mm, Ta 1.2 mm. Prosoma brown with a distinct broad white-haired median band, no lateral markings. Chelicerae proximally yellowish-brown with darker stripes, distally brown. Sternum brown with white and some stronger black hairs. Opisthosoma brown with some large dark spots, distinct lanceolate stripe sometimes bordered by dark spots. Venter light brown. Anterior spinnerets in Netherlands populations darker than general colour of opisthosoma (Roberts, 1998); not observed in Bavarian populations. Legs light brown with clear annulations, especially on dorsal parts of femora. Epigyne with anchor-shaped



Figs. 30–33: Right male palps (ventral and prolateral views). **30, 31** *P. pertinax*, paratype from northern Greece, Vernon Mts. (CvH, 1989); **32, 33** *P. caucasica*, from Caucasus (ex Coll. Buchar). Scale line=0.5 mm. Drawings by Ch. Voigt.

medium septum typical for species group (see Tongiorgi, 1966a).

Diagnosis: Males can be distinguished from males of the other species by the dorsal surface of the cymbium (Fig. 21) being comparatively convex when seen in lateral view, and by the comparatively short cymbium tip. The cymbium of *lugubris* is also characterised by the prominent cymbial claw, which is easily visible even in unshaved palps. In our experience this difference is expressed more conspicuously than shown in Kronstedt (1999; fig. 6) for *P. baehrorum*, *alacris* and *lugubris*. The palpal tibia of *lugubris* has a relatively sparse covering of dark hairs compared with all other species and the dorsal cymbium (especially the cymbium tip) is often greyish-brown and not blackish-brown as in the other species, except *alacris* (see below).

Males as well as females (and this is the only recently found diagnostic character for females) can be distinguished by having dark anterior spinnerets — in males they may even be black (Roberts, 1998). All other species are characterised by brown spinnerets in males as well as in females. However, this character has not been found in the Bavarian populations that were studied in detail here; possibly it is only present in populations of the Netherlands.

Habitat and distribution: *Pardosa lugubris* is a widespread species in Europe and occurs in a variety of forest types ranging from oak and beech to pine (*Pinus silvestris*) woods. Additionally the species can be found in woodland clearings, on forest borders and along hedges (ecotones). It seems to be more euryoek than the other species.

According to our study all the faunistic records of *P. lugubris* (*s.lato*) made before *c.* 1990 cannot be trusted unless the material has been reviewed. Only those records are used here that were revised by the authors. They prove the occurrence of *P. lugubris* in the following countries: Austria, Czech Republic, Estonia, France, Germany, Italy, "Jugoslavia", Netherlands (A. Noordam, in litt.), Poland, Slovakia, Sweden, Switzerland. *P. lugubris* also occurs in Japan, as shown

by the examination of a sample from the Tanaka Collection (see also Tanaka, 1993).

***Pardosa alacris* (C. L. Koch 1833)** (Figs. 19, 24, 25, 34)

Lycosa alacris C. L. Koch, 1833: hft 120, pl. 17, 18.

Lycosa silvicultrix C. L. Koch, 1836: 25, pl. 82, figs. 182–183.

Lycosa lugubris: Thorell, 1872: 277.

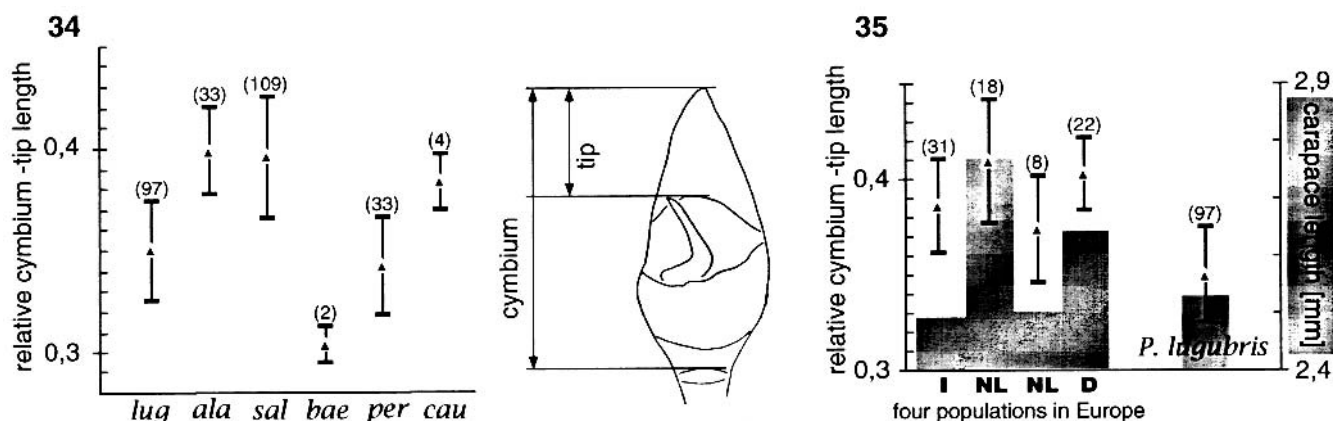
Pardosa pseudolugubris Wunderlich, 1984: 3, figs. 1–13.

Pardosa alacris: C. L. Koch, 1848b: 39, pl. 514, figs. 1443–1444; Kronstedt, 1992: 179–182; 1999: figs. 1b, 3l–p, 5d,e, 6c, 8c, 9.

Remarks on synonymy: Type material of the two *Pardosa lugubris*-group species described by C. L. Koch is deposited in Berlin, whereas collection material of both father and son, C. L. and L. Koch, is housed in London.

The description given for *Lycosa alacris* by C. L. Koch (1833) leaves no doubt, as discussed in Kronstedt (1992); the taxon is characterised by the variable reddish-coloured cymbial bases that in living individuals can easily be seen in dorsal view. In preserved animals the colour of the cymbium base can change to an opaque yellow.

In the case of *Lycosa silvicultrix*, C. L. Koch (1836) provides enough information to allow a decision on its identity. The only type material deposited in Berlin is a female specimen that cannot be reliably identified. However, Koch's description is based on a very good colour illustration of male and female. The male is described as having a brown (as opposed to bright red in *alacris*) spot on the cymbium dorsum. Also Thorell (1872) treats *L. silvicultrix* C. L. Koch as a synonym of *L. alacris* C. L. Koch because of its reddish cymbium ("lamina") base. The variability of this character is well known to us from *P. alacris* males from southern Germany, the same region where Koch lived and collected. Therefore we also believe that the specimens which Koch drew under the new name *silvicultrix*, in reality belong to his earlier described *P. alacris* because the brown area on the cymbium lies at exactly the place where *alacris* has the variable red coloration. Specimens from the Koch Coll.



