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## Social cleptogamy in the ant subgenus *Chthonolasius* Ruzsky, 1912 – survival as a minority

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### Abstract

Improvement of stereomicroscopic equipment as well as of recording and evaluation of data since 1992 enables a much better interpretation of the extremely complicated situation within the ant subgenus *Chthonolasius* Ruzsky, 1912 compared to earlier revisions by the author. Very high frequencies of the interspecific hybrids *Lasius jensi* x *umbratus* and *L. meridionalis* x *umbratus* are recognised for the territory of Central Europe. The ratio of properly identified worker nest samples is 41 : 31 in the *L. jensi*/*L. jensi* x *umbratus* pair and 19 : 9 in the *L. meridionalis*/*L. meridionalis* x *umbratus* pair. In the latter pair, the ratio of randomly collected gyne individuals is 54 : 25 while in the former pair no hybrid gynes are produced. According to an estimation considering the real abundance ratios in the given region, assuming a 1 : 1 sex ratio and equal colony foundation success of heterospecifically mated gynes, as much as 27 % of the *L. jensi* alates and 19 % of *L. meridionalis* alates should have mated with the heterospecific partner *L. umbratus*. There are no indications for a seasonal, daytime or spatial segregation of swarming in any of these three species. Confined to their rather small oligotrophic and xerothermous habitat areas, both *L. jensi* and *L. meridionalis* have been encircled by 10 – 15-fold larger populations of *L. umbratus* over a very long historical period. Reconstruction of postglacial natural and anthropogenous landscape development in Central Europe indicates that *L. meridionalis* and *L. jensi* have been in close contact with *L. umbratus* for more than 7000 and 1100 years respectively and that the overall habitat frequencies have little changed since the big clear cuttings in 1100 BP. Social cleptogamy, as the asymmetric, unidirectional form of social hybridogenesis, is an apparent strategy for rare species to survive when confronted with a superior force of heterospecific hybridisation partners. If a gyne of a rare species does not meet a conspecific male, she will readily accept heterospecific males and establish a productive colony with the help of a vital population of sterile hybrid workers. During some 20 years of colony life, she can then send, in the form of numerous sons produced, 100 % of her own alleles into the gene pool. In other words the heterospecific genes are only »stolen« to use them as a vehicle to propagate the own genes but are excluded from reproduction. In *Chthonolasius*, the optimum solution for social cleptogamy has been developed by *L. jensi* in which the expensive and useless production of hybrid gynes is suppressed, which is not the case in *L. meridionalis*. Social cleptogamy has been found so far in *Lasius*, *Acanthomyops*, *Solenopsis* and *Temnothorax* while symmetric social hybridogenesis is only known in *Pogonomyrmex*.

### Zusammenfassung

**Soziale Kleptogamie im Ameisensubgenus *Chthonolasius* Ruzsky, 1912 – das Überleben als Minderheit** – Seit 1992 erfolgte Verbesserungen in stereomikroskopischer Ausrüstung, Meßverfahren und Datenauswertung ermöglichen gegenüber früheren Revisionen des Autors eine bessere Deutung der komplizierten Situation im Subgenus *Chthonolasius* Ruzsky,

1912. Sehr hohe Häufigkeiten der Hybriden *Lasius jensi* x *umbratus* und *L. meridionalis* x *umbratus* wurden für das Territorium Mitteleuropas festgestellt. Das Verhältnis der determinierten Nestproben ist 41 : 31 für *L. jensi* gegen *L. jensi* x *umbratus* und 19 : 9 für *L. meridionalis* gegen *L. meridionalis* x *umbratus*. Für das letztere Phänotypen-Paar war die Zahl der zufallsverteilt gesammelten Gynen 54 : 25, während im ersteren Fall keine Hybridgynen produziert werden. Unter Berücksichtigung der realen Häufigkeitserhältnisse in Mitteleuropa und unter Annahme eines Geschlechtsverhältnisses von 1 : 1 und gleicher Koloniegründungschancen heterospezifisch begatteter Gynen ergibt sich, dass sich 27 % der *L. jensi*- und 19 % der *L. meridionalis*-Geschlechtstiere mit *L. umbratus* gekreuzt haben. Es gibt keine Anzeichen für eine saisonale, tageszeitliche und räumliche Trennung des Hochzeitfluges zwischen den drei Arten. Beschränkt auf ihre relativ kleinflächigen, oligotrophen und xerothermen Habitatinseln, sind *L. jensi* und *L. meridionalis* über einen langen historischen Zeitraum von 10 – 15mal mächtigeren Populationen von *L. umbratus* umstellt. Eine Rekonstruktion der natürlich und anthropogen bedingten postglazialen Landschaftsentwicklung in Mitteleuropa zeigt, daß *L. meridionalis* und *L. jensi* seit mehr als 7000 bzw. 1100 Jahren in engem Kontakt mit *L. umbratus* gewesen sein müssen, und dass sich die grundsätzlichen Habitathäufigkeiten nur wenig seit den großen Rodungen vor 1100 Jahren geändert haben. Soziale Kleptogamie als die asymmetrische, unidirectionale Form der Sozialen Hybridogenese ist eine offenkundige Überlebenstrategie seltener Arten unter den Bedingungen einer Konfrontation mit zahlenmäßig weit überlegenen Hybridisierungspartnern. Wenn eine Gyne einer seltenen Art kein konspezifisches Männchen findet, wird sie bereitwillig ein artfremdes Männchen akzeptieren und dann mit Hilfe einer vitalen Population steriler Hybridarbeiter eine produktive Kolonie aufbauen. Während ihrer 20 – 25 Jahre währenden Reproduktionszeit kann sie dann – in der Form zahlreicher Söhne – 100 % ihrer eigenen Allele in den Genpool ihrer Art entsenden. Die artfremden Gene werden also nur »gestohlen«, um sie als Vehikel zur Vermehrung arteigener Gene zu nutzen, werden aber andererseits von der eigenen Reproduktion ausgeschlossen. Die optimale Lösung für Soziale Kleptogamie wurde bei *L. jensi* realisiert, wo die teure und nutzlose Produktion von Hybridgynen unterdrückt wird, während sie aber bei *L. meridionalis* x *umbratus* noch erfolgt. Soziale Kleptogamie ist damit bislang bekannt für *Lasius*, *Acanthomyops*, *Solenopsis* und *Temnothorax*, während Symmetrische Soziale Hybridogenese nur für einen Fall bei *Pogonomyrmex* bekannt ist.

## 1. Introduction

Considerable improvements of equipment and methodology and a much wider sampling basis have been achieved since the author's last revisions (SEIFERT 1988, 1990, 1992) on taxonomy of the genus *Lasius* Fabricius, 1804 had appeared. The use of a high-resolution stereomicroscope with a numeric aperture of 0.25 instead of only 0.10, improved knowledge on errors of stereomicroscopic morphometry together with a reduction of other sources of variance (SEIFERT 2002), extension of the character system and the use of modern computers instead of a pocket calculator provided a much better approach to the real taxonomic structure of a complicated genus.

Separation of the species of the subgenus *Chthonolasius* Ruzsky, 1912 based upon workers is one of the most difficult tasks in ant determination while gyne discrimination is much easier in the majority of cases. Unfortunately, gynes are rarely collected together with workers in clean nest samples – most of the gynes are randomly collected during trapping projects or when they move over the ground in search of a host colony. As consequence, the quality of studies on ecology, distribution or interspecific relations such as hybridisation strongly depends upon worker discrimination. According to recent studies (SEIFERT in prep.), about 23

species of *Chthonolasius* are found in the Palaearctic, three of which have to be described as new.

Unexpectedly high hybridisation frequencies between W Palaearctic ant species of different tribes have already been reported by SEIFERT (1999). Results since then, obtained in ants of the *Formica rufa* group (SEIFERT & GOROPASHNAYA 2004) and in *Chthonolasius* (presented here), have shown that even these figures were underestimates. For the Nearctic range, extreme regional hybridisation frequencies have been reported between *Acanthomyops claviger* (Roger, 1862) and *A. latipes* (Walsh, 1863) for SW Ontario (UMPHREY & DANZMANN 1998) and *Solenopsis geminata* (Fabricius, 1804) and *S. xyloni* McCook, 1879 for E Texas (HELMS-CAHAN & VINSON 2003). In the former case, as much as 50 % *A. latipes* queens had mated with a heterospecific partner. A most fascinating phenomenon, recently termed »symmetric social hybridogenesis«, SSH, (PARKER 2004), has been found in the example of two *Pogonomyrmex* species in the SW United States (HELMS-CAHAN et al. 2002, HELMS-CAHAN & KELLER 2003). Here, interspecific hybridisation is essential for survival of both parent genomes. However, because evolution of SSH in monogynous societies requires a high frequency of multiple mating, which is rare in social hymenoptera (STRASSMANN 2001), this phenomenon should be quite exceptional. A wider distribution is predicted here for the asymmetric, unidirectional cases, in which only one species uses heterospecific sperm in order to establish highly productive colonies managed by hybrid workers. This form of social hybridogenesis is termed here social cleptogamy.

This paper reports on social cleptogamy within the subgenus *Chthonolasius*, which was undetected or unknown 15 years ago. Interspecific hybridisation between three *Chthonolasius* species apparently does not affect the genetic integrity of parent species and may be a strategy of rare species to survive when confronted with overwhelming masses of heterospecific hybridisation partners. The phenomenon became obvious for some landscapes of Central Europe where the *Lasius* fauna is best-studied on a worldwide scale and where a high density of sampling is given.

## 2. Materials and methods

### 2.1. Specimens examined

The following material of three species and of their hybrids was morphometrically investigated (w = sample with workers, g = sample with gynes). About twice the number of specimens from the same samples were only subjectively inspected.

*Lasius jensi* Seifert, 1982:

41 nest samples with 128 workers, and 48 samples of gynes with 68 specimens from the following sites were morphometrically investigated:

**ARMENIA:** Delizhan, 1930.07, g. **AUSTRIA:** Burgenland: Jois, 1983, w; Spitz, Setzberg, 1994.05.13, w. **BELGIUM:** Yvoir R.D. (4°52'W, 50°19'N), 1910. **BULGARIA:** Rhodopen: Dobrostan, 1982.09.11, w; Rhodopen: Dobrostan, 1982.09.10, g. **CZECHIA:** Bohemia: Koněprusy, 1980.08.09 w, g; Bohemia: Zdice, 1976.08.03, g. **GERMANY:** Bad Kösen, Himmelreich, 1951.08.05, g; Badra: Numburg, 1987.05.27, w; Balgstädt, 1975.06.09, w; Balgstädt, 1979.06.11, w; Balgstädt, 1980.05.04, w; Balgstädt, 1980.07.12, w; Balgstädt, 1980.08.27, w; Balgstädt, 1980.09.04, w; Balgstädt, 1981.06.01, w; Balgstädt, 1981.07.08, w,

