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NEW DATA ON THE DISTRIBUTION OF *POLISTES BISCHOFFI WEYRAUCH, 1937* AND *POLISTES HELVETICUS NEUMEYER, 2014*, A SYNONYM OF *POLISTES ALBELLUS GIORDANI SOIKA, 1976* N. STAT. (HYMENOPTERA: VESPIDAE)

Rainer Neumeyer^{1*}, Bruno Gereys² & Leopoldo Castro³

¹ Probsteistrasse 89, CH-8051 Zürich, (Switzerland) — neumeyer.funk@bluewin.ch

² 4, rue des Escaranches, F-04700 Oraison, (France) — bruno.gereys04@orange.fr

³ Av. Sanz Gadea 9, E-44002 Teruel (Spain) — discoelius@discoelius.jazztel.es

Abstract: *Polistes helveticus* Neumeyer, 2014 is synonymised with *Polistes albellus* Giordani Soika, 1976 n. stat., n. syn. Additionally, *Polistes bischoffi* Weyrauch, 1937 is recorded from the Iberian Peninsula for the first time. New records and world distribution maps are provided for both species. The available data suggest that *P. albellus* and *P. bischoffi* are vicariant taxa.

Key words: Hymenoptera, Vespidae, Polistinae, nomenclature, taxonomy, distribution, Belgium, France, Germany, Gibraltar, Italy, Kazakhstan, Mongolia, Russia, Spain, Switzerland.

Données nouvelles sur la distribution de *Polistes bischoffi* Weyrauch, 1937 et *Polistes helveticus* Neumeyer, 2014, ce dernier étant synonyme de *Polistes albellus* Giordani Soika, 1976 n. stat. (Hymenoptera: Vespidae)

Résumé: *Polistes helveticus* Neumeyer, 2014 est mis en synonymie avec *Polistes albellus* Giordani Soika, 1976 n. stat., n. syn. De plus, *P. bischoffi* Weyrauch, 1937 est cité pour la première fois de la Péninsule Ibérique. Des citations nouvelles et des cartes de distribution mondiale sont fournies pour les deux espèces. Les données disponibles laissent suggérer que *P. albellus* et *P. bischoffi* sont des taxons vicariants.

Mots clés: Hymenoptera, Vespidae, Polistinae, nomenclature, taxonomie, distribution, Allemagne, Belgique, Espagne, France, Gibraltar, Italie, Kazakhstan, Mongolie, Russie, Suisse.

Neue Verbreitungsdaten von *Polistes bischoffi* Weyrauch, 1937 und *Polistes helveticus* Neumeyer, 2014, einem Synonym von *Polistes albellus* Giordani Soika, 1976 n. stat. (Hymenoptera: Vespidae)

Zusammenfassung: *Polistes helveticus* Neumeyer, 2014 wird zum Synonym von *Polistes albellus* Giordani Soika, 1976 n. stat. erklärt. Des weiteren wird *Polistes bischoffi* Weyrauch, 1937 zum ersten Mal auf der Iberischen Halbinsel nachgewiesen. Gemäß der weltweiten Verbreitungskarte mit neuen Fundorten für beide Arten scheinen diese zu vikariieren.

Schlüsselwörter: Hymenoptera, Vespidae, Polistinae, Nomenklatur, Taxonomie, Verbreitung, Belgien, Deutschland, Frankreich, Gibraltar, Italien, Kasachstan, Mongolei, Russland, Schweiz, Spanien.

Nuevos datos sobre la distribución de *Polistes bischoffi* Weyrauch, 1937 y *Polistes helveticus* Neumeyer, 2014, que se sinonimiza con *Polistes albellus* Giordani Soika, 1976 n. stat. (Hymenoptera: Vespidae)

Resumen: Se sinonimiza *Polistes helveticus* Neumeyer, 2014 con *Polistes albellus* Giordani Soika, 1976 n. stat., n. syn. Por otra parte, se cita a *P. bischoffi* Weyrauch, 1937 por primera vez de la Península Ibérica. Se incluyen citas nuevas y mapas con la distribución mundial de ambas especies, que según todos los indicios constituyen taxones vicariantes.

Palabras clave: Hymenoptera, Vespidae, Polistinae, Nomenclatura, Taxonomía, Distribución, Alemania, Bélgica, España, Francia, Gibraltar, Italia, Kazajistán, Mongolia, Rusia, Suiza.

Introduction

When separating *Polistes helveticus* Neumeyer, 2014 from *Polistes bischoffi* Weyrauch, 1937 the authors also provided a distribution map (Neumeyer *et al.*, 2014: 105) suggesting a chiefly southern European range from France to eastern Turkey for *Polistes bischoffi* and a rather small, merely Central European range for *Polistes helveticus*. In the meantime we have collected and received new material from sites which altogether increase the known range of both species substantially, as published here. However, after examining some of the new material we realised that *Polistes helveticus* is identical to the taxon traditionally known as *Polistes foederatus albellus* Giordani Soika, 1976.

Material and Methods

TAXONOMIC TREATMENT

For taxonomy, classification and identification we followed Neumeyer *et al.* (2014). Stack-photographs of mounted

specimens were taken with a Keyence VHX-2000 digital microscope at the NMBe. Abbreviations used for specimen depositaries, private collections and other institutions cited in this study are given here:

AM – American Museum of Natural History, New York (USA).

BMNH – Natural History Museum (London, U.K.).

CBG – Bruno Gereys collection (Oraison, France).

CCDB – Canadian Centre for DNA Barcoding (Guelph, Canada).

CLC – Leopoldo Castro collection (Teruel, Spain).

HNHM – Hungarian Natural History Museum, Budapest (Hungary).

MMML – Městské muzeum Mariánské Lázně (Czech Republic).

MSNM – Museo Civico di Storia Naturale, Milano (Italy).

MSNV – Museo di Storia Naturale, Venezia (Italy).

NMBe – Naturhistorisches Museum der Burgergemeinde Bern (Switzerland).

RAM – Royal Alberta Museum, Edmonton (Canada).

RN – Rainer Neumeyer collection (Zürich, Switzerland).

SMNS – Staatliches Museum für Naturkunde Stuttgart (Germany).

UoN – University of Neuchâtel (Switzerland).

ZSM – Zoologische Staatssammlung München (Germany).

Tab. I. Data for sequenced specimens. S = Sex; The abbreviations in the country column mean: C = Country; ES = Spain, KZ = Kazakhstan, RU = Russia. The abbreviations in the collection (coll.) column are explained under "Material and Methods". • Datos de los especímenes secuenciados. S = Sexo. Las abreviaturas de la columna de países significan: C = País; ES = España, KZ = Kazajistán, RU = Rusia. Las abreviaturas de la columna de colecciones (coll.) se explican en "Material and Methods".

S	Unique Identifier		Date	C	Region, MUNICIPALITY, Site	Coordinates		Alt (m)	Leg.	Coll.
	RN	ZSM HYM				latitude	longitude			
<i>Polistes albELLus</i>										
♀	571	22709	14.07.2011	KZ	East Kazakhstan, MAY-TEREK, Kurchum mountains	48°34'N	84°46'E	1150	R.V. Yakovlev	RN
♀	567	22706	18.07.2011	KZ	East Kazakhstan, ZAISAN, Bolshoi Zhemenei valley	47°14'N	84°56'E	1650	R.V. Yakovlev	RN
♀	404	-	7/12.07.2011	RU	Orenburg Oblast, DONSKOYE, 5 km W of village	52°3'28"N	55°25'12,6"E	-	V. Višinskas	MSNM
♀	405	-	7/12.07.2011	RU	Orenburg Oblast, DONSKOYE, 5 km W of village	52°3'28"N	55°25'12,6"E	-	V. Višinskas	MSNM
<i>Polistes bischoffi</i>										
♀	570	22711	7.07.2014	ES	Andalucía, GUARDIAS VIEJAS—	36°42'10,8"N	2°51'32,6"W	5	L. Castro	CLC
♂	569	22710	10.08.2014	ES	Andalucía, GUARDIAS VIEJAS—	36°42'10,8"N	2°51'32,6"W	5	L. Castro	CLC
♀	566	22707	6.09.2014	ES	Aragón, POMAR DE CINCA, Arroyo de la Clamor	41°53'2,9"N	0°5'24"E	250	L. Castro	CLC
♀	568	22708	4.08.2014	ES	Aragón, ALCAÑÍZ, Salada Grande	41°2'0,4"N	0°12'19,2"W	345	L. Castro	CLC

Since there are no reliable external caste differences, we do not distinguish gynes from workers in *Polistes* but call both of them just *females* (♀).