Figs. 34, 35: Morphometrics of *P. lugubris*-group species. **34** Comparison of relative cymbium tip length (tip length divided by total length of cymbium) between the species: *P. baehrorum* has the shortest tip whereas *P. alacris* and *P. saltans* have the longest. The difference between the tip length of *P. lugubris* and *P. saltans* is usually sufficient to distinguish the species in most populations; **35** Variation of the relative cymbium tip length in four *P. saltans* populations (Netherlands, Italy, Germany): populations with smaller body size (carapace length) have relatively shorter cymbium tips.

(deposited in NHM, London) were reviewed and belong to *P. alacris* and *P. lugubris*. It is not clear whether the collections were made by C. L. Koch or by his son L. Koch (see data on the labels) who in 1878 did not list the two taxa described by his father.

Type material: C. L. Koch Coll. (*L. alacris*, 1♂, ZMB 1986, Berlin, examined); C. L. Koch Coll. (*L. silvicultrix*, 1♀, ZMB Berlin, not examined); Wunderlich (*P. pseudo-lugubris*, 1♂, SMF 31914, examined).

Other material examined: C. L. & L. Koch Coll. (NHM London), 5 tubes, labelled “*Lycosa lugubris*”; [5♂, no label] [3♂, no label] [1♂ 1♀, in copula leg., 13 May 1868] [14♂, no label], many females not identified! AUSTRIA: Gleinalpe near Graz, deciduous forest, 1♂ 1♀, 15 May 1968 (v. Helversen leg., CvH. Northern Tirol: near Innsbruck, Martinsrand, 19♂, 1964 (SMF 31594, Thaler leg.); near Innsbruck, Ötztal, Brunau, 1♂, 1973 (SMF 30686, Thaler leg.); near Innsbruck, Stanis, 1♂, April/May 1974 (SMF 36314, Thaler leg.); near Innsbruck, Stillschlucht, 1♂, 1977 (SMF 29864, Thaler leg.); Innsbruck, Kranebitten, 2♂, 1977 (SMF 29855, Thaler leg.). CZECH REPUBLIC: *Biele Karpaty*: Krivoklatska Tiesnava, 1♂, 25 September 1990 (Devon leg., CSv); Krivoklatska Tiesnava, many ♂♀, 4 October 1990 (Devon leg., CSv). FRANCE: MNHN No. B2202–(441 c.st.). GERMANY: *Baden-Württemberg*: southern “Black Forest”, Wutach-Gorge, slope (beech forest) north of “Schattenmühle” near Göschweiler, 9♂, 16–17 April 1966 (v. Helversen leg., CvH); “Black Forest”, Utzenfluh, 5♂ 1♀, 10 May 1970 (v. Helversen leg., CvH); southern “Black Forest”, Wutach-Gorge, beech forest, 7♂ 2♀, 12 May 1988 (Cordes leg., CvH). *Bavaria*: Murnauer Moos, 10♂, 1977–78, 1983 (SMF 33054, Löser leg.); Steinbach, old vineyard, 70♂♀, 1986 (SMF 35634, Bauchhens leg.); Steinbach, old vineyard, oak and beech forest, 12♂ 12♀, 25 April 1989 (T.-Hofmann leg., CTH); same locality, 6♂, 21 March 1990 (T.-Hofmann leg., CTH); Rhön, Weissbach, dry pasture on chalk (480 m), 1♂ 1♀, 9 June 1986 (Leipold/Fischer leg., CvH); Aschenroth, oak forest, 2♂, 10 April 1989 (T.-Hofmann leg., CTH); Stetten, dry pasture on chalk, near bushes, 4♂ 12♀, 11 April 1989 (T.-Hofmann leg., CTH); riparian forests near Isar river, beech forest near Bad Tölz, 1♂ 3♀, 4 May 1990 (T.-Hofmann leg., CTH); Mittelehrenbach, beech forest, 10♂ 3♀, 16 May 1990 (T.-Hofmann leg., CTH); same locality, 4♂ 4♀, 19 May 1992 (T.-Hofmann leg., CTH). *Hessen*: Odenwald, 1♂, c. 1830 (SMF 2317, Wider leg.); Vogelsberg, Künanzhorn, 1♂, 6 June 1967 (Pieper leg., CvH). Hardt, 1♂, 1905 (SMF 2323, Wolf leg.). *Rheinland-Pfalz*: Bonn/Rhein, 1♂, 1883 (SMF 2318, Bertkau leg.); “Gonsenheimer Wald” near Mainz, 2♂, 13 May 1963 (v. Helversen leg., CvH). GREECE: Karpathos, Forest of Aperi, 1♂ (SMF 15504, Kinzelbach leg.); Katára-pass (1400 m), beech forest, 5♂ 4♀, 27 April 1992 (Cordes leg., CTH). ITALY: South Tyrol, Tisens near Meran (630 m), 2♂ 1♀, 5 May 1969 (Uhrig leg., CvH). SLOVENIA: Karawanken Mts., Kl. Orbir (1200 m), 1♂, 29 May 1966 (Wasserthal leg., CvH).

Male: Carapace length 2.4 mm, width 1.84 mm, total length 4.5 mm. Leg I (right): Fe 1.86 mm, Pt 0.74 mm, Ti 2.0 mm, Mt 2.13 mm, Ta 1.35 mm. Prosoma dark brown covered with dense black hairs and a broad contrasting white-haired median band dorsally; no lateral markings. Sternum light brown with dark hairs. Opisthosoma brown with dark spots on margins of lanceolate stripe, laterally greyish-brown covered with yellow hairs. Spinnerets medium to light brown. Legs: proximal parts of femora black, distal parts and remaining segments light yellow. Palps: femur, patella and tibia blackish-brown, densely covered with black hairs. Cymbium dark with a large light yellow spot (dark red in living individuals, see Kronstedt, 1992) in proximal half; comparatively slim with long cymbium tip (Fig. 34) and a distinct depression in its distal half (Fig. 25); tegular apophysis characterised by straight anterior branch.