g; Balgstädt, 1981.08.25, w; Beierstedt, 1991.08.01, w; Creutzburg 0.7 km NNE, 1999.08.12, w; Creutzburg (No162), 1999.08.12, w; Erfurt: Edelberg, 1987.07.23 (BF2), g; Erfurt: Edelberg, 1987.08.21 (Bf2, Bf3, Bf5), g; Erfurt: Ringelberg, 1987.07.23 (Bf1, Bf2), g; Erfurt: Steinberg, 1987.08.21 (Bf1, Bf2), g; Effringen/Rheinland, pre 1930, w; Etdorf, 1971.07.28, g; Falken 0.7 km NE, 1999.08.13, w; Freyburg, 1983.07.10, w, g; Großvargula, 1998.05.10, w; Günserode, 1983.06.02, w; Halle-Trotha, 1938.07.23, g; Hausneindorf, 2002.05.13, w; Hohenburg 0.9 km SW, 2002, w; Hohenburg 4.5 km NW, 2002, g; Kaiserstuhl, 1990.06 (BK1, BK5), g; Leutra, Arrhen 1, 1972.05.23, w; Leutra, Arrhen 2, 1972.05.23, w; Leutra, Gebüsch 1, 1972.05.23, w; Leutra, Gebüsch 2, 1972.05.24, w; Leutra, 1972.07.25, g; Leutra, 1972.08.08, g; Leutra, 1973.08.11, g; Leutra, 1981.08/09, g; Leutra, 1981.08.06 (9, 10), g; Leutra, Arrhen, 1981.08.06, g; Leutra, Mesobrom, 1981.08.06, g; Leutra 1983.08.11 (M1-5), g; Leutra, 1993.07.19, g; Grosswilsdorf, NSG Tote Täler, 1980.08.23, w; Grosswilsdorf, NSG Tote Täler, 1981.09.06, w; Muldingen, 1986.07/08, g; Müheln, 1994.08.03, g; Quedlinburg, Seweckenberge, 1980.03.08, w; Quedlinburg, Seweckenberge, 1980.08.09, w; Römhild: Milz, 1999.08.02, g; Schwarza, 1986.07.22 (BF5+6), g; Schwarza, 1986.08.05, g; Steudnitz, 1979.07.13 (Bf4), g; Steudnitz, 1979.07.27, g; Steudnitz, 1979.08.10, g; Steudnitz, 1979.08.24, g; Steudnitz, 1979.10.22, g; Steudnitz, 1980.08.10, g; Steudnitz, 1980.08.11 (Bf3-4), g; Steudnitz, 1981.07.22 (Bf3), g; Udersleben, 1998.07.08, g; Weddersleben, 1979.05.26, w; Weischütz (sample W), 1981.09.05, w; Weischütz (sample E), 1981.09.05, w; Wormsleben, 1982.05.28, w; Würzburg: Retzbach, 1990, w; Zappendorf, 1942.07.05, g; Zscheiplitz, 1981.06.01, w; Zscheiplitz, 2002.06.14 (563), w. **GREECE**: Mount Olympos: Agia Dimitrios, 1988.05.21, w. **KAZAKHSTAN**: Saur Mountains (47°20'N, 85°31'E), 2001.07.25 (51), g. **POLAND**: Pulawy, Kazimierz, 1962.07.07, w, g. **ROMANIA**: Medias-Birtheim, 1987.07.27, g. **SLOVAKIA**: Hor. Dolny Almas, 1938.07.20, w; PR Palanta, 2000.08.08 S47, w. **TURKEY**: Bolu: Abant Gölü, 1994.06.26.

*Lasius jensi* x *umbratus*:

31 nest samples with 115 workers from the following sites were morphometrically investigated (gynes of this hybrid combination are unknown):

**AUSTRIA**: Schildbachgraben, 2003.09.03, w. **CZECHIA**: Bohemia: Koněprusy, 1976.07.31, w; Nenačovice, 2000.07.21, w. **GERMANY**: Bad Kösen, 1975.09.25, w; Badra 1 km N, 1987.05.27 (N1), w; Balgstädt, 1981.06.01 (Lip1), w; Bendorf, Landeskrone, 1991.07.16 (with *L. jensi* males), w; Camburg, 1980.09.08, w; Würzburg: Dürrbach, 1991.05.27 (No 235), w; Würzburg (laboratory colony of K. Sommer, with *L. umbratus* mother), 1990.07, w; Freyburg, 1983.07.10, w; Freyburg, 1983.07.14 (1), w; Friedrichsaue, 2002.05.13 (168), w; Gatersleben, 1980.05.19, w; Großvargula, 1998.05.10 (235), w; Heterborn, 1980.08.01, w; Kleinjena, 1982.09.17, w; Leutra, Arrhen, 1983.07.28, w; Leutra, Arrhen, 1984.06.13, w; Lorch 0.2 km N, 1995.06.12 (3N5), w; Naumburg, 1982.09.17, w; Oberbergen, 1993.05.01 (g), w; Quedlinburg 4 km ESE, 2002.05.15, w; Reinstädt 1 km NW, 1993.07.20 (g5, with *L. jensi* males), w; Sondershausen, 1983.05.30, w; Sättelstädt 0.4 km N, 2002.06.12, Sättelstädt 0.5 km NNW, 1984.09.05 (with *L. jensi* males), w; Sättelstädt, 1984.09.04, w; Grosswilsdorf, NSG Tote Täler, 1977.06.27, w; Zscheiplitz, 1981.06.01 (Lip1), W; Zscheiplitz, 1981.09.03, w. **SLOVAKIA**: Zádielska Planina, 2000.08.09 (S45), w.

*Lasius meridionalis* (Bondroit, 1920):

19 nest samples with 87 workers, and 30 samples of gynes with 54 specimens from the following sites were morphometrically investigated:

**AUSTRIA:** Stubai Alp, Krössbach, 1948, g. **BELGIUM:** Oostduinkerke, 2001 (OPN32), w; Oostduinkerke, 2001 (OPN51), w. **CZECHIA:** Bohemia: Kam. Přívoz, 1985.07.06, w; Bohemia: Putim, 1987.08, w, g; Borotín u Tábora, 1984.08, w, g; Krivoklátsko Kublov, 2002.07.05, w, g. **FRANCE:** Aveyron, 1917, g. **GERMANY:** Bad Brambach, 1983.08.20, w, g; Boek, 1983.07.30, g; Dahlen, 1981.06.16, w; Dahlen, 1981.08.22, w; Dübener Heide: Roitzscher Wiese, 1995, g; Gartz, Silberberge, 1987.08.05 (114), w; Gartz, Silberberge, 1987.08.05 (12), w; Gartz, Silberberge, 1987.08.05 (74), w; Hannover, Umgebung, 1984, w; Hohenferchesar, 2003.07.27, w; Koblenz/Hoyerswerda, 1984.08.05, g; Kostebrau, 1984.08.06, g; Langebrück, 1988.07.21, g; Lauchhammer, FND Laug, 1984.09.17, g; Lodenau 0.5 km S, 1993.07.10 (59), w; Lüneburger Heide, Heymons, pre 1920, w; Neureddewitz, 1973.07.31, g; Premnitz, 1982.07.22, g; Premnitz, 1983.06/07, g; Premnitz, 1983.07.18/30, g; Premnitz, Schwarzer Weg, 1985.07, g; Premnitz, Eisberg, 1985.07.24, g; Schwarza, 1986.08.05 (BF3, Bf4), g; Schwarza, 1987.08.19, g; Sorno 3.7 km NE, 1994.07.20, g; Urwald Fünfeichen, 1987.08.12, g; Waren: Feissnecksee, 1988.07.27, w; Wittersroda, 1993.07.20, g; Wölper, 1981.03.22, w; Wölper, 1981.06.29, w; Wölper, 1981.09.06 (2), w; Wölper, 1984.10.30, g; Wölper, 1989.08.15, g. **ITALY:** S-Tirol: Stilsfser Joch, 1998.08.22, g. **NETHERLANDS:** Bergen, 1988.07.21, g. **SWEDEN:** Skåne: Falsterbo, 1960, w. **SWITZERLAND:** Alagna, 1917.07.14, w; Domleschg, 1939.08.20, g; Il Fuorn, 1998.07.26, g; Isonne, 1983.08.18, g; Montana, 1800 m, 1983.07.09, w; Pradella, Schuls, 1955.07.23, w, g; **YUGOSLAVIA:** Brezovica, 1986.08, w.

*Lasius meridionalis* x *umbratus*:

9 nest samples with 35 workers, and 17 samples of gynes with 25 specimens originating from the following sites were morphometrically investigated:

**AUSTRIA:** Stotzing, 1999.06, g. **CZECHIA:** Studenec, 1984.08.12, g; **GEORGIA:** 44°37'E, 42°41'N, 1985.08.08, w; **GERMANY:** Apfelstädter Ried, 1989.08.20, g; Bertelsdorf/Sebnitz, 1986.08.02, g; Casslau, 1975.08.19 (2), g; Dahlen, 1982.05.25, w; Dubring 2 km N, 1986.07/08 (2), g; Erfurt: Steinberg, 1987.07.09, g; Gallen, 1981.07.06, w; Garmisch-Partenkirchen 12 km W, 1994.08.23 (2), g; Greiz, 1982.05.15, w; Gross-Luja, 1993.07.29 (65-2), g; Halle: Zool. Institute, 1988.06.15, w, g; Kaiserstuhl, 1990.06 (BK1), g; Kromlau 0.5 km SE, 2002.08.18, w; Premnitz, 1983.06/07 (2), g; Rössenbergheide, 1986.09.08, w; Schlepzig, 1987.08.09, g; Schlossböckelheim, 1995.08.26, w; Wetzlar: Eibelshausen, 1996.07, g; Sächsische Schweiz: Zeughaus, 1971, g. **KAZAKHSTAN:** Saur Mountains (47°20'N, 85°31'E), 2001.07.25 (51), g; **SLOVAKIA:** PR Palanta, 2000.08.08 (S44), w. **SWITZERLAND:** Alagna, 1917.07.14, g.

*Lasius umbratus* (Nylander, 1846):

97 nest samples with altogether 303 workers, and 81 samples of gynes with 113 specimens from the following sites were morphometrically investigated:

**AUSTRIA:** Bad Gleichenberg, 1994.07.10, w; Berndorf, 1999.06, g; Erbreichsdorf, 2001.04.02 (No 6635), w; Forchach, 2001.07.31, g; Gertenberg, 2002.05.04 (No 10975), w;

Großheinrichschlag, 2002 (8929), w; Habersdorf, 2002.09.01 (No 11262), w; Hirm, 1999.06, g; Hundsheimer Berge, 2000.06.18 (No 193), g; Innsbruck: Arzl, 1994.08.02, w; Innsbruck: Arzl, 1995.09.27 (S12), w; Krems: Theiss, 1969.07.20, g; Markleiten, 2002.08.31 (No 11290), w; Nötsch, 1995.05.22, w; Oberdachsberg, 2002.08.03 (No 11025), w; Oberdachsberg, 2002.08.03 (No 11027), w; Radbrunn S, 2001.09.23 (No 8661), w; St.Pölten, 1994.07.12, w, g; St.Pölten, 1994.07.12 (g84), g; Zwingendorf, 2001.10.03 (No 10410), w.

