Mimumesa littoralis (Bondroit), *M. oresterus* (van Lith), and *M. unicolor* (Vander Linden): notes on similarity, synonymy, and identification (Hymenoptera: Crabronidae)

EDUARDAS BUDRYS

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Mimumesa oresterus (van Lith) was found to be less different from regional populations of *M. unicolor* (Vander Linden) than are regional populations of the closely related species *M. littoralis* (Bondroit) among themselves, and *M. oresterus* is therefore synonymized with *M. unicolor*. The East Asiatic population of *M. littoralis* is comparatively dissimilar to conspecific European and Central Asiatic populations morphometrically and in some details of male genitalia, and after additional studies it might be considered as a subspecies. An identification key with new structural and morphometric characters to distinguish *M. littoralis* and *M. unicolor* is presented.

E. Budrys, Institute of Ecology, Akademijos 2, 2600 Vilnius, Lithuania (ebudrys@ekoi.lt).

Introduction

The Old World faunas of the genus *Mimumesa* have been reviewed by van Lith (1949, 1973, 1974), Tsuneki (1959, 1984), Budrys (1990, 1991), Else & Felton (1994). The taxonomic status of the two Palearctic subboreal-temperate species, which have the widest distribution, *M. littoralis* (Bondroit, 1934) and *M. unicolor* (Vander Linden, 1829), has been stated as 'not completely clear' (Schmidt et al. 1995).

Specimens of *M. littoralis* from Europe and Central Asia differ from those of *M. unicolor* by usually having a smoother and shinier vertex, a less developed or absent longitudinal rugosity of the mesopleuron, weaker defined male tyloidea (Else & Felton 1994), a pale brownish or brownish-yellow ventral surface of the flagellum in both sexes, and a thicker, rounded ventral subapical lobe of the penial valve (Budrys 1990, 1991). However, limits of variability of these characters seem to overlap in the two species, especially in males. A third species close to *M. littoralis* and *M. unicolor*, *M. oresterus* (van Lith, 1976), has also been described from Pakistan. The description of *M. oresterus* does not contain clear diagnostic characters to differentiate the species from *M. littoralis* or *M. unicolor*, except for a less dense punctuation of the male vertex in comparison with *M. unicolor*.

The objectives of this research were (1) to discover new structural and morphometric characters to differentiate *M. littoralis* and *M. unicolor*, and (2) to clarify the status of *M. oresterus*.

Material and methods

A total of 405 specimens were studied as follows: *M. littoralis* (260), *M. oresterus* (4), and *M. unicolor* (141). The material come from various parts of the Palearctic region (Fig. 1) and belongs to the following institutions and collections:

Biology and Pedology Institute, Vladivostok, Russia (BPIV);
British Museum (Natural History), London, UK (BMNH);
Institut Royal Sciences Naturelles de Belgique, Brussels, Belgium (IRSNB);
Institute of Ecology, Vilnius, Lithuania (IEV);
National Museum of Natural History, Washington, USA (USNM);

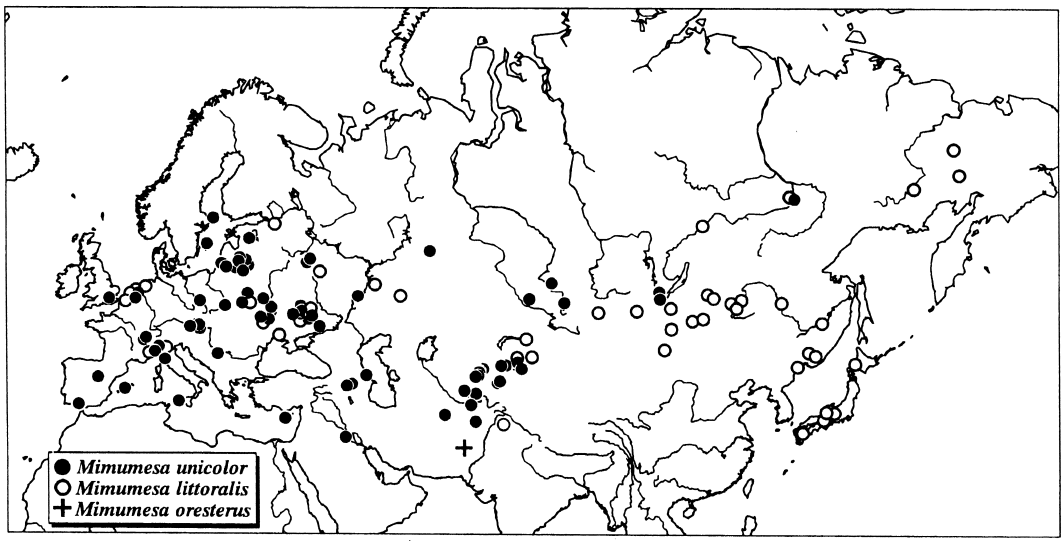


Figure 1. Distribution of *Mimumesa littoralis*, *M. unicolor*, and *M. oresterus*.

Oxford University Museum, Oxford, UK (OUM);
Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands (RMNH);
T. Ivanauskas Zoological Museum, Kaunas, Lithuania;
Zoological Institute, Kiev, Ukraine;
Zoological Institute, Sanct Petersburg, Russia (ZISP);
Zoological Museum of Moscow University, Moscow, Russia (ZMMU);
Zoologie generale & appliquee, Faculte des Sciences Agronomiques, Gembloux, Belgium;
Zoologisk Museum, Copenhagen, Denmark;
collections of Dr. S. F. Gayubo (Salamanca University, Spain) and Dr. G. Pagliano (Turin University, Italy).

A subsample of 44 females and 41 males of *Mimumesa littoralis*, *M. oresterus*, and *M. unicolor* were measured for the morphometric similarity analysis. In order to establish whether differences between the species exceed differences between regional populations of the species, the measured specimens were grouped into 7 sets by the region of their capture locality:

Mimumesa littoralis

Europe. – Belarus: Pinsk env., 1 ♀ 2.viii.1979, A. S. Lelej (BPIV); Belgium: Ostende, 1 ♂ lectotype, 5.viii.1933, 1 ♀ paralectotype, 1.ix.1933 (IRSNB); Italy: Piemonte, Racconigi, 1 ♀ viii.1985, Curletti (coll. Pagliano); The Netherlands: Drenthe, Emmen, 1 ♂ 24.vii.1970, 1 ♀ 13.viii.1970, 1 ♀ 10.vi.1971, 1 ♂ 21.vii.1971, 1 ♂ 16.vi.1972, 1 ♀ 20.vi.1972, K. Vegter (RMNH); Russia: Orenburg reg., Spasskoye env., 1 ♀, 14.vi.1930, Rysakov; Leningrad reg., Shapki, 1 ♂ 18.vii.1972, D. R. Kasparyan (both ZISP); Saratov reg., Voskresensk, 2 ♂ 27.vi.1961, G. Viktorov (ZMMU).