Female: Carapace length 2.7 mm, width 2.3 mm, total length 4.9 mm. Leg I (right): Fe 2.33 mm, Pt 0.94 mm, Ti 2.1 mm, Mt 2.05 mm, Ta 1.3 mm. Appearance similar to *P. lugubris*.

Diagnosis: Males can be easily distinguished from all other taxa by the bi-coloured cymbia. The base is dark red covered with light hairs in live spiders and bleaches into yellow in preserved specimens. The distal parts of the cymbia are dark. Females appear to be the same size as those of *P. lugubris* (Fig. 19).

Habitat and distribution: Palaearctic, with syntopic occurrences found with *P. lugubris*, *saltans* and *pertinax* (see Fig. 2). The species seems to be more restricted to deciduous oak and beech woods. *P. alacris* has been reported from Austria, Czech Republic, France, Germany, Greece, Italy, Poland, Romania, Slovenia, Sweden and Switzerland.

Pardosa saltans Töpfer-Hofmann, new species (Figs. 19, 26, 27, 34, 35)

Lycosa lugubris: Blackwall, 1861: 27, fig. 10.

Lycosa chelata: Dahl, 1908: 216.

Pardosa lugubris: Locket & Millidge, 1951: 266, figs. 129e,f, 130e; Tongiorgi, 1966a: 296, figs. 56–59; Wunderlich, 1984 (in part): 6–8; Roberts, 1985: 134, 140, fig. 59b; 1995: 219.

Pardosa saltans / *silvicultrix*: Roberts, 1998: 232–233.

Remarks on synonymy: This species is similar to *P. lugubris* (*s.str.*) and therefore has not been recognised until in this study populations were sorted by means of their sexual behaviour. Nevertheless, some authors who published accurate drawings of the genitalia or habitus provide information on which species they described. One such author is Blackwall (1861) who published a drawing of “*L. lugubris*” which obviously shows *P. saltans* with its strong bristles on the palpal femur and patella. Additionally he shows the cymbium completely dark, a trait that is typical for *P. saltans* and different from *P. lugubris* (*s.str.*).

Pardosa saltans / *silvicultrix* (*sensu* Roberts, 1998): the author names the species *P. saltans* (section header), but in the text the name *P. silvicultrix* is used; the usage of two names must be the result of a typing error. The description in Roberts (1998) fits exactly the taxon that is described here under the name *saltans*, and both share the same differences from C. L. Koch’s description of *Lycosa silvicultrix* (for synonymy see also *P. alacris*).

Etymology: The specific name refers to a characteristic behavioural element during the males’ courtship, when the male approaches the female in several jumping steps and tries to mount. The behaviour appears similar to a certain style of dancing.

Type material: Holotype ♂ (to be deposited in SMF), Germany, Bavaria, Steinbach, beech forest, 25 April 1989 (T.-Hofmann, leg.). Paratypes: 7♂ 3♀, same locality, 25 April 1989 and 21 March 1990 (T.-Hofmann leg., CTH).

Other material examined: AUSTRIA: Reschen, Scheidegg, 1♂ (SMF 30357, Roewer leg.). CZECH REPUBLIC: Lovos, hill near Lovosice, *Quercus pubescens* forest, pitfall trap, 2♂, spring 1968 (Buchar leg., CTH). FRANCE: *Pyrénées Orientales*: Banyuls s. M.,

1♂ (SMF 31922, Wunderlich det. 1983, sub *lugubris*); Mt. Canigou, 2♂ (SMF 16939, Grasshoff leg.); Mt. Canigou, 7♂ 2♀, 18 May 1970 (v. Helversen leg., CvH); *Corsica*: Zonza, 3♂, 1953 (SMF 9054, Kahmann leg.); same data, 3♂ (SMF 9059, Kahmann leg.). *Seine et Marne*: Fontainebleau, beech-oak-pine wood, 6♂, 16 April 1992 (T.-Hofmann leg., CTH). GERMANY: *Baden-Württemberg*: Freiburg/Br., "Zähringer Burg", deciduous wood, 7♂ 5♀, 16 May 1971 (v. Helversen leg., CvH); Kaiserstuhl, forest edge south of Badloch, beech forest, 1♂, 1965 (SMF 17633, Wiehle leg.); Kaiserstuhl, Oberrotweil, vineyard, 1♂, 1965 (SMF 17558, Wiehle leg.); Kaiserstuhl, Niederrotweil, 1♂, 1966 (SMF 28529, Wiehle leg.); Freiburg/Br., Wild-Tal, 7♂ 5♀, 11 April 1966 (v. Helversen leg., CvH); Gundelfingen, Rebberg, pitfall traps, 2♂ 1♀, 26 April-1 May 1966 (v. Helversen leg., CvH); Kaiserstuhl near Schelingen, pitfall traps, 3♂, 9 April-23 July 1967 (v. Helversen leg., CvH); Kaiserstuhl, 1♂, 1 June 1968 (v. Helversen leg., CvH). *Bavaria*: Adelsdorf, Neuhaus, 1♂, May 1983 (v. Helversen leg., CvH); Rhön near Burkhardroth (350 m), deciduous forest, 2♂, 16 May 1987 (v. Helversen leg., CvH); Herbststadt, 13♂ 7♀, 11 April 1989 (T.-Hofmann leg., CTH). *Berlin*: Pfaueninsel, 3♂, 1968 (SMF 24068, Wunderlich leg.); Nikolskoe, oak forest, 10♂ 29♀, June 1970 (Wadmann leg., CvH). *Hessen*: Taunus, Altkönig, 3♂, 1948 (SMF 5724, Zilch leg.); Spessart, Jossa, 5♂, 1949 (SMF 10164, Braun leg.); same data, 1♂ (SMF 10021, Braun leg.); same data, 1♂ (SMF 10007, Braun leg.); Harz, oak forest, 2♂, 1952 (SMF 20506, Wiehle leg.); between Wetzlar and Weidenhausen, pine forest, 2♂, 1983 (SMF 31991, Müller leg.); same data, 2♂ (SMF 31992, Müller leg.); same data, 2♂ (SMF 31994, Müller leg.); Hohenahr, deciduous forest, 12♂, 1987 (SMF 36738, Allspach leg.). *Niedersachsen*: Osterholtz-Scharmbeck/Hellingst, oak wood, 3♂ 1♀, April 1989 (Cordes leg., CTH). *Rheinland-Pfalz*: Gonsenheimer Forest, near Mainz, 1♂, 1954 (SMF 26051, Braun leg.); same locality, 1♂, 1956 (SMF 15956, Braun leg.); Eifel, Jünkerath, 1♂, 1957 (SMF 26052, Braun leg.); Dahn, 2♂, 13 May 1973 (v. Helversen leg., CvH). ITALY: Valtelluna, near Sondrio, 600-700 m, 1♂, 1975 (SMF 32974, Martens leg.); Valle di Corteno, south of Tirako, 700 m, 1♂, 1975 (SMF 32962, Martens leg.); Tuscany, chestnut forest, 3♂ 11♀, March 1991 (Edrich leg., CTH); Liguria, P.v. Genova, St. Stefano d'Aveto, beech forest, 1400 m, 31♂ 18♀, 15 April 1991 (Cordes leg., CTH). NETHERLANDS: Ede, beech forest, 19♂ 26♀, 15 April 1991 (Kessler leg., CTH); same locality, coastal land, mixed deciduous forest, 9♂ 18♀, 1 May 1991 (Kessler leg., CTH). POLAND: Kartuzy, Ciche Lake, Melico-Fagetum, 3♂, 1980 (SMF 35829, Staręga leg.). SWITZERLAND: Near Basel, 21♂ (Schenkel leg.); near Vierwaldstätter Lake, 5♂ (Müller & Burckhardt leg.); Maggia valley, 1♂, 12 April 1969 (v. Helversen leg., CvH); Tessin, 6♂, 11 April 1969 (v. Helversen leg., CvH).

