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Wing Venation Abnormalities in the Solitary Wasp Family Crabronidae (Insecta: Hymenoptera)

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ABSTRACT

Insect wings are flexible structures composed of tubular veins and thin wing membranes. In many insect groups, wings contain distinct taxonomic characters which are easy to describe (e.g., the number and length of veins, the wing size, etc.). However, some insects may have abnormal specimens that have some veins or their parts missing, or to the contrary have additional veins on the wings. In this study, forewing abnormalities in 248 species of 53 solitary wasp genera belonging to the family Crabronidae (Hymenoptera) collected from Turkey were investigated for the first time. As a result, forewing abnormalities were detected in 37 species belonging to 18 genera from five subfamilies. In total, 20 cases of wing venation abnormalities, classified as: a) supernumerary veins, b) defective veins and c) supernumerary cells, were observed in 67 of 3244 specimens. The abnormalities were rather common in following three species *Psammaecius punctulatus* (Vander Linden, 1829) (n = 8, 11.94%), *Bembix bidentata* Vander Linden, 1829 (n = 6, 8.95%), and *Bembecinus tridens* (Fabricius, 1781) (n = 4, 7.46%). *Nysson interruptus* (Fabricius, 1798) and *Nysson maculosus* (Gmelin, 1790) are species with more than one abnormality on the same wing. Abnormalities were generally observed in males (n=50, 74.63%) rather than females (n=17, 25.37%). The mechanism of this phenomenon, which is thought to occur due to genetic, environmental or pathogenic reasons, has not yet been clarified in many insect groups, including Crabronidae.

Key words: abnormalities, Crabronidae, defective veins, Hymenoptera, supernumerary cells, supernumerary veins.

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INTRODUCTION

Crabronidae is one of the most diverse families in the order Hymenoptera which collectively includes over 200 genera, containing well over 9000 species (Pulawski, 2022). The family consists of solitary and predatory wasps. This family includes quite different groups according to the variety of forewing veins and cells. Members of some groups of subfamilies such as Pemphredoninae and Crabroninae have different submarginal cell numbers in the forewings due to a reduction in some veins. Also, in some genera, the second submarginal cell is petiolated.

As in other families of the order Hymenoptera, the wing has a very important taxonomic characters in family Crabronidae. The following wing characters are frequently used for classification and identification of subfamilies, genera and species belonging to this family: number of submarginal cells, number of discoidal and subdiscoidal cells, whether submarginal and discoidal cells are separate or fused, size of stigma, terminal structure of the marginal cell, whether the second submarginal cell is petiolated or not, the shape and size of submarginal cells and the number and termination of recurrent veins (Bohart & Menke, 1976; Bitsch & Leclercq, 1993). However, due to wing abnormalities, changes may occur in these taxonomic characters and may lead to the misidentification of taxa or systematic problems (Gülmez, 2019).

Abnormalities are defined as physical developmental defects or malformations, and the exact causes are not known. Although abnormalities appear very rare in nature, abnormal specimens have been described in almost all animal groups, including insects. Balazuc (1958) provided a comprehensive classification of abnormality phenomena in the order Hymenoptera. Following this study, abnormalities such as gynandromorphism, irregularities in segmentation of gaster and antennae, supernumerary ocelli, loss of ocelli, loss of compound eye, and wing vein abnormalities have been reported in that order (Gülmez, 2019).

Mostly honey bees, *Apis mellifera* Linnaeus, 1758, have been well studied in terms of wing venation abnormalities within the order Hymenoptera (Soose, 1954; Akahira & Sakagami, 1959; Bährman, 1963; Torres & Ramos, 2000; Schneider & Feitz, 2003; Penteado-Dias, Nunes & Shimbori, 2005; Tan, Fuchs & Engel, 2008; Węgrzynowicz, Gerula, Panasiuk & Bieńkowska, 2010; Mazeed, 2011; Porporato, Laurino, Balzola & Manino, 2014; Caomério, Perioto & Lara, 2015; Eligül, Koca & Kandemir, 2017). A few studies on wing abnormalities of some ant species of the same order have also been reported (Perfilieva, 2000). Scarpulla (2018) summarized the cases with atypical and variable submarginal cell numbers on specimens belonging to the families Colletidae, Andrenidae, Halictidae and Apidae. Recently, wing abnormalities related to the Sphecidae family, which is in the same superfamily as honey bees in Hymenoptera, have been reported by Gülmez (2019). There is no record of any wing abnormalities related to the Crabronidae family.

In this study, various wing abnormalities were recorded for 69 specimens representing 37 species in the solitary wasp family Crabronidae (Hymenoptera). Abnormalities detected in specimens belonging to different genera from the Crabronidae family are presented.