Central Asia. – Kazakhstan: East-Kazakhstan reg., 30 km E Altay, 1 ♀ 5.viii.1979, V. L. Kazenas; Taldy-Kurgan reg., 25 km N Lepsy, 1 ♀ 29.vi-2.vii.1978, I. M. Kerzhner (both ZISP); India: Kashmir, 2 ♂ paralectotypes of *Psen kashmirensis* Nurse (= *Psenulus kashmirensis*), v.1901; Pakistan: Quetta, 1 ♂ viii.1903, all C. G. Nurse (BMNH).

East Asia. – China: Manchuria, lake Dalaj-nor, 1 ♀ 10.viii.1909, Sergeev, Mongolia: the Bomyn river, 1 ♂ vi.1895, R. Kozlov; Tov aym., Songino, 1 ♂ 12.vi.1980, I. M. Kerzhner; Hentiy aym., 8 km N Binder, 1 ♀ 5.vii.1976; Uvs aym., 50 km ESE Ulaangom, 1 ♂ 7.viii.1970, M. A. Kozlov; Russia: Chita reg., Adrianovka, 1 ♂ 2.viii.1975, 7 km W Priargunsk, 1 ♂ 25.vii.1975, D. R. Kasparyan (all ZISP); Aleksandrovskij Zavod, 1 ♀ 17.vii.1977, A. S. Lelej (BPIV); Klyuchi, 1 ♀ 1.viii.1947, Zhelokhovtsev; Olochi env., 1 ♀ 16.viii.1984, 1 ♀ 18.viii.1984, D. Shcherbakov (all ZMMU); Buryatiya, Kyakhta, 1 ♀ 28.vii.1977; Amursk reg., Natalyino, 1 ♀, 1 ♂ 13.vii.1975; Khabarovsk terr., Khabarovsk, 1 ♀ 5.viii.1982; Primorsk terr., Novomikhailovka, 1 ♂ 26.vii.1986; 7 km E Khasan, 1 ♀ 21.ix.1974, all A. S. Lelej (BPIV); Japan: Hossaka, 1 ♀ 17.ix.1955; Simizuyama, 1 ♀ 20.ix.1970, both K. Tsuneki (USNM).

Mimumesa unicolor

Europe. – Armenia: Parakar, 1 ♂ 11.ix.1962, Richter (ZISP); Austria: Burgenland, 5 km S Frauenkirchen, 1 ♀ 5.viii.1973, Ph. Pronk (RMNH); Byelorussia: Pinsk env., 1 ♀ 2.viii.1979, A. S. Lelej (BPIV); Cyprus: 1 ♀, G. A. Mavromoustakis (RMNH); Italy:

Piemonte, S. Benedetto Belbo, 1 ♀ 12.viii.1985, G. Pagliano; Stupinigi, 1 ♂ 21.viii.1950, C. Casolari (both coll. Pagliano); Sicilia, Fiume Belice env., 1 ♂ 8.vi.1974, Ph. Pronk (RMNH); Lithuania: Ignalina, Antagave, 1 ♂ 1.vi.1993, V. Jonaitis; Kaunas, Pavejuonis reserve, 1 ♀ 16.viii.1990; Panevezys, Piniava forestry, 1 ♂ 26.vi.1972; Pasvalys, Naradava arboretum, 3 ♂ 12.vi.1971; Silute, Piktupenai, 1 ♀ 20.vii.1968, all A. Jakimavicius; Vilnius, Salote, 1 ♂ 4.vi.1977, E. Budrys; Russia: Belgorod distr., Borisovka, 4 ♂ 1.vii.1981, E. Budrys (all IEV); Spain: Soria, Velilla de Medinaceli, 1 ♀ 15.vi.1990, J. Garcia (coll. Gayubo); Mayorca, 2 ♂ syntypes of *M. palliditarsis*, 9.vii.1901, E. B. Poulton, A. H. Hamm, W. Holland (OUM).

Central Asia. – Kazakhstan: 10 km SSE Kaskasu, 1 ♀ 10.vii.1983; 30 km S Lenger, 1 ♀ 17.vii.1981; 15 km SE Lenger, 1 ♂ 9.vii.1983; Sosnovka env., 1 ♀ 6.viii.1983; Alma-Ata reg., Talgar env., 1 ♂ 23.viii.1983; 33 km NE Tarbagatay, 1 ♀ 8.vii.1986; Uzbekistan: 20 km N Parkent, 4 ♀ 9.vi.1982, all V. L. Kazenas (ZISP); Khodzha-Kurgan valley, 1 ♂ 15.vii.1985, E. Budrys (IEV); Kirgizia: Belovodskoe, 1 ♀ 15.viii.1931, Zimin (ZISP); 20 km ESE Karakuldzha, 1 ♀, 1 ♂ 16.viii.1985, E. Budrys (IEV); Tadzhikistan: Dushanbe, 1 ♂ 5.ix.1969; Yangiabad, 1 ♀ 22.v.1978, both Nazarova (ZISP).

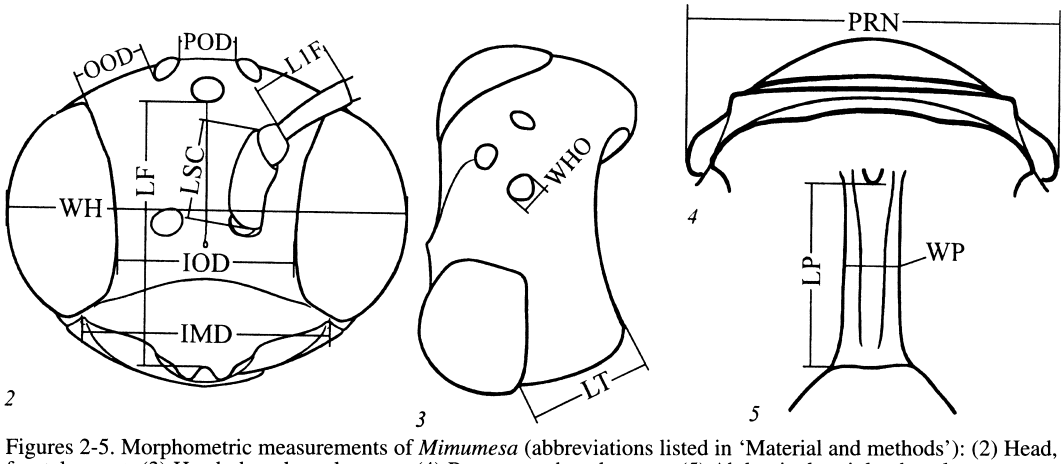
East Asia. – Russia: Irkutsk terr., Irkutsk, 1 ♀, 1 ♂ (no dates), Jakovlev; Padun', 1 ♀ 1867, Chekanovskij; Yakut-Sakha: Yakutsk, 1 ♀ 22-23.vii.1927; 1 ♂ 24.vii-1.viii.1927, both Moskvin (all ZISP).