MOLECULAR ANALYSES

Eight specimens, four from Spain (BC ZSM HYM: 22707, 22708, 22710, 22711), two from Russia (RN0404, RN0405) and two from Kazakhstan (BC ZSM HYM: 22706, 22709) have been subjected to a molecular analysis of the 658 bp "barcode" region of their mitochondrial gene COX1. For the specimens from Spain and Kazakhstan, both mtDNA sequencing and data analysis were performed by the staff of the ZSM and the CCDB, according to the procedure described in Schmidt *et al.* (2015). However, the specimens from Russia were sequenced and analysed by C. Praz (UoN), who carried out maximum likelihood analyses using RAXML (Stamatakis *et al.*, 2005), performing 1000 bootstrap replicates (Neumeyer *et al.*, 2014: 73).

DISTRIBUTION

For the distribution map we have used not only records listed under "Material examined" here, but also sites already published in Castro & Dvořák (2010: 45), Dvořák *et al.* (2006: 536), Mauss (2001), and Neumeyer *et al.* (2014). Of course, all but Neumeyer *et al.* (2014) still used the name *bischoffi* Weyrauch, 1937 for *helveticus* Neumeyer, 2014, but from the key in Mauss & Treiber (2004) it is clear that *helveticus* was meant at least in Mauss (2001). Moreover, *Polistes bischoffi* Weyrauch, 1937 rev. stat. not only has not yet been found in Germany to date, but most probably would also have been confused with *P. gallicus* (Linnaeus, 1767) at that time (Neumeyer *et al.*, 2011: 9). As far as Dvořák *et al.* (2006: 536) and Castro & Dvořák (2010: 45) are concerned, we know that the corresponding individuals indeed have dorsally black flagella (L. Dvořák pers. comm.) and therefore must have been *helveticus*.

Results

• *Polistes albELLus* Giordani Soika, 1976, n. stat.

Polistes bischoffi Weyrauch, 1937: 274, in part.

Polistes foederatus albELLus Giordani Soika, 1976: 272.

Polistes helveticus Neumeyer, 2014: 101 ff. n. syn.

From eastern Kazakhstan we received nine female specimens which one of us (LC) determined as *Polistes helveticus*, but another (RN) as *Polistes foederatus albELLus*. Later, we borr-

owed five more females (SMNS coll.) from the Kazakh Almaty region. Four of them are also mentioned in Dvořák *et al.* (2006: 536). In fact, all 14 females are virtually indistinguishable from the paratype (Fig. 1, 2) of *Polistes foederatus albELLus*, except for the ivory maculation, which is a little bit more reduced in the paratype. On the other hand, the only western Palaearctic taxon we know to share the trait of a reduced or lacking epicnemial carina with the sibling taxa *P. helveticus* and *P. bischoffi* is *Polistes f. albELLus*. So, we decided to subject two of the Kazakh specimens (BC ZSM HYM 22706, BC ZSM HYM 22709) to barcoding (Tab. I). Since they turned out to group in the same clade (Fig. 3) as *P. helveticus* from central Europe (Neumeyer *et al.* 2014) and the Orenburg Oblast of Russia (Fig. 4), we conclude that there is no specific difference between the taxa *helveticus* and *albellus*. Thus, the taxon *helveticus* Neumeyer, 2014 is a junior synonym of *Polistes albellus* Giordani Soika, 1976 n. stat., which is in this way raised to species status.

Distribution. Up to the present, *Polistes albellus* has been found in a considerable range extending from France to the Pacific coast of Russia but latitudinally remaining roughly between the 44th (FR, Lardiers: 44°03'28,1"N) and the 53rd (RU, Donskoye: 52°03'28"N) northern parallels (Fig. 5). Remarkably, the localities in Russia (Barabash-Levada, Donskoye), Kazakhstan (Koktal, May-Terek, Tekeli, Zaisan) and Mongolia (Namnan Uul mountains, Töv) are so far from Europe and in part also from each other that we cannot yet reject the idea of a disjunct area, for now. On the other hand, barcoding showed hardly any difference among the COX1 genes of all examined individuals from Central Europe, Russia (Orenburg Oblast), and Kazakhstan (Fig. 3), suggesting rather a connected, but partially unexplored area between Slovakia and Vladivostok. However, when considering five known populations (Central Europe, Orenburg Oblast of Russia, Kazakhstan, Mongolia, Primorsky Krai of Russia) there seems to be a cline from Central Europe to Mongolia, with the black surface on the female body gradually increasing at the cost of the pale (yellow or white) markings (Fig. 1, 2). Some effects of this change we may nevertheless perceive as abrupt when regarding the paired yellow blotches on tergite II which western females (Central Europe, Orenburg Oblast of Russia) have but eastern ones (Kazakhstan, Mongolia, Primorsky Krai of Russia) lack (Fig. 2). Furthermore, somewhere between Donskoye (Orenburg Oblast of Russia) and eastern Kazakhstan the lemon yellow colour of western fe-

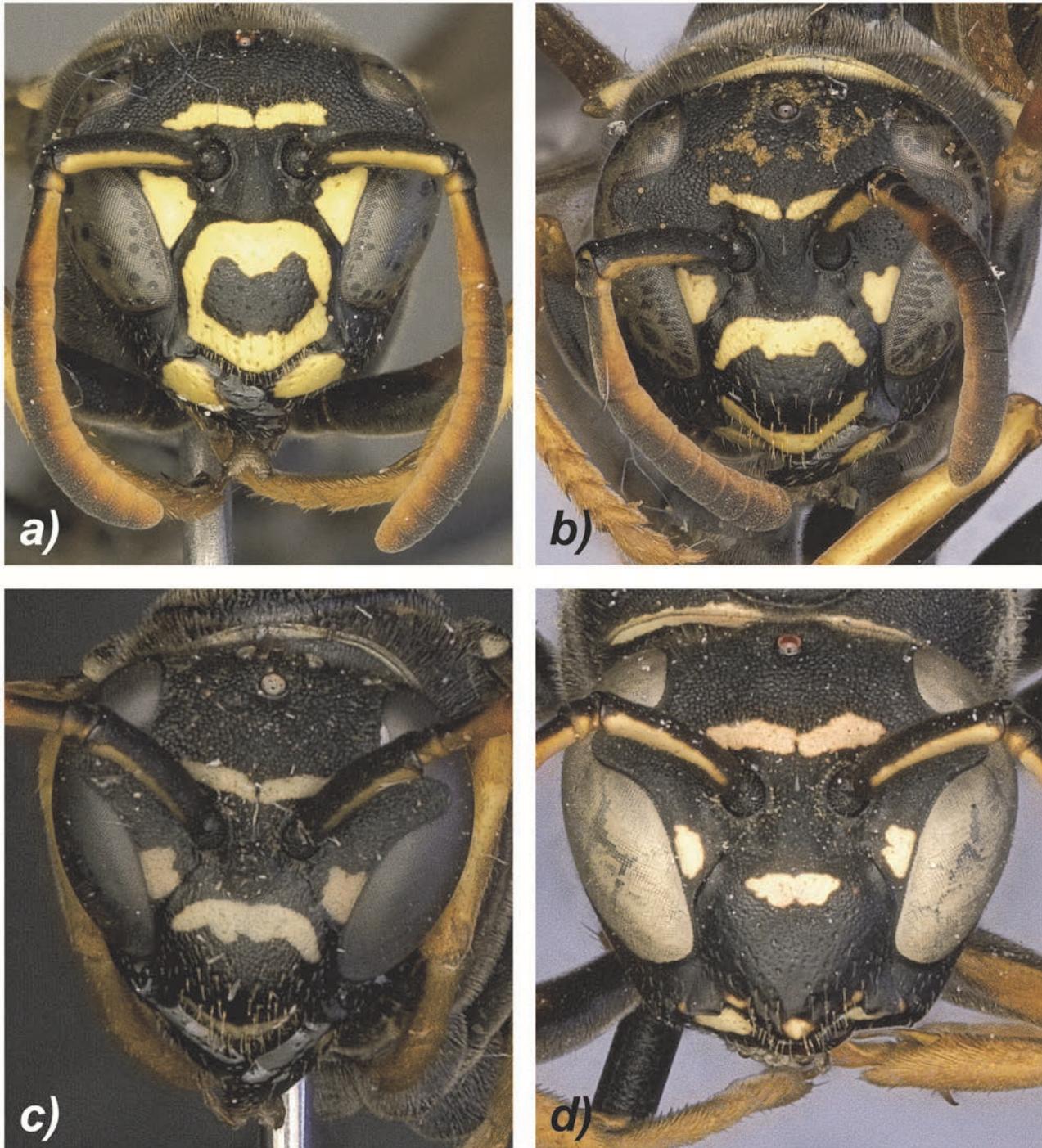


Fig. 1. Frontal view of head of female *Polistes albellus* Giordani Soika, 1976 from Switzerland (a, individual RN0138), Orenburg Oblast of Russia (b, RN0404), Kazakhstan (c, RN0567), and Mongolia (d, paratype). / Vista frontal de la cabeza de hembras de *Polistes albellus* Giordani Soika, 1976 de Suiza (a, individuo RN0138), la provincia de Orenburg en Rusia (b, RN0404), Kazajistán (c, RN0567) y Mongolia (d, paratipo).

males changes to the ivory white of eastern females (Fig. 1, 2). Remarkably, this colour trend does not seem to go on east of Mongolia, since the markings of the individual (RN0641) from Barabash-Levada (Primorsky Krai of Russia) are by no means ivory-white, but as yellow as those of the specimens (RN0401, RN0404, RN0405, RN0406) from Donskoye (Orenburg Oblast of Russia). Unfortunately, no male of *P. albellus* has ever been collected east of Slovakia yet.