**BULGARIA:** Srebarna, 1988.07.14 (1880), g. **CZECHIA:** Bohemia: Srbsko, 1973.04.08, w; Bohemia: Vitín, 1983.07.19, w; Tvoršovice u Benešov, 1985.06.28, w. **ENGLAND:** S Wales: Kenfig, 1960, w. **FRANCE:** Grande Chartreuse, 1917, g. **GEORGIA:** Tiflis, 1918.08.30, g. **GERMANY:** Apfelstädter Ried, 1984.07.11, g; Apfelstädter Ried, 1984.07.31 (1, 2), g; Apfelstädter Ried, 1984.08.11, g; Apfelstädter Ried, 1984.08.31, w, g; Bad Kösen, 1981.09.21, w; Bad Lippspringe, 1988.08.27, g; Badra 1 km N, 1987.05.27 (N2), w; Balgstädt, 1977.06.20, w; Balgstädt, 1981.05.21, w; Balgstädt, 1981.06.01, w; Balgstädt, 1981.08.25, w; Balgstädt, 1982.04.05, w; Belzig, 1984.08.16, w; Berlin-Müggelsee SW, 1979.08.12, g; Bernsdorf 5 km NE, 1989.08.08, g; Bertelsdorf, 1986.08.02, g; Casslau, 1975.08.19, g; Dammer Moor/Beeskow, 1982.06/07, g; Demitz-Thumitz, 1986.07.17, g; Dessau, 1985.09.26, w; Dresden, pre 1920, g; Dresden-Langebrück, 1988.07.21, g; Dresden-Klotzsche, 1989.08.08, g; Drohmburg, 1962.04.09, w; Dubring 2 km N, 1986.07/08 (2), g; Dübener Heide, 1993 (UG10, UG40, UG44), g; Dübener Heide: Mühlbachwiesen, 1995, g; Dübener Heide: Roitzscher Wiese, 1995, g; Dübener Heide: Siedegrabenwiese, 1995, g; Eifel: Mechernich, 1986.09.12, w; Eisenach, 1983.08.01, w; FND Laug, 1984, g; Fünfichen, Urwald, 1987.08.12, g; Freyburg, 1982.07.15, w; Freyburg, 1983.07.10 (2), w; Garmisch-Partenkirchen 12 km W, 1994.08.23, g; Gatersleben, 1980.07.29, g; Gartz 1 km NW, 1987.08.05 (85), w; Gleiberg, 1998.10, w; Görlitz, 1982.07.11, g; Görlitz, 1984.10.11, g; Gross-Luja, 1993.07.29 (3, 65-1), g; Gross-Luja, 1993.07.29 (59), w; Groß-Luja, 1993.07.29 (65), w; Grosswilsdorf, Tote Täler, 1982.05.27, w; Gräfenhainichen, 1982.05.31, w; Hamburg-Bergedorf, 1999.10.06, w; Hamburg-Bergedorf W, 2003.05.17, w; Heimbürg, 1980.09.20 (180), w; Heimbürg, 1980.09.20 (181), w; Jänkendorf 2 km NNW, 1981.06.08, w; Kaiserstuhl, 1990.06 (BK2, BA2), g; Kaiserstuhl, 1991.06 (BA2), g; Kaiserstuhl, 1990.07 (BA3), g; Koblenz/Knappensee, 1984.08.05, g; Königshain, 1994.09.29, w; Kr. Beeskow: Schwarzberge, 1983, g; Kr. Senftenberg: Seewald, 1983, g; Kulkwitz, Tagebau, 1982.10.17, w; Leissling, 1986.10.01, w; Lenggries 9 km S, 1994.08.23, w; Leutra, 1993.07.19, g; Leutra, Arrhen, 1981.07.09, g; GER: Lömischau, 1965.08.07, g; Lorch 0.2 km N, 1995.06.12 (3M18), w; Ludwigsfelde, 1987, w, g; Ludwigsdorf, 1983.09.27, g; Ludwigslust, 1986.08.01, w; Lütgenziatz 1.6 km SW, 1999.09.04, w; Lützow/Gadebusch, 1984.07.17, w; Mainz-Finthen W, 1990.09/10, w; Marburg, 1954.09.04, g; Marke/Dessau, 1984.05.20, w; Marke/Dessau, 1984.09.08, w; Martinfeld/Eichsfeld, 1984.06, w; Meissen: Bosel, 1995.08, g; Gehren, 1981.06.25 (1), w; Gehren, 1981.06.25 (2), w; Müritzhof, 1984.06.28, w; Müritzhof, 1985.10.07, w; Naumburg, 1979.05.11, w; Neuenhagen, 2000.07.08, w, g; Neustrehlitz, 1986.06.04, w; Neustrehlitz: Grünplan, 1984, w, g; Niederoderwitz, 1920.05.28, w; Niesky: Steinbach, 1983, w; Nöda, 1987.07.20, g; NSG Pulsnitz, 1984, g; Nürnberg, Reichswald, 1991.06, w; Pommern/Mosel, 1993.07/08, g; Premnitz, 1983.06/07, g; Premnitz, 1983.10.23, w; Premnitz, 1984.07/08, g; Premnitz, 1985.07.14, g; Pressel 2.8 km NNE, 1994.08.19, w; Reinstedt 1 km NW, 1993.07.20 (g29), Rotes Haus, 1981.05.09, w; Reinstädt, 1993.07.20, g; Salem, 1988.07.28, g; Sargstedt, 1979.05.30, w; Steinhalleben, 1987.05.24, w; Steudnitz, 1979.07.13 (Bf1), g; Steudnitz, 1979.07.27, g; Steudnitz, 1979.08.10, g; Steudnitz,

1980.08.11 (Bf3), g; Steudnitz, 1981.07.08 (Bf4, Bf5), g; Steudnitz, 1981.07.22, g; Steudnitz, 1981.08.04 (Bf5), g; Steudnitz, 1982.07.15, g; Steudnitz, 1983.07.13 (Bf3), g; Steudnitz, 1984.08.09 (Mf1), g; Tübingen: Spitzberg, 1993.05.06, w; Untergrombach, 1990.05.06, w; Waren: Feissnecksee, 1987.07.27 (2), w; Waren/Müritz, 1983.04.18, w; Weltersbach, 1995.07.21, w, g; Wormsleben, 1982.05.28, w; Wölper, 1979.05.08, w; Wölper, 1979.09.17, w; Wölper, 1980.05.24, w; Wölper, 1980.06.14, w; Wölper, 1980.10.16 (2), w; Wölper, 1980.10.16 (3), w; Wölper, 1981.03.22 (2), w; Wölper, 1981.05.22, w; Wölper, 1981.09.06 (1), w; Wölper, 1982.09.26, w; Wölper, 1984.10.30, g; Zittau: Hainewalde, 1989.07.21, g. **GREECE:** Xanthi, Stavroupoli, 2002.10.16, w. **NETHERLANDS:** Bergen, 1988.07.21, g. **POLAND:** Pieniny, 1989.09.15, g. **SLOVAKIA:** Hačava, Luky Miglinec, 2000.08.09, w; Zádielska Planina, 2000.08.09 (S48), w. **SLOVENIA:** Postojna 12 km W, Mt. Nanos, 1997.05, w. **SPAIN:** La Seu de Urgell 17 km W, 1991.05.15 (158), w; La Seu de Urgell 17 km W, 1991.05.15 (2), w. **SWEDEN:** Öland: Esö, 1983.07.26, w; Öland: Glömminge 3 km SSW, 1992.06.13, w. **SWITZERLAND:** Basel, Badischer Bahnhof, 1996.08.07, g; Basel, Badischer Bahnhof, 1996.09.04, g; VS: Brig 24 km E, Bodmen, 1994.05.16, w. **YUGOSLAVIA:** Brezovica, 1986, g.

## 2.2. Equipment, measuring, and data evaluation

Workers were numerically evaluated for 14 and gynes for 13 characters, at magnifications of 80 – 320x using a Wild M10 high-performance stereomicroscope equipped with a 1.6x planapochromatic objective. Illumination was provided by a Schott KL 1500 cold-light source with two flexible light-cables mounted at a ring support at the objective. In contrast to the frequently used goose necks, this system provides a focus-stable illumination independent of focusing movements and allows a rotation of the light-cable support around the optical axis. The latter is important for precise measuring of pubescence distance. All measurements were made on mounted and dried specimens using a pin-holding stage, permitting endless rotations around X, Y, and Z axes. A Leica cross-scaled ocular micrometer with 120 graduation marks ranging over 65 % of the visual field was used. A cross-scale is inevitable for exact measurements of characters such as PEAS, PECR, Smax, Smin or HTmax. A mean measuring error of  $\pm 0.6 \mu\text{m}$  was calculated for small and well-defined structures such as setae length, but one of  $\pm 3 \mu\text{m}$  for larger structures such as gyne CW showing positioning and desiccation errors (SEIFERT 2002). To avoid rounding errors, all measurements were recorded in  $\mu\text{m}$  even for characters for which a precision of  $\pm 1 \mu\text{m}$  is impossible. In order to reduce irritating reflections of the cuticular surfaces, a plastic diffuser was sometimes positioned as close as possible to the specimen. This method considerably improved the resolution of microsculpture and other tiny structures.

The process to discriminate the most similar sister species included (a) the reduction of variance in primary data (SEIFERT 2002), (b) the removal of allometric variance by specific functions valid for species pairs (SEIFERT 2002), (c) the generation of nest sample means in workers and (d) a canonical discriminant analysis with an SPSS 10.0 statistical package.

Removal of allometric variance was performed in workers by overall functions computed as average of species specific functions of 12 *Chthonolasius* entities with sufficient data available: *Lasius balcanicus* Seifert, 1988, *L. bicornis* (Förster, 1850), *L. citrinus* Emery, 1922, *L. distinguendus* (Emery, 1916), *L. jensi* Seifert, 1982, *L. meridionalis* (Bondroit, 1920), *L. mixtus* (Nylander, 1846), *L. nitidigaster* Seifert, 1996, *L. sabularum* (Bondroit, 1918), *L. umbratus*

*tus* (Nylander, 1846), *L. jensi* x *umbratus*, *L. meridionalis* x *umbratus*. This overall correction was preferred to enable a direct comparison of data in tables and because pair-specific corrections did not provide significant improvement. The overall allometric corrections for workers transform data for the assumption of each individual having a head size CS of 1.05 mm:

|                   |   |             |   |                                    |
|-------------------|---|-------------|---|------------------------------------|
| $CL/CW_{cor}$     | = | $CL/CW$     | / | $(-0.11451*CS + 1.1707)*1.0505$    |
| $SL/CS_{cor}$     | = | $SL/CS$     | / | $(-0.01560*CS + 0.9035)*0.8871$    |
| $GHL/CS_{cor}$    | = | $GHL/CS$    | / | $(-0.05470*CS + 0.1495)*0.09207$   |
| $Smax/CS_{cor}$   | = | $Smax/CS$   | / | $(+0.003536*CS + 0.09171)*0.09542$ |
| $Smax/Smin_{cor}$ | = | $Smax/Smin$ | / | $(+0.40038*CS + 1.0589)*1.4793$    |
| $HTmax/CS_{cor}$  | = | $HTmax/CS$  | / | $(+0.00887*CS + 0.1297)*0.13901$   |
| $PDF_{cor}$       | = | $PDF$       | / | $(+3.121*CS + 4.96)*8.237$         |
| $PDG_{cor}$       | = | $PDG$       | / | $(-7.564*CS + 16.42)*8.478$        |
| $nHT_{cor}$       | = | $nHT$       | / | $(+29.57*CS - 15.06)*15.99$        |
| $PECR/CS_{cor}$   | = | $PECR/CS$   | / | $(+0.0768*CS + 0.0004)*0.0810$     |
| $PEAS/CS_{cor}$   | = | $PEAS/CS$   | / | $(+0.519*CS - 0.102)*0.443$        |
| $PEW/CS_{cor}$    | = | $PEW/CS$    | / | $(-0.0189*CS + 0.3022)*0.2824$     |
| $PEH/CS_{cor}$    | = | $PEH/CS$    | / | $(+0.1274*CS + 0.1269)*0.2607$     |

Removal of allometric variance was performed in gynes as average of species specific functions of only those entities considered here: *L. meridionalis*, *L. umbratus* and *L. meridionalis* x *umbratus*. These corrections for gynes transform data for the assumption of each individual having a head size CS of 1.5 mm:

|                   |   |             |   |                                   |
|-------------------|---|-------------|---|-----------------------------------|
| $CL/CW_{cor}$     | = | $CL/CW$     | / | $(-0.0674*CS + 0.9628)*0.8617$    |
| $SL/CS_{cor}$     | = | $SL/CS$     | / | $(-0.1647*CS + 1.0996)*0.8526$    |
| $Smax/CS_{cor}$   | = | $Smax/CS$   | / | $(-0.00747*CS + 0.10996)*0.09876$ |
| $Smax/Smin_{cor}$ | = | $Smax/Smin$ | / | $(-0.0137*CS + 1.6539)*1.6334$    |
| $HTmax/CS_{cor}$  | = | $HTmax/CS$  | / | $(+0.03416*CS + 0.11233)*0.16357$ |
| $IF2_{cor}$       | = | $IF2$       | / | $(-0.0447*CS + 1.7454)*1.6784$    |
| $sqPDF_{cor}$     | = | $sqPDF$     | / | $(-0.103*CS + 2.970)*2.816$       |
| $sqPDG_{cor}$     | = | $sqPDG$     | / | $(+0.0096*CS + 2.213)*2.227$      |
| $nHT_{cor}$       | = | $nHT$       | / | $(51.37*CS - 51.53)*25.52$        |
| $GHL/CS_{cor}$    | = | $GHL/CS$    | / | $(-0.01216*CS + 0.08752)*0.06928$ |
| $MnHL/CS_{cor}$   | = | $MnHL/CS$   | / | $(+0.00040*CS + 0.06175)*0.06235$ |
| $ScHD/CS_{cor}$   | = | $ScHD/CS$   | / | $(-0.00424*CS + 0.02935)*0.02299$ |

### 2.3. Definition of morphometric characters

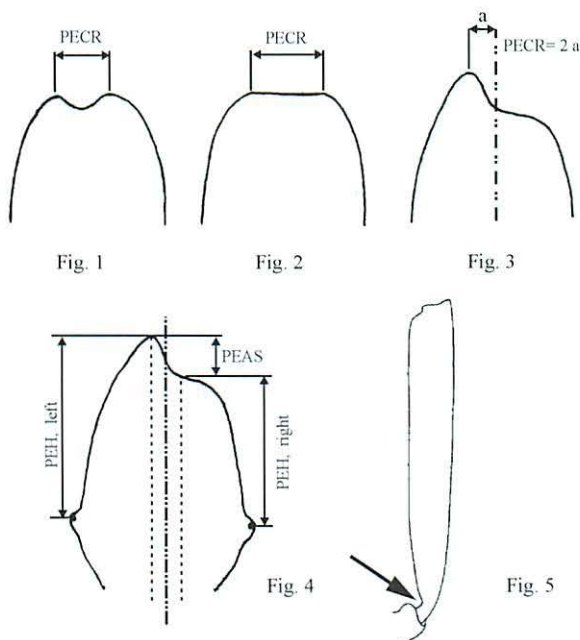
Any metric measurement refers to real cuticular surface and not to the diffuse pubescence surface (most important in CW, IF2, Smax, Smin, HTmax). All setae counts include setae pro-

jecting  $> 10 \mu\text{m}$  from cuticular profile with no change of viewing position. In cases of ambiguous projecting distance or unclear hair type (is it a fine seta or only a larger pubescence hair?) countings of 0.5 are applied.