Mimumesa oresterus

Oriental Region. – Pakistan: Quetta, all C. G. Nurse leg.: 1 ♀ (BMNH), 1 ♀ (RMNH) viii.1903, and 1 ♂ (BMNH) vi.1902 (holotype and 2 paratypes of *Psen* (*Mimumesa*) *oresterus* Lith); 1 ♂ viii.1903 (BMNH), aberrant specimen with very short petiole, measurements of which were not used in morphometric analyses.

The selection of an informative set of morphometric measurements for *Mimumesa* was made using the same principles as in the earlier study of the genus *Diodontus* (Budrys 1996); 14 measurements were found useful:

IMD – inter-mandibular distance (distance between outer margins of small swellings of genae just above fore mandibular condyles, frontal aspect; used for females only) (Fig. 2).
IOD – inter-ocular distance (shortest distance between inner margins of eyes, frontal aspect) (Fig. 2).
LF – length of face (distance between anterior margin of mid ocellus and mid point of apical margin of clypeus, frontal aspect) (Fig. 2).
LP – length of petiole (distance between hind margin of visible part of attachment area of dorsal petiolar apodeme and anterior margin of first abdominal tergum, dorsal aspect) (Fig. 5).
LSC – length of scape (maximum visible length of scape, usually frontal aspect) (Fig. 2).
LT – length of temple (longest line between hind margin of eye and rectangular to it, and occipital carina, posterolateral aspect; used for females only) (Fig. 3).
L1F – length of the first flagellomere (maximum visible length of first flagellomere, usually measured dorsally; used for females only) (Fig. 2).
OOD – oculo-ocellar distance (shortest distance between outer margin of hind ocellus and margin of eye) (Fig. 2).
POD – post-ocellar distance (shortest distance between inner margins of hind ocelli) (Fig. 2).
PRN – width of pronotum (distance between tips of pronotal lobes, dorsal aspect) (Fig. 4).
WH – width of head (frontal aspect) (Fig. 2).
WHO – width of hind ocellus (maximum visible diameter of hind ocellus) (Fig. 3).
WP – width of petiole in the middle (dorsal aspect) (Fig. 5).



Figures 2-5. Morphometric measurements of *Mimumesa* (abbreviations listed in 'Material and methods'): (2) Head, frontal aspect. (3) Head, dorsolateral aspect. (4) Pronotum, dorsal aspect. (5) Abdominal petiole, dorsal aspect.

3FL – length of three flagellomeres (maximum visible combined length of first three flagellomeres, excluding pedicel, usually in dorsal aspect; used for males only).

Raw morphometric measurements of *M. littoralis*, *M. oresterus*, and *M. unicolor* were used for the discriminant and canonical analysis. Standardized measurements were used for the morphometric similarity (cluster) analysis. The standardisation was performed using the formula:

$$\frac{X_i}{\overline{X}} \Big/ \frac{WH_i}{\overline{WH}}$$

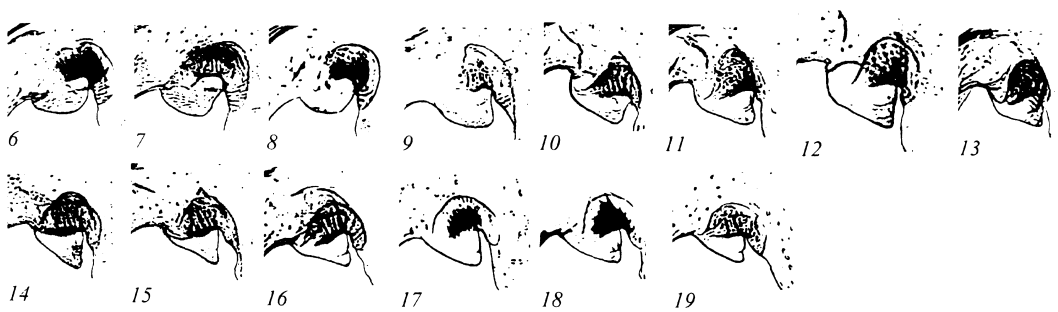
where X_i = an individual measurement, $\overline{X}$ = the overall average of the measurement, WH_i = the width of the head of the specimen (reflecting an individual body size), and $\overline{WH}$ = the overall average of the width of the head. By this means the influence of the absolute size of a particular measurement and an individual body size were eliminated from the analysis.

Examination of the wasps and morphometric measurements were made using an MBS-10 binocular microscope with an ocular micrometer, mostly at a magnification of 56x. Morphometric measurements were made with the line between the two limiting points of the measured structure forming an angle of 90° with the optical axis of the microscope. Part of the drawings of genitalia (Fig. 6-19) were made using Olympus BX40 microscope and the program MicroImage 3.0.01 for video-digital capture of images. Discriminant, canonical and cluster analyses were made using the program Statsoft Statistica for Windows, release 4.5. The faunal and morphometric data were processed using the database managing system Borland Paradox 4.5 for DOS; relational structure and tools of the database was detailed in Budrys (1999). The distribution map was prepared using the mapping program Carto Fauna-Flora, version 1.2, by Yvan Barbier & Pierre Rasmont (Université de Mons-Hainaut, Mons, Belgium).

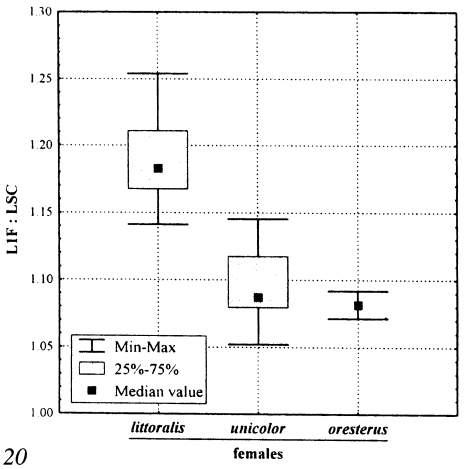
Results

Mimumesa littoralis and *M. unicolor* were preliminary separated using the most stable morphological characters: relative length of the first flagellomere of females, expressed in the morphometric ratio L1F : LSC (Fig. 20), and the form of the ventral lobe of the penial valve in males (Fig. 6-18). The penial valve has a thick, semielliptically or nearly trapezoidally widened base and a rounded apex in *M. littoralis* (Fig. 6-9), but it is not widened basally and has an acute apex in *M. unicolor* (Fig. 14-18). Other morphological characters, namely the structure of the tyloidea, the dorsal apodeme of the 7th sternite (Fig. 35, 38), as well as the form and sclerotization of the dorsal edge of the gonostylus (Fig. 37, 40) were used as subsidiary diagnostic features. These were found to be less reliable than the form of the ventral lobe of the penial valve because of greater variation.