While in Europe *P. albellus* mainly lives in fens (Neumeyer *et al.*, 2011, 2014), we have no habitat information from Russia (Barabash-Levada, Donskoye) and only a

short note ("upper stream Bolshoi Zhemenei riv.") about habitat (Bolshoi Zhemenei valley) in Kazakhstan (Rubin & Yakovlev, 2013: 140). The habitat in Mongolia (Namnan Uul mts.), however, was described by Kaszab (1968: 435 ff.) as a mountain valley with wooded slopes (young coniferous forest and old birch forest with Siberian cedars) and a vast mountain steppe [“ausgedehnte Gebirgssteppe”] at the bottom, with some willow shrubbery [“Weidengebüsch”] next to a creek. There was also a very rich herbaceous layer with Apiaceae (on July 21) in the aquiferous cracks [“in den Wasserrissen”] and at the forest edges.

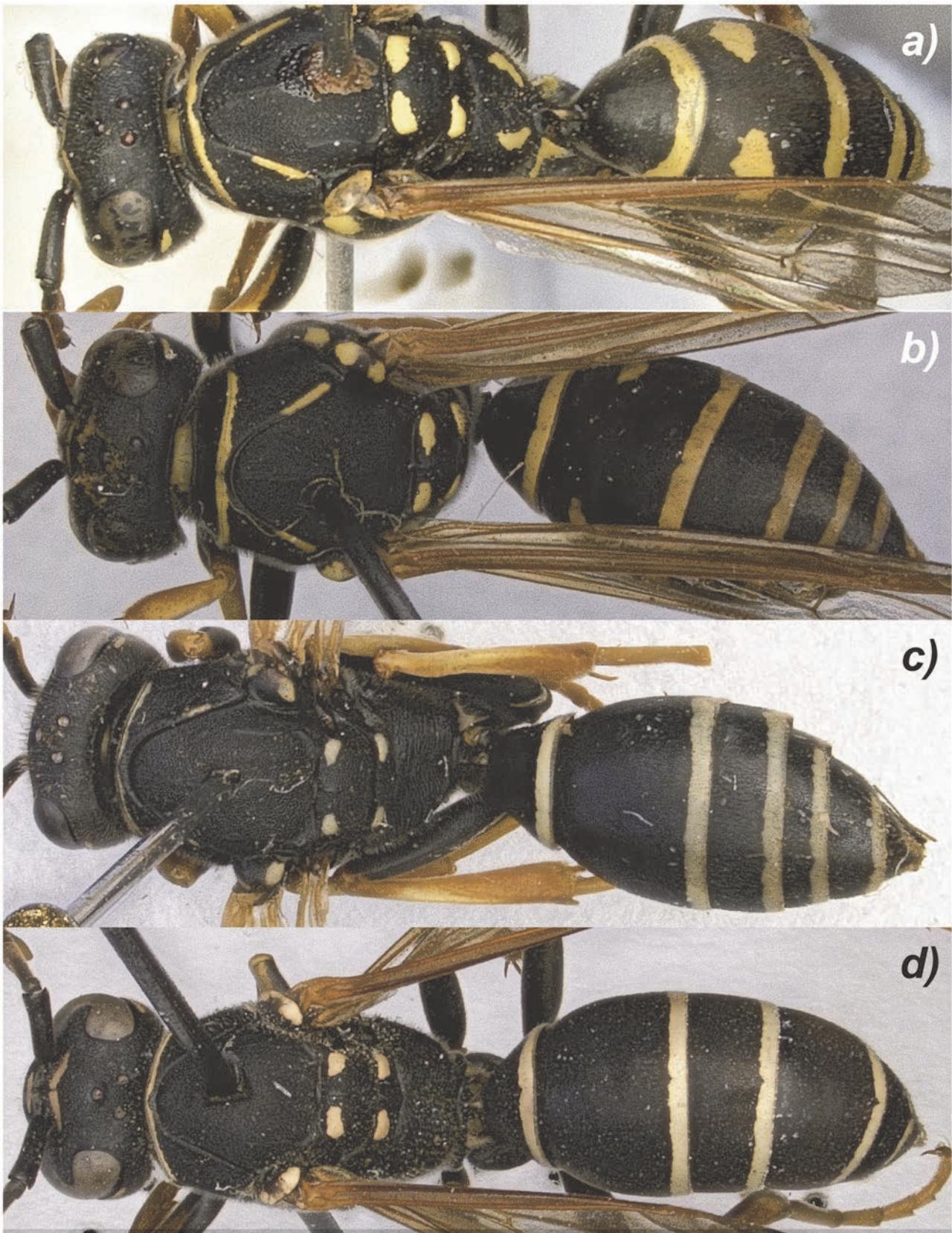


Fig. 2. Dorsal view of body of female *Polistes albellus* Giordani Soika, 1976 from Switzerland (a, RN0138), Orenburg Oblast of Russia (b, RN0404), Kazakhstan (c, RN0567), and Mongolia (d, paratype). / Vista dorsal del cuerpo de hembras de *Polistes albellus* Giordani Soika, 1976 de Suiza (a, RN0138), la provincia de Orenburg en Rusia (b, RN0404), Kazajistán (c, RN0567) y Mongolia (d, paratipo).