Male (holotype): Carapace length 2.7 mm, width 2 mm, total length 4.7 mm. Leg measurements: see Table 1. Prosoma dark brown with a distinct broad white-haired median band, no lateral markings. Sternum yellowish-brown with short dark hairs. Opisthosoma brown with a light brown lanceolate stripe bordered by dark markings; lateral parts with grey spots covered with whitish and some stout dark hairs. Venter

Male	Fe	Pa	Ti	Mt	Ta	Total
Leg I	2.1	0.8	1.9	1.9	1.4	8.1
Leg II	1.9	0.7	1.6	1.9	1.2	7.3
Leg III	1.7	0.7	1.6	1.9	1.3	7.2
Leg IV	2.4	0.9	2.3	1.6	1.1	8.3
Female	Fe	Pa	Ti	Mt	Ta	Total
Leg I	2.5	1.2	2.1	2.1	1.5	9.4
Leg II	2.4	0.9	1.9	1.8	1.3	8.3
Leg III	2.5	0.9	1.8	2.2	1.3	8.7
Leg IV	3.2	0.9	2.7	3.8	1.8	12.4

Table 1: *Pardosa saltans*, leg measurements of male holotype and female paratype.

yellowish-brown with dark spots. Spinnerets brown. Legs: coxae, trochanters and femora black, femora distally light, both femora IV with slight annular pattern; patella, tibia, metatarsus and tarsus yellow. Palps (Figs. 26, 27): femur, patella and tibia blackish-brown; tibia and proximal parts of cymbium densely covered with long black bristles, especially on prolateral sides of tibia. Short claw hidden in bristles. Cymbium with characteristic straight shape (Fig. 27), dark brown, distal part (cymbium tip) comparatively long (Figs. 34, 35) giving the cymbium a slim appearance.

Female (paratype): Carapace length 2.85 mm, width 2.5 mm, total length 5.7 mm. Leg measurements: see Table 1. Appearance similar to *P. lugubris*, though slightly larger (see Fig. 19).

Diagnosis: In general *P. saltans* males can be distinguished from *P. lugubris* males by the long distal part of the cymbium (Figs. 34, 35) giving it a long and slim appearance, and the small claw at the cymbium tip, both characters contrasting with *lugubris*. Also the general shape of the cymbium in lateral view is straight (Fig. 27) whereas the dorsal surface is convex (Fig. 21) in *lugubris*. In females there is no reliable character to distinguish the species. On average they appear to be slightly larger than females of both *P. lugubris* and *alacris* (Fig. 19), but this difference may be valid only for Bavarian populations. More morphometric data are needed to verify this possible difference, which in cases of sympatry with *lugubris* and *alacris* may turn out to be a diagnostic character.

Morphological variation: Some populations were found where males of *P. saltans* were distinctly smaller in body size (Fig. 35). In these cases, the relative size of the two parts of the cymbium, otherwise a good character for distinguishing between *P. saltans* and *P. lugubris*, is less reliable. Nevertheless, it is possible to separate nearly all males from *P. lugubris* by a combination of the characters: shape of the cymbium, indistinct claw, and hairiness of the palpal tibia and tarsus.

Habitat and distribution: *P. saltans* is a widespread species, but seems to be restricted to the more western parts of Europe. No records are available from the south-eastern parts of Europe. The species occurs in Austria (as already presumed by Buchar & Thaler, 1997), Belgium, Czech Republic, France, Germany, Great Britain, Italy, Netherlands (also data from A. Noordam, in litt.), Poland and Switzerland. Recently records have been published from southern Sweden (Jonsson, 1998) and from the Czech Republic (Vlček, 1995; Buchar, 1997). Syntopic occurrences with *P. lugubris* and *P. alacris* have been found in several habitats in Bavaria (Fig. 2). Many collections, not reviewed so far, will also contain the species combination: *P. saltans* and *P. lugubris*.

Pardosa baehrorum Kronstedt, 1999 (Figs. 19, 28, 29, 34)

Pardosa baehrorum Kronstedt, 1999: 3-10, figs. 1a, 2, 3a-e, 4, 5a, 6a, 7, 9, 10.

Type material: Holotype ♂, Germany, Bavaria, Pupplinger Au (south of Munich), riparian forest near river Isar, 13 May 1983 (M. Baehr leg., ZSM), not examined.

Material examined: From type-locality, 3♂, 8–21 April 1989 (T.-Hofmann leg., CTH).

Diagnosis: A detailed description of this taxon is given in Kronstedt (1999). He includes a comparison with *P. lugubris* and *P. alacris*.

Males of *P. baehrorum* are easily distinguishable from all other European species by (1) being the smallest species (Fig. 19), and (2) by having conspicuous annulations on the pale yellow femora of all legs instead of being darkened as in all other species (see Kronstedt, 1999: fig. 1). The cymbium (Figs. 28, 29) has the shortest cymbium tip (Fig. 34).

