

Comparative Morphology and Morphometry of *Badister* (s. str) Species (Coleoptera: Carabidae), Occur in Baltic States, with Notes on Their Distribution in Local Fauna

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ABSTRACT

The results of studied problems of identification and distribution in the Baltic countries of four species of *Badister* (s. str.) subgenus: *B. unipustulatus*, *B. meridionalis*, *B. bullatus*, and *B. lacertosus*, are presented in the current paper. The relevance of a number of diagnostic body traits both in males and females is widely discussed and illustrated by original drawings. The morphological traits of some structures of the reproductive tract of females and their utility for identification of species have described for the first time. Based on analysis of published sources and on available material, the distribution of these species in Estonia, Latvia and Lithuania is specified and reviewed.

Key words: Coleoptera, Carabidae, *Badister*, taxonomy, faunistic review, Baltic countries.

INTRODUCTION

The genus *Badister* Clairville, 1806 is included to the tribe Licinini which comprises of 235 species worldwide that had been identified until 2005 (Lorenz, 2005). The ground beetles of this tribe are characterized by modified mouthparts (the mandibles are robust and shorter than in other ground beetles) and by more or less flattened head (Ball, 1959). Three subgenera which are characterised by the following details of mandibular structure and tarsal setation are classified within the genus: right mandible with dorsal surface notched and tarsomere 5 with row of setae on ventro-lateral margin (*Badister* (s. str.)); right mandible with dorsal surface notched and tarsomere 5 with ventro-lateral margins aseptose (*Trimorphus* Stephens, 1828); and left mandible notched and tarsomere 5 with ventro-lateral margins aseptose (*Baudia* Ragusa, 1884) (Ball, 1959). By the number of species, it is a relatively small genus worldwide presently comprising 48 species placed in 3 subgenera: *Badister* (s. str.); 23, *Trimorphus*; 3, and *Baudia*; 22 (Anichtchenko *et al.*, 2007-2017). Among 26 species distributed in

the Palaearctic region, only 11 occur in Europe (Baehr, 2003). Nine species having wider distribution ranges are known in the Baltic countries as well (Silfverberg, 2010). Despite a small number of species and a relatively large body size, the taxonomy of this genus has quite a controversial history and is problematic till nowadays. Generally, the faithful identification of all European *Badister* species is based on the morphology of male genitalia (Makólski, 1952; Komarov, 1991; Hurka, 1996; Assman, 2004) while females remain poorly identifiable. Four species of subgenus *Badister* (s. str.) are reported in the Baltic countries (Silfverberg, 2010). Indeed, the extant distribution of these species is difficult because they are very similar morphologically and often are not identified safely. Although the morphology of the European species of *Badister* (s. str.) is described and the keys of their identification are well presented in several most recent publications (Komarov, 1991; Hurka, 1996; Assman, 2004; Puchkov, 2013), however some morphological characters are specified differently or even controversially and make some confusion for users. Indeed, no particular attention to *Badister* species has been paid in the Baltic countries before, and available knowledge is far from the real situation of their prevalence in the territory of this region. Such circumstances were the main reason to compile a comprehensive review of ground beetles of *Badister* (s.str.) genus in the Baltic countries. Seeking trustworthy identification, we aimed to study the morphological structures of adults, both males and females, from different regions of Europe, to compare the variance of body and genitalic characters between and within species, and to find correct morphological characters which could be useful for an easier identification of “problematic” species.

MATERIAL AND METHODS

Specimens examined

All available specimens deposited in collections of museums and scientific institutions and held by private collectors in Baltic countries were examined in this study: altogether 583 specimens. The material from the following institutional and private collections was examined: Kaunas Tadas Ivanauskas Zoological Museum, Lithuania (KZM), Latvian Museum of Natural History, Latvia (LMNH), Daugavpils University, Coleopterological Research Centre, Latvia (DUBC), Estonian Museum of Natural History, Estonia (EMNH), Private collection of Florian Savich (FS), University of Latvia, Faculty of Biology, Zoology and Animal Ecology Department (LUFB); Private collection of Alexander Napolov (AN), Private collection of Aleksandr Meržijevskij.

Additionally, the specimens for comparative studies were loaned from the following collections: Berlin Nature Museum, Germany (BNM): 27 specimens of *B. meridionalis*, Bavarian State Collection of Zoology, Germany (BSCZ): 9 specimens of *B. bullatus* and 1 specimen of *B. lacertosus*, Museum and Institute of Zoology, Polish Academy of Science (MIZPAS): 5 paratypes of *Badister kineli* Makólski, 1952, Private collection of Dr. Oleg Aleksandrowich (Poland) (OA): 2 specimens of *B. meridionalis*, and Private collection of H. Ljungberg (Sweden) (HL): 1 specimen of *B. meridionalis*.

The classifications of chorotypes were used following Gorodkov (1983).

Dissection and depiction methods

Male and female genitalia were prepared for the study following the instruction described by Liebherr and Will (1998) and Will (1998). Male genitalia were removed after softening the specimens. For this reason dry specimens were placed in 70-80°C temperature water for 30-60 minutes, than using stereo-microscope and dissecting needles was made section throughout membrane between 5th and 6th abdomen tergites. Removed genitalia gently cleared in 50°C of 10% KOH for 10-15 minutes. Further dissections of genitalia were done in the drop of glycerine after neutralization of dissected material by 10% acetic acid and dehumidification. Females were softened like males, than using the same entomological equipment dissected abdomen throughout pleural membrane and removed dorsal part of abdomen with entrails. Removed material was cleared in 50°C of 10% KOH for 10-15 minutes. Further dissections of females genitalia were done in the drop of distilled water after neutralization of dissected material by 10% acetic acid. Dissected genitalia plus reproductive tract was placed in a saturated Clorazol Black[®] dye and distilled water solution. Than tracts were slide mounted in glycerine and examined using phase-contrast compound microscope. Examined genitalia and reproductive tracts both males and females were placed in genitalia micro vials in glycerine and pinned on the same pin as examined specimen. The terms for the parts of genitalia are either standard among carabidologists or taken from Ball and Shpeley (2009) and Erwin and Ball (2011). Drawings were made using an ocular grid. A stereomicroscope SMZ-168 Motic, digital camera Nikon D3100, and digital camera Canon EOS 400D DIGITAL with objective Canon EF 100 mm f/2.8 L IS USM were used for taking photographs. A confocal laser scanning microscope Zeiss LSM 5 Pascal and its software LSM 5 Pascal Release version 4.0 were used for the investigation of surface structures of elytra and acquisition of pictures. Distribution maps were prepared with the ArcGIS software.

Morphometric analyses

All measurements were made using a stereoscopic microscope Motic and a calibrated ocular grid with magnification of 40 and 20 times. For each measured specimen, seven distance variables were measured, including: width of head (WH), measured between inner margins of eyes (shortest distance); length of head (LH), measured along the midline from the apical margin of the clypeus to the cervical suture; length of pronotum (LP), measured midline from the apical margin to the basal margin; width of pronotum (WP), measured latitudinal distance beside the insertion of midlateral setae (widest distance); width of elytra (WE), measured maximum width of both elytra combined; length of elytra (LE), measured from the humeral carina to the apical margin (tips) of elytra; longitudinal distance between the humeral carina of elytra and the anterior side of the lunular black spot of elytra (BS); and length of body (LB), measured from the apical margin of the clypeus to elytra tips, or $LB = LH + LP + LE$. The scheme of morphological measurements of the body and used special terms of genitalia of *Badister* (s. str.) species are given in figures (Figs. 1, 2).

For statistic analysis, we used software Past version 3.11 (Hammer, 1999-2015).

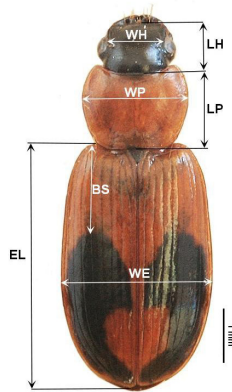


Fig.1. Habitus of *B. meridionalis* specimen collected in Sweden: KZM, IC-68557 and scheme of morphological measurements.

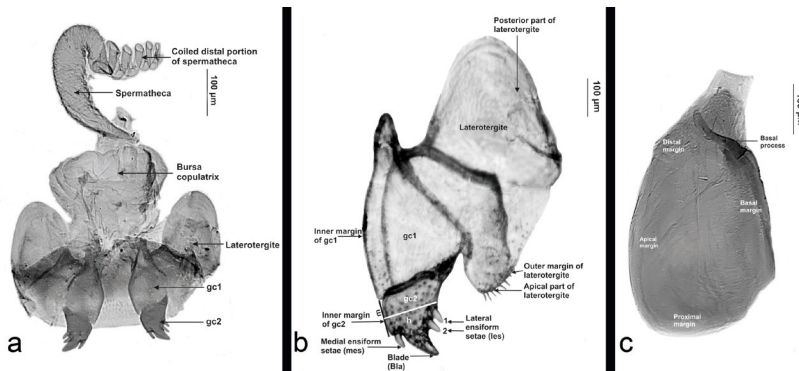


Fig. 2. Scheme of used special terms of genitalia of *Badister* (s. str.) species: b. ventral aspect of the reproductive tract of female of *B. bullatus* (KZM, IC-60106), b. ventral aspect of a complex of right gonocoxites and laterotergite of female of *B. meridionalis* (paratype of *B. kineli*) (MIZPAS, Pol-2); c. ventral aspect of the left paramere of *B. unipustulatus* (KZM, IC-60113); gc: gonocoxite, m: length f inner margin of gonocoxite 2, h: width of gonocoxite 2; scale 100 μ m.

For graphically depicting groups of numerical data through their quartiles we used a boxplots. The length of the box is the interquartile range (IQR). A line inside the box is a median. The boundaries of the box are Tukey's hinges. An asterisk (*) is an extreme outlier that is calculated as the value more than 3 IQR's. A circle (o) is an outlier that is calculated as the value more than 1.5 IQR's but less than 3 IQR's. Usually, extreme outliers are taken away from analysis but not in this case due to limited data in the analysis.

RESULTS

Review of the material

Subgenus *Badister* sensu stricto Clairville, 1806*B. (s. str.) unipustulatus* Bonelli, 1813

Examined material. Estonia: Tartu: Emajõgi, 23.04.1938 leg. H. Kuusik (1 ♂, EMNH); Ropka, 09.1831 leg. H. M. Asmuss (1 ♂, EMNH); Tartu, 05.1846 leg. H. M. Asmuss (1 ♀, EMNH); Valga: Helme, 2.07.1956 leg. R. Marivae (1 ♀, EMNH), 22.04.1958 leg. E. Marivae (1 ♀, EMNH), 12.06.1965 leg. O. Marivae (1 ♂, EMNH); Latvia: Aglona: Šķeltova, 26.08.1985, 5.04.1986 leg. A. Barševskis (1 ♂, 1 ♂, DUBC); Carnikava: Kalngale, Garciems, 3.05.1995 leg. R. Matrozis (2 ♀♀, FS); Daugavpils: Elerne, 30.09.1993 leg. A. Barševskis (1 ♂, DUBC); Ilgas, 8.04.1994, 21-24.04.1995, 5.07.1995, 18.06.1996 leg. A. Barševskis (2 ♂♂/1 ♀, 1 ♀, 1 ♂, 1 ♂, DUBC), 16.06.2008 leg. R. Cibulskis (2 ♀♀, DUBC), 8.04.1994 leg. F. Savich (1 ♂, FS); Slutiški, 10.06.1996 N. Savenkovs (1 ♀, DUBC); Vabole, 20.07.1994, 14.10.1994 leg. R. Cibulskis (1 ♂, 1 ♂, DUBC); Gulbene: Stradi, Pededze Lower Reaches Nature Reserve, 06.2001 leg. A. Napolov (1 ex., AN); Ilūkste: "Straumēni", 16.03.2008, 23-26.06.2010 leg. M. Janovska (1 ex., 2 ♂♂, DUBC); Jēkabpils: Dunava, 10-13.08.1995, 24.08.1995 leg. A. Barševskis (1 ♂, 1 ♀, DUBC); Jelgava: Jelgava, 1.05.1997 leg. R. Matrozis (1 ♀, FS); Riebiņi: Stabulnieki, 20.04.1991 leg. A. Barševskis (1 ♂, DUBC); Rīga: Daugavgrīva isl., Garciems, Garupe, 29.05.1994, 3 05.1995, 16.05.1995 leg. R. Matrozis (2 ♀♀/1 ♂, 1 ♀, 1 ♀, FS); Gauja, Garupe, 25.05.1996 leg. F. Savich (5 ♀♀/1 ♂, FS); Talsi: Mazirbe, 06.2002, leg. A. Barševskis (1 ex., DUBC); Ventspils: Moricsala Nature Reserve, 05.2003 leg. U. Valainis (1 ex., DUBC); Lithuania: Akmenė: Kamanos Strict Nature Reserve, 15.05.1991, 18.07.1991, 18.10.1991 leg. Vidm. Monsevičius (1 ♂, 1 ♂, 1 ♀, KZM); Alytus: Punios šilas forest, 27.06.2008 leg. V. Tamutis (1 ex., KZM); Jonava: Šėta, 08.1954 leg. S. Pileckis (1 ♀, KZM); Kazlų Rūda: Kazlų Rūda, 23.03.1966 leg. E. Gaidiene (1 ♂, KZM); Kaunas: Braziūkai, 15.08.2015 leg. V. Tamutis (5 ♂♂/3 ♀♀, KZM); Dubrava forest, 11.05.1999, leg. P. Zolubas (1 ♀, KZM); Margininkai, 2.07.1997 leg. V. Tamutis (1 ♂, KZM); Romainiai, 7.04.1966 leg. E. Gaidienė (3 ♂♂, KZM); Klaipėda: Giruliai, 20.04.1994, leg. S. Karalius (1 ♂, KZM); Neringa: Lapnugaris Landscape Reserve, 20.06.2007 leg. R. Ferenc (1 ♀, KZM); Pervalka, 2.06.1995 leg. B. Šablevičius (1 ♀, KZM); Palanga: Monciškė, 9.05.2001, 27.06.2010 leg. R. Ferenc (1 ♀, 1 ♀, KZM); Plungė: Grigaičiai, 7.10.1998 leg. A. Gedminas (1 ♀, KZM); Tauragė: Buveiniai lake env., Viešvilė Strict Nature Reserve, 27.07.2008 leg. V. Tamutis (1 ex., KZM); Utena: Antalgė, 26.04.1977, leg. A. Kaulinis (1 ♂, KZM).