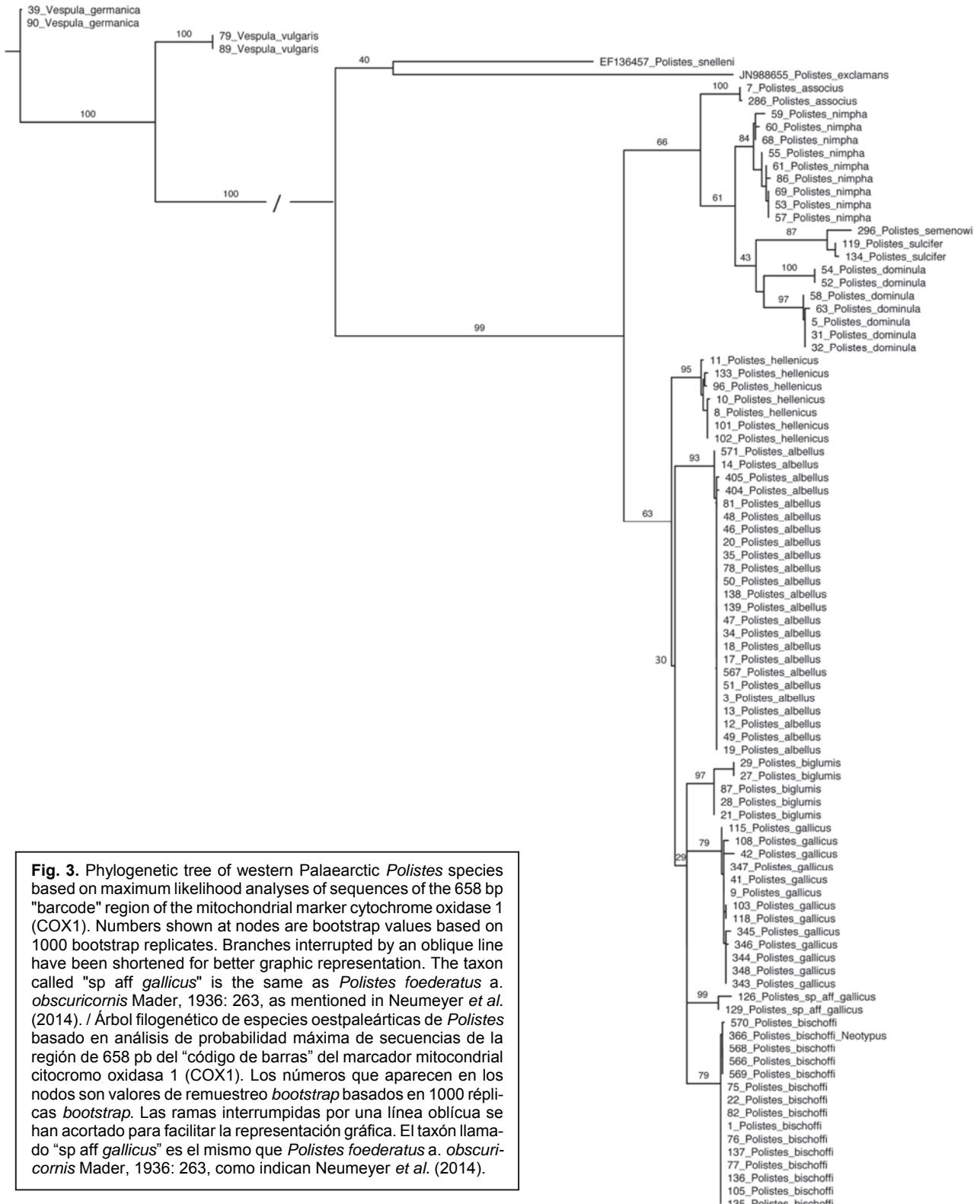


Fig. 3. Phylogenetic tree of western Palaearctic *Polistes* species based on maximum likelihood analyses of sequences of the 658 bp "barcode" region of the mitochondrial marker cytochrome oxidase 1 (COX1). Numbers shown at nodes are bootstrap values based on 1000 bootstrap replicates. Branches interrupted by an oblique line have been shortened for better graphic representation. The taxon called "sp aff *gallicus*" is the same as *Polistes foederatus* a. *obscuricornis* Mader, 1936: 263, as mentioned in Neumeyer et al. (2014). / Árbol filogenético de especies oestpaleárticas de *Polistes* basado en análisis de probabilidad máxima de secuencias de la región de 658 pb del "código de barras" del marcador mitocondrial citocromo oxidasa 1 (COX1). Los números que aparecen en los nodos son valores de remuestreo bootstrap basados en 1000 réplicas bootstrap. Las ramas interrumpidas por una línea oblicua se han acortado para facilitar la representación gráfica. El taxón llamado "sp aff *gallicus*" es el mismo que *Polistes foederatus* a. *obscuricornis* Mader, 1936: 263, como indican Neumeyer et al. (2014).

Material examined. Paratype of *P. foederatus albellus*: MONGOLIA, BULGAN AIMAG, Namnan Uul mountains (approx. 49°27'07"N 102°16'00"E, 1150 m), 1 ♀ (MSNV-04702), 21 Jul 1968, Zoltán Kaszab leg., MSNV coll. Further material: BELGIUM, WALLONIA, Marbehan (approx. 49°43'21"N 05°32'02"E; 360 m), 1 ♂ (CLC-JR08), 02 Sep 2006, 1 ♂ (CLC-JR09), 08 Sep 2006, J.L. Renneson leg., CLC coll.; FRANCE, ALPES-DE-HAUTE-PROVENCE, Lardiers (44°03'28.1"N 05°42'46.1"E), 1 ♀, 14 Jul 1996, B. Gereys leg., RN coll.; CÔTE-D'OR, Broin (approx. 47°04'47"N

05°06'35"E), 1 ♂, H. Fonfria leg., CBG coll.; HAUTE-SAÔNE, Port-sur-Saône (approx. 47°41'16"N 06°03'00"E), 1 ♀ (CLC-BG434/296), 06 Aug 1929, 1 ♀ (CLC-BG435/298), 11 Aug 1929, Vandel leg., CLC coll.; 4 ♀, 1 ♂, 16 Aug 1929, H. Nouvel leg., CBG coll.; HAUTE-SAVOIE, Thonon (approx. 46°22'21"N 06°29'13"E), 1 ♂ (CLC-BG436/293), CLC coll.; 6 ♀ (BG282, BG283, BG284, BG285, BG286, BG287), 6 ♂ (G289, BG290, BG291, BG292, BG294, BG295), CBG coll.; 2 ♀ (BG288, BG297), 1 ♂ (BG288), RN coll.; all (16) specimens emerged 28 Jul 1982 from a nest collected 14 Jul 1982,

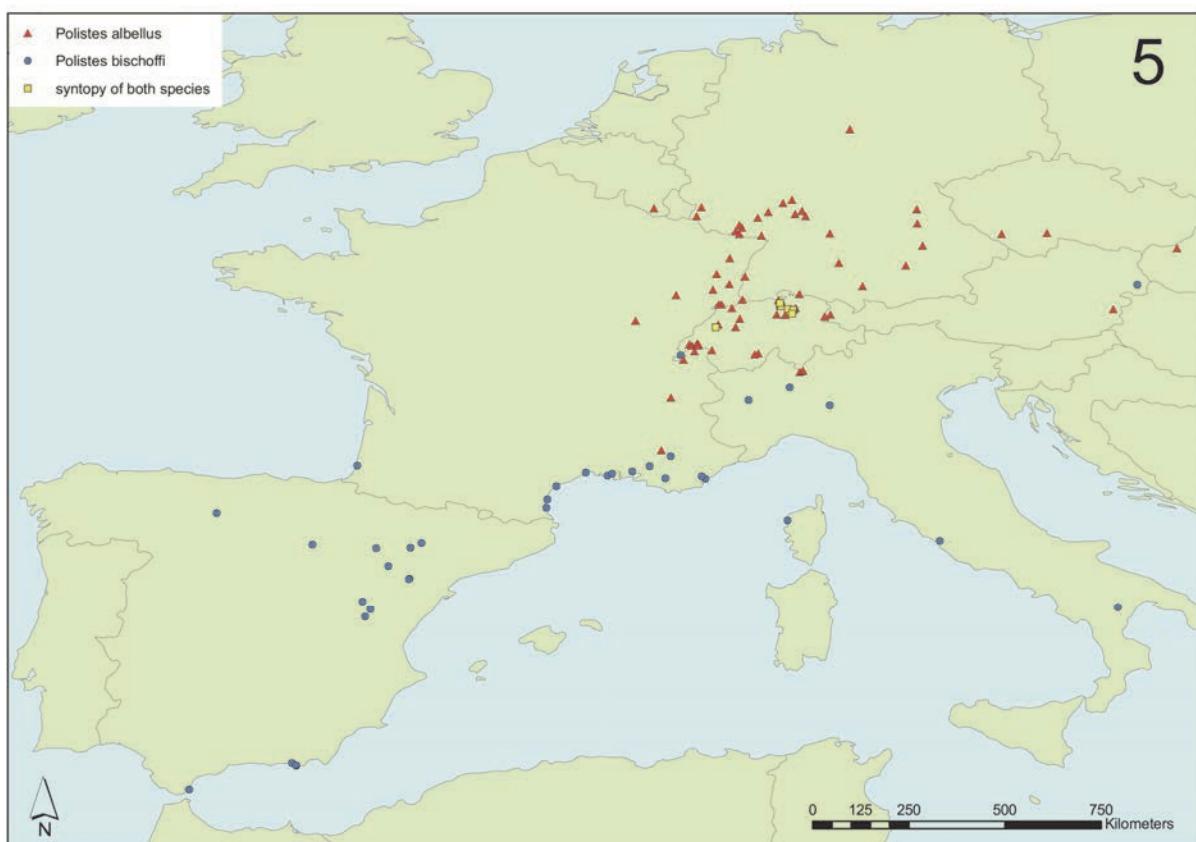
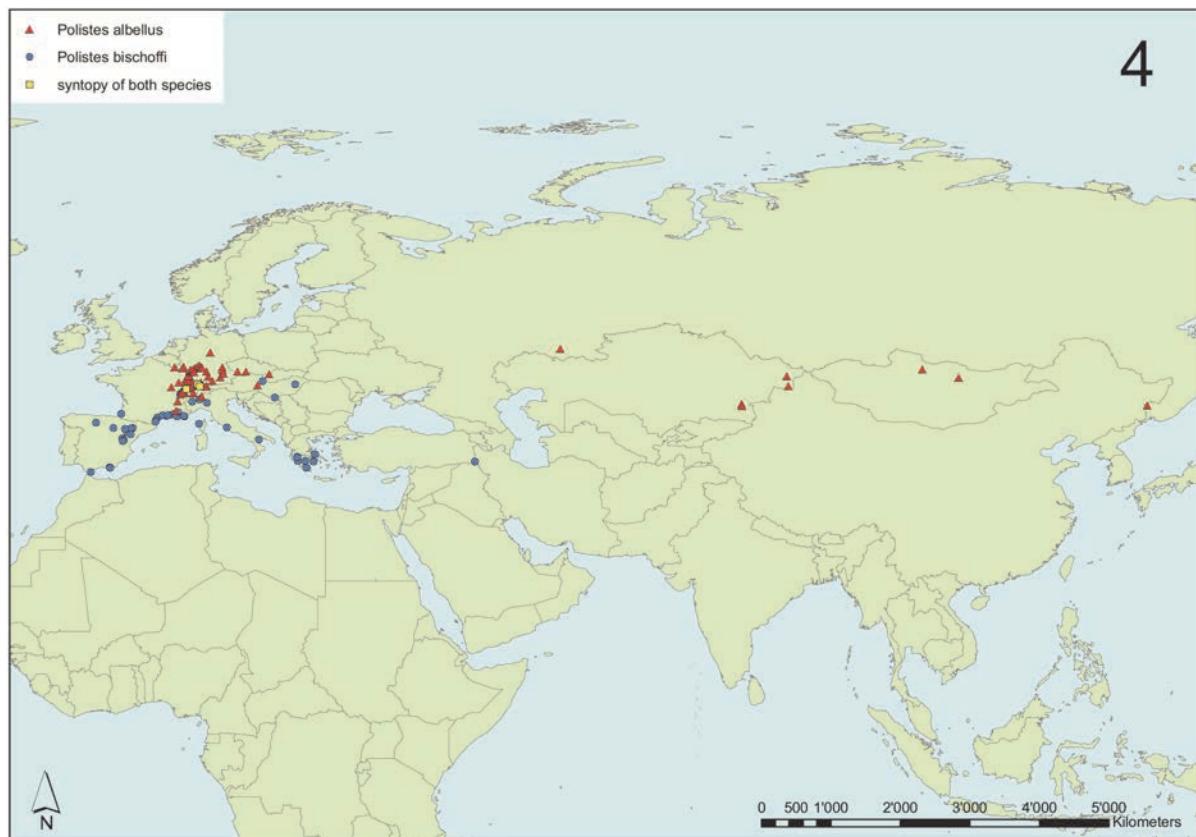