- CL** – maximum cephalic length in median line; the head must be carefully tilted to the position with the true maximum. Excavations of posterior vertex reduce CL.
- CS** – cephalic size; the arithmetic mean of CL and CW, used as a less variable indicator of body size.
- CW** – maximum cephalic width – either across, anterior or posterior of eyes, which ever yields the maximum measurement.
- GHL** – length of longest seta on dorsal plane of first gaster tergite excluding setae near the posterior margin. The anterior area of dorsal plane where it slopes down to anterior face is included, but do never include areas sloping  $> 50^\circ$  (here setae are significantly longer!).
- Htmax** – maximum width of hind tibia at midpoint. The reference points to determine the midpoint are the distal end of tibia and the point of strongest constriction of the tibia's flexor side at the tibio-femoral joint (arrow in Fig. 5). In some species with dense and long pubescence (as exemplary in *L. mixtus*) visualisation of the cuticular surface is difficult and measuring errors are expected. However, control measurements after removal of pubescence have shown subjective and real HTmax not to differ considerably. Users should test their subjective errors at the beginning of a measuring series.
- IF2** – ratio of median length/maximum width of second funiculus (third antennal) segment when viewing perpendicular to the moving plane of the hinge joint of the pedicel with scape. Use median length because of frequent length differences between inner and outer margin and modify incidence of illumination.
- MnHL** – length of longest seta on mesonotum.
- NHT** – number of setae projecting more than  $10 \mu\text{m}$  above the extensor profile of hind tibia. Apical setae at distal end are excluded.
- PEAS** – bilateral height asymmetry of petiolar crest. Height difference of the corners of petiolar crest. If only one side shows a corner, height measurement on the other side is performed at a sagittal level, the distance of which from the median is equal to that of the sagittal level of the corner from the median (Fig. 4).
- PEH** – petiolar height measured from centre of spiracle to dorsalmost point of petiolar crest. In case of asymmetric crests, the average of both sides is taken (Fig. 4).
- PEW** – maximum width of petiole.
- PECR** – width of petiolar crest. In case of an average *Chthonolasius* scale shape (Fig. 1), PECR is measured from corner centre to corner centre. If the crest is straight, PECR is measured between the lateralmost points of the straight section (Fig. 2). If only one side shows a corner in asymmetric scales, PECR is twice the distance **a** of the corner centre from the median (Fig. 3). PECR is 0 in case of symmetric crests without any corners (rounded or tipped crests).
- PDF** – transverse pubescence distance on vertex frontal of mid ocellus. To avoid damaged and oily surface areas, countings are done as an average of three or four

shorter sections of 90  $\mu\text{m}$ . A section crossing the frontal line is always included. Hairs crossing/just touching the 90  $\mu\text{m}$  reference lines are counted as 1/0.5. A rather flat incidence of light ( $30^\circ$ ) is advantageous. To visualise the full length of pubescence hairs, short to-and-fro rotations of the light-cables around the optical axis are permanently performed during counting. Use objectives with numeric apertures  $> 0.2$ . In gynae, the square root of PDF (sqPDF) is applied to normalise positively skewed distributions.

- PDG** – transverse pubescence distance on dorsum of first gaster tergite. Measuring is basically done as in PDF. In species with high pubescence distance and undamaged, clean surfaces, larger sections of up to 400  $\mu\text{m}$  should be combined but do not exceed this length to minimise errors caused by surface convexity. In gynae, the square root of PDG (sqPDG) is applied to normalise positively skewed distributions.
- ScHD** – viewing on the small diameter of scape, maximum projecting distance of setae from dorsal profile of scape. Any seta, projecting more than 10  $\mu\text{m}$  or not, is considered with exception of the apical ones.
- SL** – maximum straight line scape length excluding the articular condyle.
- Smax** – maximum scape diameter at midpoint.
- Smin** – minimum scape diameter at midpoint.



Figs 1 – 4 mode of measuring the characters PECR, PEH, and PEAS

Fig. 5 proximal end point (arrow) of measuring hind tibia length

### 3. Results

To understand the hybrid scenario described below, biology, habitat selection, postglacial immigration, overall abundance and swarming of the hybridising species must be considered. All *Chthonolasius* species are temporary social parasites of species of the subgenus *Lasius* s. str. and to a lesser degree of the subgenus *Cautolasius* Wilson, 1955. The rarity of direct evidence does not allow to conclude that host specificity is widespread, though it is obvious that main hosts can be recognised, and regional host species seem to exist according to distributional data (SEIFERT 1988, 1996, SEIFERT & BUSCHINGER 2001, SCHLICK-STEINER et al. 2002a, 2002b). If not explicitly stated otherwise, any information given on the postglacial landscape development in Central Europe is derived from BICK (1984), GREIG (1988), KÖRBER-GROHNE (1990) and LANG (1994).

#### 3.1. Habitat selection, host species and putative postglacial immigration history

*L. umbratus* is the least xerothermophilous of the three species considered here and occurs in semidry to moist sites, both in open habitats as well as in shady woodland (Tab. 1). As a consequence, the spectrum of habitats of *L. umbratus* is much wider and it is clearly the most abundant of the 10 *Chthonolasius* species known from Central Europe. Its main host species, *Lasius niger* (Linnaeus, 1758), is euryoecious and extremely abundant in Central Europe. The composition of the ant fauna in some of the *L. umbratus* sites suggests *L. brunneus* (Latreille, 1798), *L. psammophilus* Seifert, 1992, and *L. platythorax* Seifert, 1991 to be supplementary host species but direct evidence by discovery of mixed nest populations is still missing. The comparably wide ecological potency of *L. umbratus* (if a social parasite can ever bear this attribute!) indicates that postglacial immigration to Central Europe must have started soon and that *L. umbratus* should have been a normal faunal element between 7500 and 2000 BP. The landscape in this period was largely dominated by dense woodland, but interrupted by lakes, bogs, river plains and small to medium sized clear cuttings of the Neolithic, Bronze Age and Early Iron Age cultures.

Tab. 1 Frequency of nest findings in Central Europe grouped in four main habitat categories

|                                             | open,<br>xerothermous,<br>natural to<br>semi-natural | open, fresh-dry<br>to moist<br>cultivated land | xerothermous to<br>moist woodland | peat bogs    |
|---------------------------------------------|------------------------------------------------------|------------------------------------------------|-----------------------------------|--------------|
| <i>L. jensi</i>                             | 30<br>(= 91 %)                                       | 3<br>(= 9 %)                                   | 0                                 | 0            |
| <i>L. jensi</i> x<br><i>umbratus</i>        | 14<br>(= 74 %)                                       | 5<br>(= 26 %)                                  | 0                                 | 0            |
| <i>L. umbratus</i>                          | 20<br>(= 32 %)                                       | 22<br>(= 35 %)                                 | 19<br>(= 30 %)                    | 2<br>(= 3 %) |
| <i>L. meridionalis</i> x<br><i>umbratus</i> | 4<br>(= 57 %)                                        | 3<br>(= 43 %)                                  | 0                                 | 0            |
| <i>L. meridionalis</i>                      | 13<br>(= 93 %)                                       | 1<br>(= 7 %)                                   | 0                                 | 0            |

*L. meridionalis* is significantly more xerothermophilous than *L. umbratus* and occurs mainly in open sites. However, occurrence in S Fennoscandia and mountain ranges of Central Europe indicates tolerance against lower winter temperatures. Major habitats are dry heath land or xerothermous grassland, preferentially on sandy soils but also on silicate rock. Its main host is *Lasius psammophilus* Seifert, 1992, a proved secondary host is *L. paralienus* Seifert, 1992, while direct proof for *L. niger* is still lacking. The ecology of *L. meridionalis* indicates a high potency for early postglacial immigration beginning with 10 000 BP or even earlier – sandy grasslands with plant species typical for recent *L. meridionalis* habitats such as *Jasione* or *Helianthemum* were already detected in Germany in the early Alleröd 13 500 BP (FRIEDRICH et al. 2001). Immigration may have happened very fast over corridors provided by warm dune areas on glacial outwash plains, stretching over hundreds of miles along Pleistocene watercourses. These sand dunes remained open for a longer period and are the primary habitats for its main host species.

*L. jensi* is the most thermophilous of the three species. In Central Europe, it preferentially occurs in xerothermous grassland on limestone in landscapes with warm local climate. In fact, the distribution of *L. jensi* in Central Europe largely overlaps with areas of historic or present wine growing and zoogeographically it is a Submediterranean element. Its major host species is *Lasius alienus* (Förster, 1850), a widespread but xerothermophilous species. The ecology of *L. jensi* does not indicate a potency for early postglacial immigration beginning with 10 000 BP and it is also not likely that *L. jensi* could settle in the small open areas in the Central European landscape between 7500 and 2500 BP. Indirect support for this idea is given by the absence of pollen or other fossil traces of Mediterranean or Submediterranean steppe plants such as *Salvia pratensis* or *Bromus erectus* that are typically found in recent *L. jensi* habitats. As a consequence, substantial immigration of *L. jensi* to SW Central Europe should not have proceeded earlier than 2100 BP with the extended Roman cultivation, while E Central Europe was not reached earlier than 1100 BP with the big clear-cuttings of the Middle Ages and simultaneous temperature increase between 1100 and 700 BP.

### 3.2. Relative population size in Central Europe

The relative population size of *L. jensi*, *L. meridionalis* and *L. umbratus* in Central Europe is important for our considerations but not easily estimated. Sampling activities of the author and many other myrmecologists are biased in Central Europe to open xerothermous sites where ant biodiversity is largest, with limestone regions being most attractive. Furthermore, it is a rule for abundant species that only a fraction of the specimens really collected is finally incorporated into collections in order to save storage capacity and time for preparing and proper labelling of specimens. Rare species, in contrast, are usually stored completely. As a consequence, the abundance of *L. jensi* is strongly over- and that of *L. umbratus* strongly underestimated when simply using the number of samples stored in the collections. In this study, the ratio of *L. jensi* : *L. meridionalis* : *L. umbratus* is 38 : 19 : 97 in morphometrically investigated worker nest samples and 78 : 54 : 169 in gyne individuals. It becomes clear that both ratios are most unrealistic when considering that potential habitats of the three species available in Central Europe have an area ratio of about 3 : 10 : 100. If considering that *L. jensi* reaches about twice the density in rich limestone grasslands than *L. umbratus* or *L. meridionalis* in their main habitats (SEIFERT, unpublished results), it follows that *L. jensi* should have about 6 % and *L. meridionalis* about 10 % of the overall population size of *L. umbratus*.