Additional material. Germany: Brandenburg Nauen, 29.03.1910 leg. M. Ude (2 ♀♀, BNM).

Published records. Estonia: Harju, Pärnu, Tartu, Valga (Haberman, 1968); Hiiumaa (Miländer, 1993). Latvia: Livland, Curland (Seidlitz, 1872, 1887); Liepāja, Ventspils (Lackschewitz and Mikutowicz, 1939); Rīga (Stiprais, 1973); Garciems, Kalngale (Stiprais, 1975); Sigulda (Spuris, 1975); Melliži, Jumala (Stiprais, 1984); Šķeltova (Barševskis, 1987); Šķeltiņi (Aglona), Stabulnieki (Riebiņi) (Barševskis, 1993), Līksna, Vabole, Daugavpils (Cibuļskis, 1994); Moricsala Nature Reserve (Barševskis *et al.*, 2004); Gauja National Park (Kalniņš *et al.*, 2007); Šedere (Barševskis *et al.*, 2008); Mazirbe (Talsi), Ilgas (Daugavpils) (Barševskis *et al.*, 2009); Butiški (Bukejs, 2011). Lithuania: Kaunas (Heyden, 1903); Žuvinas Nature Reserve, Alytus, Meteliai (Sharova and Grūntal, 1973), Juodkrantė, Neringa (Žiogas, Zolubas, 2005).

Description. The body pattern is typical of this group of species: black-colored head, metathorax, abdomen, and a single entire or divided transversely semi-lunular spot on each elytron and yellow-red pronotum, scutellum, mesothorax, and the remaining part of elytra, palpi and legs. Antennomeres are often red-brown or yellow-red, usually 2-6 antennomeres and the last palpomeres are darkened. The black pattern of elytra is usually composed of two spots on each elytron: a large irregular spot beside the middle and a narrow, falcate spot along the posterior margin of elytra (Fig. 3a, ♂). Occasionally, these spots join on 1-2 last marginal intervals in the anterior third of elytra by a slightly darkened interval (Fig. 3a, ♀). The larger spots on elytra vary in the shape of the front margin, which can be straight transversely, denticulate or convex, while their posterior margin usually has a constant distinct protrusion beside 5-7 rows of elytra. The row of distinct setae is visible on the apical margin of elytra (Fig. 4a).

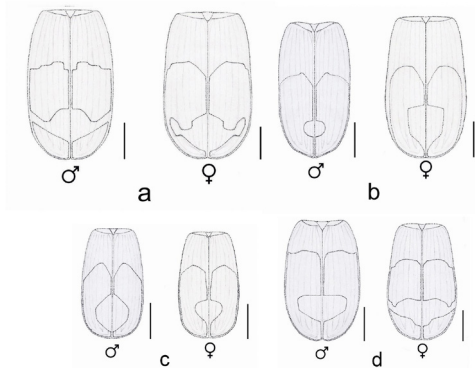


Fig. 3. Scheme of the pattern of elytra: a. ♂ - *B. unipustulatus* (KZM, IC-68686), a. ♀ *B. unipustulatus* (KZM, IC-1932), b. ♂ *B. meridionalis* (paratype of *B. kineli*) (MIZPAS, Pol-1), b. ♀ *B. meridionalis* (BNM, Ger-B-18), c. ♂ *B. bullatus* (KZM, IC-68680), c. ♀ - *B. bullatus* (KZM, IC-60109); d. ♂ *B. lacertosus* (KZM, IC-68680), d. ♀ *B. lacertosus* (KZM, IC-60118); scale 1mm.

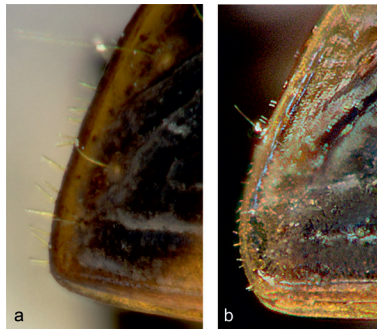


Fig. 4. Fragment of the apex of elytra: a. *B. unipustulatus* (KZM, IC-11514), b. *B. meridionalis* (paratype of *B. kineli*) (MIZPAS, Pol-3).

The microsculpture of elytra is very fine, composed by very fine transversal fissures, the contours of which are blind even magnified 150 times. Four to five fissures are distributed along the distance of 10 μm of the surface of elytra (Fig. 5a). The surface of elytra is strongly iridescent. The length of bodies is quite similar among genders: 6.1-7.3 mm of males and 6.4-7.4 mm of females. The sexual dimorphism is distinct. Despite the dilated first three tarsomeres of males, the bodies of both genders slightly differ in shapes of their parts. The WH and LH in males average 1.132 and 1.102, respectively, and are significantly lower compared to those in females ($U = 56.5$; $p < 0.01$; $U = 15.5$; $p < 0.001$). The pronotum slightly differs in the straightness of lateral margins and roundness of posterior angles (Fig. 6a), but its width and length values in males (1.96 and 1.288 mm, respectively) are not significantly differing from those in females (Table 1). However, the ratio of LH/LP in males is 0.86, and it is significantly lower than in females ($U = 30$; $p < 0.001$). The ratio of LP/WP in males is about 0.657, which is significantly higher than in females ($U = 51.5$; $p < 0.001$). The females have significantly wider elytra ($U = 81.5$; $p < 0.0259$). The distance between the anterior

Comparative Morphology and Morphometry

margin of the base of elytra and the anterior side of the lunular black spot of elytra (BS) in males is about 1.517 mm, which is significantly shorter than in females ($U = 73.5$; $p < 0.0107$). The median lobe of the aedeagus is distinctly asymmetric in ventral view (Fig. 7a), apically inclined ventrally with an inflated protuberance (Fig. 9a). The left paramer is wide, its proximal margin is broadly rounded, and apical margin is slightly convex, with distinct indentation in the basal part of the proximal margin (Fig. 8. a). The right paramer is triangular, its proximal margin is slightly rounded (Fig. 10. a). The genital ring is wide and oval, rather asymmetric, with a fairly short apex which is curved right (Fig. 11a). Gonocoxite 1 is triangular, funnelliform, the inner margin is gradually convex, without distinct punctation. Gonocoxite 2 is elongated, rather curved, blade sharp in the apex; a dorso-median ensiform, slightly curved seta is situated slightly above the middle of the gonocoxite. All setae located on the apical margin of the ventral surface of laterotergites are directed forward, more or less perpendicular to the margin.

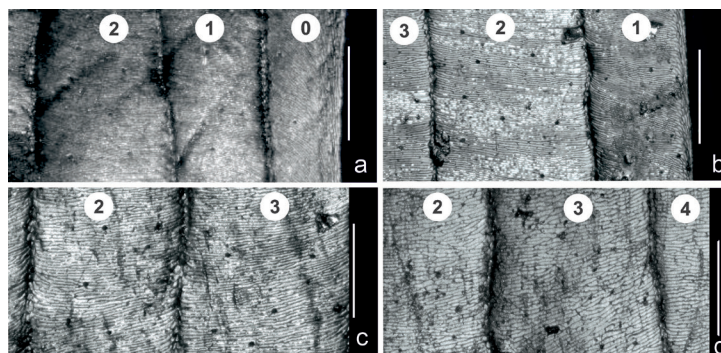


Fig. 5. Fragments of the first half of the base of surface of elytra (intervals are numbered): a. *B. unipustulatus* (KZM, male, IC-68687), b. *B. meridionalis* (KZM, male, IC-68335), c. *B. lacertosus* (KZM, male, IC-68205; d. *B. bullatus* (KZM, male, IC-68219)

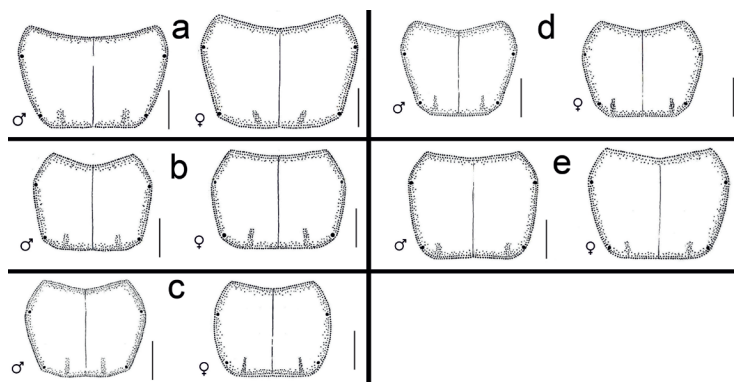


Fig. 6. Pronotum: a. *B. unipustulatus* (♂ KZM, IC-68920; ♀ KZM IC-20346); b. *B. meridionalis* (♂ paratype of *B. kineli*, MIZPAS, Pol-3; ♀ paratype of *B. kineli*, MIZPAS, Pol -2); c, d *B. bullatus* (c, ♂ KZM IC-68223, d, ♂ KZM, IC-60108, c, ♀ KZM, IC-68226; d, ♀ KZM, IC-60103); e. *B. lacertosus* (♂ KZM, IC-60123, ♀ KZM, IC-60116); scale 500µm.

Table 1. Sex differences in body traits (means and Standard Error of means) in four species of *Badister* (s.str.). The Mann-Whitney test results are shown; with significance levels estimated using the permutation procedure (P_{MonteCarlo}). Statistically significant results are in bold, M - males, F - females, N - number of specimens, LB - length of body, WH - width of head, LH - length of head, WP - width of pronotum, LP - length of pronotum, WE - width of elytra, LE - length of elytra, BS - distance between the base and the apical margin of the lunular black spot of elytra).

Species	Traits	Male		Female		Mann-Whitney test				
		Mean	SEM	Mean	SEM	U	P _{MonteCarlo}	Z		
<i>B. unipustulatus</i>	LB	6.79	17	0.063	6.87	17	0.060	103	0.2378	-1.174
	WH	1.132	17	0.017	1.232	17	0.020	56.5	0.0016	3.060
	LH	1.102	17	0.014	1.222	17	0.010	15.5	<0.001	-4.485
	WP	1.96	17	0.024	2.019	17	0.021	94.5	0.0832	-1.721
	LP	1.288	17	0.018	1.257	17	0.017	107.5	0.1926	-1.289
	WE	2.761	17	0.036	2.894	17	0.044	81.5	0.0259	-2.218
	LE	4.355	17	0.056	4.385	17	0.038	129.5	0.6193	-0.504
	BS	1.517	17	0.014	1.594	17	0.026	73.5	0.0107	-2.491
	Ratio LH/LP	0.860	17	0.020	0.973	17	0.011	30	<0.001	-3.934
	Ratio LP/WP	0.657	17	0.008	0.622	17	0.005	51.5	<0.001	-3.190
	Ratio LE/LP	3.385	17	0.036	3.494	17	0.036	89	0.051	-1.897
Ratio LE/BS	2.870	17	0.026	2.760	17	0.041	82.5	0.033	2.122	
<i>B. meridionalis</i>	LB	6.19	22	0.078	6.18	19	0.047	169	0.9838	0.015
	WH	0.93	22	0.016	0.99	19	0.012	77	0.0038	-2.85
	LH	0.93	22	0.016	0.98	19	0.014	86	0.0078	-2.596
	WP	1.75	22	0.025	1.78	19	0.022	159	0.7437	-0.322
	LP	1.24	22	0.019	1.23	19	0.011	147	0.4866	0.700
	WE	2.47	22	0.038	2.55	19	0.021	130	0.2176	-1.215
	LE	4.00	22	0.047	3.97	19	0.029	154.5	0.6509	0.463
	BS	1.38	22	0.034	1.39	19	0.038	151.5	0.5754	-0.575
	Ratio LH/LP	0.760	22	0.011	0.804	19	0.010	113.5	<0.011	-2.488
	Ratio LP/WP	0.71	22	0.005	0.697	19	0.005	139	<0.068	-1.819
	Ratio LE/LP	3.220	22	0.029	3.225	19	0.019	177.5	0.414	-0.811
Ratio LE/BS	2.910	22	0.053	2.872	19	0.070	169	0.293	1.033	
<i>B. bullatus</i>	LB	5.359	72	0.033	5.414	72	0.044	2118	0.0552	-1.90
	WH	0.785	72	0.006	0.864	72	0.008	906.5	0.0001	-6.809
	LH	0.824	72	0.007	0.882	72	0.009	1423	0.0001	-4.179
	WP	1.59	72	0.010	1.629	72	0.015	2039	0.0264	-2.216
	LP	1.165	72	0.008	1.171	72	0.010	2545	0.8502	-0.189
	WE	2.139	72	0.022	2.186	72	0.019	2071	0.0360	-2.093
	LE	3.361	72	0.023	3.368	72	0.027	2448	0.5604	-0.577
	BS	0.965	72	0.010	0.960	72	0.012	2483	0.6572	-0.442
	Ratio LH/LP	0.704	72	0.005	0.750	72	0.006	1328	<0.001	-5.142
	Ratio LP/WP	0.738	72	0.002	0.720	72	0.002	1502	<0.001	-4.452
	Ratio LE/LP	2.852	72	0.010	2.880	72	0.011	2398	0.363	-0.907
Ratio LE/BS	3.493	72	0.046	3.540	72	0.050	2475	0.5416	-0.605	

Comparative Morphology and Morphometry

Table 1. Continued.