MATERIALS AND METHODS

In this study, 3244 specimens belonging to 248 species of Crabronidae family were examined for wing venation abnormalities. Specimens were collected from Erzincan, Giresun, Gümüşhane, and Sivas provinces of Turkey between 2015 and 2020 and are deposited in the Entomology Research Laboratory, Department of Biology, Tokat Gaziosmanpaşa University (Tokat, Turkey). Abnormal wings (right or left) were removed from the specimens, placed between glasses in a slide frame and then photographed with a Leica M205C stereomicroscope controlled by the Leica Application Suite 3 software. The distribution of abnormalities among species is given in Table 1. The general shapes of the different types of forewings in the Crabronidae family are given in Fig. 1 with the names of veins and cells according to Bohart & Menke (1976) except for the terms “1st abscissa” and “2nd abscissa” which are from Porporato et al. (2014). Photographs representing the types of wing abnormalities belonging to different genera are given in the Figs. 2 - 9. In the present study, Porporato et al. (2014) was followed for the classification and naming of abnormalities.

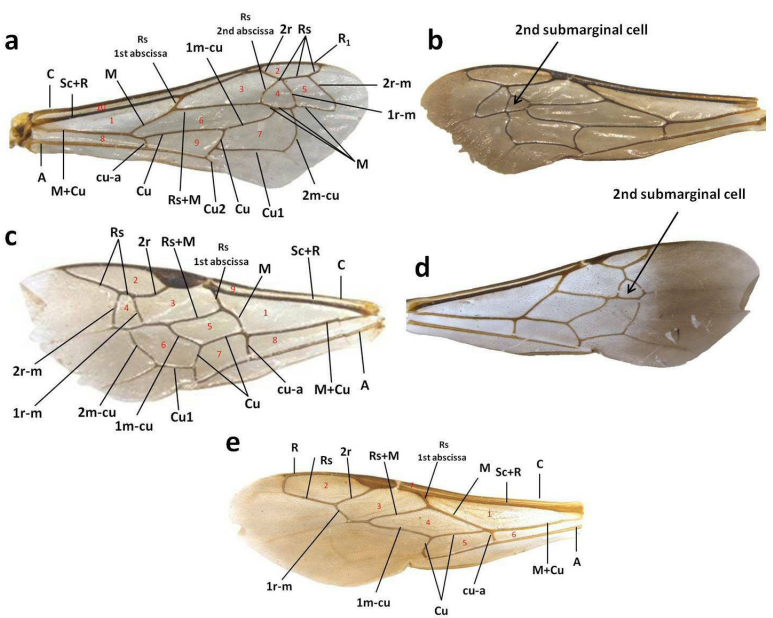

Fig. 1. Different types of forewings in the Crabronidae family in terms of cell number and veins. **a)** Right forewing of *Bembecinus tridens* with three submarginal cells representing cell and vein names. Cell names (1–10): 1. Medial, 2. Marginal, 3. Submarginal I, 4. Submarginal II, 5. Submarginal III, 6. Discoidal I, 7. Discoidal II, 8. Submedial, 9. Subdiscoidal, 10. Costal. Vein names: A. Anal, C. Costal, Cu. Cubital, M. Medial, R. Radial, Rs. Radial sector, Sc. Subcostal; **b)** Left forewing of *Brachystegus scalaris* with a petiolated second submarginal cell; **c)** Left forewing of *Diodontus minutus* with two submarginal cells representing names of cells and veins. Cell names (1-9): 1. Medial, 2. Marginal, 3. Submarginal I, 4. Submarginal II, 5. Discoidal I, 6. Discoidal II, 7. Subdiscoidal, 8. Submedial, 9. Costal. **d)** Right forewing of *Miscophus pretiosus* with a petiolated second submarginal cell; **e)** Left forewing of *Ectemnius crassicornis* with one submarginal cell representing names of cells and veins. Cell names (1-7): 1. Medial, 2. Marginal, 3. Submarginal, 4. Discoidal, 5. Subdiscoidal, 6. Submedial, 7. Costal.

Table 1. Distribution of abnormality types among species and their proportions.