Specimens of *M. littoralis* from the Far East of Russia, Mongolia, and Japan often have a trans-



Figures 6-19. Ventral lobe of the male penial valve of *Mimumesa littoralis* (6-13), *M. unicolor* (14-18), and *M. oresterus* (19). Localities and dates of capture of specimens: (6) Shapki, 18.vii.1972. (7) Voskresensk, 27.vi.1961. (8) The Bomyn river, vi.1895. (9) Kashmir, v.1901. (10) 50 km ESE Ulaan-gom, 7.viii.1970. (11) 7 km W Priargunsk, 25.vii.1975. (12) Adrianovka, 2.viii.1975. (13) Novomikhailovka, 26.vii.1986. (14) Salote, 4.vi.1977. (15) Borisovka, 1.vii.1981. (16) 15 km SE Lenger, 9.vii.1983. (17) Irkutsk (no date). (18) Yakutsk, 24.vii.1927. (19) Quetta, viii.1903.



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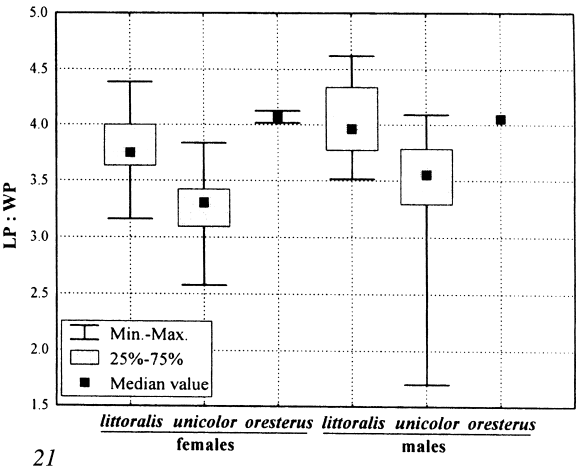

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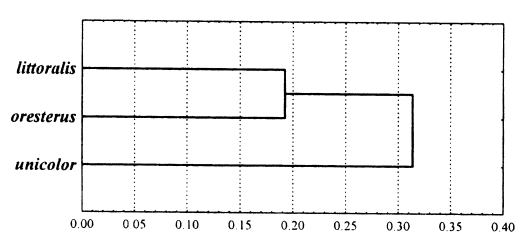
Figures 20-21. Morphometric ratios L1F : LSC and LP : WP of *Mimumesa littoralis, M. oresterus*, and *M. unicolor*. Abbreviations of measurements: see 'Material and methods'.

versely rugose vertex and a rather dark flagellum, similar to *M. unicolor*. The structure of their penial valves seems to be intermediate between other *M. littoralis* and *M. unicolor*, having the ventral subapical lobe with a rather thick base but a more or less acute apex (Fig. 10-13).

Mimumesa oresterus was found to be very close to *M. unicolor*. Females of *M. oresterus* have a short first flagellomere (L1F : LSC < 1.15), similar to *M. unicolor* (Fig. 20); males have an acute, not bulged basally ventral subapical lobe of the penial valve (Fig. 19), which is very similar to the structure of Central Asiatic *unicolor* (Fig. 16), but clearly different from that of the Central Asiatic *M. littoralis* (Fig. 8-9). The only morphological character distinguishing *M. oresterus* from *M. unicolor* I could find was a comparatively long and slender (4-4.2 times as long as wide) petiole in female (2.5-3.8 times as long as wide in *M. unicolor*, 3.2-4.4 times as long as wide in *M. littoralis*). However, observed variability in the length/width ratio of the petiole (LP : WP) in male *M. unicolor* is 1.7-4.1 (fig. 21), so that I do not regard this character as a reliable one for females. Nevertheless, the morphometric similarity analysis (Euclidean distances, complete linkage method[1])



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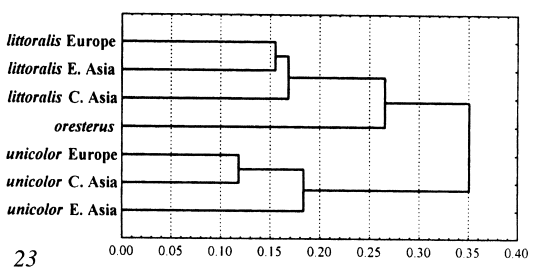

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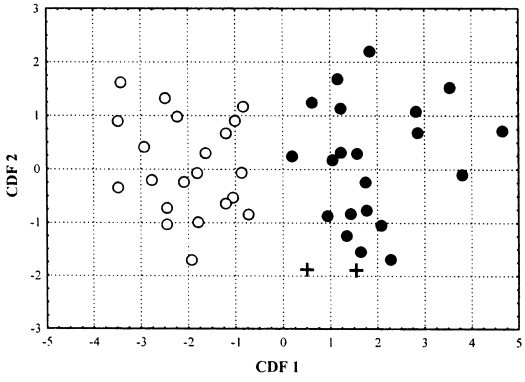
Figures 22-23. Tree diagrams of general morphometric similarity (complete linkage, Euclidean distances) of *Mimumesa littoralis, M. oresterus* and *M. unicolor* (22) and their regional populations (23), using averages of 12 standardised measurements of females and 10 standardised measurements of males combined (all but WH, which was used for the standardisation). List of the measurements: see 'Material and methods'.

[1] Complete linkage method was used as corresponding with the usual sequence of study in taxonomy: starting from general differences, then going to details. Other linkage methods (unweighted pair group average and single linkage) were also tried and mostly lead to similar results.



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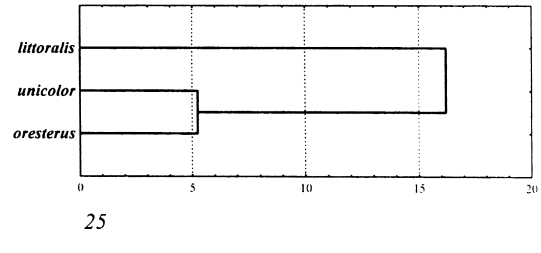

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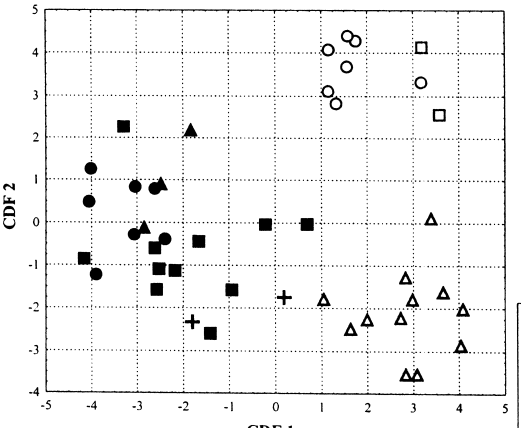
Figures 24-25. Canonical discriminant function (CDF) analysis of females of *Mimumesa littoralis, M. oresterus* and *M. unicolor*, measurements with significant influence on the discrimination (LT, LSC, L1F) in the model: (24) Individual CDF values (CDF coefficients in Tab. 1). (25) Tree diagram of similarity: complete linkage, squared Mahalanobis distances (Tab. 2, upper left part) between centroids of groups of individual CDF values.

using averages of all the standardized measurements of both the sexes combined showed that generally *M. oresterus* was closer to *M. littoralis* than to *M. unicolor*. The same result was obtained comparing the whole species (Fig. 22) and regional populations of the species (Fig. 23). Twelve measurements of females and 10 measurements of males were used, listed in 'Material and methods', except for the width of the head (WH), which was used for the standardization as a measure of body size.