Species	Traits	Male		Female		Mann-Whitney test				
		MeanN	SEM	MeanN	SEM	U	P _{MonteCarlo}	Z		
<i>B. lacertosus</i>	LB	6.217	21	0.050	6.295	21	0.079	173.5	0.2410	-1.171
	WH	0.886	21	0.009	0.941	21	0.009	83	<0.001	-3.516
	LH	0.883	21	0.009	0.939	21	0.014	110.5	0.0052	-2.828
	WP	1.763	21	0.014	1.810	21	0.019	128	0.0206	-2.234
	LP	2.279	21	0.010	2.271	21	0.015	207.5	0.7493	0.3218
	WE	2.455	21	0.025	2.488	21	0.037	162.5	0.1473	-1.461
	LE	3.705	21	0.034	3.728	21	0.047	194	0.5167	-0.658
	BS	1.152	21	0.020	1.133	21	0.022	197	0.5565	-0.585
	Ratio LH/LP	0.691	21	0.006	0.732	21	0.009	95.5	0.0017	-2.979
	Ratio LP/WP	0.726	21	0.005	0.702	21	0.005	119.5	0.01	-2.531
	Ratio LE/LP	2.899	21	0.023	2.935	21	0.029	187	0.4063	-0.830
	Ratio LE/BS	3.231	21	0.050	3.306	21	0.053	182.5	0.3367	-0.944

The posterior part of laterotergites is slightly prolonged, bell-shaped (Fig. 12a), well sclerotized. The reproductive tract is proximally with a short, broad, cap-shaped bursa copulatrix and a long C-shaped spermatheca with a coiled distal portion (Fig. 13a).

Variations. A few variations of the pattern of elytra were previously noted for this species (Puel, 1925; Jeannel, 1942). But most of our examined specimens have the black lunular spot on elytra divided transversely by a narrower or wider space into a broad semi-rounded spot in the middle of elytra and a narrow, falciform spot in the apex. The shape and size of these spots slightly differ between individuals. The pronotum slightly varies by the shape of the lateral margin and basal angle both in males and females. The lateral margin can be almost straight or slightly convex on the posterior half of the pronotum. Posterior angles of the pronotum can be distinct or slightly rounded. No distinct variations in the structures of genitalia were detected.

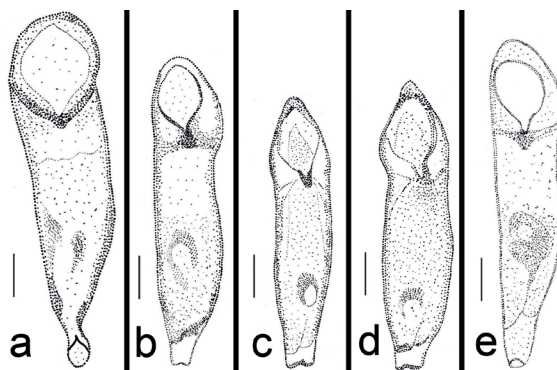


Fig. 7. Aedeagus, ventral side: a. *B. unipustulatus* (KZM, IC-60113), b. *B. meridionalis* (BNM, Ger-B-16); c. *B. bullatus* (KZM, IC-60103), d. *B. bullatus* (KZM, IC-68227), e. *B. lacertosus* (KZM, IC-68685), scale 200 μ m.

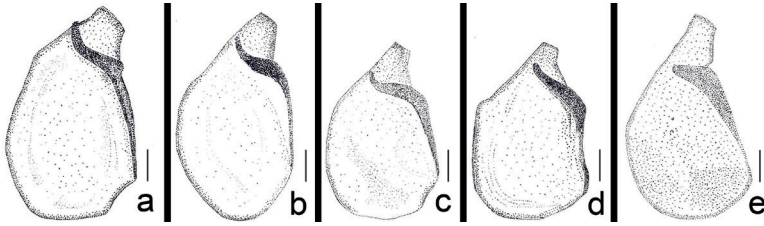


Fig. 8. Left paramere, ventral side: a. *B. unipustulatus* (KZM, IC-60113), b. *B. meridionalis* (BNM, Ger-B-16); c. *B. bullatus* (KZM, IC-60103), d. *B. bullatus* (KZM, IC-68227), e. *B. lecertosus* (KZM, IC-68685), scale 200 μ m.

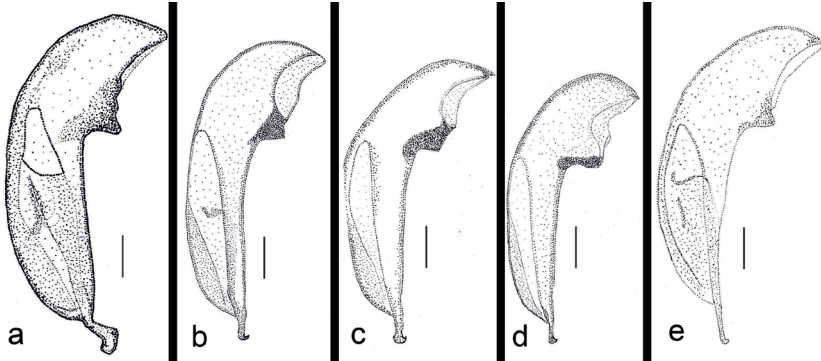


Fig. 9. Aedeagus, lateral side: a. *B. unipustulatus* (KZM, IC-60113), b. *B. meridionalis* (BNM, Ger-B-16); c. *B. bullatus* (KZM, IC-60103), d. *B. bullatus* (KZM, IC-68227), e. *B. lecertosus* (KZM, IC-68685), scale 200 μ m.

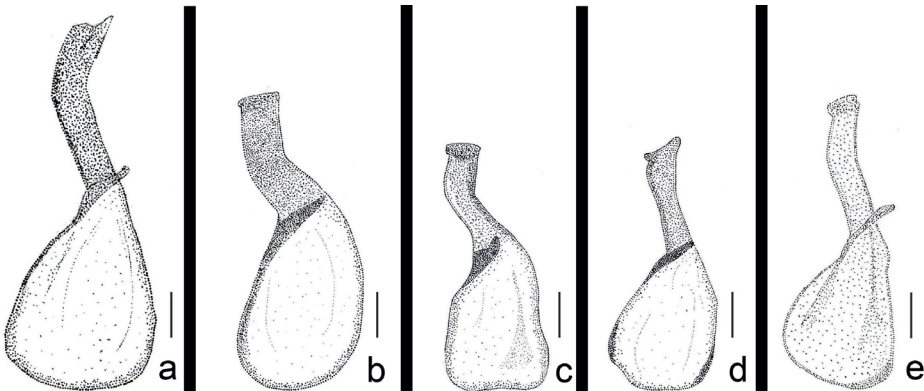


Fig. 10. Right paramere, ventral side: a. *B. unipustulatus* (KZM, IC-60113), b. *B. meridionalis* (BNM, Ger-B-16); c. *B. bullatus* (KZM, IC-60103), d. *B. bullatus* (KZM, IC-68227), e. *B. lecertosus* (KZM, IC-68685), scale 200 μ m.

Differential diagnosis. *Badister unipustulatus* is a well distinguished species among other Central European *Badister* (s. str.) species by parameters of a number of its body traits: largest head, widest pronotum, longest elytra, etc. However, sometimes small specimens of *B. unipustulatus* can be confused with *B. meridionalis*, or conversely

Comparative Morphology and Morphometry

large *B. meridionalis* can be confused with *B. unipustulatus*. Especially it could happen in case of females. The most characteristic body traits of this species are a row of well visible setae on the apical margin of elytra (Fig. 4a) and longer blades of gonocoxite 2. Contrary to *B. unipustulatus*, the black lunule spot on elytra of *B. meridionalis* is generally complete, not divided transversely (Fig. 3b).

General distribution. Euro-Sibero-Central Asiatic species widely distributed in Europe, from the coasts of the Mediterranean Sea in the south to southern Finland in the north (Lindroth, 1992; Hristovski and Guéorguiev, 2015); from British Islands in the west to Western Siberia in the east (Krizhanovskiy *et al.*, 1995; Dudko, Lyubchanskii, 2002; Baehr, 2003), also known in Kazakhstan, Uzbekistan and Turkey (Baehr, 2003).

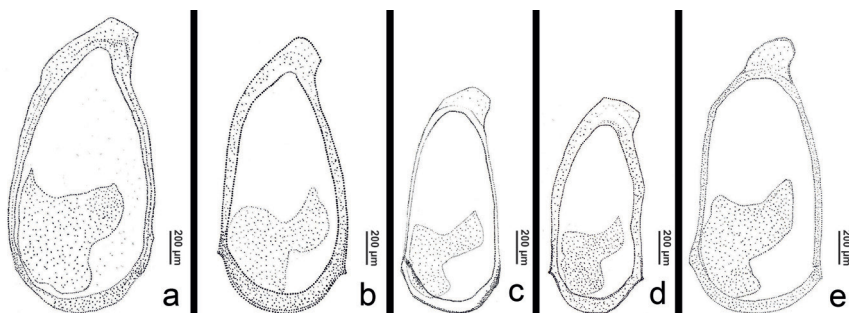


Fig. 11. Genital ring, ventral side: a. *B. unipustulatus* (KZM, IC-60113), b. *B. meridionalis* (BNM, Ger-B-16); c. *B. bullatus* (KZM, IC-60103), d. *B. bullatus* (KZM, IC-68227), e. *B. lacertosus* (KZM, IC-68685), scale 200 μ m.

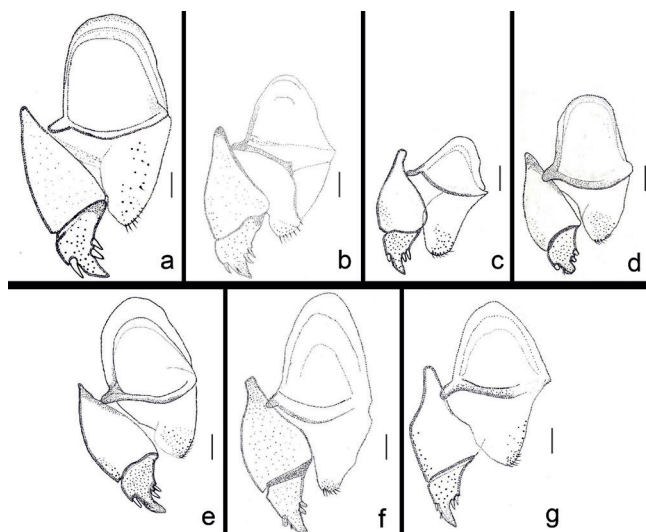


Fig. 12. Right complex of gonocoxites and laterotergite of females: a. *B. unipustulatus* (KZM, IC-60112), b. *B. meridionalis* (paratype of *B. kineli*, MIZPAS, Pol-2); c. *B. bullatus* (KZM, IC-68226); d. *B. bullatus* (KZM, IC-60106); e. *B. bullatus* (KZM, IC-20345); f. *B. lacertosus* (KZM, IC-68338); g. *B. lacertosus* (KZM, IC-68332)

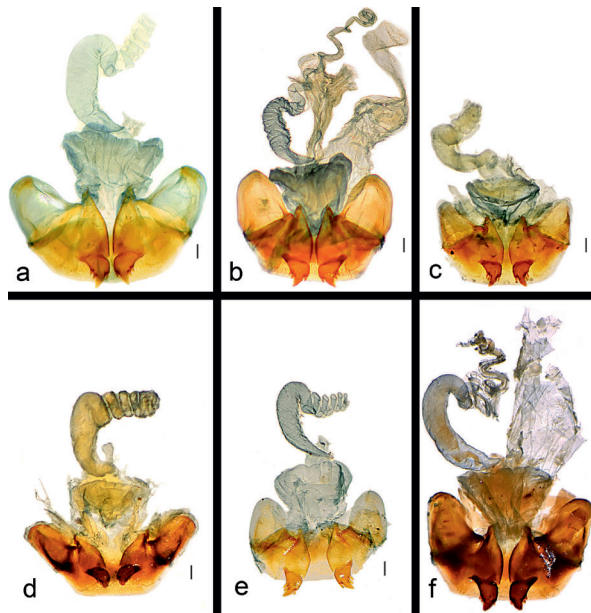


Fig. 13. Reproductive tract of females: a. *B. unipustulatus* (KZM, IC-60112); b. *B. meridionalis* (BNM, Ger-B-15); c. *B. bullatus* (KZM, IC-60103); d. *B. bullatus* (KZM, IC-60106), e. *B. bullatus* (KZM, IC-20314); f. *B. lacertosus* (KZM, IC-68338), scale 75 μ m.