Fig. 4. Worldwide distribution of examined specimens of *Polistes albellus* Giordani Soika, 1976 and *Polistes bischoffi* Weyrauch, 1937 based on new material and data provided by Castro & Dvořák (2010: 45), Dvořák *et al.* (2006: 536), Mauss (2001), and Neumeyer *et al.* (2014). / Distribución mundial del material examinado de *Polistes albellus* Giordani Soika, 1976 y *Polistes bischoffi* Weyrauch, 1937, en base al material nuevo y a datos aportados por Castro & Dvořák (2010: 45), Dvořák *et al.* (2006: 536), Mauss (2001) y Neumeyer *et al.* (2014).

Fig. 5. European distribution of *Polistes albellus* and *P. bischoffi* (enlarged from Fig. 4). / Distribución europea de *Polistes albellus* y *P. bischoffi* (ampliación a partir de la Fig. 4).

H. Tussac leg.; GERMANY, NIEDERSACHSEN, Ebergötzen (approx. 51°34'22"N 10°06'57"E, garden), 1 ♂, 11 Sep 2010 T. Meineke photographic record; RHEINLAND-PFALZ, Monsheim, Im Pflänzer (49°38'26"N 08°12'41"E, 150 m, clay pit), 1 ♂, 17 Oct 1995, G. Reder leg. et coll.; KAZAKHSTAN, ALMATY, 20 km NE of Tekeli, Kora valley (approx. 44°56'N 78°53'E, > 1300 m) in the western part of the Dzungarian Alatau, 2 ♀, 23 Jul 2002, T. Osten leg., SMNS coll.; gorge (1650 m) of Koktal, southern part of the Dzungarian Alatau, 3 ♀, 26 Jul 2002, T. Osten leg., SMNS coll.; EAST KAZAKHSTAN, Kurchum mountains (48°34'N 84°46'E, 1150 m) 3 km W of May-Terek, 6 ♀ (1 ♀ RN0571, 5 ♀ CLC-RY01), 14 Jul 2011, R.V. Yakovlev leg., CLC & RN coll.; Bolshoi Zhemenei valley (47°14'N 84°56'E, 1650 m) in the Saur mountains 24 km S of Zaisan, 3 ♀ (1 ♀ RN0567, 2 ♀ CLC-RY03), 18 Jul 2011, R.V. Yakovlev leg., CLC & RN coll.; RUSSIA, ORENBURG OBLAST, 5 km W of Donskoye vill. (approx. 52°03'28"N 55°25'12.6"E), 4 ♀ (RN0401, RN0404, RN0405, RN0406), 07-12 Jul 2004, V. Višinskas leg., MSNM coll.; PRIMORSKY KRAI, Barabash-Levada (approx. 44°45'N 131°25'E), 1 ♀ (CLC-IO296 / RN0641), 22 Jul 2002 [collector unknown], CLC coll.; SWITZERLAND, VALAIS, Visp (approx. 46°17'40"N 07°53'05"E; 650 m), 1 ♀ (CLC-VZ07a), 24 Jul 1964, V.S. van der Goot & J.A.W. Lucas leg., CLC coll.; ZÜRICH, Hirzel, Chrutzelenmoos (47°13'25.0"N 08°36'29.3"E, 670 m, fen), 1 ♀ (RN0634), 08 Sep 2014, R. Neumeyer leg. et coll.; Hombrechtikon, Lützelsee, Lutikon (47°15'28.1"N 08°46'12.6"E, 503 m, fen), 1 ♀ (RN0635), 04 Aug 2014, R. Neumeyer leg. et coll.

• *Polistes bischoffi* Weyrauch, 1937

Polistes bischoffi Weyrauch, 1937: 274, in part

Presence on the Iberian Peninsula

In the present interpretation of the taxon (Neumeyer *et al.* 2014), *Polistes bischoffi* is known from continental France, Corsica, Italy, Switzerland, Austria, Greece and Turkey. Previously published records of the species were provisionally disregarded, pending verification of the material on which they were based, given the fact that the wasp has been confused up until now with *P. gallicus*, *P. albellus* (= *helveticus*) and quite possibly *P. hellenicus* Arens, 2011.

The latest works dealing with the Iberian distribution of the Polistini (Madero Montero 1988; Diniz 1960, 1978; Castro 2001) did not mention *P. bischoffi*, and isolated records from “Spain” by other authors (Schmid-Egger & Treiber 1989: 601-602; Dvořák *et al.* 2006: 536) may or may not correspond to the current interpretation of the taxon.

In early 2014, on a visit to London’s British Museum, RN was able to examine a specimen of *P. bischoffi* from Gibraltar, which prompted LC to visit a series of potentially suitable sites in Spain. These expeditions revealed the presence of the species in several Spanish provinces, and a revision of previously collected material has produced further records from other areas of the country.

Material examined (Iberian Peninsula). GIBRALTAR, Gibraltar (approx. 36°08'N 05°21'W), 1 ♀ (1910-266), [no date], J.J.W. [= J. J. Walker] [leg.], BMNH (E. Saunders coll.); SPAIN, ANDALUCÍA, ALMERÍA, Adra, Venta Nueva (36°45'25.7"N 02°56'51.8"W, 15 m), 2 ♀ (CLC-2014/A42), 10 Aug 2014, L. Castro leg. et coll.; Guardias Viejas (36°42'10.8"N 02°51'32.6"W, 5 m), 7 ♀ (6 at *Tamarix* flo-

ers, 1 at *Limonium*; 1 ♀ RN0570, 6 ♀ CLC-2014/A21), 7 Jul 2014, L. Castro leg., CLC & RN coll.; 5 ♂ (at *Crithmum maritimum*; 1 ♂ RN0569, 4 ♂ CLC-2014/A43), 10 Aug 2014, L. Castro leg., CLC & RN coll.; Guardias Viejas (36°41'55.0"N 02°50'33.4"W, 8 m), 3 ♀ (at *Tamarix*; CLC-2014/A22), 7 Jul 2014, L. Castro leg. et coll.; CASTILLA Y LEÓN, PALENCIA, Villasur (42°34'55"N 04°41'57"W, 990 m), 1 ♀ (CLC-2002/A37), 7 Aug 2002, L. Castro leg. et coll.; CASTILLA Y LEÓN, SORIA, Chavaler (approx. 41°51'N 02°28'W; 1250 m), 1 ♀ (white Malaise trap; CLC-AN13), 18 May 1998, A. de la Nuez leg., CLC coll.; ARAGÓN, HUESCA, Pomar de Cinca, Arroyo de la Clamor (41°53'02.9"N 00°05'24.0"E, 250 m), 4 ♀ 3 ♂ (at *Foeniculum* flowers; 1 ♀ RN0566, rest CLC-2014/A55), 6 Sep 2014, C. Latorre leg., CLC & RN coll.; Sariñena, El Puyalón (41°46'07.3"N 00°10'30.3"W, 285 m), 2 ♀ (at *Eryngium campestre* flowers; CLC-2015/A04), 4 Jul 2015, L. Castro leg. et coll.; ARAGÓN, TERUEL, Alcañiz, Salada Grande (41°02'30.1"N 00°11'46.0"W, 340 m), 2 ♀ (at nest; CLC-2014/A33), 4 Aug 2014, L. Castro leg. et coll.; Alcañiz, Salada Grande (41°02'00.4"N 00°12'19.2"W, 345 m), 3 ♀ (at unidentified flowers; 1 ♀ RN0568, 2 ♀ CLC-2014/A34), 4 Aug 2014, L. Castro leg., CLC & RN coll.; Libros (40°09'09.79"N 01°13'55.84"W; 755 m), 3 ♀ (at *Foeniculum* flowers; CLC-2015/A25), 5 Sep 2015, L. Castro leg. et coll.; Teruel, rambla Franquia (40°19'09"N 01°06'18"W, 910 m), 1 mature nest with 5 unemerged subadults (1 ♀ 4 ♂; CLC-1977), 13 Apr 1977, L. Castro leg. et coll.; Villarquemado (40°30'14.9"N 01°17'19.6"W, 985 m), 3 ♀ (CLC-2014/A51), 25 Aug 2014, L. Castro leg. et coll.; ARAGÓN, ZARAGOZA, Alfocea, Acampo de Cuéllar (41°45'29"N 00°58'01"W, 300 m), 1 ♀ (no other collecting data; CLC-1979), 11 May 1979, L. Castro leg. et coll.; Codo, Balsa del Margen (41°20'35.9"N 00°40'53.0"W, 290 m), 3 ♀ (at *Limonium* flowers; CLC-2014/A36), 4 Aug 2014, C. Latorre leg., CLC coll..