In order to assess the value of each morphometric character in distinguishing the species, the discriminant analysis of raw measurements of females and males (separately) was applied. As a grouping variable, the 3 species, *M. littoralis*, *M. oresterus*, and *M. unicolor*, and their 7 regional populations (measured specimens listed in



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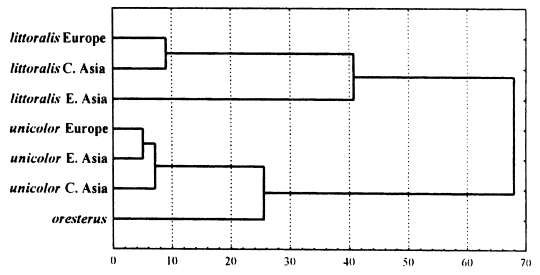

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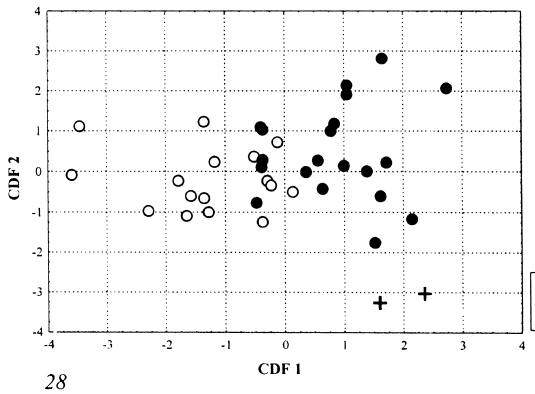
Figures 26-27. Canonical discriminant function (CDF) analysis of females from the regional populations of *Mimumesa littoralis, M. oresterus* and *M. unicolor*, measurements with significant influence on the discrimination (IMD, LF, POD, OOD, LSC, L1F, PRN, LP, WP) in the model: (26) Individual CDF values (CDF coefficients in Tab. 1). (27) Tree diagram of morphometric similarity: complete linkage, squared Mahalanobis distances (Tab. 3, upper left part) between centroids of groups of individual CDF values.



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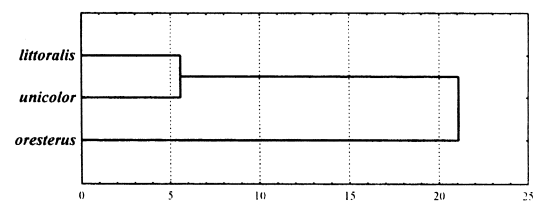

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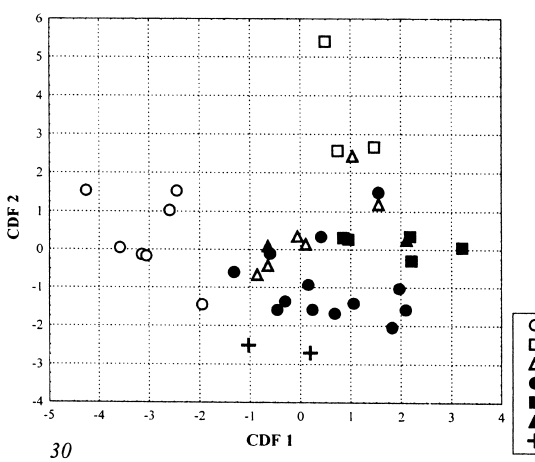
Figures 28-29. Canonical discriminant function (CDF) analysis of males of *Mimumesa littoralis, M. oresterus* and *M. unicolor*, measurements with significant influence on the discrimination (WH, LF, OOD, PRN, LP, WP) in the model: (28) Individual CDF values (CDF coefficients in Tab. 4). (29) Tree diagram of similarity: complete linkage, squared Mahalanobis distances (Tab. 5, upper left part) between centroids of groups of individual CDF values.

'Material and methods') were used. The measurements that had influence on the discrimination, which was statistically insignificant at the available number of measured specimens (their *p*-level, related to the corresponding *F to remove*, exceeded 0.05), were excluded from the model using the backward stepwise discriminant analysis. Raw coefficients of the calculated canonical discriminant functions (CDF) and standardised coefficients, showing relative 'weight' of a particular measurement in discrimination between groups, are presented in Tab. 1 and 4. The squared Mahalanobis distances between the centroids of groups of the individual CDF values, showing the calculated differences between the groups, are presented in Tab. 2, 5 (species) and 3, 6 (regional populations). The same tables contain the *p*-levels related to respective *F*-values, giving the probability



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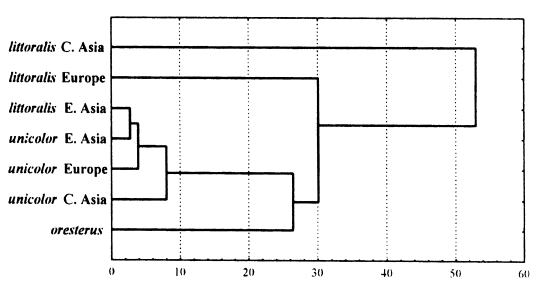

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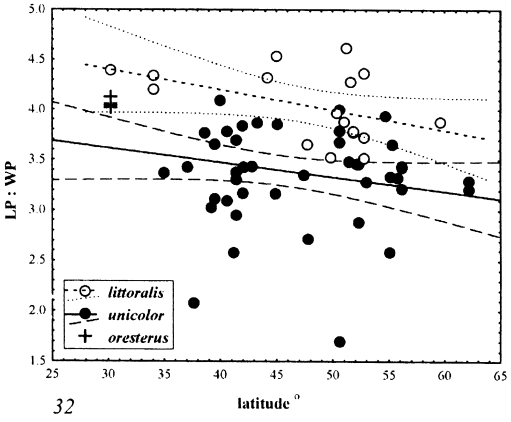
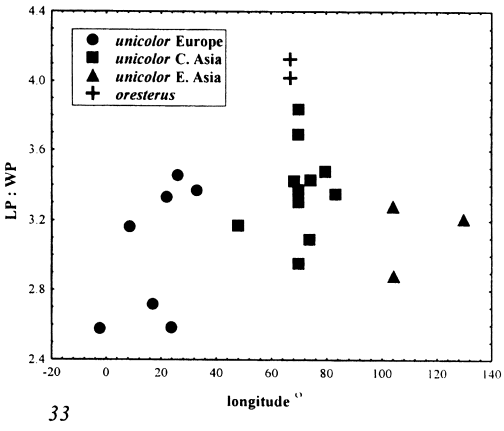
Figures 30-31. Canonical discriminant function (CDF) analysis of males from the regional populations of *Mimumesa littoralis, M. oresterus* and *M. unicolor*, measurements with significant influence on the discrimination (WH, LF, OOD, PRN, LP, WP) in the model: (30) Individual CDF values (CDF coefficients in Tab. 4). (31) Tree diagram of morphometric similarity: complete linkage, squared Mahalanobis distances (Tab. 6, upper left part) between centroids of groups of individual CDF values.