Remarks. Contrary to the description of the elytral pattern of *B. unipustulatus* presented in previous well known identification keys of Central European *Badister* species (Makólski, 1952; Freude, 1976; Hurka, 1996; Assman, 2004; Arndt *et al.*, 2011), almost all examined specimens have the semi-lunular spot on elytra divided into two parts transversally. Similar observations on the pattern of elytra are described by Lindroth (1986) and Komarov (1991). Such aberration of *B. unipustulatus* was described and named *ab. quadripustulatus* by Letzner (1851). A second controversial point we found was on parameters of the head and the pronotum and their ratios described by Hurka (1996). This incongruence is perhaps related to different means of morphometrical measurements used in the studies.

***Badister* (s. str.) *meridionalis* Puel, 1925**

Examined material. Livonia (a historical region on the eastern shores of the Baltic Sea): leg. Bolz (3 ♂♂/1♀, EMNH); Lithuania: Kaunas: Kamša forest, 3.05.1938 leg. A. Palionis (1 ♀, KZM), Nevėžis Landscape Reserve, 4.07.2007, leg. R. Ferenca (1 ♂ KZM).

Additional material. Belarus: Žitkavičy: Hlupin, 20.07.2014 leg. A.V. Kulak (2 ♂♂, OA); Czech: Bohemia: Čelakovice, 1924 leg. Z. Tesar (1 ♂, KZM); Croatia: Gunja, 1929, 1930 leg. Bischoff (1 ♂, 1 ♀, BNM), Račinovci, 1930 leg. Bischoff (1 ♀, BNM); Germany: Brandenburg, Neuendorf, 12.05.1991 leg. W. Renner (1 ♀, BNM); Zarentin am Schaalsee, 1.05.2005 leg. Materlik (1 ♂, BNM); Hungary: Kiskunsag, National Park Bugac, 06.1979, 12-13.06.1979 leg. Uhlig (8 ♂♂/7♀♀, 5 ♀♀, BNM); Poland: Warszawa: Goclawek, 23-25.03.1947 leg. J. Makolski (2 ♂♂/2♀♀, paratypes of *B. kineli*, MIZPAS); Sweden: Öland: Vickleby, 08.05.2000 leg. H. Ljungberg (1 ♂, HL); Ukraine: Kherson: Novochornomoria (label data: Falzfeinowo am Dniepr), 12.05.1914, 7.06.1914 leg. W. Ramme (1♂/1♀, BNM), Dnepropetrovsk: Pavlograd, Levadki environments, 10-20.06.1994, leg. V. Brygadyrenko (1♂/1♀, KZM).

Comparative Morphology and Morphometry

Published records: Estonia: Harju, Järva, Tartu, Valga (Haberman, 1968), these records were based on misidentified material which specimens belong to *B. bullatus*; Latvia: Ilgas (Daugavpils), Šķeltiņi, "Barševski" (Aglona), Jersika (Līvāni) (Barševskis, 1993), Līksna (Cibulskis, 1994), Gauja National park (Kalniņš *et al.*, 2007), Skrīveri (Aizkraukle) (Bukejs *et al.*, 2009), Sakas Island, Salas parish (Jēkabpils) (Bukejs, 2009), but these records were not confirmed in our study, because the material was not available. We related these records to *B. bullatus* as most presumable for this species. In Rubeņi (Leskina, 2000), Jersika (Barševskis *et al.*, 2009), and these records were based on misidentified material, it was related to *B. bullatus*; Lithuania: Zarasai (Barševskis, 2001) not confirmed in our study, because the material is not available. We related this record to *B. bullatus* too.

Description. The body pattern: black-colored head, metathorax, abdomen, and semi-lunular spot on each elytron and yellow-red pronotum, palpi, legs and the remaining part of elytra; however, scutellum and mesothorax can be red-yellow or entirely black. Antennomeres are often red-brown or yellow-red, usually the upper sides of antennomere 1, antennomeres 2-6 are completely and the last palpomeres partly darkened. The black pattern of elytra is composed of one semi-lunular spot on each elytron (Figs. 1, 3b); occasionally this spot is divided into two parts transversely. The interior margins of semi-lunules are curved and forming a yellow-red spot on both sides of the suture, which can vary in shape from round to trapeziform or rectangular (Figs. 1, 3b). The black semi-lunule is confined in the front usually by a broadly curved line running from the first row to the exterior side of the elytron (Figs. 1, 3b); occasionally this line is denticulate or bracket formed. The row of very short, indistinct setae is situated on the apical margin of elytra (Fig. 4b). The microsculpture of elytra is very fine, composed of very fine transversal fissures, the contours of which are blind even magnified 150 times. Five to six fissures are arranged along the distance of 10 μm of the surface of elytra (Fig. 5b). The surface of elytra is strongly iridescent. The sexual dimorphism is less distinct than that of *B. unipustulatus*. The length of bodies is quite similar among genders: 5.6-6.8 mm in males and 5.8-6.5 mm in females. However, WH and LH in males average 0.93 and are significantly lower compared to those of females ($U = 77$; $p < 0.01$; $U = 86$; $p < 0.01$). The pronotum slightly varies in straightness of lateral margins and roundness of posterior angles, but differences are weak among genders (Fig. 6b), the ratio of LP/WP is 0.697 of females and 0.71 of males (Table 1). However, the ratio of LH/LP in males is 0.76, and it is significantly lower than that of females ($U = 113.5$; $p = 0.011$). The distance between the anterior margin of the base of elytra and the anterior side of the lunular black spot of elytra (BS) differs insignificantly between genders and the mean varies from 1.38 to 1.39 mm. The median lobe of the aedeagus is smooth and has a small kink directed toward the ventral side on the apex (Fig. 8b). The median lobe is slightly asymmetric and distinctly incurved on the apex in ventral view (Fig. 7b). The left paramer is wide, the proximal margin is rounded; the apical margin is gradually convex (Fig. 9b). The right paramer is trowel-form, rounded, rarely obtuse in the apex (Fig. 10b). The genital ring is wide and slightly oval, rather asymmetric, with a fairly short apex which is curved right (Fig. 11b). Gonocoxite 1 is triangular, funnellform, the inner margin is gradually convex, without distinct punctation. Gonocoxite 2 is like that of *B. unipustulatus*, but shorter; rather less curved. All setae deposited on the apical margin of the ventral surface of laterotergites are directed forward, more or less perpendicular to the margin.

The posterior part of laterotergites is less prolonged, bell-shaped, well sclerotized (Fig. 12b). The reproductive tract is proximally with a short, broad, cap-shaped bursa copulatrix and a long C-shaped spermatheca with a coiled distal portion (Fig. 13b).

Variations. The pattern of elytra is quite uniform, but anterior and interior margins of black semi-lunules vary in shape. Its anterior margin is often confined by a broadly or sharply curved line (Fig. 3b ♀), but it also could be denticulate or angulate (Fig. 3b ♂). Also, a different shape of the interior margin can make various forms of the bright spot between semilunules: circular, drop-like, rectangular, trapeziform or cordiform. No substantial variations of the shape of the pronotum and of structures of genitalia were detected.

Differential diagnosis. *Badister meridionalis* seems quite a problematic species regarding its faithful identification. Due to the variety of some traits of the body, such as: its length, shape of pronotum, pattern of elytra, color of mesothorax, and this species is often confused with other species of the group. The most characteristic body traits we found are fine microsculpture, strong iridescence, and the distance from the base to the anterior side of the lunular black spot of elytra, which generally is at least 1.4 times longer than that of *B. bullatus* and at least 1.2 times longer than that of *B. lacertosus*. The median lobe of the aedeagus is smooth in the dorsal side of *B. meridionalis* unlike in *B. bullatus* (Figs. 8c, d), and contrary to *B. lacertosus* (Fig. 7e) it has a distinct sag in the apex. A narrower and more convex upper side of the body, lack of a row of long, well visible setae on the apical margin of elytra, and a specific curvature of the median lobe of the aedeagus can be good differential characters for the separation of this species from *B. unipustulatus*. The blade of gonocoxite 2 and the posterior part of laterotergites are less prolonged (Figs. 2b, 12b) compared with those of *B. unipustulatus* (Fig. 12 a); spermathecal walls are finer, distinctly wrinkled transversely (Fig. 13 b). *B. meridionalis* has more convexed dorsally and longer elytra than *B. lacertosus* and *B. bullatus* have. The ratio of length of elytra and length of pronotum of *B. meridionalis* is average 3.22, while those are 2.86 of *B. bullatus* and 2.91 of *B. lacertosus*.

General distribution. Western-Palearctic species widely distributed in Central and Southern Europe, also known in Northern Africa, Kazakhstan (Baehr, 2003), West Siberia (Novosibirsk region, Russia) (Dudko, Lyubechanskii, 2002). The northern border of the distribution range of this species reaches Denmark, southern Sweden, Lithuania, Belarus, central part of the Russian Plain (Lindroth, 1992; Krizhanovskij *et al.*, 1995).

Remarks. *B. meridionalis* was briefly described as an aberration of *B. bipustulatus* = *bullatus* by Puel in 1925. Subsequently Jeannel (1942) after revision of Puel's material concluded that *B. meridionalis* should be considered a Mediterranean region race of *B. bipustulatus*, because male genitalia are similar to those of *B. bipustulatus*. The status of valid species of this form was established only in 1952 by Makólski and it was named *Badister kineli*. Later this name was placed to the status of junior synonym of *B. meridionalis* by Lohse (1954). It is interesting to note that it was made without any comments on similarity of these taxa. Makólski's description is the most comprehensive and assuredly proving the status of valid species of this taxon. The

Comparative Morphology and Morphometry

microsculpture of elytra and the shape of the aedeagus were taken as the main assent of characters of *B. kineli* distinguishing it from *B. bipustulatus*. Indeed, we did not find any substantial differences between specimens determined as *B. meridionalis* from Croatia (specimens from the locality closest to the locality of Puel's material) and Hungary and paratypes of *B. kineli*. The means of the length and width of the pronotum of our examined paratypes of *B. kineli* slightly differed from the means of the holotype described by Makólski (1952) and did not exceed 1.225 and 1.75 mm, respectively, while the means for the holotype indicated by Makólski (1952) were 1.4 and 2.2, respectively. In case of coloration of scutellum and mesothorax, our observations completely fit descriptions of Komarov (1991) and Arndt *et al.* (2011), but partly disagree with Hurka (1996). The coloration of these parts of body of our examined specimens varies from black to red-brown or orange, or some specimens' mesothorax is bicolored: black with a reddish anterior part.

Badister (s. str.) *bullatus* Schrank, 1798

Examined material. Estonia: Harju: Keila, 06.1938 leg. Anonymous (1♀, EMNH); Nissi, 8.06.1936 leg. A. Juris (1♂, EMNH); Paaskula, 4.05.1983 leg. G. Milländer (1 ex., EMNH); Padise, 24.06.1929 leg. H. Haberman (1♂, EMNH); Tallin, 23.04.1935 leg. B. Gebauer (1♂, EMNH), 30.09.1956 leg. G. Milländer (1♂, EMNH); Marivalja, 25.04.1953 leg. G. Milländer (1♀, EMNH); Lääne Viru: Tapa, Läste, 18.04.1935 leg. Anonymous (1♀, EMNH); Põlva, 05.1897 leg. Anonymous (1♀, EMNH); Rapla: Kehna, Saarepõllu, 15.06.1956 leg. H. Haberman (1♀, EMNH); Lipstu, 1.06.1957 leg. H. Haberman (1♂, EMNH); Raikküla, 14.09.1956 leg. H. Haberman (1♂, EMNH); Vigala, 28.07.1952 leg. H. Haberman (1♂, EMNH); Saare: Kiirassaare, 10.06.1911 leg. K. Krausp (1♀, EMNH); Tartu: Rõngu, Valguta, 1846 leg. L. Schrenk (1♂, EMNH); Ropka, 06.1827 leg. H. M. Asmuss (1♂, EMNH); Tähtvere, 1834 leg. A. Lejmann (1♂, EMNH); Tartu, 1829 leg. H. Haberman (1♂, EMNH), 10.03.1846 leg. Chleboforf (1♀, EMNH), 04.1861 leg. L. Schrenk (1♂, EMNH), 04.1880 leg. Anonymous (3♂♂/2♀♀, EMNH), - 04.1881 leg. Anonymous (1♂/1♀, EMNH), 14.05.1938 H. Kuusik (1♀, EMNH); Karlova park, 04.1831 leg. H. M. Asmuss (1♀, EMNH), Toomemägi, 17.05.1930 leg. H. Haberman (1♀, EMNH); Võnnu, 1.06.1986, leg. J. Vilbaste (1♂, EMNH); Valga: Helme, Kirikuküla, 27.03.1958 leg. E. Marivee (1♂, EMNH); Helme, 13.04.1963 leg. R. E. Marivee (1♀, EMNH); 7.09.1963 leg. R. E. Marivee (1♂, EMNH); Viljandi: Vöhma, 14.05.1939 leg. Anonymous (1♀, EMNH); Livonia (a historical region on the eastern shores of the Baltic Sea): 1858 leg. Anonymous (1♀, EMNH); Latvia: Aglona: Kastuļina, Stivrīni, 28.08.1989 leg. A. Barševskis (1♂, DUBC); Šķeltova, Suveizdi, 8.04.1995, 29.04.1995 leg. A. Barševskis (1♀, 1♂, DUBC); Šķeltova, 5.04.1986, 29.03.1987, 18-19.03.1989, 8.04.1991, 17.10.1992, 4.04.1993, 25.02.1995, 17.03.1995, - 07.2002, 10.04.2009 leg. A. Barševskis (1♂, 1♀, 3♀♀, 2♀♀, 1♂/1♀, 3♂♂/1♀, 1♂/2♀♀, 1♂/♀, 1♂, 1 ex., DUBC); Aknīste: Aknīste, - 05.1993 leg. A. Barševskis (1♀, DUBC); Daugavpils: Ambeļi, - 04.1988 leg. A. Barševskis (1♂, DUBC); Elerne, 24.05.2007 leg. A. Pankjans (1♀, DUBC); Ilgas, 10.10.1992, 14.05.1993, 18.06.1993, 29.06.1995, 1-30.06.2002, 22.04.2009 leg. A. Barševskis (3♂♂, 1♂/1♀, 1♀, 1♂, 1♂/1♀, 1♂, DUBC), 5-10.06.2006 leg. M. Verdenfelde (1♂, DUBC); Stropi, 11.06.2009 leg. A. Barševskis (1♂, DUBC); Višķi, 30.03.1986, 12-27.04.1991, 14.12.1991 leg. A. Barševskis (2♂♂, 1♂/1♀, 1♂, DUBC); Engure: Abragciems, 18.07.2001 leg. A. Napolov (1 ex., AN); Ilūkste: Bebrene, 18.09.2006, 28.10.2006, leg. E. Rudans (1♀, 2♂♂/1♀, DUBC); Dviete, - 07.2006 leg. Anonymous (1♀, DUBC); Ilūkste, 17.04.1993 leg. A. Barševskis (1♂, DUBC); Šarlote, 14.09.1991 leg. A. Barševskis (1♂/1♀, DUBC), 4.05.2009 leg. K. Aksjuta (1♂, DUBC); Šedere, 12.06.2007 leg. M. Murd (1 ex., DUBC); Jēkabpils: Dunava, 11.04.1993, 1.01.1995, 15.04.1995, 6.04.1996, 22.09.1996, 10-30.06.2007, 12-18.07.2009 leg. A. Barševskis (2♂♂, 1♂, 2♂♂, 1♀, 1♀, 1♂/1♀, 1♀, DUBC); Rubeni, 1.06.1997, 28.03.1999 (published as *B. meridionalis* (Leskina 2000), 4.04.1999 leg. I. Leiskina (1♂, 1♀, 1♂, DUBC); Jelgava: Jelgava, 1.05.1997 leg. R. Matrozis (2♂♂/1♀, FS); Jūrmala: Kauguri, 1.05.1992 leg. A. Barševskis (1♂, DUBC); Krāsava: Ūdrīši, "Zapoļņiki", 8-10.05.2009 leg. M. Janovska (1 ex., DUBC); Kaplava, Varnaviči, 27.05.1990 leg. A. Barševskis (1♀, DUBC); Madona: Bērzaune, Gaiziņkalns, 5.11.2005, leg. A. Barševskis (2♀♀, DUBC); Arona, Lautere, 1-3.06.2006 leg. A. Ilzēna-Rozentāle (1♀, DUBC); Preiļi: Jersika, 21.05.2005, 7.09.2008, 1-10.05.2009,