### 3.3. Temporal and spatial features of swarming

Direct observations of alates flying-off from the nests are very rare in *Chthonolasius*. However, daily flight hours may be roughly estimated from the frequent observations of dealate gynes moving over ground. When subtracting one hour from the observation time, it follows that both *L. jensi*, *L. meridionalis* and *L. umbratus* should fly between 2.00 and 7.00 p.m. on warm summer days with high air humidity and weak or no air movement. Catches of alate gynes of all three species (and of *L. nitidigaster* Seifert, 1996) in light-traps indicate extension of flights to late evening or early night. The data as a whole do not allow to conclude on interspecific daytime separation of nuptial flight – if any temporal segregation should exist, it cannot be conspicuous. On several occasions it was observed that dealate gynes of all three species moved over the ground at the same site and same hour of the day.

More precisely documented are the seasonal flight periods expressed by observation of alate and dealate, walking or flying gynes. A total of 172 flight days in Central Europe, mainly from the period 1975 – 2003, was evaluated for *L. jensi*, *L. meridionalis*, *L. umbratus* and the hybrid *L. meridionalis* x *umbratus* (Tab. 2). There are no significant differences of annual flight periods in each possible comparison when tested in a nonparametric U test. The percentage of observations outside the overlap range is 1.3 % between *L. jensi* and *L. meridionalis*, 6.7 % between *L. jensi* and *L. umbratus* and 5.5 % between *L. umbratus* and *L. meridionalis*. Hybrids *L. meridionalis* x *umbratus* seem to fly a little earlier but this difference is also insignificant.

The question of a spatial separation of mating places cannot be answered clearly. Since mating on the ground or exposed structures has never been observed by any myrmecologist, mating most probably occurs during flight high up in the air and the simultaneous and syntopic landing of mated gynes of different species suggests no clear spatial separation.

Tab. 2 Observation days of alate or dealate gynes moving outside the nests. Days are continuously numbered with day 1 = 1 June and day 123 = 1 October; n = number of observations

|                                             | mean $\pm$ SD   | range     | n  | mean date |
|---------------------------------------------|-----------------|-----------|----|-----------|
| <i>L. jensi</i>                             | 58.1 $\pm$ 20.2 | [23, 129] | 46 | 28 July   |
| <i>L. meridionalis</i>                      | 61.9 $\pm$ 22.9 | [23, 137] | 32 | 1 August  |
| <i>L. umbratus</i>                          | 58.7 $\pm$ 26.4 | [10, 137] | 77 | 29 July   |
| <i>L. umbratus</i> x<br><i>meridionalis</i> | 49.8 $\pm$ 19.5 | [15, 77]  | 17 | 20 July   |

### 3.4. The hybrid case *L. meridionalis* x *umbratus*

In gynes, the three entities *L. umbratus*, *L. meridionalis* x *umbratus* and *L. meridionalis* can be fully separated on the individual level by a canonical discriminant analysis computing the characters CS, CL/CW<sub>cor</sub>, Smax<sub>cor</sub>, Smax/Smin<sub>cor</sub>, HTmax<sub>cor</sub>, IF2<sub>cor</sub>, sqPDF<sub>cor</sub>, nHT<sub>cor</sub> and GHL/CS<sub>cor</sub> (Fig. 6). All 192 determinations show error probabilities of  $p < 0.05$ . Safer determinations can be achieved by pairwise considerations. In the case of *L. meridionalis* vs *L. meridionalis* x *umbratus* a discriminant D(10) with

$$D(10) = -47.56 -4.65 \text{ CS} +22.06 \text{ CL/CW}_{\text{cor}} -9.15 \text{ SL/CS}_{\text{cor}} +11.90 \text{ Smax/CS}_{\text{cor}} +6.126 \text{ Smax/Smin}_{\text{cor}} +151.02 \text{ HTmax/CS}_{\text{cor}} +3.76 \text{ IF2}_{\text{cor}} +0.66*\text{sqPDF}_{\text{cor}} +0.014*\text{nHT}_{\text{cor}} -25.61*\text{GHL/CS}_{\text{cor}}$$

shows for all 79 determinations error probabilities of  $p < 0.002$ :

$$L. \text{ meridionalis} \quad D(10) +3.150 \pm 1.005 [1.32, +6.67] \text{ n} = 54$$

$$L. \text{ meridionalis} \text{ x } \text{umbratus} \quad D(10) -3.659 \pm 0.989 [-5.46, -1.32] \text{ n} = 25$$

and in the case of *L. meridionalis* x *umbratus* vs *L. umbratus* a discriminant

$$D(10) = 73.50 +2.46 \text{ CS} +22.56 \text{ CL/CW}_{\text{cor}} +13.63 \text{ SL/CS}_{\text{cor}} +18.30 \text{ Smax/CS}_{\text{cor}} +8.93 \text{ Smax/Smin}_{\text{cor}} +106.72 \text{ HTmax/CS}_{\text{cor}} +3.04 \text{ IF2}_{\text{cor}} +1.60*\text{sqPDF}_{\text{cor}} -0.033*\text{nHT}_{\text{cor}} -6.55*\text{GHL/CS}_{\text{cor}}$$

shows for all 113 determinations error probabilities of  $p < 0.013$ :

$$L. \text{ meridionalis} \text{ x } \text{umbratus} \quad D(10) +3.352 \pm 1.329 [0.86, +5.91] \text{ n} = 25$$

$$L. \text{ umbratus} \quad D(10) -3.005 \pm 0.915 [-5.08, -0.86] \text{ n} = 113.$$

Comparative data of all three entities are given in Tab. 3. Hybrid gynes are in seven characters intermediate between the parent species, approach in two characters to *L. umbratus* and in only one to *L. meridionalis*.

Compared to the comfortable situation in gynes, identification of hybrids by worker nest samples is problematic and some samples are most doubtful. Three entities can be clustered by canonical discriminant analysis computing the 14 standard characters CS, CL/CW<sub>cor</sub>, Smax/CS<sub>cor</sub>, Smax/Smin<sub>cor</sub>, HTmax/CS<sub>cor</sub>, PDF<sub>cor</sub>, PDG<sub>cor</sub>, nHT<sub>cor</sub> and GHL/CS<sub>cor</sub>, PECCR/CS<sub>cor</sub>, PEW/CS<sub>cor</sub>, PEH/CS<sub>cor</sub> and PEAS/CS<sub>cor</sub> but only 82.4 % of 125 cases have error probabilities of  $p < 0.10$  (Fig. 7). The identification is improved when pairwise discriminant analysis is applied. Unproblematic is the separation of the parent species. A discriminant D(14) determines 98.3 % of 116 cases with error probabilities of  $p < 0.005$ :

$$D(14) = -35.45 -3.80 \text{ CS} -27.38 \text{ CL/CW}_{\text{cor}} +33.10 \text{ SL/CS}_{\text{cor}} -4.92 \text{ Smax/CS}_{\text{cor}} +9.37 \text{ Smax/Smin}_{\text{cor}} +81.54 \text{ HTmax/CS}_{\text{cor}} -0.02 \text{ PDF}_{\text{cor}} +0.36 \text{ PDG}_{\text{cor}} +0.01 \text{ nHT}_{\text{cor}} -71.75 \text{ GHL/CS}_{\text{cor}} +1.53 \text{ PECCR/CS}_{\text{cor}} +57.49 \text{ PEW/CS}_{\text{cor}} -10.96 \text{ PEH/CS}_{\text{cor}} -0.38 \text{ PEAS/CS}_{\text{cor}}$$

$$L. \text{ meridionalis} \quad 2.525 \pm 0.828 [0.72, 4.29] \text{ n} = 19$$

$$L. \text{ umbratus} \quad -3.347 \pm 1.024 [-5.74, -0.72] \text{ n} = 97.$$

Tab. 3 Primary (uncorrected) morphometric data of gynes of *Lasius meridionalis*, *L. meridionalis* x *umbratus* and *L. umbratus*. Given are arithmetic mean  $\pm$  standard deviation [minimum, maximum] and the significance levels of a *t* test on difference of the means.

|              | <i>L. meridionalis</i><br>(n = 54)  |        | <i>L. meridionalis</i><br>x <i>umbratus</i><br>(n = 25) |        | <i>L. umbratus</i><br>(n = 113)     |
|--------------|-------------------------------------|--------|---------------------------------------------------------|--------|-------------------------------------|
| CS [mm]      | 1.514 $\pm$ 0.043<br>[1.443, 1.627] | 0.0001 | 1.581 $\pm$ 0.046<br>[1.510, 1.654]                     | n.s.   | 1.563 $\pm$ 0.044<br>[1.465, 1.699] |
| CL/CW        | 0.862 $\pm$ 0.013<br>[0.829, 0.897] | n.s.   | 0.859 $\pm$ 0.011<br>[0.840, 0.881]                     | 0.030  | 0.853 $\pm$ 0.013<br>[0.829, 0.894] |
| SL/CS        | 0.864 $\pm$ 0.016<br>[0.830, 0.908] | 0.0001 | 0.843 $\pm$ 0.017<br>[0.812, 0.886]                     | 0.0001 | 0.813 $\pm$ 0.018<br>[0.775, 0.887] |
| Smax/CS [%]  | 10.76 $\pm$ 0.40<br>[9.80, 11.49]   | 0.0001 | 9.90 $\pm$ 0.40<br>[9.02, 10.64]                        | 0.0001 | 8.88 $\pm$ 0.32<br>[8.12, 9.63]     |
| Smax/min     | 1.983 $\pm$ 0.105<br>[1.776, 2.269] | 0.0001 | 1.595 $\pm$ 0.089<br>[1.413, 1.758]                     | 0.0001 | 1.316 $\pm$ 0.061<br>[1.184, 1.459] |
| HTmax/CS [%] | 18.65 $\pm$ 0.54<br>[17.45, 19.88]  | 0.0001 | 16.59 $\pm$ 0.58<br>[15.46, 17.56]                      | 0.0001 | 14.32 $\pm$ 0.59<br>[12.98, 15.58]  |
| IF2          | 1.823 $\pm$ 0.097<br>[1.570, 2.010] | 0.0001 | 1.657 $\pm$ 0.068<br>[1.560, 1.823]                     | 0.0001 | 1.549 $\pm$ 0.073<br>[1.401, 1.805] |
| MnHL/CS [%]  | 7.06 $\pm$ 0.54<br>[6.0, 8.4]       | 0.0001 | 6.11 $\pm$ 0.69<br>[5.3, 7.5]                           | 0.003  | 5.56 $\pm$ 0.76<br>[4.15, 10.21]    |
| GHL/CS [%]   | 7.11 $\pm$ 0.53<br>[5.5, 8.1]       | n.s.   | 6.94 $\pm$ 0.48<br>[6.2, 7.9]                           | 0.011  | 6.61 $\pm$ 0.92<br>[4.7, 10.2]      |
| nHT          | 31.3 $\pm$ 7.9<br>[17.0, 51.0]      | n.s.   | 27.8 $\pm$ 11.6<br>[6.5, 47.0]                          | n.s.   | 28.8 $\pm$ 10.5<br>[0.9, 51.1]      |
| sqPDF        | 2.98 $\pm$ 0.19<br>[2.61, 3.48]     | 0.001  | 2.81 $\pm$ 0.20<br>[2.53, 3.55]                         | 0.0001 | 2.61 $\pm$ 0.17<br>[2.05, 3.01]     |
| sqPDG        | 2.35 $\pm$ 0.15<br>[2.10, 2.74]     | 0.01   | 2.23 $\pm$ 0.17<br>[2.00, 2.61]                         | 0.001  | 2.07 $\pm$ 0.15<br>[1.82, 2.77]     |
| ScHD/CS [%]  | 2.11 $\pm$ 0.54<br>[1.1, 3.2]       | n.s.   | 2.14 $\pm$ 0.70<br>[1.0, 3.6]                           | 0.0001 | 2.72 $\pm$ 0.53<br>[1.1, 4.7]       |