Abnormality	Species	n	%a	%b
Supernumerary veins		**39**		
Spur protruding from 1r-m into the 2nd submarginal cell	*Astata kashmirensis* (1 ♂)	1	1.45	0.03
Spur protruding from 1m-cu into the 2nd discoidal cell	*Astata minor* (1 ♀) *Cerceris quinquefasciata* (1 ♂) *Nysson interruptus* (1 ♂)	3	4.35	0.09
Spur protruding from 2r into marginal cell	*Bembecinus tridens* (1 ♂) *Nysson pratensis* (1 ♂)	2	2.90	0.06
Spur protruding from Rs into marginal cell	*Bembecinus tridens* (1 ♀)	1	1.45	0.03
Spur protruding from 2m-cu	*Bembix bidentata* (1 ♀) *Bembix tarsata* (1 ♂) *Larra anathema* (1 ♀) *Tachysphex incertus* (1 ♂) *Tachysphex obscuripennis* (1 ♀) *Tachysphex panzeri* (1 ♂) *Tachysphex tessellatus* (1 ♂)	7	10.14	0.22
Spur protruding from 2m-cu into the 2nd discoidal cell	*Bembix bidentata* (1 ♂) *Nysson gerstackeri* (1 ♀) *Tachysphex incertus* (1 ♂)	3	4.35	0.09
Spur protruding from 2nd abscissa of Rs into 1st submarginal cell	*Bembecinus tridens* (1 ♂) *Gorytes quinquefasciatus* (1 ♂) *Prosopigastra bulgarica* (1 ♂) *Psammaecius punctulatus* (2♀♀, 5 ♂♂)	10	14.49	0.31
Spur protruding from RS+M into the 1st submarginal cell	*Nysson interruptus* (1 ♀) *Nysson variabilis* (1 ♂)	2	2.90	0.06
Spur protruding from 2nd abscissa of Rs into the 2nd submarginal cell	*Psammaecius punctulatus* (1 ♂)	1	1.45	0.03
Spur protruding from 2nd abscissa of Rs	*Ectemnius crassicornis* (1 ♀) *Nitela truncata* (1 ♀)	2	2.90	0.06
Spur protruding from 2r-m	*Astata kashmirensis* (1 ♂) *Astata minor* (1 ♂) *Cerceris stratiotes* (1 ♂) *Tachysphex pompiliformis* (1 ♂)	4	5.80	0.12
Spur protruding from 1m-cu into 1st discoidal cell	*Prosopigastra orientalis* (1 ♂)	1	1.45	0.03
Spur protruding from R1 into the marginal cell	*Nysson maculosus* (1 ♂) *Philanthus triangulum* (1 ♂)	2	2.90	0.06
Defective veins		**11**		
Incomplete 2r-m crossvein	*Nysson maculosus* (1 ♂)	1	1.45	0.03
Incomplete 1r-m crossvein	*Cerceris specularis* (1 ♂) *Miscophus pretiosus* (1 ♂) *Tachysphex brevipennis* (1 ♂) *Philanthus triangulum* (1 ♂) *Diodontus luperus* (2 ♂♂) *Diodontus minutus* (1 ♀) *Nysson interruptus* (1 ♂)	8	11.59	0.25
Incomplete 2m-cu crossvein	*Miscophus pretiosus* (1 ♂)	1	1.45	0.03
Incomplete 1m-cu crossvein	*Prosopigastra bulgarica* (1 ♂)	1	1.45	0.03

Table 1. Continued.

Abnormality	Species	n	%a	%b
Supernumerary cells		**19**		
Supernumerary submarginal cell	*Astata affinis* (1 ♀) *Bembecinus tridens* (1 ♂) *Bembix bidentata* (1 ♀, 3 ♂♂) *Brachystegus scalaris* (1 ♀) *Gorytes albidulus* (1 ♂) *Gorytes quinquecinctus* (1 ♀) *Nysson variabilis* (1 ♀) *Tachysphex fulvitarsis* (2 ♂♂) *Tachysphex graecus* (1 ♂) *Tachysphex obscuripennis* (1 ♂) *Tachysphex psammobius* (1 ♂)	15	21.74	0.46
Supernumerary discoidal cell	*Bembecinus tridens* (1 ♂) *Gorytes quinquefasciatus* (2 ♂♂)	3	4.35	0.09
Incomplete supernumerary discoidal cell	*Tachysphex brevipennis* (1 ♂)	1	1.45	0.03

%a Rate of total abnormal forewings

%b Rate of total examined material

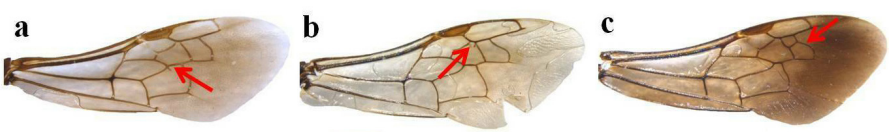

Fig. 2. Forewing abnormalities in the genus *Astata*. a) *A. minor* (♀), spur protruding from 1m-cu into 2nd discoidal cell; b) *A. kashmirensis* (♂), spur protruding from 1r-m into 2nd submarginal cell; c) *A. affinis* (♀), supernumerary submarginal cell.