28.06.2009, leg. A. Barševskis (1♂, 1♂ 1♀, DUBC), 7.09.2008 leg. A. Barševskis and K. Barševska, published as *B. meridionalis* (Barševskis *et al.* 2009) (1♀, DUBC); Rēzekne: Rēzekne, 8. 11.2008, leg. J. Kupce (1♂/1♀, DUBC); Rīga: Rīga, 8.05.1994, 29.04.1997 leg. R. Matrozis (1♀, 1♀, FS), 5.06.1994 leg. F. Savich (1♂, FS); Garciems, Garupe, 3.05.1995 leg. F. Savich (1♀, FS); Garupe, 14.05.1994 leg. F. Savich (1♀, FS); Rumbula, 12.04.1994 leg. F. Savich (1♂, FS); Rucava: Pape, 24.06.1998 leg. F. Savich (1♀, FS); Saldus: Šķēde, 7.10.1995 leg. F. Savich (1♂, FS); Sigulda: Allaži, Kangarnieki, 29.04.2006 leg. M. Kalniņš (1♂, DUBC); Talsi: Slīteres Nacionālais parks, 13.06.2007 leg. K. Aksjuta (1♂, DUBC); Vārkava: Vārkava, 25.06.1992 leg. G. Spuriņš (1♀, DUBC); Ventspils: Moricsala Nature Reserve, - 10.2010 leg. U. Valainis (1 ex., DUBC); Usma, 19.07.2007, 5-6.10.2011 leg. A. Barševskis (1♀, 1♂, DUBC); Zilupe: Pasiene, 19.07.1989, leg. A. Barševskis (1♂, DUBC); Lithuania: Akmenė: Gimbetišké, 9.05.1995 leg. Vidm. Monsevičius (1♀, KZM); Kamanos Strict Nature Reserve, 4.05.1992 leg. R. Ferenca (1♂, KZM), 2.05.1984, 11.06.1984, 19.08.1984, 19.10.1997, 31.05.2002 leg. Vidm. Monsevičius (1♂, 1♀, 1♀, 1♂, 1♀, KZM); Alytus: Žuvintas Strict Nature Reserve, 15.04.1979, leg. Vidm. Monsevičius (1♂, KZM); Anykščiai: Deveniai, 19.06.1989 leg. B. Šablevičius (1♂, KZM); Katlėriai, 19.08.1988 leg. S. Karalius (1♀, KZM); Kurklė, 14.05.2016, 26.05.2016, 9.06.2016, leg. Ž. Obelevičius (2♀♀, 1♀, 1♂, KZM), Maciūnai, 14.05.2016, 26.05.2016, 19.06.2016 leg. Ž. Obelevičius (3♀♀, 1♀ 1♀, KZM) Surdaugiai, 26.05.2016, 9.06.2016, 19.06.2016, 13.07.2016, 28.07.2016, 14.08.2016, 26.08.2016 leg. Ž. Obelevičius (1♀/1♂, 1♀, 1♀/1♂, 1♂, 1♀/1♂, 1♂, 2♀♀/1♂, KZM); Kaišiadorys: Kruonis, 20.04.2002 leg. A. Meržijevskij (1♂, AM); Vaiguva forest, 27.05.2003 leg. R. Ferenca (1♂/1♀, KZM); Kalvarija: Juodeliai, 27.06.1995 leg. H. Ostrauskas (3♂♂, KZM), Norvydai, 19.08.1981 leg. R. Ferenca (1♀, KZM); Kaunas: Akademija, 3.05.2004 leg. V. Tamutis (1♀, KZM); Aleksotas, 19.03.2002 leg. V. Tamutis (1♂, KZM); Braziūkai, 15.07.2004, 26.06.2006, 10.09.2016 leg. V. Tamutis (1♀, 1♂, 1♀, KZM); Dubrava forest, 29.07.1984, leg. R. Ferenca (1♂, KZM), -- 1987 leg. A. Ragelis (1 ex., KZM); 2.05.1999 leg. P. Zolubas (1 ex., KZM); Ežerėlis, 25.06.2008 leg. A. Meržijevskij (1 ex., AM); Jiesia Landscape Reserve, 25.05.1984, 9.04.1989, 18.09.1992, 31.05.2001, 10.05.2008, leg. R. Ferenca (1, 1, 1, 2, 1 ex., KZM), 30.05.2010 leg. A. Meržijevskij (1♂, AM); Kamša forest, 6.05.1992, 20.05.1992 leg. V. Tamutis (1♂/1♀, 1♂/1♀, KZM); Kaunas, 15.09.1989 leg. R. Ferenca (1♀, KZM); Margininkai, 31.08.1997, 9.05.1999, 20.06.1999 leg. V. Tamutis (1♀, 1♂, 1♂, KZM); Noreikiškės, 23.05.1995, 22.09.1995, 15.11.2008, leg. V. Tamutis (2♂♂, 2♂♂, 1♀, KZM); Pajiesiai, 7.05.1938 leg. A. Palionis (1♀, KZM); Papiškės, 31.03.2007 leg. V. Tamutis (1♂, KZM); Papiškinė forest, pheromone trap for *Ips typographus*, 10.05.2016 leg. V. Tamutis (1♀, KZM), Ringaudai, 22.10.2003 leg. V. Tamutis (2♂♂, KZM); Klaipėda: Klaipėda, 27.04.1990, 12.05.1990, leg. S. Karalius (1♂, 1♂, KZM); Smiltynė, 22.07.1988, 17.07.1991 leg. S. Karalius (1♂, 1♀, KZM), 11.04.2004, leg. R. Ferenca (1♂, KZM); Palanga: Manciskė, 9.05.2001 leg. R. Ferenca (3♀♀, KZM); Palanga airport env., 8.05.2001 leg. R. Ferenca (1♂, KZM); Šakiai: Tervydoniai, 8.05.1988, 27.09.2014, 27.06.2015, 27.03.2016 leg. R. Ferenca (1♀, 1♂, 1♀, 1♂, KZM); Šiauliai: Dzidai, 4.08.2002 leg. V. Tamutis (2♀♀, KZM); Šilalė: Juodžiai, 4.04.2010, leg. R. Ferenca (3♂♂, KZM); Medvėgalis, 7.07.2005 leg. P. Ivinskis (1 ex., KZM); Švenčionys: Jakeliai, 1.05.2015 leg. R. Patapavičius (1♂, KZM); Trakai: Bitiškieji Lake env., 12.08.1927 leg. B. Ogijewicz (1 ex., KZM); Galvė Lake env., 13.08.1927, 10.07.1929, 28.07.1929, 9.08.1929 (leg. B. Ogijewicz (1♀, 1♂, 1♂, 1♂/1♀, KZM); Skaistis Lake env., 1.09.1928, 23.06.1929, 6.10.1929 leg. B. Ogijewicz (1 ex., 1♀, 1♀, KZM); Trakai, 6.08.1896, leg. Markiewicz (1♂, KZM), 2.01.1937, leg. Anonymous (1♀, KZM); Varnikai, 30.06.1994 leg. H. Ostrauskas (1 ex., KZM); Ukmergė: Zujai -Vidiškiai, 30.10.1983, leg. L. Tiškevičius (1♀, KZM), 17-25.04.1984, 5-24.05.1984 3-24.07.1984 leg. R. Dvilevičius (1♂/3♀♀, 2♂♂/5♀♀, 2♂♂, KZM), 8.11.1983 leg. A. Čepelė (1♀, KZM), 21.04.1984 leg. G. Švitra (1♀, KZM); Utena: Utena, 7.06.1964 leg. E. Gaidienė (1 ex., KZM); Varėna: Jablanavas, 13.06.1998 leg. A. Gedminas (1 ex., KZM); Vilnius: Dūkštų ažuolynas forest, 1.06.2003 leg. S. Morkūnas (2♀♀, KZM); Veliučionys, 13.05.1971 leg. A. Manikas (1♂.); Vilnius, 12.08.1927 21.05.1930, 27.07.1930, leg. B. Ogijewicz (1♀, 1♀, 1♀, KZM); Zarasai: Salakas, 24.06.1996 leg. H. Ostrauskas (2♀♀, KZM).

Additional material: Germany: Bavaria: München: Schleisheim, 19.06.2005 leg. H. Kulzer (1♂, BSCZ), Wessling, 11.05.1994 leg. O. Bühlmann (1♀, BZCZ), Überlingen - 03. 1994, leg. A. Horion (1♀, BSCZ), Aschau, 4.04.1946 leg. H. Freude (1♂, BSCZ), Garhing, - 04.1950, - 05.1955, leg. K. E. Hüdephil (1♀, BSCZ), Sammlung, 9.06.1948, 7.08. 1948 leg. O. Bühlmann (1♀, 1♂, BSCZ); Berlin: Müllkippe Marienfelde, 16.07.1971, leg. H. Korge (1♂, BNM), Berlin-Biesdorf, Süd Garten, 4.06.2005 leg. H. Wendt (1♂/1♀, BNM); Mecklenburg: Vorpommern, LSG Schlosspark, 12-21.05.2007, leg. M. Grünwald (1♂, BNM); Dorf Wehlen; Turkey: Kastamonu, 25 km SE Tosya, 1600 altitude, pine forest, 6.04.2009 leg. V. Assing and P. Wunderle (1♂, 1♀, BNM),

Comparative Morphology and Morphometry

Published records: Estonia: Harju, Lääne, Lääne Viru, Põlva, Rapla, Saaremaa, Tartu (Haberman, 1968); Hiiumaa (Miländer, 1993). Latvia: Kurzeme (Kawall, 1866); Koknese (as synonym of *B. bipustulatus*) (Seidlitz, 1872, 1887); Melluži (Jūrmala) (Stiprais, 1984); Arņe, Daugavpils, Ilgas, Svete, Krauja, Medumi, Naujene, Nīcgale, Vasargēlišķi, Višķi (Daugavpils), Šarlote, Eglaine, Pilskalne (Ilūkste) Šķeltiņi, Šķeltova (Aglona), Izvalta, Krāslava, Kombuļi, Piedruja (Krāslava), Kuprava (Viļaka), Stabulnieki (Riebiņi), Koknese, Viskāļi (Koknese), Teiču Nature Reserve, Krustkalni Nature Reserve (Barševskis, 1987, 1993); Līksna, Vabole (Daugavpils) (Cibulskis, 1994); Silene (Daugavpils) (Barševskis *et al.*, 2002); Moricsala Nature Reserve (Barševskis *et al.*, 2004); Gauja National Park (Kalniņš *et al.*, 2007); Bebrene, Šedere (Ilūkste), Ūdrīši (Krāslava), Dunava (as *B. lacertosus*) (Jēkabpils), Jersika (as *B. lacertosus*) (Preiļi), Slitere National Park (Talsi) (Barševskis *et al.*, 2009), Skrīveri (Aizkraukle) (Bukejs *et al.*, 2009), Poki (Jelgava) (Gailis and Turka, 2014). Lithuania: Kaunas (Heyden, 1903, Ferenc, 2006); Trakai, Vilnius (Roubal, 1910, Ogjiewicz, 1933); Panevėžys (Ferenc, 2006); Žuvinas Nature Reserve, Lazdijai, Alytus (Sharova and Grūntal, 1973); Ukmergė (Dvilevičius *et al.*, 1988).