Clearly separate discriminant values and low error probabilities suggest also a powerful separation of *L. meridionalis* from the hybrid. However, because of the low sample size of the hybrid which is lower than the number of characters evaluated, the discriminant function should be unstable. Nevertheless, the discriminant D(14) with

$$D(14) = -43.71 - 7.52 \text{ CS} - 78.18 \text{ CL/CW}_{\text{cor}} + 100.47 \text{ SL/CS}_{\text{cor}} + 114.55 \text{ Smax/CS}_{\text{cor}} + 7.60 \text{ Smax/Smin}_{\text{cor}} + 110.61 \text{ HTmax/CS}_{\text{cor}} - 0.14 \text{ PDF}_{\text{cor}} + 0.51 \text{ PDG}_{\text{cor}} + 0.02 \text{ nHT}_{\text{cor}} - 71.75 \text{ GHL/CS}_{\text{cor}} - 44.46 \text{ PECR/CS}_{\text{cor}} + 65.96 \text{ PEW/CS}_{\text{cor}} - 17.92 \text{ PEH/CS}_{\text{cor}} - 0.76 \text{ PEAS/CS}_{\text{cor}}$$

shows for all 28 determinations error probabilities of  $p < 0.001$ :

$$L. \text{ meridionalis} \quad 5.407 \pm 0.992 [2.67, 6.63] \quad n = 19$$

$$L. \text{ meridionalis} \times \text{umbratus} \quad -4.159 \pm 1.018 [-5.39, -2.67] \quad n = 9.$$

Most problematic is the separation of the hybrid from *L. umbratus*. A discriminant D(14) determines only 91.5 % of 106 cases with error probabilities of  $p < 0.10$ :

$$D(14) = -65.79 + 4.95 \text{ CS} - 29.94 \text{ CL/CW}_{\text{cor}} + 81.50 \text{ SL/CS}_{\text{cor}} + 172.42 \text{ Smax/CS}_{\text{cor}} - 9.38 \text{ Smax/Smin}_{\text{cor}} - 8.66 \text{ HTmax/CS}_{\text{cor}} + 0.78 \text{ PDF}_{\text{cor}} - 0.52 \text{ PDG}_{\text{cor}} + 0.06 \text{ nHT}_{\text{cor}} - 34.95 \text{ GHL/CS}_{\text{cor}} + 11.38 \text{ PECR/CS}_{\text{cor}} + 53.94 \text{ PEW/CS}_{\text{cor}} - 7.80 \text{ PEH/CS}_{\text{cor}} - 0.92 \text{ PEAS/CS}_{\text{cor}}$$

$$L. \text{ meridionalis} \times \text{umbratus} \quad -1.588 \pm 0.944 [-3.13, -0.38] \quad n = 9$$

$$L. \text{ umbratus} \quad 2.117 \pm 1.004 [0.38, 5.37] \quad n = 97.$$

The problematic separation of the hybrid from its *L. umbratus* parent is also reflected in Tab. 4. Among 14 characters tested, the hybrid significantly differs from *L. umbratus* in only 43 % but from *L. meridionalis* in 79 % of characters.

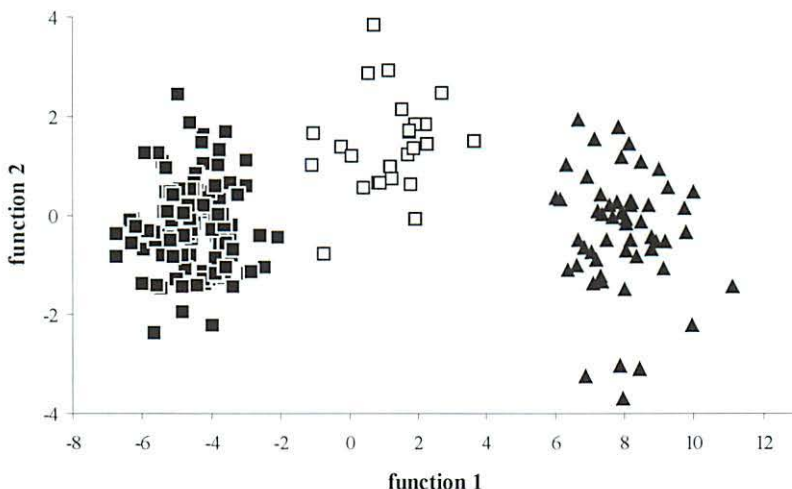


Fig. 6 Canonical discriminant analysis of gyne individuals. Filled squares = *L. umbratus*, empty squares = *L. meridionalis*  $\times$  *umbratus*, filled triangles = *L. meridionalis*.

Tab. 4 Allometrically corrected morphometric data of worker nest sample means of *Lasius meridionalis*, *L. meridionalis* x *umbratus* and *L. umbratus*. Given are arithmetic mean  $\pm$  standard deviation [minimum, maximum] and the significance levels of a *t* test on difference of the means; n = number of nest samples (basis of statistics), i = number of individuals.

|                                       | <i>L. meridionalis</i><br>(n = 19, i = 67) |        | <i>L. meridionalis</i><br>x <i>umbratus</i><br>(n = 9, i = 35) |        | <i>L. umbratus</i><br>(n = 97, i = 303) |
|---------------------------------------|--------------------------------------------|--------|----------------------------------------------------------------|--------|-----------------------------------------|
| <b>CS [mm]</b>                        | 1.010 $\pm$ 0.076<br>[0.851, 1.121]        | n.s.   | 0.988 $\pm$ 0.101<br>[0.812, 1.124]                            | 0.0001 | 1.089 $\pm$ 0.073<br>[0.848, 1.211]     |
| <b>CL/CW<sub>cor</sub></b>            | 1.034 $\pm$ 0.014<br>[1.002, 1.064]        | 0.017  | 1.047 $\pm$ 0.009<br>[1.030, 1.055]                            | n.s.   | 1.042 $\pm$ 0.013<br>[1.004, 1.075]     |
| <b>SL/CS<sub>cor</sub></b>            | 0.894 $\pm$ 0.007<br>[0.880, 0.903]        | 0.0001 | 0.868 $\pm$ 0.007<br>[0.857, 0.877]                            | 0.036  | 0.878 $\pm$ 0.013<br>[0.842, 0.919]     |
| <b>Smax/Smin<sub>cor</sub></b>        | 1.640 $\pm$ 0.068<br>[1.512, 1.767]        | 0.0001 | 1.456 $\pm$ 0.096<br>[1.331, 1.602]                            | 0.05   | 1.393 $\pm$ 0.078<br>[1.204, 1.547]     |
| <b>Smax/CS<sub>cor</sub><br/>[%]</b>  | 10.02 $\pm$ 0.25<br>[9.54, 10.50]          | 0.0001 | 9.30 $\pm$ 0.38<br>[8.63, 10.01]                               | n.s.   | 9.36 $\pm$ 0.31<br>[8.64, 10.04]        |
| <b>HTmax/CS<sub>cor</sub><br/>[%]</b> | 14.62 $\pm$ 0.32<br>[14.03, 15.33]         | 0.0001 | 13.47 $\pm$ 0.49<br>[12.47, 14.00]                             | n.s.   | 13.37 $\pm$ 0.39<br>[12.15, 14.13]      |
| <b>GHL/CS<sub>cor</sub><br/>[%]</b>   | 8.87 $\pm$ 0.67<br>[7.52, 10.07]           | 0.004  | 9.65 $\pm$ 0.48<br>[9.07, 10.49]                               | n.s.   | 9.44 $\pm$ 0.56<br>[8.20, 10.84]        |
| <b>nHT<sub>cor</sub></b>              | 21.2 $\pm$ 7.7<br>[9.8, 40.9]              | 0.012  | 13.8 $\pm$ 4.1<br>[7.1, 17.7]                                  | 0.041  | 17.7 $\pm$ 5.6<br>[5.7, 32.6]           |
| <b>PDF<sub>cor</sub></b>              | 8.24 $\pm$ 0.78<br>[7.0, 9.6]              | 0.0001 | 6.75 $\pm$ 0.42<br>[6.1, 7.2]                                  | n.s.   | 6.85 $\pm$ 0.65<br>[4.6, 8.7]           |
| <b>PDG<sub>cor</sub></b>              | 8.41 $\pm$ 1.60<br>[6.3, 13.9]             | 0.002  | 6.87 $\pm$ 0.82<br>[5.7, 8.3]                                  | 0.088  | 6.41 $\pm$ 0.76<br>[4.6, 8.6]           |
| <b>PECR/CS<sub>cor</sub></b>          | 0.096 $\pm$ 0.014<br>[0.071, 0.133]        | n.s.   | 0.089 $\pm$ 0.010<br>[0.078, 0.108]                            | n.s.   | 0.090 $\pm$ 0.014<br>[0.064, 0.137]     |
| <b>PEW/CS<sub>cor</sub></b>           | 0.300 $\pm$ 0.014<br>[0.278, 0.331]        | 0.0001 | 0.275 $\pm$ 0.010<br>[0.259, 0.289]                            | 0.001  | 0.288 $\pm$ 0.011<br>[0.268, 0.321]     |
| <b>PEH/CS<sub>cor</sub></b>           | 0.266 $\pm$ 0.015<br>[0.231, 0.286]        | 0.0001 | 0.260 $\pm$ 0.015<br>[0.237, 0.284]                            | n.s.   | 0.254 $\pm$ 0.014<br>[0.223, 0.285]     |
| <b>PEAS/CS<sub>cor</sub><br/>[%]</b>  | 0.42 $\pm$ 0.28<br>[0.00, 0.94]            | 0.091  | 0.62 $\pm$ 0.31<br>[0.00, 1.12]                                | 0.014  | 0.37 $\pm$ 0.30<br>[0.00, 1.36]         |

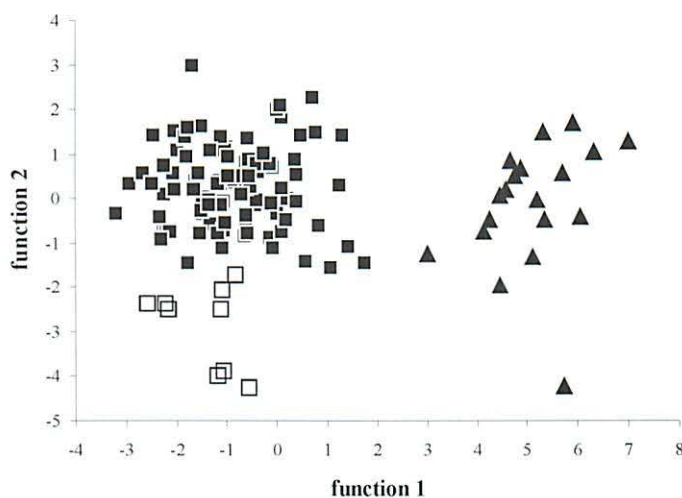


Fig. 7 Canonical discriminant analysis of worker nest samples. Filled squares = *L. umbratus*, empty squares = *L. meridionalis* x *umbratus*, filled triangles = *L. meridionalis*.

### 3.5. The hybrid case *L. jensi* x *umbratus*

Gynes of *L. jensi* x *umbratus* should be easily identified because of the extreme morphological differences of the parent species (SEIFERT 1988). However, despite intensive sampling in habitats with *L. jensi* populations, not a single gyne suspected to be hybrid has ever been discovered throughout an observation period of 27 years in which the author has seen about 89 gynes of *L. jensi* and 330 gynes of *L. umbratus*. As a matter of fact, *L. jensi* x *umbratus* gynes are apparently not produced.