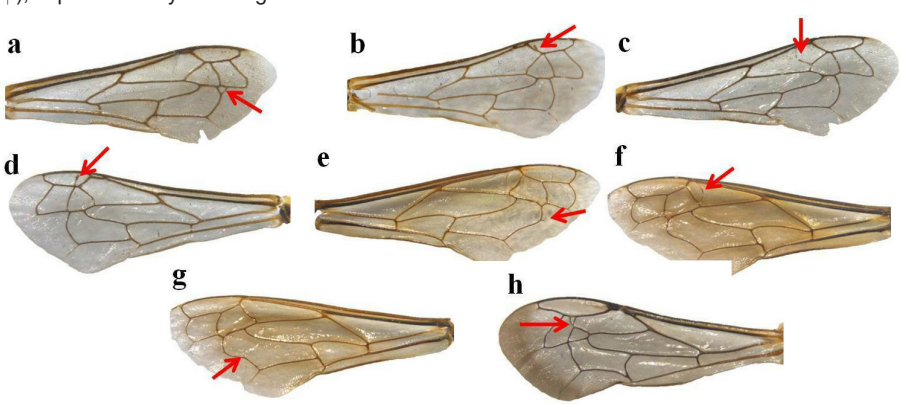

Fig. 3. Forewing abnormalities in the genus *Bembecinus*, *Bembix* and *Brachystegus.* a) *Bembecinus tridens* (♂), supernumerary discoidal cell; b) *Bembecinus tridens* (♂), spur protruding from 2r into marginal cell; c) *Bembecinus tridens* (♂), spur protruding from 2nd abscissa of Rs into the 1st submarginal cell; d) *Bembecinus tridens* (♀), spur protruding from Rs into marginal cell; e) *Bembix bidentata* (♀), spur protruding from 2m-cu; f) *Bembix bidentata* (♂), supernumerary submarginal cell; g) *Bembix bidentata* (♂), spur protruding from 2m-cu into the 2nd discoidal cell; h) *Brachystegus scalaris* (♀), supernumerary submarginal cell.

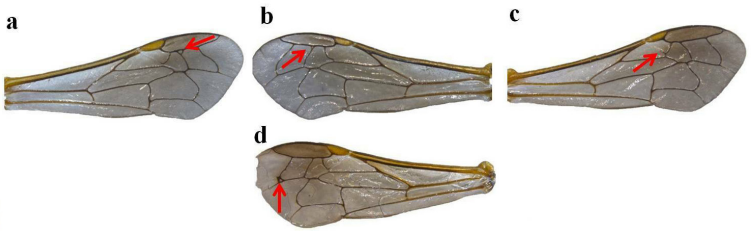

Fig. 4. Forewing abnormalities in the genus *Gorytes*. a) *Gorytes albidulus* (♂), supernumerary submarginal cell; b) *Gorytes quinquecinctus* (♀), supernumerary submarginal cell; c) *Gorytes quinquefasciatus* (♂), spur protruding from 2nd abscissa of RS into 1st submarginal cell; d) *Gorytes quinquefasciatus* (♂), supernumerary submarginal cell.

RESULTS

In this study, various forewing abnormalities were documented in 67 out of 3244 specimens (2.07%). Twenty different abnormalities have been identified which can be grouped under three main headings: a) supernumerary veins n = 39 (56.52%), b) defective veins n = 11 (15.94%) and c) supernumerary cells n = 19 (27.54%) (Table 1). The most common wing abnormalities are supernumerary veins which arise as spurs protruding from various veins, mostly from transverse ones. Reduction or deletion of some veins, defective vein abnormality, is the least common abnormality type which is found in transverse veins. Supernumerary cell formation is determined in submarginal and discoidal cells. The most common individual cases are: 1) supernumerary submarginal cell (n = 15, 21.74%), 2) spur protruding from 1st abscissa of Rs to 1st submarginal cell (n = 10, 14.49%) and 3) spur protruding from 2m-cu (n = 7, 10.14%). More than one abnormality in a same wing was observed in *Nysson interruptus* and *N. maculosus* (Figs. 5b and 5c).

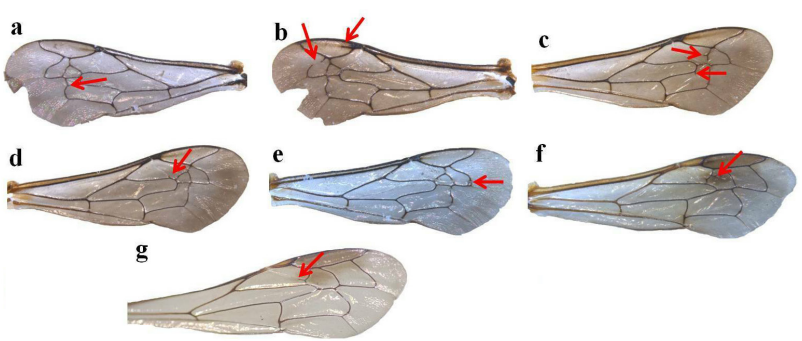

Fig. 5. Forewing abnormalities in the genus *Nysson*. a) *Nysson gerstaeckeri* (♀), spur protruding from 2m-cu into the 2nd discoidal cell; b) *N. maculosus* (♂), incomplete 2r-m crossvein and spur protruding from R1 into the marginal cell; c) *N. interruptus* (♂), spur protruding from 1m-cu into the 2nd discoidal cell and partially incomplete 1r-m crossvein; d) *N. interruptus* (♀), spur protruding from RS+M into the 1st submarginal cell; e) *N. variabilis* (♀), supernumerary submarginal cell; f) *Psammaecius punctulatus* (♂), spur protruding from 2nd abscissa of Rs into the 2nd submarginal cell; g) *Psammaecius punctulatus* (♀), spur protruding from 2nd abscissa of Rs into 1st submarginal cell.