Description. The body pattern is almost similar to that of *B. meridionalis*; however, scutellum and mesothorax are constantly black to black-brown, the first antennomere is entirely yellow or red-yellow, 2-6 antennomeres are darkened. The black pattern of elytra is generally composed of one semi-lunular spot on each elytron (Fig. 3c); occasionally this spot is divided into two parts transversely. The interior margins of semi-lunules are curved variously and forming various shape yellow-red spots on both sides of the suture. The black semi-lunule is confined mostly by a more or less convex line, occasionally by a wiggle in the front. Short setae are absent from the apical margin of elytra. The microsculpture of elytra is fine, composed of transversal fissures, the contours of which can be well visible magnified 80 times. Two or three fissures are arranged along the distance of 10 μm of the surface of elytra (Fig. 5d). The surface of elytra is distantly iridescent.

The sexual dimorphism is distinct by the width diameters of the head, pronotum and elytra (Table 1). The means of WH and LH in males average 0.785 and 0.824 mm, respectively, and are significantly lower compared to females ($U = 906.5$; $p < 0.01$; $U = 1423$; $p < 0.01$). The pronotum slightly varies in the straightness of lateral margins and roundness of posterior angles by both genders (Figs. 6c, d), but it is significantly wider in females (1.629 mm) than in males (1.59 mm) ($U = 2039$; $p < 0.0264$) (Table 1). Also, the mean of the width of elytra, LH/WH and LP/WP are significantly higher in females ($P < 0.05$) (Table 1). The distance from the base of elytra to the anterior side of the lunular black spot of elytra (BS) differs insignificantly between genders and varies from 0.7 to 1.2 mm.

The aedeagus has a relatively short ending part of the median lobe (Figs. 7c, d). A small kink directed toward the ventral side on the apex and a small tooth or knoll (sometimes indistinct) directed upward and situated in the apex of the median lobe are visible in lateral view (Figs. 9c, d). The median lobe is distinctly asymmetric and distinctly incurved on the apex (Figs. 7. c, d). The left paramer is wide, the proximal margin is broadly rounded, the basal margin varies from almost straight to convex, without distinct indentation or slightly indented in the proximal margin (Figs. 8c, d); the apical margin ungradually rounded; the basal process is curved variously. The right paramer is trowel-form, confined by a blunt to slightly rounded margin in the apex (Figs. 10c, d). The genital ring is elongated, with straight or slightly convex margins, rather asymmetric, with a fairly short apex which is curved right (Figs. 11. c, d). Gonocoxite 1 is triangular or funnelform, the inner margin is convex, without

distinct punctation. Gonocoxite 2 is curved, disorderly punctate; the blade is blunt and short (Fig. 12d) to sharp, rather elongated finger-form and curved (Figs. 12c, e). The median and lateral ensiform setae are sharp (Figs. 12c, e) to short and blunt (Fig. 12 d). All setae on the apical margin of laterotergites are directed outward, more or less by a sharp angle to the margin (Figs. 12c, d, e). The posterior part of laterotergites varies from more or less prolonged (Figs. 12 d, e) to short, bell-shaped (Fig. 12 c). The reproductive tract is with a short, broad, cap-shaped bursa copulatrix and a diverse by thickness C-shaped spermatheca and a coiled distal portion (Figs. 13c-e).

Variations. It is a very polymorphic species. Some of aberrations and variations of this species based on different shape of semi-lunular black spots of elytra have been mentioned by Puel (1925) and Jeannel (1942). Two of them, *B. meridionalis* and *B. lacertosus*, presently have the status of valid species (Baehr, 2003). Actually, this species varies not only by the pattern of elytra, but also by the shape of the pronotum, color of the scutellum, depth of elytral striae, and shapes of structures of genitalia. Interior margins of black semi-lunules on elytra are curved variously and forming various shape yellow-red spots on both sides of the suture: round, trapeziform, rectangular, semi-lunular, cordiform or wedgeform; also, its front line is confined variously: sharply or broadly curved, denticulate or bracketformed. In combination of these characters, almost each specimen of this species is different. One more strongly varying character is the shape of the pronotum. Despite differences of pronotum width among genders, the lateral margins and roundness of posterior angles vary within genders as well (Figs. 6. c, d). The small tooth directed upward of the apex of the median lobe of the aedeagus is mentioned as a certain character for distinguishing this species, but it can be reduced to an indistinct knoll in some males. Also, very interesting is variability of shape of left parameres from almost oval to rather rectangular (Figs. 8c, d). Basal processes both of left and right parameres vary by their falling to the basal margin of the paramer from angles of 45° up to 80°. The gonocoxites 2 of females vary by their length and apex of blades from rather long, sharp, fingerform, with normal ensiform, slightly curved setae (Figs. 12c, e) to short and blunt, with short and blunt setae (Fig. 12d). The shape of spermatheca and its coiled distal portion varies as well (Figs. 13c-e).

Differential diagnosis. Due to the variety of some of above-mentioned traits of body, this species is often confused with *B. meridionalis* and *B. lacertosus*. It seems quite explainable that these currently valid species were previously regarded as variations of *B. bullatus* (Puel, 1925; Jeannel, 1942). We found that the most characteristic body traits could be the thinner fissures of elytral microsculpture and distant iridescence compared with the same traits of *B. meridionalis* and *B. lacertosus*. Of course, *B. bullatus* seems to be the smallest species and it significantly differs from other species of this subgenus by its body length, width and length of the head, pronotum and elytra, distance from the base of elytra to the anterior side of the lunular black spot (Table 2), but sometimes these parameters overlap (Figs. 14a-h.). The median lobe of the aedeagus is quite characteristic by its small tooth directed upward on the apex (Fig. 9c), but it could be reduced to weak and indistinct (Fig. 9d). In that case the ventral view could be helpful, where the apex of the median lobe is rather broader than that

Comparative Morphology and Morphometry

of *B. meridionalis* and *B. lacertosus* and there is distinct sag on the apex, which is absolutely missing in *B. lacertosus*. The shape of gonocoxite 2 and setation of the apical margin of laterotergites could be helpful for identification of females. Differently from *B. meridionalis* and *B. lacertosus*, the blade of gonocoxites 2 is usually prolonged (has some distance with parallel margins in the basal half), the inner margin is less convexed than in *B. meridionalis* (Fig. 12b), but distinctly shorter than in *B. lacertosus* (ratio h/m = 1.4-1.9) (Figs. 12f, g). The setae on the apical margin of laterotergites are directed by a more or less sharp angle to the margin (Figs. 12c-e), differently from *B. meridionalis* (Figs. 2b; 12b).

General distribution. Euro-Sibero-Central Asiatic species widely distributed in Europe, known in Caucasus, Turkey, Iraq, Iran, Uzbekistan, Kazakhstan, Siberia (Baehr, 2003). The northern border of its distribution range reaches 62° latitude in Europe and 60° latitude in Siberia, and the eastern border goes as far as the Amur River lowland (Lindroth, 1992; Krizhanovskiy *et al.*, 1995). This species is still unknown in Portugal, Spain, southern Italy, Macedonia, Tadjhikistan, China.

Table 2. Inter-specific differences in body morphological traits (pair groups with significant differences of mean values $p \leq 0.05$ are showed) in four species of *Badister* (s.str.). The Kruskal-Wallis test results estimated with the permutation procedure (PMonteCarlo) are reported (M - males, F - females, a, b, c, d, e, f, g, h - codes of groups, LB - length of body, WH - width of head, LH - length of head, WP - width of pronotum, LP - length of pronotum, WE - width of elytra, LE - length of elytra, BS - distance between the base of elytra and the black spot)

Traits	Species									
	<i>B. unipustulatus</i>		<i>B. meridionalis</i>		<i>B. bulatus</i>		<i>B. lacertosus</i>		Chi square	
	M	F	M	F	M	F	M	F	M	F
	a	b	c	d	e	f	g	h		
LB	c, e, g	d, f, h	a, e	b, f	a, c, g	b, d, h	a, e	b, f	95.3	90.41
WH	c, e, g	d, f, h	a, e	b, f, h	a, c, g	b, d, h	a, c, e	b, d, f	89.47	78.97
LH	c, e, g	d, f, h	a, e	b, f	a, c, g	b, d, h	a, e	b, d, f	68.26	64.91
WP	c, e, g	d, f, h	a, e	b, f	a, c, g	b, d, h	c, e	b, f	78.53	72.12
LP	e	f	e	-	a, c, g	b, d, h	a, e	b, f	36.44	31.16
WE	c, e, g	d, f, h	a, e	b, f, h	a, c, g	b, d, h	a, c, e	b, f	87.75	85.74
LE	c, e, g	d, f, h	a, e, g	b, f, h	a, c, g	b, d, h	a, c, e	b, d, f	92.79	88.97
BS	c, e, g	d, f, h	a, e, g	b, f, h	a, c, g	b, d, h	a, c	b, d, f	95.38	87.9
Ratio LH/LP	c, e, g	d, f, h	a, e, g	b, f, h	a, c	b, d, h	a, e	b, d	56.8	60.21
Ratio LP/WP	c, e, g	d, f, h	a, e	b, f, h	a, c	b, d	a	b, d	46.36	56.98
Ratio LE/LP	c, e, g	d, f, h	a, e, g	b, f, h	a, c	b, d, h	a, c	b, d	82.74	79.51
Ratio LE/BS	e, g	f, h	e, g	f, h	a, c, g	b, d	a, c, e	b, d, f	57.73	62.22

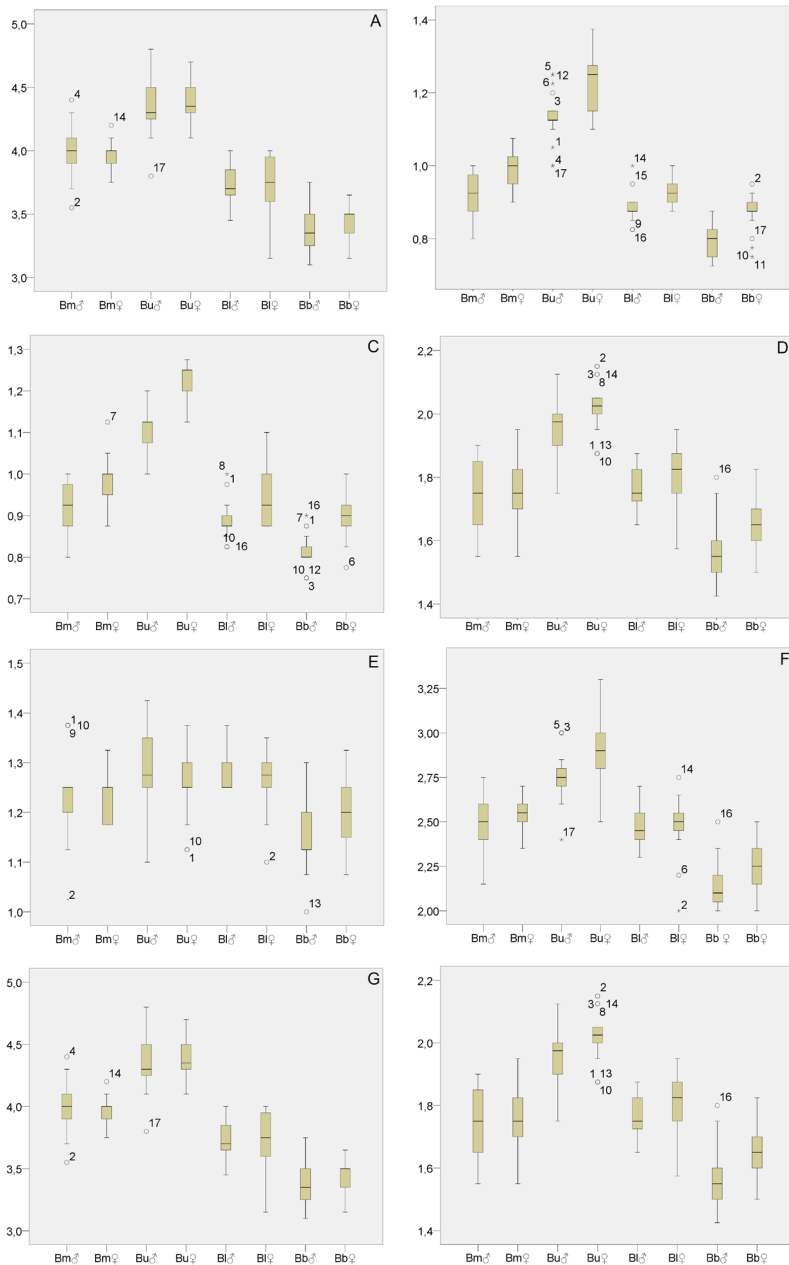


Fig. 14. Measured traits: A. body length; B. width of head (WH), C. length of head (LH), D. width of pronotum (WP), E. length of pronotum (LP), F. width of elytra (WE), G. length of elytra, H. distance between base and apical margin of lunular black spot of elytra; Bm. *Badister meridionalis*, Bu. *Badister unipustulatus*, Bl. *Badister lacertosus*, Bb. *Badister bullatus*.