Material from other European countries. FRANCE, ALPES-DE-HAUTE-PROVENCE, Oraison (43°55'05"N 05°55'09"E), 1 ♀, 06 Aug 1995, B. Gereys leg. et coll.; AUDE, Leucate (42°54'38"N 03°01'46"E), 1 ♀, 10 Jul 1984, J. Hamon leg., CBG coll.; BOUCHES-DU-RHÔNE, Camargue (approx. 43°31'N 04°33'E), 1 ♀ (CLC-VZ04 / RN0447), 2-9 Aug 1963 [collector unknown], CLC coll.; PYRÉNÉES-ORIENTALES, Canet-en-Roussillon, plage (42°42'24"N 03°00'28"E), 1 ♀, 17 Aug 1957, H. Ribaut leg., CBG coll.; ITALY, BASILICATA, MATERA, Craco, Masseria del Monte (40°22'13.1"N 16°22'40.5"E, 320 m), 1 ♀ (CLC-2011/A78), 21 Jul 2011, L. Castro leg. et coll.; SWITZERLAND, ZÜRICH, Hombrechtikon, Lützelsee: Lutikon (47°15'32.8"N 08°45'59.7"E, 503 m, fen), 1 ♀ (RN0533), 02 Sep 2014, R. Neumeyer leg., ZSM coll.; Neerach, Neeracherried, Langenteilen (47°29'54.7"N 08°28'55.2"E, 410 m, fen), 1 ♀ (RN0532), 26 Jun 2014, R. Neumeyer leg., ZSM coll.

Notes on habitat (material from Spain and Italy):

ADRA: Permanent coastal lagoon with natural, mostly dense, vegetation in the immediate vicinity but surrounded by agricultural land. *Polistes nimpha* was also collected, and *P. gallicus* specimens were observed but not collected.

ALCAÑIZ (both sites): Area covered by steppe vegetation around a group of nearly permanent brackish lagoons, with scattered *Tamarix* bushes (Fig. 6); in very hot years these lagoons can run completely dry. *Polistes gallicus* was also



Fig. 6. *Polistes bischoffi* Weyrauch, 1937 habitat at Alcañiz (Teruel province, Spain). / Hábitat de *Polistes bischoffi* Weyrauch, 1937 en Alcañiz (provincia de Teruel, España).



Fig. 7. *Polistes bischoffi* Weyrauch, 1937 locality near Codo (Zaragoza prov., Spain). / Localidad de *Polistes bischoffi* Weyrauch, 1937 junto a Codo (provincia de Zaragoza, España).

collected, and *P. dominula* was observed at the locality. The nest was attached to a standing but dead *Foeniculum* stalk. **CODO:** Seasonally flooded ground with a number of small permanent ponds but otherwise devoid of surface water in summer; numerous patches (some of them large) of *Tamarix* bushes (Fig. 7). Other *Polistes* species collected: *P. gallicus*, *P. nimpha*.

CRACO: Specimen collected by a very small stream in steep terrain; there were reed patches on the banks, and a small river some 350 m. below. Other *Polistes* species collected: *P. gallicus*, *P. nimpha*.

GUARDIAS VIEJAS, 5m. alt.: Seasonally flooded ground inland of the coastal dunes, in the vicinity of a beach; mostly low vegetation with quite a few *Tamarix* bushes around the main flood plain (Fig. 8). Other *Polistes* species collected: *P. dominula*, *P. gallicus*, *P. nimpha*; *P. bischoffi* was the most abundant social wasp at the site.

GUARDIAS VIEJAS, 8 m. alt.: Area behind the coastal dunes bordering the beach; low vegetation with *Tamarix* patches. There were no wet areas in the vicinity, but the locality is not far from the seasonally flooded area at the other Guardias Viejas site. No other *Polistes* species were collected, but *P. nimpha* was also present.

LIBROS: Very shallow depression, about 100 x 30 m., close to the bank of a river, almost entirely covered by reeds, without any surface water at the time of the visit (Fig. 9). Other *Polistes* species collected at the site: *P. dominula*, *P. gallicus*, *P. nimpha*.

POMAR DE CINCA: No wetlands or wet spots were detected at the site, but there may be seasonal flooding or individual pools, as suggested by the presence of some reed patches; in the vicinity there is a permanent stream with very abundant *Tamarix* bushes along its banks. Besides *P. bischoffi*, *P. gallicus* and *P. nimpha* were also collected.

Fig. 8. One of the seasonally flooded areas behind the beach at Guardias Viejas (Almería prov., Spain), completely dried up at the time of the visit, in July. *P. bischoffi* Weyrauch, 1937 was very abundant at this site, outnumbering syntopic *Polistes* species. / Una de las zonas de inundación estacional tras la playa de Guardias Viejas (provincia de Almería, España), completamente seca en el momento de la visita, en julio. *P. bischoffi* Weyrauch, 1937 era muy abundante en este lugar, superando en número a las demás especies de *Polistes*.



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Fig. 9. *Polistes bischoffi* Weyrauch, 1937 locality near Libros (Teruel prov., Spain). / Localidad de *Polistes bischoffi* Weyrauch, 1937 junto a Libros (provincia de Teruel, España).



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SARIÑENA: A short distance from the southern banks of the Sariñena lake, which has water all year long; patches of steppe vegetation surrounded by agricultural and developed land. Other *Polistes* species collected: *P. dominula*, *P. gallicus*, *P. nimpha*, *P. semenowi* Morawitz, 1889.

TERUEL: Banks of a small stream surrounded by steppe and agricultural land. There are no wetlands in the area, although the site is not far (ca. 1 km) from a river. The nest was attached to a reed stalk. LC originally (1977) determined the specimens as “*P. foederatus*”. *P. dominula*, *P. gallicus*, *P. nimpha* and *P. semenowi* have also been collected at this site.

VILLARQUEMADO: The site was originally a (shallow) lake, but it was drained in the 18th century. It is now a seasonally flooded depression with a few permanent ponds but with very little surface water in summer. *Tamarix* patches are present. Other *Polistes* species collected: *P. dominula*, *P. nimpha*, *P. semenowi*.

Discussion

Taxonomy

When describing *Polistes helveticus* Neumeyer, 2014, the author was quite aware the paratype of *P. foederatus albellus* (MSNV-04702) was not only morphologically similar "to a very dark *P. helveticus* sp. n." (Neumeyer *et al.*, 2014: 98), but also morphometrically plotting among other females of *P. helveticus*, even if in the intersection with *P. gallicus* (Neumeyer *et al.*, 2014: 83). However, since no specimens of intermediate colour pattern such as those (RN0401, RN0404, RN0405, RN0406) from the Russian Orenburg Oblast were known yet, the striking differences in colour patterns between Mongolian and Kazakh females on the one hand and Central European individuals (Fig. 1, 2) on the other hand had obviously been overvalued when attributing the taxa *helveticus* and *albellus* to different species, then. Besides, Neumeyer *et*

Tab. II. Recognition in the field of *Polistes bischoffi* Weyrauch, 1937 females in the Iberian Peninsula. The shaded areas correspond to the main characters separating pairs of species. • Identificación en el campo de las hembras de *Polistes bischoffi* Weyrauch, 1937 en la Península Ibérica. Las zonas sombreadas corresponden a los principales caracteres que diferencian pares de especies.