Habitat and distribution: This species has so far been found only in Austria near Vienna (Thaler *et al.* (1984) and Thaler & Steiner (1989) sub *P. lugubris*, Buchar & Thaler (1997) sub *P. baehrorum*) and in Bavaria (Germany) in riparian forests near the Isar river (M. Baehr leg.). In Bavaria it was found in small numbers syntopic with dense populations of *P. lugubris* (*s.str.*). The populations may be extinct now in these habitats since no specimens could be found there in the years following 1989.

***Pardosa pertinax* von Helversen, new species** (Figs. 19, 30, 31, 34)

Etymology: The specific name refers to the persistent and long-lasting courtship of the males.

Type material: Holotype ♂ (to be deposited in SMF), northern Greece, Vernon Mts., beech wood, 1500 m, 28 August 1989 (leg. as juv., v. Helversen). Paratypes: 15♂ 4♀, same data (v. Helversen leg., as juv., CvH).

Other material examined: GREECE: Northern Greece, Vernon Mts., beech wood, 1300 m, 3♂ 1♀, 28 July 1990 (v. Helversen leg., CvH); central Greece, Nómois Ioanninon, Katára Pass, oak and beech wood, 1400–1700 m, 19♂ 3♀, 28 April 1992 (Cordes leg., CTH).

Male (holotype): Carapace length 2.9 mm, width 2.2 mm, total length 5.4 mm. Leg measurements: see Table 2. Prosoma dark brown covered with small black bristles, median band distinct and white-haired. Chelicerae dark brown. Sternum dark brown with black

hairs. Opisthosoma dark brown with white hairs; no lanceolate stripe. Venter and spinnerets dark. Legs: coxae, trochanters and femora dark brown with long dark hairs; distal parts of femora as well as remaining segments pale yellow. Palps (Fig. 31): wholly black with long black bristles on tibia and cymbium base; claw indistinct; tegular apophysis with characteristic shape, being almost round (shape of a sickle) in ventral view, the two processes forming half a circle (Fig. 30).

Female (paratype): Carapace length 2.9 mm, width 2.3 mm, total length 5.0 mm. Leg measurements: see Table 2. Appearance similar to *P. lugubris*, but distinctly larger (Fig. 19).

Diagnosis: Apart from the characteristic courtship behaviour in the male, this species can be recognised by being distinctly larger in both sexes than the other European species (Fig. 19), and additionally can be distinguished by the sickle-shaped tegular apophysis (Fig. 30). The palpal tibia and tarsus are covered with long, strong bristles, similar to those of *P. saltans*.

Habitat and distribution: The species has so far been found only in montane areas of northern and central Greece (above 1300 m). In some places it is syntopic with *P. alacris*. The species can be expected from other montane regions in the eastern Mediterranean. Both populations in Greece were found on the leaf litter on and near the borders of beech forests.

***Pardosa caucasica* Ovtsharenko, 1979** (Figs. 19, 32, 33, 34)

Pardosa caucasica Ovtsharenko, 1979: 39–58.

Type material: Not examined.

Material examined: Caucasus, Guseri pl. near Majkop, 6♂ (received from J. Buchar, CTH).

Male: Carapace length 3.0 mm, width 2.2 mm, total length 5.4 mm. Prosoma dark brown covered with small black bristles, median band distinct and white-haired. Chelicerae dark brown. Sternum light brown with brown dots. Opisthosoma light brown, lanceolate stripe dark brown. Venter and spinnerets dark. Legs: coxae, trochanters and femora dark brown with long dark hairs; distal parts of femora as well as remaining segments pale yellow, without annulations. Palps (Figs. 32, 33): broad with a broad cymbium tip, wholly black with long black bristles on tibia and cymbium base; claw indistinct; tegular apophysis very strong and broad (Fig. 32).

Female: Carapace length 2.9 mm, width 2.3 mm, total length 5.0 mm. Appearance similar to *P. lugubris*; females were not available for this study.

Diagnosis: This species is the largest of the *lugubris*-group species (carapace length ≥ 3 mm). The cymbium is large and broad and the tegular apophysis is very strong. The palpal tibia has long bristles.

Habitat and distribution: So far this species is known only from montane areas of the north-western Caucasian mountains. According to Ovtsharenko (1979) it is sympatric with another species of the *P. lugubris*

Male	Fe	Pa	Ti	Mt	Ta	Total
Leg I	2.3	0.9	2.8	2.2	1.7	9.9
Leg II	2.2	0.9	1.9	2.2	1.6	8.8
Leg III	2.3	0.9	1.7	2.5	1.4	8.8
Leg IV	3.1	1.1	2.4	4.4	1.9	12.9
Female	Fe	Pa	Ti	Mt	Ta	Total
Leg I	2.6	1.0	2.0	2.0	1.4	9.0
Leg II	2.4	0.9	1.9	1.9	1.3	8.4
Leg III	2.4	0.9	1.8	2.3	1.2	8.6
Leg IV	3.2	1.1	2.7	3.9	1.8	12.7

Table 2: *Pardosa pertinax*, leg measurements of male holotype and female paratype.

group. *P. caucasica* was found at elevations between 500 and 1900 m, while the other *lugubris*-group species was found between 500 and 700 m.

The *Pardosa lugubris* group

Diagnosis

This study provides strong evidence that all species included in this study form a monophyletic group, the *Pardosa lugubris* group. At least five of the species are shown to be biologically isolated species. All taxa are characterised by a high degree of similarity in appearance as well as in the morphology of the genitalia. Living specimens of most of the species look almost identical.