Comparative Morphology and Morphometry

Remarks. The pattern of elytra is regarded as a valuable character for distinguishing this species (Makólski, 1952; Komarov, 1991; Arndt *et al.*, 2011; Puchkov 2013). But we found that this character is very variable and has a low value for identification of the *Badister bullatus* species group. The shape of the median lobe of the aedeagus seems to be the most faithful character, but its variations (mentioned above) should be considered.

Badister (s. str.) lacertosus Sturm, 1815

Examined material. Estonia: Harju: Kaila, Laulasmaa, - 06.1938 leg. Anonymous (2 ex., EMNH); Keila, 07.1939 leg. Anonymous (1 ex., EMNH); Lääne: Nõva, 28.05.1956 leg. J. Viibaste (1 ex., EMNH); Tartu: Tartu, 1827 leg. Anonymous (1 ex., EMNH); Valga: Helme, Kirikuküla, 24.09.1956 leg. E. Marivee (1 ex., EMNH); Latvia: Aglona: Kastuļina, Stivriņi, 06.10.1986 leg. A. Barševskis (1♀, DUBC); Šķeltova, 27.10.1991 leg. A. Barševskis (1♀, DUBC); Auce: 6 km E. Auce, 12.06.2015 leg. M. Balalainis (2♂♂/4♀♀, KZM); Daugavpils: Elerne, 04.2002 leg. A. Barševskis (1♀, DUBC); Ilgas, 19.06.1994 leg. A. Barševskis (2♂♂/2♀♀, DUBC); Naujene, 16.04.1987 leg. A. Barševskis (1♂, DUBC); Ilūkste: Pilskalne, 16.03.1989, 29.04.1994 leg. A. Barševskis (1♀, 2♂♂, DUBC), Straumēni, 27.05.2007 leg. M. Janovska (1♂, DUBC); Jēkabpils: Dunava, 12.07.1994 leg. A. Barševskis (1♀, DUBC), 1-8.06.2009 leg. K. Barševska (1♂, DUBC); Krāslava: Izvalta, 13.09.1986 leg. A. Barševskis (1♀, DUBC); Limbaži: Vitrupe forest, 21.05.-19.06.2011 leg. V. Spungis (2 ex., LUBF); Madona: Krustkalni Nature Reserve, 17.07.2007 leg. A. Barševskis (1♀, DUBC), 4 km E Madona, 3.06.2015 leg. M. Balalainis (3♂♂, 1♀, KZM); Rīga: Rīga, 31.05.1974 leg. L. Danka (1 ex., LMNH), Rīga Mežaparks, 8.06.2005 leg. A. Napolov (1, ex., AN); Rucava: Rucava, 26.04.-29.05.1997, 23.04.-20.05.1998 leg. V. Spungis (1, 1 ex., LUBF); Vārkava: Vārkava, 09.05.1992 leg. G. Spuriņš (1♀, DUBC); Ventspils: Moricsala Nature Reserve, Viskūžu Island, 27.09.2003 leg. V. Tamutis (1♂, KZM), Moricsala Nature Reserve, 29.06.2006, 14.07.2009, 16.08. 2010 leg. A. Barševskis (1♂, 1♀, 1♀, DUBC); Vecumnieki: 6 km NW Bārbele, 16.06.2015 leg. M. Balalainis (1♂, KZM); Lithuania: Akmenė: Gimbetišké, 17.05.1991 leg. Vidm. Monsevičius (1♀, KZM); Kamanos Strict Nature Reserve, 7.07.1984, 15.09.1984, 30.06. 1997, 30.06.2002 leg. Vidm. Monsevičius (1♂, 2♂♂, 1♂, 1♂, KZM), Užpelkiai, 05.05.1999 leg. Vidm. Monsevičius (1♀, KZM); Anykščiai: Kurklė, 14.05.2016, 9.06.2016 leg. Ž. Obelevičius (2♂♂/1♀, 2♀♀, KZM), Maciūnai, 13.07.2016 leg. Ž. Obelevičius (1♂); Biržai: Miegonyš, 25.06.1973 leg. A. Manikas (1♂, KZM); Neringa: Juodkrantė, 14-15.06.2012 leg. R. Ferenc (1♂, KZM); Kaišiadorys: Kaukinė Botanical-Zoological Rezerve, 24.09. 1994 leg. B. Šablevičius (1♂, KZM), Pravieniškės, 09.05.1986 leg. R. Ferenc (1♀, KZM); Kalvarija: Trakėnai, 05.09.1999 leg. V. Monsevičius (1♀, KZM); Kaunas: Braziūkai, *Anthriscus sylvestris* overgrowth, 10.07.2007 leg. V. Tamutis (2♂♂, KZM), Dubrava forest, pheromone trap for *Ips typographus*, 02.05.1999, leg. P. Zolubas (1♂, KZM); Kamša Botanical-Zoological Rezerve, 02.04.1992, 15.04.1992, 08.04.1997 leg. V. Tamutis (1♀, 1♀, 2♂♂, KZM), Noreikiškės, 20.05.1994 leg. V. Tamutis (1♀, KZM); Šakiai: Juškinė Forest, 30.04.2000 leg. R. Ferenc (1♂, KZM), Tervydoniai, 27.09.2014, 27.03.2016 leg. R. Ferenc (1♂, 1♂, KZM); Šilalė: Juodžiai, 05.04.2010 leg. R. Ferenc (1♀, KZM); Trakai: Trakai, 23.06.1929 leg. B. Ogijewicz (1♀, KZM); Ukmergė: Dukstyna Entomological Reserve, 04.05.1984 leg. R. Dvilevičius (3♂♂, KZM), Kalnai forest, 5.04. 2017 leg. V. Tamutis (1♂, KZM), Ratakalnis forest, 5.04.2017 leg. V. Tamutis (1♂, KZM), Vytinėle forest, 20.04.2004, 10.06.2004, 21.06.2004, 30.06.2004, 19.07.2004, 29.07.2004, 18.08.2004, 28.08.2004 leg. N. Noreika (2♂♂, 4♀♀, 2♂♂/1♀, 1♂, 2♂♂, 1♀, 2♀♀, 1♀, 1♀, 1♂, KZM); Utena: Antalgė, 03.04.1977 leg. A. Kaulinis (1♀, KZM); Varėna: Pogarenda, 19.09.1981 leg. V. Monsevičius (1♂, KZM); Vilnius: Baltupiai, 14.04.1931 leg. B. Ogijewicz (1♀, KZM).

Additional material. Germany: Berlin: Tegel, Flughafensee Wald, 10.07.2004 leg. Diehr (1♂, BNM); Frankfurt (Oder), 6.05.1997 leg. A. Barševskis (1♂, DUBC); Görlitz: Weinhübel, 30.07.1962 leg. Anonymous (1♀, BNM); München: Ampermoching, 22.09.1955 leg. Dr. Engelhardt (1♀, BSCZ); Weimar: Bad Berka, - 06.1983, leg. Materlik (1♂, BNM); Russia: Kaliningrad oblast: Svetlogorsk, 26.04.1998 leg. V. I. Alekseev (1♂, DUBC); Irkutsk oblast: 17 km SW Irkutsk, 18.05.1990 leg. A. Anichtchenko (1♀, DUBC).

Published records. Estonia: Harju, Lääne, Rapla, Tartu (Haberman, 1968); Hiiumaa (Miländer, 1993). Latvia: Kurzeme (Fleischer, 1829; Kawall, 1866); Rīga (Stiprais, 1973); Ilūkste, Daugavpils, Aglona, Krāslava (Barševskis, 1993), Gauja National park (Kalniņš *et al.*, 2007); Elerne (Daugavpils,

Bebrene (Ilūkste), Šķeltova (Aglona), Slītere National Park (Talsi), Moricsala Nature rezerve (Ventspils) (Barševskis *et al.*, 2009); Lithuania: Kaunas (Tamutis and Dapkus 2008), Vilnius (Ogijewicz, 1933); Ukmergė (Dvilevičius *et al.*, 1988) and Varėna (Miländer *et al.*, 1988).

Description. The body pattern: black-colored head, mesothorax, metathorax, abdomen, and a semi-lunular spot (it can be divided into two spots transversely) on each elytron; yellow-red pronotum, scutellum, the remaining part of elytra, palpi and legs. The first antennomere is yellow or red-yellow, slightly darkened anterior, 2-6 antennomeres are darkened, the remaining are brown. The interior margins of semi-lunules, if entire, are curved variously and forming various shape yellow-red spots on both sides of the suture; its front margin is usually straight (roughly 50% of all our examined specimens) (Fig. 3d, ♂), but also can be slightly rounded (about 25 %) (Fig. 3d, ♀) or wiggled (about 25%). Short setae are absent from the apical margin of elytra. The microsculpture of elytra is fine, composed of thin transversal fissures, the contours of which are well visible magnified 150 times, but become blend magnified less than 90 times. Three or four fissures are arranged along the distance of 10 μ m of the surface of elytra (Fig5 c). The iridescence of the surface of elytra is distinct. The length of bodies is quite similar among genders: 5.7-6.7 mm in males and 5.5-6.9 mm in females. However, the head and pronotum are significantly wider in females compared to males (Table 1). The WH and LH are 0.886 and 0.883 mm, respectively, in males, and that is significantly lower than in females ($U = 83$; $p < 0.01$; $U = 110.5$; $p < 0.05$). The pronotum slightly varies in situation of lateral margins to posterior by both genders (Fig. 6e), and it is significantly wider in females (1.81 mm) than in males (1.763 mm) ($U = 207.5$; $p < 0.0206$) (Table 1). Also, the LH/LP is significantly higher in females ($p < 0.01$); however, the ratio of length and width of pronotum is significantly higher in males ($p = 0.01$) (Table 1). The aedeagus has a relatively long ending part of the median lobe (Figs. 7e, 8e). A small tooth directed toward the ventral side on the apex is well visible in lateral view (Fig. 9 e). The median lobe is slightly asymmetric without any incurvation on the apex in dorsal view (Fig. 7e). The left paramer is wide, proximal margin is broadly rounded, basal margin is almost straight, without indentation in the proximal part (Fig. 8e); the apical margin is slightly, gradually rounded; the basal process is rather curved. The right paramer is trowelform, roundly confined in the apex (Fig. 10e). The genital ring is wide and elongate, its lateral margins are weakly convex (Fig. 11. d). Gonocoxite 1 is triangular, funelform or buttleform, the inner margin is gradually convexed (Fig. 12f), or forming an obtuse angle (Fig. 12g). Gonocoxite 2 is disorderly punctate, inner margin is almost straight; its blade is blunt to sharp, rather elongated and slightly curved. The ensiform setae are fingerform, relatively long, sharpened or blunted in the apex. Most of the setae (some of them are directed differently) of the apical margin of laterotergites are directed more or less by a sharp angle to the margin. The posterior part of laterotergites is short, bell-shaped, well sclerotized (Figs. 12f, g). The reproductive tract is with a short, broad, cap-shaped bursa copulatrix and a long C-shaped, relatively fine spermatheca with a coiled distal portion directed to the left (Fig. 13f).

Variations. This species was considered a morphological variation of *B. bullatus* (*bipustulatus*) (Puel, 1925; Jeannel, 1942) till Lindberg (1948) gave a detail description

Comparative Morphology and Morphometry

and incontrovertible evidence of the valid species status of this form. Also, Lindberg (1948) described some of possible intraspecific variations of *B. lacertosus* in the shape of the median lobe of the aedeagus. However, this species varies by the pattern of elytra, shapes of the pronotum and gonocoxites like *B. bullatus* (Figs. 3.d; 6e; 12f, g). The interior margins of black semi-lunular spots are curved variously and forming various shape yellow-red spots on both sides of the suture (Fig. 3d). The front margin of black semi-lunules is confined mostly by a straight line, but we found that it can be slightly convex or wiggled as well. Despite differences of pronotum width among genders, the situation of lateral margins slightly varies within genders as well. The lateral margins of the pronotum could vary from gradually convex to almost straightly sinuate posteriorly.

The shape of the median lobe of the aedeagus both in ventral and lateral view slightly varies, but unfortunately, we did not find it to be distinct. However, gonocoxites 2 vary strongly by their length and apex of blades: they vary from rather long, sharpened to short and blunt. The same variation can be detected in the shape of medial and lateral ensiform setae of gonocoxite 2 (Figs. 12f, g).

Differential diagnosis. Due to the variety of some of body traits, this species is often confused with *B. meridionalis* and *B. bullatus*. The most characteristic body trait we have found is the microsculpture rougher than in *B. meridionalis*, but finer than in *B. bullatus* (Fig. 5b-d). The iridescence of elytra is distinct, but weaker than in *B. meridionalis*. Length of body, width of head, width of pronotum, width of elytra are often similar to these body traits in *B. meridionalis*, but length of head, length of elytra, and distance from the base of elytra to the anterior side of the lunule black spot (BS) are significantly lower. Compared with *B. bullatus*, almost all values of parameters of body traits are higher; however, their ratios are quite similar, except for the ratio of length of elytra and BS (Table 2), but sometimes these parameters overlap (Figs 14 a-h). The median lobe of the aedeagus is quite characteristic by its length, more or less gradually sinuated lateral margins and lack of distinct incurvation on the apex. The apex of the median lobe is rather slender compared with those of *B. meridionalis* and *B. bullatus*. The shape of gonocoxite 2 and setation of the apical margin of the ventral surface of laterotergites are quite similar to those of *B. bullatus*. However, the blade is generally shorter, its inner margin is longer (ratio h/m = 0.9-1.1).