The three entities *L. jensi*, *L. jensi* x *umbratus* and *L. umbratus* can be identified based upon worker nest samples by a canonical discriminant analysis computing the 14 standard characters (Fig. 8). The identification is improved when pairwise discriminant analysis is applied. Radically different are the parent species. A discriminant  $D(14)$  with

$$D(14) = -26.79 - 4.02 CS - 8.78 CL/CW_{cor} + 17.05 SL_{cor} + 4.76 Smax_{cor} + 9.30 Smax/Smin_{cor} + 23.70 HTmax_{cor} + 0.79 PDF_{cor} + 0.27 PDG_{cor} - 0.02 nHT_{cor} - 28.30 GHL/CS_{cor} - 25.70 PECR_{cor} + 37.88 PEW_{cor} - 9.80 PEH_{cor} - 0.33 PEAS_{cor}$$

determines any of 138 cases with  $p < 0.0001$ :

$$L. umbratus \quad -3.316 \pm 0.895 [-5.72, -1.72] \quad n = 97$$

$$L. jensi \quad 4.619 \pm 1.216 [1.73, 7.45] \quad n = 41.$$

Tab. 5 Allometrically corrected morphometric data of worker nest sample means of *Lasius jensi*, *L. jensi* x *umbratus* and *L. umbratus*. Given are arithmetic mean  $\pm$  standard deviation [minimum, maximum] and the significance levels of a *t* test on difference of the means; n = number of nest samples (basis of statistics), i = number of individuals.

|                                     | <i>L. umbratus</i><br>(n = 97, i = 303) |        | <i>L. jensi</i><br>x <i>umbratus</i><br>(n = 31, i = 115) |        | <i>L. jensi</i><br>(n = 41, i = 128) |
|-------------------------------------|-----------------------------------------|--------|-----------------------------------------------------------|--------|--------------------------------------|
| <b>CS [mm]</b>                      | 1.089 $\pm$ 0.073<br>[0.848, 1.211]     | 0.0001 | 0.992 $\pm$ 0.082<br>[0.838, 1.145]                       | n.s.   | 0.979 $\pm$ 0.066<br>[0.788, 1.085]  |
| <b>CL/CW<sub>cor</sub></b>          | 1.042 $\pm$ 0.013<br>[1.004, 1.075]     | 0.061  | 1.047 $\pm$ 0.011<br>[1.022, 1.076]                       | n.s.   | 1.049 $\pm$ 0.016<br>[1.021, 1.109]  |
| <b>SL/CS<sub>cor</sub></b>          | 0.878 $\pm$ 0.013<br>[0.842, 0.919]     | n.s.   | 0.878 $\pm$ 0.011<br>[0.853, 0.903]                       | 0.0001 | 0.906 $\pm$ 0.010<br>[0.881, 0.926]  |
| <b>Smax/Smin<sub>cor</sub></b>      | 1.393 $\pm$ 0.078<br>[1.204, 1.547]     | 0.0001 | 1.477 $\pm$ 0.054<br>[1.375, 1.634]                       | 0.0001 | 1.885 $\pm$ 0.103<br>[1.722, 2.154]  |
| <b>Smax/CS<sub>cor</sub></b><br>[%] | 9.36 $\pm$ 0.31<br>[8.64, 10.04]        | 0.01   | 9.57 $\pm$ 0.27<br>[8.91, 10.13]                          | 0.0001 | 10.53 $\pm$ 0.25<br>[9.91, 10.95]    |
| <b>HTmax/CS<sub>cor</sub></b>       | 13.37 $\pm$ 0.39<br>[12.15, 14.13]      | n.s.   | 13.49 $\pm$ 0.32<br>[12.82, 14.17]                        | 0.0001 | 14.72 $\pm$ 0.52<br>[13.63, 16.10]   |
| <b>GHL/CS<sub>cor</sub></b><br>[%]  | 9.44 $\pm$ 0.56<br>[8.20, 10.84]        | 0.038  | 9.21 $\pm$ 0.51<br>[8.11, 10.12]                          | 0.0001 | 8.50 $\pm$ 0.81<br>[7.26, 11.28]     |
| <b>nHT<sub>cor</sub></b>            | 17.7 $\pm$ 5.6<br>[5.7, 32.6]           | n.s.   | 19.4 $\pm$ 4.1<br>[9.5, 26.5]                             | 0.0001 | 26.4 $\pm$ 5.4<br>[3.1, 25.8]        |
| <b>PDF<sub>cor</sub></b>            | 6.85 $\pm$ 0.65<br>[4.6, 8.7]           | 0.0001 | 7.50 $\pm$ 0.73<br>[5.9, 9.1]                             | 0.0001 | 9.52 $\pm$ 1.03<br>[7.4, 11.8]       |
| <b>PDG<sub>cor</sub></b>            | 6.41 $\pm$ 0.76<br>[4.6, 8.6]           | n.s.   | 6.74 $\pm$ 1.16<br>[4.3, 9.3]                             | 0.0001 | 9.28 $\pm$ 1.51<br>[6.5, 14.0]       |
| <b>PECR/CS<sub>cor</sub></b>        | 0.090 $\pm$ 0.014<br>[0.064, 0.137]     | 0.0001 | 0.067 $\pm$ 0.015<br>[0.021, 0.096]                       | 0.0001 | 0.025 $\pm$ 0.018<br>[0.000, 0.065]  |
| <b>PEW/CS<sub>cor</sub></b>         | 0.288 $\pm$ 0.011<br>[0.268, 0.321]     | 0.0001 | 0.278 $\pm$ 0.009<br>[0.263, 0.306]                       | n.s.   | 0.281 $\pm$ 0.009<br>[0.259, 0.304]  |
| <b>PEH/CS<sub>cor</sub></b>         | 0.254 $\pm$ 0.014<br>[0.223, 0.285]     | 0.0001 | 0.266 $\pm$ 0.015<br>[0.233, 0.294]                       | 0.003  | 0.278 $\pm$ 0.019<br>[0.230, 0.322]  |
| <b>PEAS/CS<sub>cor</sub></b><br>[%] | 0.37 $\pm$ 0.30<br>[0.00, 1.36]         | 0.0001 | 1.08 $\pm$ 0.62<br>[0.00, 2.76]                           | 0.0001 | 0.13 $\pm$ 0.21<br>[0.00, 0.79]      |

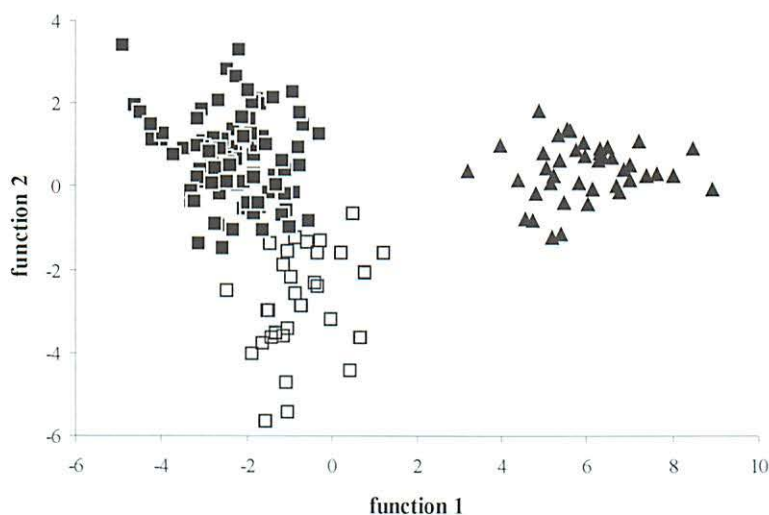


Fig. 8 Canonical discriminant analysis of worker nest samples. Filled squares = *L. umbratus*, empty squares = *L. jensi* x *umbratus*, filled triangles = *L. jensi*.

Very clear is also the distinction of the hybrid from *L. jensi*. A discriminant D(14) with

$$D(14) = -68.09 + 1.95 \text{ CS} - 6.52 \text{ CL/CW}_{\text{cor}} + 42.16 \text{ SL}_{\text{cor}} + 41.58 \text{ Smax}_{\text{cor}} + 7.78 \text{ Smax/Smin}_{\text{cor}} \\ + 71.88 \text{ HTmax}_{\text{cor}} - 0.08 \text{ PDF}_{\text{cor}} + 0.33 \text{ PDG}_{\text{cor}} + 0.05 \text{ nHT}_{\text{cor}} + 15.64 \text{ GHL/CS}_{\text{cor}} - \\ 13.03 \text{ PECR}_{\text{cor}} + 18.50 \text{ PEW}_{\text{cor}} - 1.99 \text{ PEH}_{\text{cor}} - 0.26 \text{ PEAS}_{\text{cor}}$$

determines any of 72 cases with  $p < 0.0001$ :

$$L. jensi \times umbratus \quad -3.345 \pm 0.809 [-5.09, -1.88] \quad n = 31$$

$$L. jensi \quad 3.992 \pm 1.121 [1.88, 6.66] \quad n = 41.$$

The distinction of the hybrid from *L. umbratus* by morphometry alone is less clear. A discriminant D(14) with

$$D(14) = -22.85 + 6.47 \text{ CS} - 18.34 \text{ CL/CW}_{\text{cor}} + 36.96 \text{ SL/CS}_{\text{cor}} + 52.29 \text{ Smax/CS}_{\text{cor}} - 3.63 \\ \text{Smax/Smin}_{\text{cor}} + 4.50 \text{ HTmax/CS}_{\text{cor}} - 0.17 \text{ PDF}_{\text{cor}} + 0.02 \text{ PDG}_{\text{cor}} + 0.002 \text{ nHT}_{\text{cor}} + 18.33 \\ \text{GHL/CS}_{\text{cor}} + 46.40 \text{ PECR/CS}_{\text{cor}} + 5.78 \text{ PEW/CS}_{\text{cor}} - 7.06 \text{ PEH/CS}_{\text{cor}} - 1.91 \\ \text{PEAS/CS}_{\text{cor}}$$

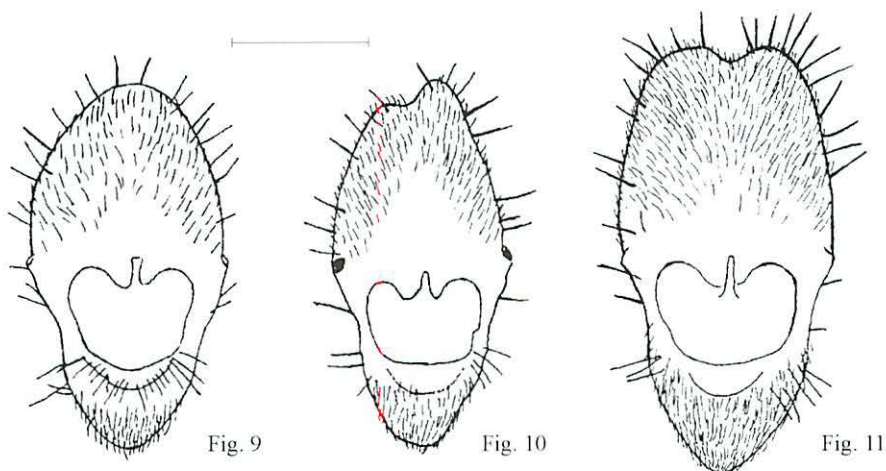
determines 89.1 % of 128 cases with  $p < 0.10$ :

$$L. jensi \times umbratus \quad -1.687 \pm 1.013 [-4.02, -0.21] \quad n = 31$$

$$L. umbratus \quad 1.938 \pm 0.996 [0.21, 5.34] \quad n = 97.$$

However, many of the doubtful cases can be decided by an eye-catching non-metric character – a pronounced scale asymmetry in the hybrid. At least a certain percentage of workers in a hybrid sample usually shows this typical petiole shape (Fig. 10). It seems as if one body half tries to form the tapering petiole scale of *L. jensi* (Fig. 9), while the other side works in the opposite direction towards the emarginated petiole crest of *L. umbratus* (Fig. 11). Numerical-

ly this hybrid asymmetry is reflected by a significantly larger PEAS compared to parent species (Tab. 5). As a consequence, the distinction of *L. jensi* x *umbratus* from *L. umbratus* is credible in the vast majority of cases. The characters of the hybrid *L. jensi* x *umbratus* are compared with those of the parent species in Tab. 6. Among 14 characters tested, the hybrid is significantly different from *L. umbratus* in 64 % and from *L. jensi* in 79 % of characters while it approaches the first in 21 % and the latter in 43 % of characters.