When sexes are considered, their distribution are as follows: 50 males (74.63%) and 17 females (25.37%). The number of normal and abnormal species in the subfamilies and the percentage of species with abnormalities among all taxa studied are as follows: three species out of 12 in the subfamily Astatinae (1.21%), 13 species out of 57 in the subfamily Bembicinae (5.24%), 15 species out of 116 (6.04%) in the subfamily Crabroninae, two species out of 36 in the subfamily Pemphredoninae (0.80%) and four species out of 26 in the subfamily Philanthinae (1.61%).

Subfamily Astatinae Lepeletier de Saint-Fargeau, 1845

Genus *Astata* Latreille, 1797

In this study, totally 183 specimens (70 ♀♀ and 113 ♂♂) of nine species of the genus *Astata* were examined for their forewing abnormalities. Abnormalities were detected in five specimens belonging to *Astata affinis* Vander Linden, 1829 (1 ♀), *A. kashmirensis* Nurse, 1909 (2 ♂♂), and *A. minor* Kohl, 1885 (1 ♀, 1 ♂). Supernumerary cell (Fig. 2c) and supernumerary veins (Figs. 2a, 2b) were observed in these specimens.

Subfamily Bembicinae Latreille, 1802

Genus *Bembecinus* A. Costa, 1859

In this study, a total of 103 specimens (47 ♀♀ and 56 ♂♂) belonging to five species of the genus *Bembecinus* were examined for their forewing abnormalities. Abnormalities were detected only in *Bembecinus tridens* (Fabricius, 1781) (1♀, 4 ♂♂). Supernumerary cell (Fig. 3a) and supernumerary veins were observed in these specimens (Figs. 3b-d).

Genus *Bembix* Fabricius, 1775

In this study, a total of 82 specimens (42 ♀♀ and 40 ♂♂) belonging to six species of the genus *Bembix* were examined for their forewing abnormalities. Abnormalities were detected in *Bembix tarsata* Latreille, 1809 (1 ♂) and *B. bidentata* Vander Linden, 1829 (2 ♀♀, 4 ♂♂). Supernumerary cell (Fig. 3f) and supernumerary veins (Figs. 3e, 3g) were observed in these specimens.

Genus *Brachystegus* A. Costa, 1859

In this study, a total of 24 specimens (22 ♀♀ and 2 ♂♂) belonging to *Brachystegus incertus* Radoszkowski, 1877 and *B. scalaris* (Illiger, 1807) were examined for their forewing abnormalities. Supernumerary submarginal cell was detected as an abnormality in a female specimen belonging to *B. scalaris* (Fig. 3h).

Genus *Gorytes* Latreille, 1805

In this study, totally 89 specimens (35 ♀♀ and 54 ♂♂) of nine species of the genus *Gorytes* were examined for their forewing abnormalities. Abnormalities were detected in five specimens belonging to *Gorytes albidulus* Lepeletier de Saint-Fargeau, 1832 (1 ♂), *G. quinquecinctus* (Fabricius, 1793) (1 ♀), and *G. quinquefasciatus* (Panzer, 1798) (3 ♂♂). Supernumerary cell (Figs. 4a, 4b, 4d) and supernumerary veins (Fig. 4c) were observed in these specimens.

Genus *Nysson* Latreille, 1802

In this study, totally 105 specimens (58 ♀♀ and 47 ♂♂) of 12 species belonging to genus *Nysson* were examined for their forewing abnormalities. Abnormalities were detected in seven specimens belonging to *Nysson gerstaeckeri* Handlirsch, 1887 (1 ♀), *N. interruptus* (Fabricius, 1798) (1♀ 1 ♂), *N. maculosus* (Gmelin, 1790) (1 ♂), *N. pratensis* Mercet, 1909 (1 ♂), and *N. variabilis* Chevrier, 1867 (1♀ 1 ♂). Supernumerary cell (Fig. 5e), supernumerary veins (Figs. 5a-d) and defective vein (Fig. 5b) were observed in these specimens. Although both *Nysson interruptus* (♂) and *Nysson maculosus* (♂) are represented with one specimen, they are included in two different abnormality sections in Table 1 since they have more than one abnormality on the same wing.

Genus *Psammaecius* Lepeletier de Saint-Fargeau, 1832

In this study, a total of 37 specimens (17 ♀♀ and 20 ♂♂) belonging to *Psammaecius punctulatus* (Vander Linden, 1829) were examined for their forewing abnormalities. Supernumerary veins were detected in eight specimens (2 ♀♀ 6 ♂♂) (Figs. 5f, 5g).

Subfamily Crabroninae Latreille, 1802

Genus *Ectemnius* Dahlbom, 1845

In this study, a total of 96 specimens (40 ♀♀ and 56 ♂♂) of 13 species belonging to genus *Ectemnius* were examined for their forewing abnormalities. Only, a spur protruding from 2nd abscissa of Rs was detected in *Ectemnius crassicornis* (Spinola, 1808) (1 ♀) (Fig. 6a).