	<i>P. bischoffi</i>	<i>P. biglumis</i>	<i>P. nimpha</i>	<i>P. gallicus</i>
Dorsum of antennal flagella III-X	Orange to very faintly darkened.	Distinctly black.	Orange to black.	Orange.
Malar-mandibular area	Dark above, light below (malar space black [there may be specimens with a yellow dot] / mandible always with a large yellow area).	Dark above, variable below (malar space black or black with a small yellow patch / mandible usually with a yellow area of variable size).	Light above, dark below (malar space predominantly yellow / mandible usually black, but sometimes with a very small yellow spot).	Dark above, light below (malar space black or black with a very small yellow patch / mandible always with a large yellow area).
Black markings on the clypeus	A large round discal patch, usually as large as in fig. XX.3 of Guiglia (1972) and sometimes larger.	Generally, a discal patch or a crossband (fig. XX.3-4 in Guiglia, 1972), often more extensive and occasionally taking up the whole of the clypeus.	Generally, a crossband, sometimes reduced to a transverse patch or small discal spots and occasionally absent (fig. XIX in Guiglia, 1972).	Generally absent; often there is a discal dot (fig. XXIV.2 in Guiglia, 1972); if there is a discal patch, it is usually relatively small and always much smaller than in <i>bischoffi</i> .
Yellow scutal marks	Usually absent.	Usually absent.	Usually absent.	Apparently always present, and usually well developed (states "a" to "d" in figure XII of Guiglia, 1972).
Yellow blotches on tergum II	Small to relatively small, and not connected to the apical band; typically as in fig. 6e of Neumeyer et al. (2014) or fig. XIId of Guiglia (1972).	Very small to relatively small, and not connected to the apical band (as in fig. XIId and XIle of Guiglia, 1972).	Small to relatively small, and usually isolated from the apical band (similar to <i>bischoffi</i> s).	Large and usually connected to the apical band (intermediate between states "b" and "c" in fig. XII of Guiglia, 1972)
Yellow bands on terga II-IV	Relatively narrow (those on terga III-IV distinctly narrower than the tergum's basal black band).	Relatively narrow (similar to <i>bischoffi</i> s).	Usually relatively narrow (similar to <i>bischoffi</i> s).	Broad (those on terga III-IV about twice the breadth of the basal black band).

al. (2014) were not yet aware of the Kazakh individuals mentioned in Dvořák *et al.* (2006: 536). Of course it would have been also desirable to see and sequence a female (8-13 Aug 2008, J. Halada leg.) from Mongolia mentioned (as "*bischoffi*") in Castro & Dvořák (2010: 45), but unfortunately it is currently missing (J. Macek pers. comm.). The same can be said of the holotype of *P. foederatus albellus* Giordani Soika, 1976 (HNHM coll.), which we have not been able to examine because it is still loaned elsewhere (Neumeyer *et al.*, 2014: 96).

Under the microscope *Polistes bischoffi* is quite distinctive and relatively easy to separate from other species of the genus with the keys in Neumeyer *et al.* (2014). In the field, and in the Iberian context, *P. bischoffi* females can be easily identified by their colour pattern; *P. biglumis*, sometimes *P. nimpha* and perhaps also *P. gallicus* may look similar at first sight, but a closer inspection will soon reveal the relevant diagnostic characters (Tab. II).

Colour variation

Polistes albellus is not the only vespid wasp to show a variation of colour and colour pattern as mentioned above. In fact, females of *Polistes biglumis* (Linnaeus, 1758) have a pattern of yellow to whitish patches on a black background which are fewer, smaller and paler in Sweden than in central Europe (Blüthgen, 1955: 398). Also in the Eurosiberian *Dolichovespula norwegica* (Fabricius, 1781) the patches are yellow in central Europe but paler right up to whitish in northernmost Europe (du Buysson 1905: 596), northeastern Siberia or central Mongolia (Birula 1930). In *Polistes fuscatus* (Fabricius, 1793) colour and colour pattern could be experimentally manipulated by nest temperature and relative humidity (Mac-

Lean *et al.*, 1978). On the other hand, there are also vespid wasps, such as the highly polymorphic *Vespa velutina* Lepeletier, 1836 whose colour variation seems predominantly due to genetic influence rather than to abiotic pressures (Perrard *et al.*, 2014). In the case of *Polistes albellus*, we can only guess which factors may influence its colour variation. However, we assume that climatic factors are involved, insofar as we have observed some associations between colour morphs (Fig. 1, 2) and climate types (Kottek *et al.*, 2006; Peel *et al.*, 2007). So, the "bright and yellow" morph of Central Europe (Fig. 1a, 2a) is the only one to occur in a moderate climate, while the others from Russia (Fig. 1b, 2b), Kazakhstan (Fig. 1c, 2c) and Mongolia (Fig. 1d, 2d) have more extensive black pigmentation and occur in cold climates. These "other" morphs with more extensive black pigmentation we can further separate into a "black and yellow" morph (Fig. 1b, 2b) from Russia (Orenburg Oblast and Primorsky Krai) and a "very black and whitish" morph from Kazakhstan (Fig. 1c, 2c) and Mongolia (Fig. 1d, 2d). Then we see (Fig. 4) that the black and yellow morph occurs in relatively moist lowland climates with warm summers, but the very black and whitish morph in relatively dry highland climates with cool summers. Thus, it primarily looks as if the colder the climate gets, the more extensive the black pigmentation becomes in *P. albellus*. This is a correlation already postulated by Zimmermann (1931) for *Polistes* and other Vespidae in general. The reason behind a transition from yellow to whitish seems, however, less obvious. It could be simply the effect of an even colder climate than the Russian sites have or it could be the effect of strong daily oscillations of temperature and relative humidity, typical of higher altitudes.

The study of the new *Polistes bischoffi* material has failed to produce any reliable evidence of geographical variability in its colour pattern, in line with the conclusions of Neumeyer *et al.* (2014); additionally, the new data suggest that the species is rather constant in this respect at the individual level as well. In the Iberian specimens variability seems restricted to the tone of the flagellar dorsum, which can be orange or slightly darkened, to a limited oscillation in the size of the clypear patch and to small differences in the extent of the yellow maculation of head and body.

Distribution

The amount of data about the distribution of *P. albellus n. stat.* has increased enormously since Neumeyer *et al.* (2014). While no records outside Central Europe were known then, we now know that its range is huge (Fig. 4), quite comparable with those of other Palaearctic species of the genus *Polistes* (Carpenter, 1996) such as e.g. *P. biglumis* (Linnaeus, 1758), *P. dominula* (Christ, 1791) or *P. nimpha* (Christ, 1791). While *P. dominula* has expanded its European range in a northern direction (Sprichardt, 2011: 89) and also invaded the Nearctic as well as other regions since the late seventies (Liebert *et al.*, 2006: 598), *P. albellus* is known to have spread northwards as well, at least in Germany since the seventies (Mauss, 2001). Our current knowledge of these species' ranges suggests a nearly vicariant distribution, with *P. albellus* occurring in the north and *P. bischoffi* in the south of their joint range, with just a narrow zone of sympatry (Fig. 4). Furthermore, the largely eastern range of *P. albellus* (apparently ranging no farther west than eastern France) and the mostly western range of *P. bischoffi* (not found farther east than Turkey so far) (Fig. 4, 5), suggest separate Pleistocene refuges for the two sibling species considered to be conspecific before Neumeyer *et al.* (2014), namely an eastern refuge for *P. albellus* and a southwestern one for *P. bischoffi*. However, this hypothesis does not explain the fact that *P. albellus* is present in Switzerland at least since 1882 (Neumeyer *et al.*, 2014: 107), but entered neighbouring Austria apparently only much later (Gusenleitner, 1995: 164). Another fact challenging the concept of sibling species is the phylogenetic tree of the mitochondrial marker COX1 (Fig. 3), where the sister clade of *P. albellus* contains three other species besides *P. bischoffi*. However, when we consider the phylogenetic tree of the nuclear marker ITS1 (Neumeyer *et al.*, 2014: 79), *P. albellus* (= *P. helveticus*) and *P. bischoffi* in fact form two sister clades. Moreover, the reduced or absent epicnemial carina (Neumeyer *et al.*, 2014: 106) seems to be a synapomorphic trait of *P. albellus* and *P. bischoffi* only, at least insofar as no other *Polistes* species with this trait are known.

Based on the new records, it is reasonable to expect that future collecting efforts will find *P. bischoffi*, in suitable habitats, in many other parts of the Iberian Peninsula; also, a re-examination of collections may very well bring to light *P. bischoffi* specimens misdetermined as some of the other Iberian members of the genus.

The overall distribution of *P. bischoffi* is not very well-known yet. The latitudinal range of the verified populations extends approximately from the 48th parallel (ca. 47°56'N, in Austria) to the 36th (ca. 36°08'N, in Gibraltar). It may occur further to the north in some areas, but, as mentioned above, the distribution of the species is apparently vicariant relative to that of *P. albellus*, which seems to largely replace it north of roughly the 44th to 47th parallels. On the other hand, its

presence at the southern extreme of the Iberian Peninsula, in habitats similar to those in the Maghreb, makes its presence in suitable enclaves of northern Africa very plausible. The eastern boundaries of the species are uncertain, due to insufficient data; the record from eastern Turkey does suggest the species might range into western and central Asia.