Figures 32-33. Individual relative length of petiole, expressed by ratio LP : WP, of *Mimumesa littoralis, M. oresterus* and *M. unicolor*: (32) Dependence from the latitude (lines - linear regression fit and 0.95 confidence), both sexes. (33) Dependence from the longitude, females only.

that the corresponding pair of the analysed groups is identical. The specimen values of the first two CDFs, which provided the greatest overall discrimination between the groups, were used to plot scatterplots, which show the variability and overlapping between the species (Fig. 24, 28) and their regional populations (Fig. 26, 30). The complete linkage method and the squared Mahalanobis distances between the CDF value group centroids were used to construct tree diagrams, quantitatively showing the calculated morphometric differences between the species (Fig. 25, 29) and their regional populations (Fig. 27, 31).

Discussion and taxonomic conclusions

In all the analyses of morphometric measurements, the first canonical discriminant function (CDF 1) showing the highest discriminating significance separated *M. littoralis* from *M. unicolor* and *M. oresterus* (Fig. 24, 26, 28). An exception was the analysis of males of regional populations

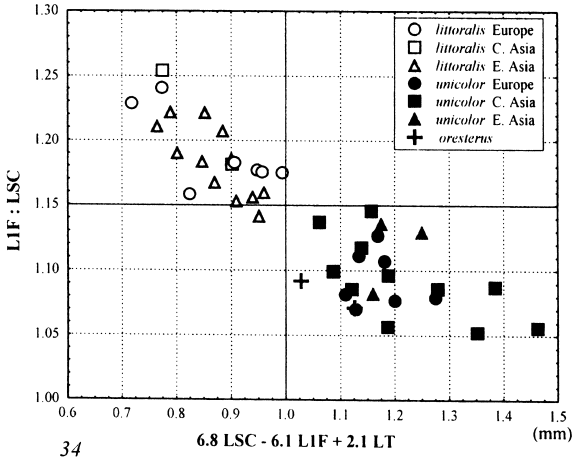


Figure 34. Diagram for separation of females of *Mimumesa littoralis* and *M. unicolor* by discriminant equation and relative length of the first flagellomere, expressed by morphometric ratio L1F : LSC.

Table 1. Raw and standardized coefficients of the canonical discriminant functions (CDF) separating measurements (mm) of females of *Mimumesa littoralis*, *M. oresterus,* and *M. unicolor* (24) and of their regional populations ((26). Only measurements with significant influence on the discrimination (*F to remove* of the measurement has $p < 0.05$) in the model. See explanation of the abbreviations of the measurements in 'Material and methods'.

FEMALES	CDF coefficients for 3 species				CDF coefficients for 7 regional populations			
	1 CDF		2 CDF		1 CDF		2 CDF	
Morphometric measurement	raw coeff.	standard. coeff.	raw coeff.	standard. coeff.	raw coeff.	standard. coeff.	raw coeff.	standard. coeff.
IMD					-39.64	-3.41	46.08	3.96
LF					18.14	1.29	-48.73	-3.46
POD					5.43	0.13	52.27	1.20
OOD					-36.66	-0.78	-55.64	-1.18
LT	20.64	0.74	35.77	1.29				
LSC	89.73	2.69	-48.21	-1.45	-95.88	-2.92	6.97	0.21
L1F	-85.69	-3.06	24.70	0.88	86.45	3.11	-8.87	-0.32
PRN					25.34	3.53	-21.94	-3.05
LP					1.30	0.08	12.92	0.83
WP					-54.45	-1.33	93.02	2.27
Constant	-7.65		-10.58		4.32		17.00	
Cumulative proportion of variance	0.955		1.000		0.531		0.891	

where CDF 1 separated the males of European *M. littoralis* from all the males of *M. unicolor*, *M. oresterus,* and Asiatic *M. littoralis* together (Fig. 30).

Ecosystem conditions and restrictions play a basic role in the process of speciation (for recent review and references see Orr & Smith 1998), including the evolutionary divergence of species morphotype (the morphological aspect of the species life form, forming the latter together with the ecological counterpart, a species niche). Wasp female is the long-lived sex, what realizes a species niche in an ecosystem, therefore I suspect the body proportions of a female to be more important than body proportions of the short-lived males (except when the proportions reflect some secondary sexual features important in mating behaviour). Considering the above, my taxonomic conclusions are based first and foremost on the results of the analysis of females (Fig. 24-27, Tab. 1-3).

Table 2. Squared Mahalanobis distances between the centroids of groups of the individual canonical discriminant function values (upper left part of table) and *p*-levels related to respective *F*-values (lower right part of table) of females of *Mimumesa littoralis*, *M. oresterus,* and *M. unicolor*. Only measurements with significant influence on the discrimination (*F to remove* of the measurement has $p < 0.05$: LT, LSC, L1F) in the model. Cluster based on the distances in Fig. 25.

FEMALES	N	*oresterus*	*unicolor*	*littoralis*
littoralis	21	13.74	16.20	
unicolor	21	5.24		0.000
oresterus	2		0.209	0.012

According to the Mahalanobis distance between the group centroids of individual CDF values, the females of *M. oresterus* were considerably closer to *M. unicolor* than to *M. littoralis*; and the difference of *M. oresterus* from *M. unicolor* was clearly less than that between the East Asiatic and other regional populations of *M. littoralis* (Tab. 2, 3; Fig. 25, 27). In the discriminant analysis of females of regional populations, the individual values of the first two CDFs (the only ones having discrimination significance $p < 0.05$) of *M. oresterus* were particularly close to the Central Asiatic *M. unicolor* (Fig. 26). The *p*-level (probability of null-hypothesis - no difference between the groups) related to the respective *F*-value was always greater than 0.05 comparing *M. oresterus* with *M. unicolor*, the difference between them being statistically insignificant (Tab. 2-3, lower right part).

I could not find reliable morphometric differences between the males of *M. littoralis* and *M.*

Table 3. Squared Mahalanobis distances between the centroids of groups of the individual canonical discriminant function values (upper left part of table) and *p*-levels related to respective *F*-values (lower right part of table) of females of *Mimumesa littoralis*, *M. oresterus*, and *M. unicolor* from the regional populations from Europe, Central Asia, and East Asia. Only measurements with significant influence on the discrimination (*F to remove* of the measurement has $p < 0.05$: IMD, LF, POD, OOD, LSC, L1F, PRN, LP, WP) in the model. Cluster based on the distances in Fig. 27.