Genus *Larra* Fabricius, 1793

In this study, a total of 15 specimens (12 ♀♀ and 3 ♂♂) belonging to *Larra anathema* (Rossi, 1790) were examined for their forewing abnormalities. Only a supernumerary vein was detected in a female specimen (Fig. 6b).

Genus *Miscophus* Jurine, 1807

In this study, a total of 108 specimens (44 ♀♀ and 64 ♂♂) belonging to 11 species of genus *Miscophus* were examined for their forewing abnormalities. Only defective veins were detected in *Miscophus pretiosus* Kohl, 1884 (2 ♂♂) (Fig. 6c, 6d).

Genus *Nitela* Latreille, 1809

In this study, a total of 3 specimens (2 ♀♀ and 1 ♂) belonging to three species of genus *Nitela* were examined for their forewing abnormalities. Only supernumerary vein was detected in *Nitela truncata* Gayubo & Felton, 2000 (1 ♀) (Fig. 6e).

Genus *Prosopigastra* A. Costa, 1867

In this study, totally 118 specimens (37 ♀♀ and 81 ♂♂) of five species of the genus *Prosopigastra* were examined for their forewing abnormalities. Abnormalities were detected in three specimens belonging to *Prosopigastra bulgarica* Pulawski, 1958 (2 ♂) and *Prosopigastra orientalis* de Beaumont, 1947 (1 ♂). Supernumerary veins (Figs. 6h, 6g) and defective vein (Fig. 6f) were observed in these specimens.

Genus *Tachysphex* Kohl, 1883

In this study, totally 786 specimens (295 ♀♀ and 491 ♂♂) of 28 species of the genus *Tachysphex* were examined for their forewing abnormalities. Abnormalities were detected in 13 specimens belonging to *Tachysphex brevipennis* Mercet, 1909 (2 ♂♂), *T. fulvitarsis* (A. Costa, 1867) (2 ♂♂), *T. graecus* Kohl, 1883 (1 ♂), *T. incertus* (Radoszkowski, 1877) (2 ♂♂), *T. obscuripennis* (Schenck, 1857) (1♀ 1 ♂), *T. panzeri* (Vander Linden, 1829) (1 ♂), *T. pompiliformis* (Panzer, 1804) (1 ♂), *T. psammobius* (Kohl, 1880) (1 ♂), and *T. tessellatus* (Dahlbom, 1845) (1 ♂). Supernumerary cells (Figs. 7e-j), supernumerary veins (Figs. 7b-d) and defective vein (Fig. 7a) were observed in these specimens.

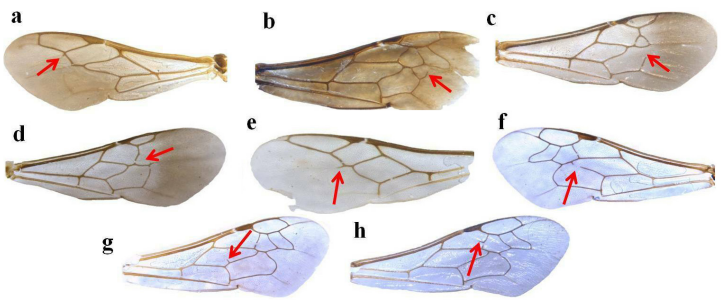

Fig. 6. Forewing abnormalities in the genera *Ectemnius, Larra, Miscophus, Nitela, and Prosopigastra.* a) *Ectemnius crassicornis* (♀), spur protruding from 1r-m; b) *Larra anathema* (♀), spur protruding from 2m-cu; c) *Miscophus pretiosus* (♂), incomplete 2m-cu crossvein; d) *Miscophus pretiosus* (♂), partially incomplete 1r-m crossvein; e) *Nitela truncata* (♀), spur protruding from submarginal cell; f) *Prosopigastra bulgarica* (♂), incomplete 1m-cu crossvein; g) *Prosopigastra orientalis* (♂), spur protruding from 1m-cu into 1st discoidal cell; h) *Prosopigastra bulgarica* (♂), spur protruding from 2nd abscissa of Rs into 1st submarginal cell.