The representatives of the *P. lugubris* group should be separated from the *P. amentata* group (*sensu* Zyuzin, 1979 and Wunderlich, 1984). This is in agreement with Wiebes (1959), who placed *P. amentata* near *P. hortensis* (Thorell) and *P. proxima* C. L. Koch, and is supported by observations on the courtship of *P. hortensis* (Cordes, unpubl.; Vlijm & Dijkstra, 1966). In general, males of the *lugubris* group can be recognised by the broad white-haired band dorsally on the carapace bordered by black lateral stripes. The broad median band with parallel borders can also be easily seen in the brown-coloured females. *Pardosa amentata* and its relatives are instead characterised by a vase-shaped light spot dorsally on the prosoma and broken lateral bands. The males of all *lugubris*-group species (except *P. baehrorum*) also have deeply darkened coxae and femora of all legs, while *P. amentata* relatives are characterised by conspicuous leg annulations or by yellowish-brown legs. Concerning the genitalia, the male bulb in all *lugubris*-group species has a typical tegular apophysis with one long, thin distal branch and one lateral branch, which resembles that of *P. amentata* and is obviously the reason why *P. amentata*, *lugubris* (*s. lato*) and *alacris* (sub *pseudolugubris*) were put together in one group. However, the anchor-shaped median septum in the female epigyne is a reason to unite all *lugubris*-group species in one group and to exclude *P. amentata* from it. Finally, the courtship display shows homologies among all observed *lugubris*-group species but is completely different from that of *P. amentata* (see Vlijm & Dijkstra, 1966; Cordes & Barth, 1997). In the species of the *lugubris* group the display is divided into distinct behavioural phases. The display of the males is only exhibited when the female stays motionless. In *P. amentata* the male displays one stereotypic sequence of palpal movements combined with fore-leg drumming while following the female in a rhythmic courting walk.

Species isolation

The data presented here indicate that courtship behaviour plays an important role in the pre-mating isolation between the species. Since many of the species live in the same habitat or at least in neighbouring habitats, isolation by different habitat preferences seems unlikely. The same is indicated from phenology: all

species have their period of sexual activity in April and May. Thus the courtship behaviour must be regarded as the most important species-barrier. Males were observed courting females of all species, but females only accepted conspecifics for copulation. Obviously it is the courtship behaviour that allows discrimination between the males. The question of which signal modality carries the species-specific information can be answered only to some extent:

(1) The visual component, the main focus of this study, may contain information on the identity of the male because movements, especially of the palps, and the temporal structure of the presentation of these conspicuously darkened appendages are different between the *lugubris*-group species. Additionally, differences between the species' displays are greater in the later phases of courtship. The visual resolution of lycosids should be good enough to recognise moving shapes at a distance of 1–3 cm (Homann, 1931), which is the usual distance between the sexes during courtship.

(2) The sensory world of spiders is greatly specialised for the perception of mechanical signals. Slit sensilla and trichobothria are extremely sensitive to vibrations of the substrate and to the flow of air currents. The vibratory sense can be expected to provide the female with precise information on the identity of the courting male. Based on knowledge from a related group of "wandering spiders" (Araneae, Ctenidae, *Cupiennius*), reviewed in Barth (1997), substrate vibrations can be regarded as powerful signals transporting specific information that is encoded in the temporal structure and frequency content of the oscillations. As shown in Cordes & Barth (1997), lycosid spiders also make extensive use of vibratory signals during courtship. All species of the *P. lugubris* group live on leaf-litter, a substrate that seems well suited for the transmission of vibratory signals, as indicated in Scheffer *et al.* (1996) for Nearctic *Schizocosa* wolf spiders that also inhabit leaf litter.

(3) Pheromones have been shown to be important transmitters of information in the sexual communication of lycosid spiders. Chemoreceptive structures (specialised hairs) have been found and mapped on the dorsal side of the male cymbium (Kronstedt, 1979b; Tietjen & Rovner, 1980), and the ability of male spiders to follow female draglines along a gradient has been demonstrated experimentally (Engelhardt, 1964; Tietjen & Rovner, 1980). The work on spider pheromones was performed on genera that at least in Europe are known to occur in relatively low population densities (*Trochosa*, *Alopecosa*). In such a situation pheromones obviously play an important role in increasing the probability of encounters between the sexes. This may be different in species that live in high densities — where both sexes meet regularly within short time intervals. The *lugubris*-group species can be found in large numbers in heaps of leaf-litter so that the whole space between the leaves might "smell" of female pheromones. In that case the role of pheromones may be as a general arousing stimulus for males. That *lugubris*-group species make use of pheromones was documented by frequent observations of searching behaviour during our experiments,

but typical courtship display was never elicited by female draglines alone. When thinking of pheromones as a species-isolating barrier it should also be borne in mind that pheromones from the *male* spider could be decisive, but data on male pheromones serving as species barriers in spiders are not available at present; a first account of male sexually-active chemicals was given by Juberthie-Jupeau *et al.* (1990), who described the tibial glands in the fore-tibia of *Alopecosa cuneata* (Clerck), a European wolf-spider that is known for its unique courtship (see Dahlem *et al.*, 1987, “gustatorische Balz”).

In conclusion, each of the three sensory modalities may contribute to the courtship. Female pheromones are likely to play a role in stimulating the males when they arrive at places where sexually active females occur in high densities. In front of a female, the male display with its combination of (possible) vibratory and (observed) visual stimuli probably will contain the most important species-specific information for the female. The importance of male pheromones has not yet been studied.