FEMALES: regional population	N	*oresterus*	*unicolor*			*littoralis*		
			E. Asia	C. Asia	Europe	E. Asia	C. Asia	Europe
littoralis Europe	7	53.17	32.38	40.20	45.56	41.89	9.94	
littoralis C. Asia	2	67.59	50.89	55.16	73.96	40.64		0.668
littoralis E. Asia	12	26.47	45.91	31.97	52.17		0.007	0.000
unicolor Europe	7	26.34	4.71	9.83		0.000	0.000	0.000
unicolor C. Asia	11	12.43	9.30		0.008	0.000	0.001	0.000
unicolor E. Asia	3	29.04		0.254	0.775	0.000	0.012	0.001
oresterus	2		0.136	0.473	0.080	0.060	0.013	0.002

unicolor using discriminant analysis (Fig. 28, 30). The measured males of *M. oresterus* morphometrically were rather different from both *M. littoralis* and *M. unicolor*, but generally closer to *M. unicolor* than to *M. littoralis*: even with a very limited number of specimens measured (N=2), the *p*-level related to the respective *F*-value was less than 0.05 comparing *M. oresterus* with any of the regional populations of *M. littoralis* (difference was always significant), but not with *M. unicolor* (difference was mostly insignificant) (Tab. 5-6, lower right part).

The relative length of the petiole, expressed as the morphometric ratio LP : WP, to separate *M. oresterus* and *M. unicolor* (Fig. 21) was assessed over the range of the species. The petiole was found to be generally longer in southern populations than in northern ones in both *M. unicolor* and *M. littoralis* (Fig. 32). Regarding *M. unicolor*, it was also found that the Central Asiatic females had the longest petiole (Fig. 33). These differences in petiole length are obscured by a wide range of individual variation and seem to have a clinal nature.

Based on the above results as well as identical male genitalia and absence of other reliable morphological differences, I consider *M. oresterus* to be just one population of *M. unicolor* on the

Table 4. Raw and standardized coefficients of the canonical discriminant functions (CDF), separating measurements (mm) of males of *Mimumesa littoralis*, *M. oresterus,* and *M. unicolor* (Fig. 28) and of their regional populations (Fig. 30). Only measurements with significant influence on the discrimination (*F to remove* of the measurement has $p <$ 0.05) in the model. See explanation of the abbreviations of measurements in 'Material and methods'.

MALES	CDF coefficients for 3 species				CDF coefficients for 7 regional populations			
	1 CDF		2 CDF		1 CDF		2 CDF	
Morphometric measurement	raw coeff.	standard. d. coeff.	raw coeff.	standar d. coeff.	raw coeff.	standar d. coeff.	raw coeff.	standar d. coeff.
WH	24.23	3.26	3.18	0.43	8.52	1.12	-27.77	-3.64
LF	-34.72	-2.63	10.80	0.82	-2.51	-0.17	55.86	3.83
OOD	103.66	2.04	-33.50	-0.66	120.53	1.91	-60.80	-0.96
PRN	-21.84	-2.99	9.67	1.32	-11.02	-1.43	17.65	2.29
LP	3.28	0.32	-18.07	-1.79	-3.36	-0.33	-6.57	-0.65
WP	21.62	0.60	-41.46	-1.16	-33.75	-0.98	-43.59	-1.27
Constant	-14.11		5.15		-26.20		-4.29	
Cumulative proportion of variance	0.666		1.000		0.475		0.823	

Table 5. Squared Mahalanobis distances between the centroids of groups of the individual canonical discriminant function values (upper left part of table) and *p*-levels related to respective *F*-values (lower right part of table) of males of *M. littoralis*, *M. oresterus,* and *M. unicolor*. Only measurements with significant influence on the discrimination (*F to remove* of the measurement has $p < 0.05$: WH, LF, OOD, PRN, LP, WP) in the model. Cluster based on the distances in Fig. 29.

MALES	N	*oresterus*	*unicolor*	*littoralis*
littoralis	17	21.08	5.57	
unicolor	22	15.60		0.000
oresterus	2		0.079	0.026

periphery of its distribution area. I conclude that the nominal species *Psen* (*Mimumesa*) *oresterus* van Lith is a junior synonym of *Mimumesa unicolor* (Vander Linden).

The East Asiatic females of *M. littoralis* (white triangles in Fig. 26) are morphometrically considerably further from the rest of their conspecific females than *M. oresterus* are from *M. unicolor* (Fig. 27). The form of the ventral lobe of the male penial valve, separating *M. littoralis* from *M. unicolor*, is more acute in East Asiatic males of *M. littoralis* (Fig. 10-13) than that of the rest of conspecific males (Fig. 6-9) is and closer to that of *M. unicolor* (Fig. 14-19). Possibly, the East Asiatic regional population of *M. littoralis* deserves a status of a subspecies. However, the studied males from Central Asia and Mongolia (Fig. 8-10) give a morphologically consequent row, linking the Eastern Asiatic (Fig. 11-13) and European (Fig. 6-7) specimens. Confirmation of a subspecific status of the East Asiatic *M. littoralis* and ascertainment of its distribution range requires further investigation of additional material, particularly from the Irkutsk territory and Yakutia were this East Asiatic form seems to be sympatric with *M. unicolor*.

Synonymy

Mimumesa littoralis (Bondroit)

Mimesa littoralis Bondroit, 1934: 61, ♂, ♀. Lectotype: ♂, Belgium: Ostende (IRSNB), designated by Leclercq 1974: 194 (as 'holotype'), examined. Beaumont 1937: 53 (*Psen* subg. *Mimumesa*); Lomholdt 1975: 157 (*Mimumesa*).

Psen (Mimesa) fulvitarsis Gussakovskij, 1934: 82 (diagnosis), 1937: 663 (description), ♀, ♂. Lectotype: ♂, Russia: Gremyachka (ZISP), designated by Budrys 1990: 945, examined. Beaumont 1941: 328 (as synonym of *unicolor*); Lith 1949: 135, 145 (as synonym of *littoralis*).

Mimesa celtica Spooner, 1948: 164, ♀, ♂. Syntypes: England, Ireland (BMNH, OUM), examined. Lith 1949: 135, 145 (as possible synonym of *littoralis*); Richards 1952: 142 (as full species); Else & Felton 1994 (as synonym of *littoralis*).

Psen (*Mimumesa*) *kashmirensis* (not *Psen kashmirensis* Nurse, 1903, now in *Psenulus* - see Budrys 2000: 65): Lith 1959: 61; Bohart et al. 1976: 164 (*Mimumesa*).

Mimumesa unicolor (Vander Linden)

Psen unicolor Vander Linden, 1829: 107. Syntypes: lost (Leclercq 1974: 194), Belgium. Shuckard 1837: 230 (*Mimesa*); Taschenberg 1858: 78 (*Mimesa*, as synonym of *borealis* Dahlbom); Beaumont 1937: 47 (*Psen* subg. *Mimumesa*); Heinrich 1967: 77 (*Mimumesa*).