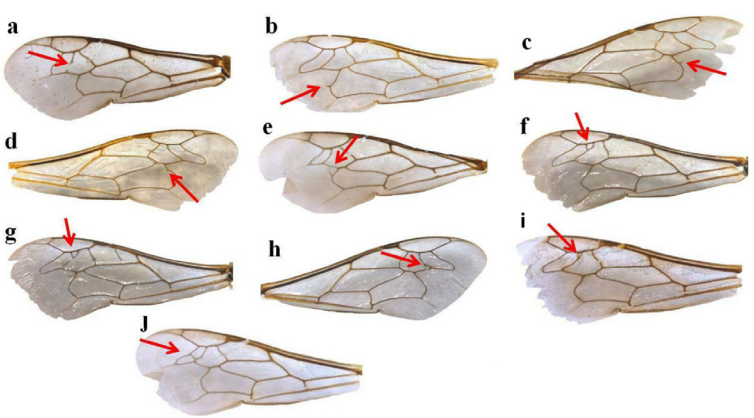

Fig. 7. Forewing abnormalities in the genus *Tachysphex*. a) *Tachysphex brevipennis* (♂), incomplete 1r-m crossvein; b) *Tachysphex incertus* (♂), spur protruding from 2m-cu; c) *Tachysphex obscuripennis* (♀), spur protruding from 2m-cu; d) *Tachysphex incertus* (♂), spur protruding from 2m-cu into the 2nd discoidal cell; e) *Tachysphex brevipennis* (♂), incomplete supernumerary discoidal cell; f) *Tachysphex fulvitarsis* (♂), supernumerary submarginal cell; g) *Tachysphex fulvitarsis* (♂), supernumerary submarginal cell; h) *Tachysphex graecus* (♂), supernumerary submarginal cell; i) *Tachysphex obscuripennis* (♂), supernumerary submarginal cell; j) *Tachysphex psammobius* (♂), supernumerary submarginal cell.

Subfamily Pemphredoninae Dahlbom, 1835

Genus *Diodontus* Curtis, 1834

In this study, a total of 87 specimens (45 ♀♀ and 42 ♂♂) belonging to five species of the genus *Diodontus* were examined for their forewing abnormalities. Abnormalities were detected in *Diodontus luperus* Shuckard, 1837 (2 ♂♂) and *Diodontus minutus* (Fabricius, 1793) (1 ♀). Defective veins were observed in these specimens (Figs. 8a, 8b).

Subfamily Philanthinae Latreille, 1802

Genus *Cerceris* Latreille, 1802

In this study, a total of 208 specimens (62 ♀♀ and 146 ♂♂) belonging to 21 species of the genus *Cerceris* were examined for their forewing abnormalities. Abnormalities were detected in *Cerceris quinquefasciata* (Rossi, 1792) (1 ♂), *C. specularis* A. Costa, 1867 (1 ♂) and *C. stratiotes* Schletterer, 1887 (1 ♂). Supernumerary veins were observed in these specimens (Figs. 9a, 9b).

Genus *Philanthus* Fabricius, 1790

In this study, a total of 79 specimens (32 ♀♀ and 47 ♂♂) belonging to four species of the genus *Philanthus* were examined for their forewing abnormalities. Abnormalities were detected in *Philanthus triangulum* (Fabricius, 1775) (2 ♂♂). Defective vein (Fig. 9d) and supernumerary vein (Fig. 9c) were observed in these specimens.

DISCUSSION

In this study, a large number of specimens belonging to the Crabronidae family were evaluated for the first time in terms of wing abnormalities. Forewing abnormalities were detected in 37 species of 18 genera out of 248 species belonging to 53 genera.

Abnormal forewing was detected in all of the studied subfamilies except the Dinetinae. The subfamily Crabroninae is the one with the highest number of abnormal species, followed by Bembicinae. While the most abnormal specimens were detected in the Bembicinae subfamily, the lowest number of abnormal species and specimens was detected in Pemphredoninae compared to other subfamilies. Although Crabroninae is twice as large as Bembicinae in terms of the number of examined specimens and species, the number of abnormal specimens is higher in the Bembicinae. The wing structures of the subfamilies and genera belonging to the Crabronidae differ considerably in terms of the number of veins and cells. While subfamilies and genera belonging to this family have one (Fig. 1e), two (Fig. 1c) and three submarginal cells (Fig. 1a); in some of these, the second submarginal cell is petiolated (Fig. 1b, 1d). The reduction in the number of veins and cells in the forewings of some subfamilies may have caused the abnormalities to be observed less frequently. However, it may not be an accurate assessment to evaluate abnormalities between subfamilies due to differences in vein and cell numbers.

The highest number of abnormal species was detected in *Tachysphex* with nine species, followed by *Nysson* with five species. *Tachysphex* is the most studied genus

with 28 species and 786 specimens, so this may have caused the overestimation of the number of abnormal species in this genus. *Psammaecius punctulatus*, *Bembix bidentata* and *Bembecinus tridens* were determined as the species with the most abnormal specimens (Table 1).

Supernumerary veins are found to be more common than other main abnormalities in this study; these results are consistent with the findings obtained by Porporato et al. (2014) and Gülmez (2019) in honey bees (*Apis mellifera*) and solitary wasps (Sphecidae), respectively. The spur protruding from 1m-cu to the 1st discoidal cell and the adventitious distal abscissa of the 2rs-m crossvein are the most frequently detected abnormalities in Gülmez (2019) and Porporato et al. (2014), respectively. However, unlike the results of those studies, the supernumerary submarginal cell is the most common abnormality in this study. It has been stated that 1r-m, 2r-m and 1m-cu veins show high variability and instability in the venation of the Aculeata wings (Akahira & Sakagami, 1959; Zimmermann, 1933; Alpatov, 1929; Porporato et al., 2014; Gülmez, 2019). In this study, 1r-m abnormalities among defective veins are common and it can be said that it is also unstable in the Crabronidae family. In both *Miscophus pretiosus* and *Nysson interruptus*, which have petiolated second submarginal cell, one edge of it is missing (Fig. 5c, 6d). In this respect, it is considered to be quite interesting among abnormal samples.