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References

- BARTH, F. G. 1997: Vibratory communication in spiders: adaptation and compromise at many levels. In: M. Lehrer (ed.), *Orientation and communication in arthropods*: 247–272. Birkhäuser Verlag, Basel.
- BLACKWALL, J. 1861: *A history of the spiders of Great Britain and Ireland*. Vol. 1: 1–174. Ray Society, London.
- BONNET, P. 1958: *Bibliographia Araneorum*. Vol. 2, part 4 (N–S): 3027–4230. Douladoure, Toulouse.
- BRISTOWE, W. S. 1929: The mating habitats of spiders, with special reference to the problems surrounding sex dimorphism. *Proc. zool. Soc. Lond.* **1929**: 309–358.
- BUCHAR, J. 1997: Supplement to the check list of spiders of the Czech Republic. In: M. Zabka (ed.), *Proceedings of the 16th European Colloquium of Arachnology*: 57–63. WSRP, Siedlce, Poland.
- BUCHAR, J. & THALER, K. 1997: Die Wolfspinnen von Österreich 4 (Schluss): Gattung *Pardosa* max. p. (Arachnida, Araneae: Lycosidae) — Faunistisch-tergeographische Übersicht. *Carinthia II* **187/107**: 515–539.
- CLERCK, C. 1757: *Aranei Svecici, descriptionibus et figuris aeneis illustrati, ad genera subalterna redacti, speciebus ultra LX determinati*. 1–154, 6 pl. Stockholm.
- CORDES, D. & BARTH, F. G. 1997: Multimodale Balz bei Wolfspinnen. *Verh. dt. zool. Ges.* **1997**: 270.
- CORDES, D. & HELVERSEN, O. von 1990: Indications for the existence of *Alopecosa barbipes* (Sundevall 1832) as a “sibling species” to *Alopecosa accentuata* (Latreille 1817). *Bull. Soc. europ. Arachnol.* vol. hors série **1**: 70–74.
- COSTA, F. G. & CAPOCASALE, R. M. 1984: *Lycosa carbonelli* sp. nov., una etoespecie simpatriada, sibilina de *Lycosa thorelli* (Keyserling) (Araneae, Lycosidae). *J. Arachnol.* **11**: 423–431.
- DAHL, F. 1908: Die Lycosiden oder Wolfspinnen Deutschlands und ihre Stellung im Haushalte der Natur. Nach statistischen Untersuchungen dargestellt. *Nova Acta Acad. Caesar Leop.-Carol.* **88**: 175–678.
- DAHLEM, B., GACK, C. & MARTENS, J. 1987: Balzverhalten von Wolfspinnen der Gattung *Alopecosa*. *Zool. Beitr. (N.F.)* **31**: 151–164.
- ENGELHARDT, W. 1964: Die Mitteleuropäischen Arten der Gattung *Trochosa* C. L. Koch, 1848 (Araneae, Lycosidae). Morphologie, Chemotaxonomie, Biologie, Autökologie. *Z. Morph. Ökol. Tiere* **54**: 219–392.
- FABRICIUS, J. C. 1775: Aranea. In: *Systema Entomologiae, sistens Insectorum classes, ordines, genera, species, adiectis, synonymis, locis descriptionibus observationibus*: 431–439. Flensburgi et Lipsiae.
- HALLANDER, H. 1967: Courtship display and habitat selection in the wolf spider *Pardosa chelata* (O. F. Müller). *Oikos* **18**: 145–150.
- HOLLANDER, J. den & DIJKSTRA, H. 1974: *Pardosa vlijmi* sp. nov., a new ethospecies sibling *Pardosa proxima* (C. L. Koch 1848), from France, with description of courtship display (Araneae, Lycosidae). *Beaufortia* **22**: 57–65.
- HOLM, Å. 1947: Fam. 8–10. Oxyopidae, Lycosidae och Pisauridae. In: *Svensk Spindelfauna* **3**: 1–48. Entomologiska Foreningen, Stockholm.
- HOLM, Å. & KRONESTEDT, T. 1970: A taxonomic study of the wolf spiders of the *Pardosa pullata*-group (Araneae, Lycosidae). *Acta ent. bohemoslovaca* **67**: 408–428.
- HOMANN, H. 1931: Beiträge zur Physiologie der Spinnenaugen: III. Das Sehvermögen der Lycosiden. *Z. vergl. Physiol.* **14**: 40–67.
- JONSSON, L. J. 1998: Spiders of the Skärälid Gorge, southernmost Sweden. In: P. A. Selden (ed.), *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997*: 273–276. British Arachnological Society, Burnham Beeches.
- JUBERTHIE-JUPEAU, L., LOPEZ, A. & KRONESTEDT, T. 1990: Structure et ultrastructure de la glande tibiale chez le mâle d'*Alopecosa cuneata* (Clerck) (Araneae, Lycosidae). *Revue arachnol.* **9**: 63–77.
- KOCH, C. L. 1833: Arachniden. In: G. W. F. Panzer, *Fauna Insectorum Germaniae initia*. Hft 120. Regensburg.
- KOCH, C. L. 1836: *Die Arachniden*. Vol. 3: 1–120, pl. 73–108. Nürnberg.
- KOCH, C. L. 1848a: *Die Arachniden*. Vol. 14: 1–210, pl. 469–504. Nürnberg.
- KOCH, C. L. 1848b: *Die Arachniden*. Vol. 15: 1–136, pl. 505–540. Nürnberg.
- KOCH, L. 1878: Verzeichnis der bei Nürnberg bis jetzt beobachteten Arachniden (mit Ausschluss der Ixodiden und Acariden) und Beschreibungen von neuen, hier vorkommenden Arten. *Abh. naturhist. Ges. Nürnberg* **6**: 1–86.
- KOOMANS, M. J., PLOEG, S. M. F. v. d. & DIJKSTRA, H. 1974: Leg wave behaviour of wolf spiders of the genus *Pardosa* (Araneae, Lycosidae). *Bull. Br. arachnol. Soc.* **3**: 53–61.
- KRONESTEDT, T. 1979a: Etologiska karaktärer vid taxonomiska studier av vargspindlar. *Ent. Tidskr.* **100**: 194–199.
- KRONESTEDT, T. 1979b: Study on chemosensitive hairs in wolf spiders (Araneae, Lycosidae) by scanning electron microscopy. *Zoologica Scr.* **8**: 279–285.