Figs 9 – 11 anterior view of petiole in *L. jensi* (Fig. 9), *L. jensi* x *umbratus* (Fig. 10) and *L. umbratus* (Fig. 11). The scale bar equals 200  $\mu$ m.

#### 4. Discussion

A *Chthonolasius* gyne mated by a heterospecific partner should have the same potency to successfully invade a host colony as a conspecifically mated gyne. Furthermore, as field observations showed, the colonies built up and maintained by hybrid workers had a normal population size and the workers themselves did not show a reduced body size or behavioural abnormalities. If there are production reductions on the colony level, e.g. because of a limited adaptation of hybrid workers to the habitat, these cannot be conspicuous. As a consequence, the number of collected nests and the number of alate gynes randomly collected should reflect in some way heterospecific mating frequencies. However, to estimate the real frequency of heterospecific mating, observed nest and gyne numbers must be calibrated with the expected real abundance ratio (Tab. 6).

According to these data and assuming an overall sex ratio of 1 : 1, absence of multiple mating and equal rate of alate production in each entity, 27 % of *L. jensi* sexuals (derived from nest samples) and 19 % of *L. meridionalis* sexuals (derived from both worker and gyne data) would mate in the region of Central Europe with *L. umbratus*. On the other hand, only 2.2 % of Central European *L. umbratus* sexuals mate with *L. jensi* and only 2.5 % of them with *L. meridionalis*. These figures raise the question why the rare species *L. jensi* and *L. meridionalis* can afford to waste such an enormous amount of genes in heterospecific matings and how they manage to maintain their genomic integrity. According to the data presented in section

3.1, *L. jensi* and *L. meridionalis* have been coexisting in Central Europe with *L. umbratus* for about 1100 years or more than 7000 years respectively. If the hybrids considered here were fertile over several generations and should not show significant fitness reductions, only 10 – 20 years of crossings with an overwhelmingly large *L. umbratus* gene pool would suffice for an almost complete elimination of *L. jensi* and *L. meridionalis* phenotypes. The conclusion is that hybrid gynes of *L. jensi* x *umbratus* and those of *L. meridionalis* x *umbratus* are either not produced or infertile with a strong epigenetic or external selection operating against the hybrid genome.

Complete hybrid infertility is apparently given in *L. jensi* x *umbratus* where no hybrid gynes are produced and, since male production by workers is not known in *Lasius*, males produced by hybrid nests are the hemizygous sons of the non-hybrid mother gyne. The lucky case of a quite easy distinction of *L. jensi* males from those of *L. umbratus* (SEIFERT 1988, 1997) allows conclusions on species identity of the mother gyne. Hybrid nests from Sättelstädt near Eisenach, 1984.09.05, from Reinstädt near Jena, 1993.07.20 and from Bendorf near Koblenz, 1991.07.16 all produced *L. jensi* males. On the other hand, the mother gyne of a hybrid nest kept by Katrin Sommer in the Würzburg laboratory of Bert Hölldobler belonged to *L. umbratus* according to the author's microscopic determination of the living gyne in Mai 1991. This gyne had been collected near Würzburg in the end of July 1990 and had been transferred for colony foundation in an orphaned worker group of *Lasius niger*.

Tab. 6 Putative relative frequencies of nests and sexuals of the parent species *Lasius jensi* (= jens), *L. meridionalis* (= meri), *L. umbratus* (= umbr) and of the hybrids *L. jensi* x *umbratus* (= jeXum) and *L. meridionalis* x *umbratus* (= meXum) in Central Europe. Calibration of data in *L. jensi* x *umbratus* was performed with the same factor as in *L. jensi* and in *L. meridionalis* x *umbratus* with that calculated for *L. meridionalis*.

|                                                                     | jens  | jeXum | meri  | meXum | umbr  |
|---------------------------------------------------------------------|-------|-------|-------|-------|-------|
| assumed real abundance ratio of parent species                      | 6     |       | 10    |       | 100   |
| worker nest samples evaluated                                       | 41    | 31    | 19    | 9     | 97    |
| calibration factor for nest samples                                 | 0.146 | 0.146 | 0.526 | 0.526 | 1.031 |
| calibrated nest sample number                                       | 6.00  | 4.54  | 10.00 | 4.74  | 100.0 |
| gyne individuals evaluated                                          | 89    | 0     | 54    | 25    | 330   |
| calibration factor for gynes                                        | 0.067 | 0.067 | 0.185 | 0.185 | 0.303 |
| calibrated number of gyne-producing nests (assumed sex ratio 1 : 1) | 6.00  | 0     | 10.00 | 4.63  | 100.0 |

Nest site selection in these weakly mobile subterranean ants is largely predetermined by the selective behaviour of the founding gyne and her adaptation to habitat-specific host species. Because habitat selection and major host are strongly different between the parent species *L. umbratus* and *L. jensi*, nest sites of hybrid nests may also give suggestions to the species identity of the mother gyne. According to the Renkonen-Schoener formula (SCHOENER 1974) and using the data of Tab. 1, nest site overlap is 83 % between *L. jensi* and *L. jensi* x *umbratus* but only 58 % between *L. umbratus* and *L. jensi* x *umbratus*. This indicates that *L. jensi* mother gynes should predominate which is in agreement with the data presented above.

Plenty of gynes are apparently produced by hybrid colonies of *L. meridionalis* x *umbratus* and only assumptions are possible on how the integrity of the parental genomes had been saved over more than 7000 years with frequent interspecific hybridisation being a »normal« situation. Unknown is also which sexes are involved in hybridisations because of the unsolved discrimination of *L. meridionalis* and *L. umbratus* males (SEIFERT 1988) and the low number of investigated *L. meridionalis* x *umbratus* nests. Nevertheless, the *L. meridionalis* x *umbratus* case is comparable to that of *Acanthomyops claviger* x *latipes* (UMPHREY & DANZMANN 1998) where also plenty of gynes are produced by hybrid nests. The genetic methods of Umphey and Danzmann allowed to show that only the *A. latipes* queens perform social cleptogamy.

Fascinating is the question how the rare species can compensate for the expected losses they would experience by hybridisations. A gyne that did not meet a conspecific male in a »panspecific« mating flock should prefer to accept a heterospecific male instead of losing the option to reproduce at all. With the help of heterospecific gametes she can then found a productive colony with a vital worker force composed of hybrids and she can send, in the form of numerous sons produced during some 20 years of colony life, 100 % of her own genes into the gene pool. In other words the heterospecific genes are only stolen to use them as a vehicle to propagate the own genes but are excluded from reproduction (SEIFERT 1999). This »social cleptogamy« differs from »individual cleptogamy« discovered in frogs of the genus *Rana* where the exclusion of the heterospecific genome proceeds during meiosis (GÜNTHER 1990).

The most perfect solution of social cleptogamy for monogynous and monoandrous societies is obviously found in *L. jensi* where the useless and expensive production of hybrid gynes is suppressed in favour of increasing the production of sons. Only a mating of an *L. umbratus* male with a *L. jensi* gyne would lead to this optimum solution while the reverse combination is fully destructive from *L. jensi*'s point of view. This may well explain the above-mentioned observation that matings between *L. umbratus* males and *L. jensi* gynes seem to be the typical case. In other words, selection should operate in the direction that *L. jensi* gynes should readily accept *L. umbratus* males while males should avoid matings with heterospecific partners.

A less perfect solution of cleptogamy is found in hybridisations of the myrmicine ant *Temnothorax albipennis* (Curtis, 1854) with *T. nigriceps* Mayr, 1855, *T. tuberum* (Fabricius, 1775) and *T. unifasciatus* (Latreille, 1798). The haploid number of chromosomes is  $n = 8$  in *T. albipennis* but  $n = 9$  in the latter three species (FISCHER 1987). For the region of Central Europe, it is estimated that 28 % of the *T. albipennis* sexuals, will mate with either *T. tuberum*, *T. nigriceps* or *T. unifasciatus* (SEIFERT 1999). The resulting aneuploidy of F1 gynes ( $2n = 17$ ) with inability to perform a balanced meiosis is thought to be the basic reason saving the

genomic integrity of involved parent species. It seems quite probable that genomic incompatibilities also save the genetic integrity of the parent species of the hybrid *Lasius meridionalis* x *umbratus*.

WING (1968) reported on hybridisations in the Nearctic genus *Acanthomyops* that is closely related and in overall biology most similar to the subgenus *Chthonolasius*. Wing recognised 15 species, five of which were involved in five hybrid combinations. He considered the phenomenon of hybridisation to be very rare within the genus except for the case *Acanthomyops latipes* x *claviger*. He identified 183 samples of *A. claviger*, 146 of *A. latipes* and 20 of *A. latipes* x *claviger*. His sample numbers will probably reflect real abundance ratios because his mode of sample selection is not suspected to be biased. For the same assumptions as presented above, about 6 % of the *A. latipes* and 5 % of the *A. claviger* alates should have mated with a heterospecific partner. However, Wing most probably underestimated overall hybridisation frequencies in *Acanthomyops* because he only investigated a single worker per sample and because the system of morphometric identification was too imprecise. According to Wing's detailed description of methods and measuring errors, he used much too low magnifications and an inappropriate ocular micrometer leading to about 500 % of the measuring error achieved with the system used in this study. Furthermore he did not use any form of a multiple discriminant analysis to evaluate his data. As a consequence, he had no chance to detect higher numbers of hybrids in his material. The extreme regional hybrid frequency of 50 % in *Acanthomyops claviger* x *latipes* reported for SW Ontario (UMPHREY & DANZMANN, 1998) will probably not hold for larger geographical areas but this well-studied example shows the importance of social cleptogamy in *Acanthomyops*.

Summing up, different forms of social hybridogenesis are apparently more widely distributed in ants and have been found in monogynous-monoandrous, monogynous-polyandrous and polygynous systems. Unidirectional, asymmetric hybridogenesis, termed here social cleptogamy because one partner is cheated, is clearly more abundant than symmetric social hybridogenesis. The less effective forms of social hybridogenesis still waste energy in producing plenty of hybrid gynes while the most evolved forms of social hybridogenesis in *Pogonomyrmex barbarus*/P. *rugosus*, *Solenopsis geminata*/S. *xyloni* and *Lasius jensi*/L. *umbratus* have in common that no or very few hybrid gynes are produced. In preferentially monogynous-monoandrous systems such as *Lasius jensi*/L. *umbratus*, production of pure species gynes is not possible. Monogynous-polyandrous systems as in *Pogonomyrmex barbarus*/P. *rugosus* (HELMS-CAHAN et al. 2002, HELMS-CAHAN & KELLER 2003) or polygynous systems as in *Solenopsis geminata*/S. *xyloni* (HELMS-CAHAN & VINSON 2003) have the option to produce pure-species gynes in addition to males when the multiple fathers of the colonies include both parent species. Productive efficiency of the latter two systems is increased by inhibition of pure-species female larvae to develop into workers. Within hybrid zones but not outside, this inhibition seems to be so strong that haplometrotic foundations of singly and homospecifically mated P. *rugosus*, P. *barbarus* and S. *xyloni* gynes are apparently no longer successful.

In conclusion a short comment on fluctuating asymmetries (FA) is given. Both hybrids *Lasius jensi* x *umbratus* and L. *meridionalis* x *umbratus* show significantly increased FA of petiole scale compared to the parent species as shown by their significantly larger PEAS data (Tab. 5). Furthermore, 45 hybrid workers of L. *jensi* x *umbratus* showed increased FA in scape length compared to 62 workers of the parent species –  $0.508 \pm 0.386$  [0, 1.38] % versus  $0.319 \pm 0.309$  [0, 1.22] % (SEIFERT, unpublished study). Thus, morphological asymmetries might

well be used as an accessory character to identify hybrids as done in this study. However, the indicative value of FA will be limited because poor environmental quality, different forms of stress during ontogenetic development or strong inbreeding may lead to increased asymmetries also in non-hybrids (MARKOV 1995, HOELZEL et al. 2002).

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