The number of submarginal cells in forewing of Crabronidae is a widely used feature to distinguish the genera. When the number is reduced to two, it is sometimes impossible to know whether the missing vein is the 2nd abscissa of Rs or 1r-m. In some previous studies on the Apoidea superfamily, it was estimated which crossvein was reduced by looking at the size of the submarginal cells. The first crossvein was considered to be missing if the first submarginal cell was longer than the second (Tofilski, 2011). In some cases, the sizes of both cells are close to each other. It has been suggested that the first crossvein is mostly missing in the Hylaeinae subfamily (Michener, 2000), while in the Panurginae subfamily the second crossvein is missing (Robertson, 1925). However, there is no information about which crossvein is missing in genera with two submarginal cells in the Crabronidae family. This situation was encountered in *Diodontus* species with two submarginal cells in which an abnormality was detected (Fig. 8a, 8b). The detected abnormality also occurred in the crossvein between the submarginal cells. In this study, it was assumed that the 2nd abscissa of Rs crossvein of the forewings was reduced in *Diodontus* forewings with two submarginal cells, since the first submarginal cell is longer than the second.

Although the exact causes of wing abnormalities are not known, there may be many different causes such as genetic origins, mutations or environmental factors. It has been suggested that abnormalities may be due to genetic reasons in some specimens from the Diptera, Lepidoptera and Coleoptera orders (Yokoyama, 1959; Barigozzi, 1963; Sokoloff, 1966). On the other hand, it is stated that various environmental effects such as physical, nutritional and chemical factors, infectious microorganisms or toxins can cause non-genetic abnormalities in wing formation by acting on the developmental stage of insects (Gülmez, 2019). It is not possible to reach a conclusion about the

effect of environmental conditions on wing abnormalities in Crabronidae, since the developmental stages of wasps in the nests cannot be followed. In this study, a case of parasitism, which is one of the environmental factors, was observed on the adult wasp with wing abnormality. A parasitic event, stylopization, produced by insects belonging to the order Strepsiptera, was detected in the abdomen of an abnormal specimen of *Bembecinus tridens*. It is not known exactly whether the parasite enters the body during the pre-adult period or in the adult period. If the parasite entered during the development period, this parasitic condition may have caused the forewing abnormality observed in this specimen.

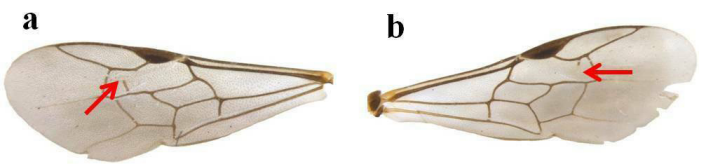

Fig. 8. Forewing abnormalities in the genus *Diodontus*. a) *Diodontus luperus* (♂), incomplete 1r-m crossvein; b) *Diodontus minutus* (♀), incomplete 1r-m crossvein.

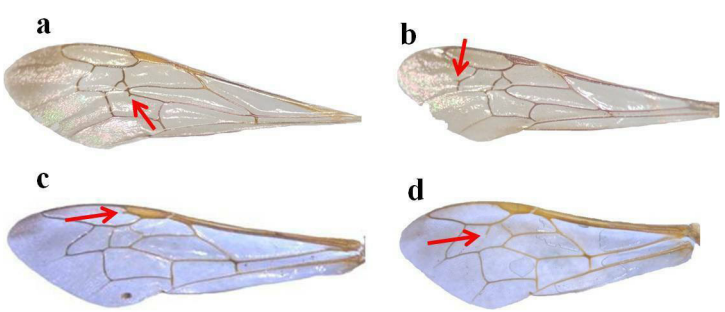

Fig. 9. Forewing abnormalities in the genera *Cerceris* and *Philanthus*. a) *Cerceris quinquefasciata* (♂), spur protruding from 1m-cu into 2nd discoidal cell; b) *Cerceris stratiotes* (♂), spur protruding from 2r-m; c) *Philanthus triangulum* (♂), spur protruding from R1 into the marginal cell; d) *Philanthus triangulum* (♂), incomplete 1r-m crossvein.

Especially in all specimens of *Psammaecius punctulatus*, the abnormalities were detected on the same veins in both wings. It has been stated that the causes of abnormalities in these species may be of either genetic or epigenetic origin (Gülmez, 2019). However, there are no studies which report the presence of genetic or epigenetic mechanisms leading to wing anomalies in solitary wasps.

The mechanism underlying wing vein formation in the vast majority of insects, including the order Hymenoptera, remains largely unexplored. The assessments regarding the causes of the wing abnormalities of the solitary wasps mentioned above generally remain at the level of predictions and assumptions. In order to find the causes of wing abnormalities, it is necessary to conduct studies on the molecular mechanisms of wing venation in solitary wasps.

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