- KRONESTEDT, T. 1990: Separation of two species standing as *Alopecosa aculeata* (Clerck) by morphological, behavioural and ecological characters, with remarks on a related species in the *pulverulenta* group (Araneae, Lycosidae). *Zoologica Scr.* **19**: 203–225.
- KRONESTEDT, T. 1992: The identity of *Pardosa alacris* (C. L. Koch 1833) (Arachnida: Araneae: Lycosidae). *Senckenberg. biol.* **72**: 179–182.
- KRONESTEDT, T. 1999: A new species in the *Pardosa lugubris* group from Central Europe. *Spixiana* **22**: 1–11.
- LOCKET, G. H. & MILLIDGE, A. F. 1951: *British spiders*. Vol. 1: 1–310. Ray Society, London.
- MAYR, E. 1963: *Animal species and evolution*. Harvard Univ. Press, Cambridge, Mass.
- MENGE, A. 1879: Preussische Spinnen, XI. Fortsetzung & Schluss. *Schr. naturf. Ges. Danzig* (N.F.) **4**: 543–560.
- MÜLLER, O. F. 1764: Aranea. In: *Fauna Insectorum Fridrichsdalina, sive Methodica descriptio Insectorum agri Fridrichsdalensis cum characteribus genericis et specificis nominibus trivialibus, locis natalibus, iconibus allegatis, novisque pluribus speciebus additis*: 92–94. Hafniae.
- OVTSHARENKO, V. I. 1979: [Spiders of the families Gnaphosidae, Thomisidae, Lycosidae (Aranei) in the Caucasus Major] In: Yu. I. Balashov (ed.), *Fauna i ekologiya paukoobraznykh. Trudy zool. Inst. Leningrad* **85**: 39–53. [In Russian with English summary.]
- REISKIND, J. 1988: *Lycosa ammophila* and *Lycosa ericeticola*: a pair of cryptic/sibling species in northern Florida (Araneae: Lycosidae). *Am. Arachnol.* **38**: 7.
- REISKIND, J. & CUSHING, P. E. 1996: Study of a narrow hybrid zone between two wolf spiders, *Lycosa ammophila* and *Lycosa ericeticola*, in north Florida (Araneae, Lycosidae). *Revue suisse Zool.* vol. hors série **2**: 543–554.
- ROBERTS, M. J. 1985: *The spiders of Great Britain and Ireland*. Vol. 1: 1–230. Harley Books, Colchester.
- ROBERTS, M. J. 1995: *Spiders of Great Britain & Northern Europe*. 1–383. HarperCollins, London.
- ROBERTS, M. J. 1998: *Spinnengids*. 1–397. Tirion, Baarn.
- SCHEFFER, S. J., UETZ, G. W. & STRATTON, G. E. 1996: Sexual selection, male morphology, and the efficacy of courtship signalling in two wolf spiders (Araneae, Lycosidae). *Behav. Ecol. Sociobiol.* **38**: 17–23.
- SIMON, E. 1876: *Les Arachnides de France*. Vol. 3: 1–364. Roret, Paris.
- SIMON, E. 1937: *Les Arachnides de France*. Vol. 6, part 5: 979–1298. Roret, Paris.
- SKINNER, E. R., THOMPSON, G. H. & COOKE, J. A. L. 1967: *Spiders, courtship, wolf spiders (Lycosidae)*. Film 4 (No. W 1010) (16 mm film). Inst. Wiss. Film: Göttingen.
- STRATTON, G. E. 1991: A new species of wolf spider, *Schizocosa stridulans* (Araneae, Lycosidae). *J. Arachnol.* **19**: 29–39.
- STRATTON, G. E. & UETZ, G. W. 1981: Acoustic communication and reproductive isolation in two species of wolf spiders. *Science, N.Y.* **214**: 575–577.
- SUNDEVALL, C. J. 1833: Svenska Spindlarmes beskrifning, Fortsättning och slut. *Nova Acta R. Soc. Scient. upsal.* **1832**: 171–272.
- TANAKA, H. 1993: Lycosid spiders of Japan IX. The genus *Pardosa* C.L. Koch — *amentata*-group. *Sonoda women's Coll. Stud.* **27**: 261–318.
- THALER, K., PINTAR, M. & STEINER, H. M. 1984: Fallenfänge von Spinnen in den östlichen Donauauen (Stockerau, Niederösterreich). *Spixiana* **7**: 97–103.
- THALER, K. & STEINER, H. M. 1989: Fallenfänge von Spinnen in abgedämmten Donau-Auen bei Wien (Österreich). *Sber. öst. Akad. Wiss.* (Abt. I) **196**: 323–339.
- THORELL, T. 1872: *Remarks on synonyms of European spiders*. Part 3: 229–374. Uppsala.
- TIETJEN, W. S. & ROVNER, J. S. 1980: Trail-following behavior in two species of wolf spiders: sensory and etho-ecological concomitants. *Anim. Behav.* **28**: 735–741.
- TONGIORGI, P. 1966a: Italian wolf spiders of the genus *Pardosa* (Araneae: Lycosidae). *Bull. Mus. comp. Zool. Harv.* **134**: 275–334.
- TONGIORGI, P. 1966b: Wolf spiders of the *Pardosa monticola* group (Araneae: Lycosidae). *Bull. Mus. comp. Zool. Harv.* **134**: 335–359.
- TÖPFER-HOFMANN, G. & HELVERSEN, O. von 1990: Four species of the *Pardosa lugubris*-group in Central Europe (Araneae, Lycosidae) — A preliminary report. *Bull. Soc. europ. Arachnol.* vol. hors série **1**: 349–352.
- VLČEK, K. 1995: The wolf spider *Pardosa alacris* (Araneae, Lycosidae): the courtship display of this and related species and pheromone communication. In: V. Růžička (ed.), *Proceedings of the 15th European Colloquium of Arachnology*: 174–183. Institute of Entomology, České Budějovice.
- VLIJM, L. & DIJKSTRA, H. 1966: Comparative research of the courtship behavior in the genus *Pardosa* (Arach., Araneae). I: Some remarks about the courtship of *P. amentata*, *P. hortensis*, *P. nigriceps* and *P. lugubris*. *Senckenberg. biol.* **47**: 51–55.
- WALCKENAER, C. A. 1802: Araignée. In: *Faune Parisienne. Insectes, ou histoire abrégée des insectes des environs de Paris*. Vol. 2: 187–250. Paris.
- WALCKENAER, C. A. 1805: *Tableau des Aranéides ou Caractères essentiels des tribus, genres, familles et races que renferme le genre Aranea de Linné, avec la désignation des espèces comprises dans chacune de ces divisions*. 1–88. Paris.
- WALCKENAER, C. A. 1837: *Histoire naturelle des Insectes. Aptères*. Vol. 1: 1–682. Paris.
- WIEBES, J. T. 1959: The Lycosidae and Pisauridae (Araneae) of the Netherlands. *Zool. Verh. Leiden* **42**: 1–78.
- WUNDERLICH, J. 1969: Zur Spinnenfauna Deutschlands, IX. Beschreibung seltener oder bisher unbekannter Arten (Arachnida: Araneae). *Senckenberg. biol.* **51**: 381–393.
- WUNDERLICH, J. 1984: Beschreibung der Wolfsspinne *Pardosa pseudolugubris* n.sp. und Revision der *Pardosa amentata*-Gruppe, zugleich ein Beitrag zur Kenntnis der innerartlichen Variabilität bei Spinnen (Arachnida: Araneae: Lycosidae). *Neue ent. Nachr.* **10**: 1–15.
- ZYUZIN, A. A. 1979: [A taxonomic study of Palaearctic spiders of the genus *Pardosa* (Aranei, Lycosidae), Part I. The taxonomic structure of the genus.] *Ent. Obozr.* **58**: 431–447. [In Russian with English summary.]