Remarks. The pattern of elytra is regarded as a valuable character for distinguishing this species (Makólski, 1952; Komarov, 1991; Arndt *et al.*, 2011; Puchkov, 2013). But we found that this character varies and is not so good for identification. It is worthy to note that the microsculpture of elytra of *B. lacertosus* is distinctly coarser than that of *B. meridionalis*, contrary to the result given by Makólski (1952) and Assman (2004). Komarov (1991) detected the microsculpture of elytra to be almost similar for all three species: *B. meridionalis*, *B. bullatus*, and *B. lacertosus*.

General distribution. Trans-Eurasian - temperate-Southern Siberian species widely distributed in Europe, known in Kazakhstan, Kyrgyzstan (Krizhanovskiy *et al.*, 1995; Baehr, 2003). The northern border of its distribution range reaches 63° latitude in

Europe and 60° latitude in Siberia, eastern border reaches as far as South Sakhalin (Krizhanovskij *et al.*, 1995) and South Primorye (Sundukov, 2009).

DISCUSSION

Analysis of morphological characters

High variability of morphological characters within species of *Badister* (s. str.) has been recognized previously and well presented, in particular for North American species (Ball, 1959), while for European species this trait is still studied incompletely. The greatest attention was paid to varieties of coloration of elytra by Puel (1925). Even five variations and aberrations for *B. unipustulatus* and eight for *Badister bipustulatus* (Fabricius, 1792) (= *Badister bullatus* (Schrank, 1798)) were presented in his comprehensive key of European *Badister* species. However, new descriptions or redescriptions of some variations or aberrations remain brief in later papers (Jeannel, 1942; Makólski, 1952). Later, two of them: *B. lacertosus* and *B. meridionalis*, were started to be ranked as valid species (Lindberg, 1948; Lohse, 1954). Additionally, some variations of the shape of the pronotum of *Badister bullatus* were presented by Komarov (1991). Despite a comparatively small dispersion of our examined material (only a small number of specimens from other regions have been additionally included in our study), we found variations of morphological characters of all species. Especially high variability was detected among specimens of *B. bullatus*. We found high variability not only in the shape of the pronotum, coloration of the scutellum and elytra, but also in the structure of genitalia both of males and females (it is described above in detail). We carefully examined each specimen of this species for variability and tried to find a complex of good indications as a background for description of new species, but our findings were not substantial. In our opinion, a deeper study including material from different parts of the distribution range and using molecular research methods could explain this phenomenon. Differences between genders and sexual dimorphism are distinct in *Badister* species, and they are mostly distinguished by dilated three first tarsomeres of the fore tarsus and two setiferous punctures on sixth abdominal sternites of males and not dilated tarsomeres of the fore tarsus and four setiferous punctures on sixth abdominal sternites of females (Ball, 1959; Lindroth, 1986; Komarov, 1991). Additionally, we found that females of all four species have a surely larger head than males; also, the pronotum is wider of females of *B. bullatus* and *B. lacertosus* (Table 1). The ratios of parameters of these parts of the body are also differentiated. The utility of the female reproductive tract for taxonomy and inferring phylogenetic relationships in Carabidae have been well demonstrated by Liebherr and Will (1998), although this system is explored particularly only for Naerctic and Neotropical species of the tribe Licinini (Will, 1998; Erwin, Ball 2011). We found that the reproductive tract of females of our studied four species of *Badister* (s. str) subgenus is markedly similar to each other and is quite analogous to homologous structures of species from the western hemisphere (Will, 1998; Erwin, Ball 2011). Differently from them, our examined species have a more intensive, generally C-shaped, basal uncoiled portion of the spermatheca. Spermathecal distal coiled portions are quite long, compact, have at least six coils;

Comparative Morphology and Morphometry

gonocoxite 1 is aetose; gonocoxite 2 is falcate, having two dorsal ensiform and one ventral ensiform setae like *Badister amazonus* Erwin and Ball, 2011 (Figs. 12, 13). The most useful character for the recognition of species we found to be the setation of the apical part of laterotergites and the shape of gonocoxites 2.

Assuming the stability of our examined morphological characters of *Badister* (s. str.) species, we propose the following key for identification of the species:

1. The mean of ratio of elytra length and distance from base of elytra to apical margin of lunular spot <3; apical margin of elytra with a row of setae (Fig. 4); microsculpture of elytra consisting of very tightly deposited transversal fissures, at least five fissures arranged along the distance of 10 µm of surface of elytra (Figs 5a, b)2

- The mean of ratio of elytra length and distance from base of elytra to apical margin of lunular spot >3; row of setae completely absents on apical margin of elytra; microsculpture of elytra consisting of tightly deposited transversal fissures, at maximum four cells arranged along the distance of 10 µm of surface of elytra (Figs. 5c, d)3

2. The setae on apical margin of elytra as long as half of second interval, well visible (Fig. 4a); mesepisternum and scutellum entirely pale; black semi-lunular spot on elytra usually divided transversely or joined narrowly beside outer margin of elytra (Fig. 3a); median lobe apically inclined ventrally with inflated protuberance (Fig. 8a); inner margin of gonocoxite 2 slightly convex, almost straight, punctation on apical margin of laterotergites dispersed along outer margin (Fig. 12a); body length 6.1-7.4 mm.....*B. unipustulatus*

- The setae on apical margin of elytra as long as ¼ of second interval, indistinct (Fig. 4b); mesepisternum and scutellum dark, black semi-lunular spot on each elytron regularly continuous, rarely divided into two parts transversely; median lobe with smooth and small kink directed toward ventral side on apex (Fig. 9b), markedly sinuated laterally, with distinct incurvation in the top (Fig. 7b); inner margin of gonocoxite 2 distinctly convex, punctation on apical margin of laterotergites more concentrated on apex, setae directed forward, more or less perpendicular to margin (Fig. 12b); body length 5.6-6.8 mm.*B. meridionalis*

3. The contours of fissures of microsculpture invisible and blended under magnification of 90 times; black semi-lunular spot on each elytron regularly confined by more or less straight or widely convex line (Fig. 3d); distal part of median lobe relatively long, with smooth and small tooth directed toward ventral side on the apex (Fig. 9e), gradually sinuated laterally, without any incurvation in the apex (Fig. 7e); inner margin of gonocoxite 2 straight almost as long as width of gonocoxite 2 measured beside first ventro-lateral ensiform seta (Figs. 12f, g).*B. lacertosus*

- The contours of fissures of microsculpture visible under magnification of 80 times; iridescence of elytra absent; black semi-lunular spot on each elytron regularly confined by more or less curved line (Fig. 3c); ending part of median lobe relatively short, with small tooth directed toward ventral side on the apex and small tooth or knoll (sometimes indistinct) directed upward at its apex (Figs. 9c, d), ungradually sinuated

laterally, with distinct incurvation in the apex (Figs. 7c, d); inner margin of gonocoxite 2 almost straight or slightly convex, but rather shorter than width of gonocoxite 2 measured beside first ventro-lateral ensiform seta (Figs. 12c, d, e).....*B. bullatus*

Ecological traits

Ecologically, most of *Badister* (sensu lato) species prefer moist or semi-moist habitats and are regarded as hygrophilous species (Lindroth, 1986, 1992), and only some of them could tolerate mesophilic stations. Particular representatives of such tolerants are *B. bullatus* and *B. lacertosus*. *B. bullatus* is regarded as the most eurytopic species occurring both in dry and moist, open and partly shaded habitats (Lindroth, 1986), but it avoids swamps or rather dark forests (Makólski, 1952). The indifference of this species to habitat conditions is well confirmed by studies of Brygadyrenko (2015) where it is presented as the most drought-resistant species of the genus in the Ukraine's steppe zone. Moreover, the findings of this species in agricultural or urban landscapes (Andersen, 2000; Elek, Lövei, 2005; Vesely, Šarapatka, 2008; Bukejs *et al.*, 2009; Galis, Turka, 2014) demonstrate its ability to survive under some anthropogenic pressure. Most of our collected specimens were found in mesophilic, open or partly shaded grasslands in the period from April to June. *B. lacertosus* is widely regarded as a mesophilic, forest species (Makólski, 1952; Komarov, 1991; Barševskis, 2003; Puchkov, 2013; Aleksandrowicz, 2014), but some authors classified it as a species that prefers wet habitats like *B. unipustulatus* (Lindroth, 1986; Hurka, 1996; Assman, 2004; Brygadyrenko, 2015). All our findings of *B. lacertosus* were done in forests (mostly in deciduous) or forest edges, in moderately moist habitats in the period from March to October. This species quite often was found together with *B. bullatus* in grasslands of forest edges or bushy areas. We found more stable positions regarding the ecology of *B. meridionalis* and *B. unipustulatus*. Makólski (1952) describing a new species *B. kineli* pointed a clear preference of the species to waters. "It lives near water in open areas with preference for wet meadows flooded in springtime" (Makólski, 1952). This position was confirmed later by other authors as well (Lindroth, 1986; Komarov, 1991; Hurka, 1996; Barševskis, 2003; Puchkov, 2013; Aleksandrowicz, 2014). Contrary to *B. meridionalis* *B. unipustulatus* prefers more shadowed habitats (Makólski, 1952; Lindroth, 1986), though its indifference to shadow was noted by Komarov (1991), Kirichenko (2000), Puchkov (2013), Brygadyrenko (2015). We can confirm the positive reaction to ultraviolet light in the night time for both these species as it was noted previously by Komarov (1991), because part of our studied specimens, according to label data, have been caught using light traps. It is interesting to note that our detected similarity of morphology of these species, particularly the row of setae on the apex of elytra, could be associated both of them to wet, often flooded habitats.

Distribution in Baltic countries

Although first data on the distribution of carabid species in the Baltic countries go back to the 19th century (Fleischer, 1829; Seidlitz, 1872; 1875), the first noticeable faunistic review on Estonian carabids was published more than 100 years later by

Comparative Morphology and Morphometry

Haberman (1968). Brief descriptions of morphology, biology and distribution of *Badister* species were published in his monograph. Later, almost similar overviews of the genus were presented in Lithuania and Latvia (Pileckis and Monsevičius, 1995; Barševskis, 2003). The data on distribution of four species, including *B. unipustulatus*, *B. bullatus* (= *bipustulatus*), *B. lacertosus* and *B. meridionalis*, in Estonia and Latvia was presented; however, the last-mentioned species was absent from Lithuanian fauna. The first record of *B. meridionalis* in Lithuania was noted by Barševskis (2001). Assuming the results of our study, we largely confirm the distribution of *B. unipustulatus*, *B. bullatus* and *B. lacertosus* in the Baltic countries; however, we suggest corrections of the data on *B. meridionalis*. We found that some previously published data on distribution of this species (Haberman, 1968; Leskina, 2000; Barševskis, 2003; Barševskis *et al.*, 2009) were based on misidentifications. Unfortunately, the material of some Latvian records of this species (Barševskis, 1993; Cibulskis, 1994; Kalniņš *et al.*, 2007; Bukejs *et al.*, 2009; Bukejs 2009) and one Lithuanian record (Barševskis, 2001) were not available for reexamination. Nevertheless, we assuredly doubt the records of *B. meridionalis* in winter rape and potato crops (Bukejs, 2009; Bukejs *et al.*, 2009) and wish to attribute them to *B. bullatus*. Four specimens of *B. meridionalis* we examined from the Estonian Museum of Natural History contained label information on two pieces of papers: "Livonia" and "Bolz". Unfortunately, these data are not enough for trustworthy confirmation of collecting these specimens in Estonia or Latvia.

Two specimens of *B. meridionalis* were examined from the Kaunas Tadas Ivanauskas Zoological Museum (Lithuania) collected in central part of Lithuania in Kaunas environs. So, currently we can confirm the distribution of all four our studied species only for Lithuania, while in Estonia and Latvia only three species: *B. unipustulatus*, *B. bullatus*, and *B. lacertosus*, are really detected (Fig. 15). It is believable that the northern border of the distribution range of *B. meridionalis* can extend further north and the occurrence of this species in Latvia and Estonia is quite realistic.

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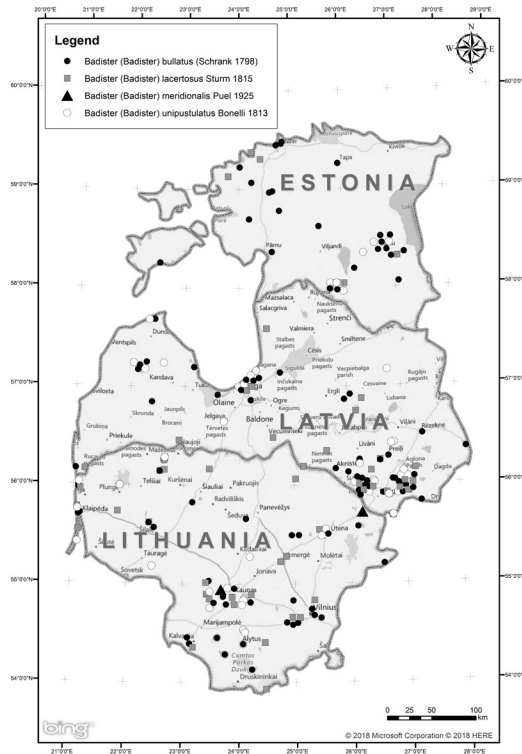


Fig. 15. Distribution maps of *Badister* (s. str.) species in Baltic countries.

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