Habitat

Whether or not they are sibling species, there is also an ecological explanation for the vicariant distribution ranges of *P. albellus* and *P. bischoffi*, since both live mostly in wetlands. In Switzerland, where *P. bischoffi* has moved northwards only in the last decades (Neumeyer *et al.*, 2014: 93), this species has colonised exclusively habitats already occupied by *P. albellus*. Only the future will show how long this contemporary syntopy will last. One of the sibling species may oust the other, thus bringing about a more clear-cut vicariance.

While in Switzerland (Neumeyer *et al.*, 2014) *Polistes bischoffi* seems to be linked to large wetlands, our data (see the "Notes on habitat" above) indicate that the habitat spectrum is much broader on the Iberian Peninsula. In some of our Spanish localities there are permanent water bodies (lakes, lagoons or ponds); in others there is only a shallow depression that dries out during the summer, with or without an adjoining stream or river; in at least one locality there is only a stream. Altitudinally, known Iberian sites range from around sea level to an altitude of 1250 m, which means the species' range overlaps with those of most of the other members of the genus occurring in Iberia, namely *P. dominula*, *P. gallicus*, *P. nimpha* and *P. semenowi*, and potentially also with that of *P. biglumis* (mostly a mountain species in this part of the world).

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References

- BIRULA, A. 1930. Über die russischen Wespen und ihre geographische Verbreitung. (Dritter Beitrag). *Annaire du Musée Zoologique de l'Académie des Sciences de l'URSS*, **31**: 291-339.
- BLÜTHGEN, P. 1955. Weitere Beiträge zur Synonymie der paläarktischen Faltenwespen. (Hym. Vespidae). *Mitteilungen der Münchner Entomologischen Gesellschaft*, **45**: 397-417.
- DU BUYSSEN, R. 1905. Monographie des guêpes ou *Vespa*; 2^e Groupe. *Annales de la Société Entomologique de France*, **73**(3): 565-634, pl. V-XV.
- CARPENTER, J.M. 1996. Distributional checklist of species of the genus *Polistes* (Hymenoptera: Vespidae; Polistinae, Polistini). *American Museum Novitates*, **3188**: 1-39.

- CASTRO, L. 2001. Vespidae: subfamilias Masarinae, Polistinae, Vespinae (Insecta: Hymenoptera. Familia 3: Vespidae (y 2)). *Catalogus de la entomofauna aragonesa*, **25**: 11-14.
- CASTRO, L. & L. DVOŘÁK 2010. New and noteworthy records of vespid wasps (Hymenoptera: Vespidae) from the Palaearctic region (III). *Acta Musei Moraviae, Scientiae biologicae (Brno)*, **95**(2): 37-53.
- DINIZ, M.A. 1960. Estado actual do conhecimento dos himenópteros portugueses. *Las ciencias*, **25**: 211-224.
- DINIZ, M.A. 1978. As espécies portuguesas de vespas (Hymenoptera Vespoidea) na coleção do Museu e Laboratório Zoológico da Universidade de Coimbra. *Ciências biológicas (Portugal)*, **4**: 7-21.
- DVOŘÁK, L., V. SMETANA, J. STRAKA & P. DEVÁN 2006. Present distribution of the paper wasp *Polistes bischoffi* Weyrauch, 1937 in the Czech Republic and Slovakia with notes to its spreading (Hymenoptera: Vespidae). *Linzer biologische Beiträge*, **38**(1): 533-539.
- GIORDANI SOIKA, A. 1976. Vespidi ed Eumenidi (Hymenoptera) raccolti in Mongolia dal Dr. Z. Kaszab. *Acta Zoologica Academiae Scientiarum Hungaricae*, **22**(3-4): 271-276.
- GUIGLIA, D. 1972. *Les guêpes sociales (Hymenoptera Vespidae) d'Europe Occidentale et Septentrionale*. Masson et Cie Editeurs, Paris, VIII + 182 pp, 3 pl.
- GUSENLEITNER, J. 1995. Hymenopterologische Notizen aus Österreich – 3 (Insecta: Hymenoptera Aculeata). *Linzer biologische Beiträge*, **27**(1): 159-167.
- KASZAB, Z. 1968. Ergebnisse der zoologischen Forschungen von Dr. Z. Kaszab in der Mongolei; 186. Liste der Fundorte der VI. Expedition. *Folia Entomologica Hungarica (Series nova)*, **21** (Suppl.): 389-444.
- KOTTEK, M., J. GRIESER, C. BECK, B. RUDOLF & F. RUBEL 2006. World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, **15**(3): 259-263.
- LIEBERT, A.E., G.J. GAMBOA, N.E. STAMP, T.R. CURTIS, K.M. MONNET, S. TURILLAZZI & P.T. STARKS 2006. Genetics, behavior and ecology of a paper wasp invasion: *Polistes dominulus* in North America. *Annales Zoologici Fennici*, **43**: 595-624.
- MACLEAN, B.K., L. CHANDLER & D.B. MACLEAN 1978. Phenotypic expression in the paper wasp *Polistes fuscatus* (Hymenoptera: Vespidae). *The Great Lakes Entomologist*, **11**(2): 105-116.
- MADER, L. 1936. Beitrag zur Kenntnis der Hymenopteren, I. *Entomologische Zeitschrift (Frankfurt a.M.)*, **50**(23): 261-263.
- MADERO MONTERO, A. 1988. Conocimiento actual de la distribución de los Véspidos en España (Hym. Vespidae). *Actas [del] III Congreso Ibérico de Entomología*: 405-416.
- MAUSS, V. 2001. Erstnachweis der Faltenwespe *Polistes bischoffi* Weyrauch 1937 (Hymenoptera, Vespidae) für Nordrhein-Westfalen mit Anmerkungen zur Arealausweitung der Art. *Decheniana (Bonn)*, **154**: 109-116.
- MAUSS, V. & R. TREIBER 2004. *Bestimmungsschlüssel für die Faltenwespen (Hymenoptera: Masarinae, Polistinae, Vespinae) der Bundesrepublik Deutschland*. Deutscher Jugendbund für Naturbeobachtung, Hamburg. pp. 2-53.
- NEUMAYER, R., A. GIGON & C. DOBLER GROSS 2011. Eine neue Feldwespe am Greifensee: Farbmorphe, Hybrid oder *Polistes gallicus* (Linnaeus, 1767)? *Entomo Helvetica*, **4**: 7-22.
- NEUMAYER, R., H. BAUR, G.D. GUEX, & C. PRAZ 2014. A new species of the paper wasp genus *Polistes* (Hymenoptera, Vespidae, Polistinae) in Europe revealed by morphometrics and molecular analyses. *ZooKeys*, **400**: 67-118.
- PEEL, M.C., B.L. FINLAYSON & T.A. McMAHON 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, **11**: 1633-1644.
- PERRARD, A., M. ARCA, Q. ROME, F. MULLER, J. TAN, S. BISTA, H. NUGROHO, R. BAUDOIN, M. BAYLAC, J.F. SILVAIN, J.M. CARPENTER & C. VILLEMAN 2014. Geographic variation of melanisation patterns in a Hornet species: genetic differences, climatic pressures or aposematic constraints? *PloS ONE*, **9**(4): 1-16.
- RUBIN, N.I. & R.V. YAKOVLEV 2013. Checklist of the butterflies (Papilioidea) of the Saur Mountains and adjacent territories (Kazakhstan), including systematic notes about the *Erebia callias* group. *Nota lepidopterologica*, **36**(2): 137-170.
- SCHMID-EGGER, C. & R. TREIBER 1989. Die Verbreitung von *Polistes bischoffi* (Hym., Vespoidea) in Süddeutschland. *Linzer biologische Beiträge*, **21**(2): 601-609.
- SCHMIDT, S., C. SCHMID-EGGER, J. MORINIÈRE, G. HASZPRUNAR & P.D.N. HEBERT 2015. DNA barcoding largely supports 250 years of classical taxonomy: identifications for Central European bees. *Molecular Ecology Resources*, **15**: 985-1000.
- SPRICHARDT, J. 2011. Bienen und Wespen naturnaher Restheiden im Raum Cuxhaven. *Drosera*, **2010**: 77-102.
- STAMATAKIS, A., T. LUDWIG & H. MEIER 2005. RAxML-III: a fast program for maximum likelihood-based inference of large phylogenetic trees. *Bioinformatics*, **21**: 456-463. doi: 10.1093/bioinformatics/bti191
- ZIMMERMANN, K. 1931. Studien über individuelle und geographische Variabilität paläarktischer *Polistes* und verwandter Vespiden. *Zeitschrift für Morphologie und Ökologie der Tiere*, **22**: 173-231.