Mimesa borealis, Dahlbom 1842: 8 (diagnose), 1843: 2 (description), ♀, ♂. Lectotype: ♀, Sweden: Gotland

Table 6. Squared Mahalanobis distances between the centroids of groups of the individual canonical discriminant function values (upper left part of table) and *p*-levels related to respective *F*-values (lower right part of table) of males of *Mimumesa littoralis*, *M. oresterus,* and *M. unicolor* from the regional populations from Europe, Central Asia, and East Asia. Only measurements with significant influence on the discrimination (*F to remove* of the measurement has $p < 0.05$: WH, LF, OOD, PRN, LP, WP) in the model. Cluster based on the distances in Fig. 31.

MALES: regional population	N	*oresterus*	*unicolor*			*littoralis*		
			E. Asia	C. Asia	Europe	E. Asia	C. Asia	Europe
littoralis Europe	7	28.90	20.32	30.10	17.97	13.78	32.85	
littoralis C. Asia	3	52.97	16.23	18.53	26.70	13.27		0.000
littoralis E. Asia	7	21.19	2.74	7.06	3.51		0.038	0.001
unicolor Europe	15	16.62	3.93	5.82		0.151	0.000	0.000
unicolor C. Asia	5	26.43	8.00		0.052	0.075	0.012	0.000
unicolor E. Asia	2	20.70		0.513	0.798	0.921	0.212	0.052
oresterus	2		0.234	0.024	0.081	0.049	0.002	0.011

(Lund University museum, designated by Lith 1949: 137). Smith, 1856: 429 (as synonym of *unicolor*).

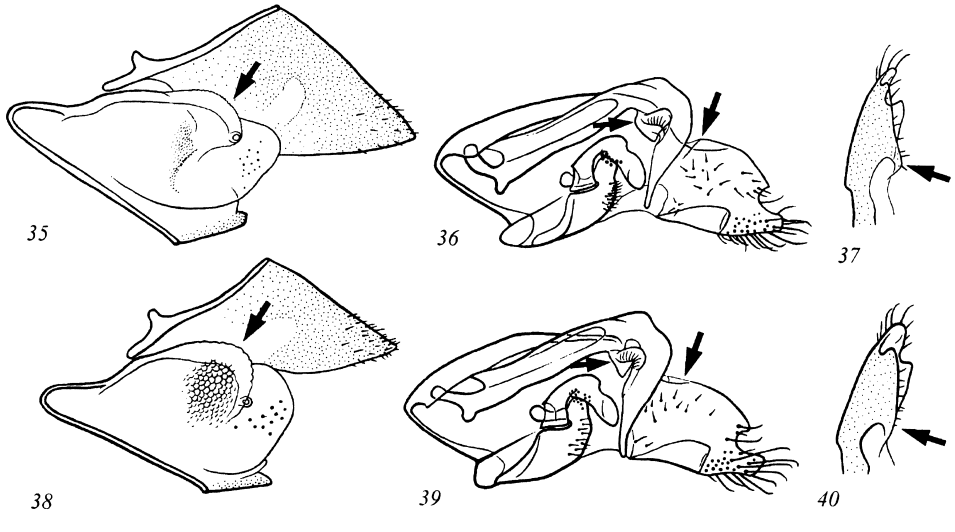
Mimesa palliditarsis, Saunders 1904: 605, ♂. Syntypes: 4♂, Spain, N. Majorca: B[ay] of Pollensa, Little Albufera (3 syntypes in OUM, examined). Beaumont 1937: 48 (as synonym of *unicolor*); Gussakovskij 1937: 661 (as probable synonym of *unicolor*).

Psen (Mimumesa) oresterus, Lith 1976: 87, ♀, ♂. Holotype: ♀, Pakistan: Quetta (BMNH), examined. Type data in the description: 'West Pakistan: Quetta, Baluchistan, 2♀, holotype and paratype, 1♂, allotype, June 1902, paratype, Aug. 1903, C. G. Nurse (BM). The last mentioned male has a deformed petiole...' Really the holotype ♀, as well as the paratype ♂ with deformed petiole, deposited at BMNH, collected Aug. 1903. Only the paratype ('allotype') ♂ with normal petiole was collected in June 1902. The paratype ♀, also collected Aug. 1903, is deposited at RMNH. Lith 1959: 61 (as an unnamed form: 'another form which is closely allied to *P. unicolor* has been taken at Quetta (Pakistan)...'). **Syn. n.**

Psen fuscipennis (not Dahlbom, 1842): Radoszkowski 1891: 587 (lapsus or misidentification); Beaumont 1937: 48 (correction of Radoszkowski 1891, and synonym of *unicolor*).

Identification key to *Mimumesa littoralis* and *M. unicolor*

1. Female 2
– Male.....3
2. Nearly always the first flagellomere more than 1.15 times as long as scape (Fig. 20), temples mostly shorter: 6.8 LSC - 6.1 L1F + 2.1 LT < 1 mm (Fig. 34; measurements in Fig. 2, 3). Flagellum ventrally often completely brownish-yellow, sometimes brown or nearly black. In comparison with *M. unicolor*, vertex usually with stronger shine and weaker rugosity ....*littoralis* (Bondroit)
– The first flagellomere less than 1.15 times as long as scape (Fig. 20), temples mostly longer: 6.8 LSC - 6.1 L1F + 2.1 LT > 1 mm (Fig. 34; measurements in Fig. 2, 3). Flagellum black, with only one or sometimes a few apical flagellomeres brownish-yellow ventrally. In comparison with *M. littoralis*, vertex usually with weaker shine and stronger rugosity..... .....*unicolor* (Vander Linden)
3. Gonostylus with angulate, slightly sclerotized dorsal edge (Fig. 36, 37). Ventral subapical lobe of penial valve basally bulged, in profile subelliptic or subtrapezoidal (Fig. 6-13, 36). Dorsal apodeme of 7th sternite usually narrower, with more finely denticulate apical edge (Fig. 35). Ventral surface of flagellum usually yellowish or brownish; tyloidea usually not very distinct, sometimes hardly visible, located on 2-8th, rarely on 9th flagellomere ....*littoralis* (Bondroit)
– Gonostylus with rounded, membranous dorsal edge (Fig. 39, 40). Ventral subapical lobe of penial valve basally flat, in profile subtriangular (Fig. 14-19, 39). Dorsal apodeme of 7th sternite usually broader, with more coarsely undulate apical edge (Fig. 38). Flagellum usually blackish, only its tip ventrally pale brownish; tyloidea more distinct, carinate, usually present on 2-9th flagellomeres, evanescent or



Figures 35-40. Lateral aspect of 7th abdominal segment (35, 38), lateral inside aspect of the right half of genitalia (36, 39) and dorsal aspect of the apical part of the right gonostylus (37, 40) of male *Mimumesa littoralis* (35-37) and *M. unicolor* (38-40). Arrows point to the dorsal apodeme of 7th sternite (35, 38), the ventral subapical lobe of penial valve (36, 39), and the dorsal edge of gonostylus (36, 37, 39, 40).

rather distinct on 1st and 10th flagellomere ....
.....*unicolor* (Vander Linden)

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