

THE FIRST RECORD OF THE FAR EASTERN GRASS-CARRYING WASP *ISODONTIA NIGELLA* (F. SMITH, 1856) (HYMENOPTERA: SPHECIDAE: SPHECINAE) FROM THE CRIMEA

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Summary. *Isodontia nigella* (F. Smith, 1856) is native to the Eastern Palaearctic, Oriental region, and Australia. A sheaf of reed canes installed as a trap nest in the Crimea was occupied with 73 nests of this species in 2021. The nests contained one to eight cells separated by partitions made of packed fragments of grass stalks and blades; the closing plug was made of the same materials. In some cases, there was no visible partition between two subsequent cells. The prey consisted of three orthopteran species with the predomination of the tree cricket *Oecanthus pellucens* (Scopoli, 1763) amounted to 95.1% of the identified specimens; three to 15 victims were stored per cell. Sex ratio was strongly male-biased, about 1♀:4♂. The species had two generations per year. Prepupae of the second generation overwintered and imagines emerged in 2022: males on 12–19 June, females on 17 June–5 July. *Melittobia acasta* (Walker, 1839) and an unidentified bombyliid fly were recorded as parasitoids that damaged only three cells. The reproductive success of the wasp was 65.2%; most deaths of the progeny were for unknown causes. This is the first record of *I. nigella* in Europe, outside its native range. *Isodontia nigella* is the second invasive species of the genus in Europe after *I. mexicana* (de Saussure, 1867) and the fifth invasive species of the family Sphecidae in the Crimea.

Key words: sphecid wasps, invasive species, trap nests, distribution, Palaearctic region.

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Резюме. Природный ареал *Isodontia nigella* (F. Smith, 1856) включает Восточную Палеарктику, Ориентальную область и Австралию. В 2021 г. 73 гнезда этого вида были найдены в Крыму в гнезде-ловушке из стеблей тростника. Гнезда содержали от

одной до восьми ячеек, разделенных перегородками из утрамбованных фрагментов стеблей и листьев травянистых растений; конечная пробка гнезда состояла из тех же материалов. В некоторых случаях явные перегородки между двумя последовательно расположенными ячейками отсутствовали. Добыча была представлена тремя видами прямокрылых с преобладанием стеблевого сверчка *Oecanthus pellucens* (Scopoli, 1763), особи которого составили 95.1% идентифицированной провизии; в одну ячейку осы заготавливали от трех до 15 жертв. Соотношение полов было сильно смещено в сторону самцов и составило около 1♀:4♂. Вид дал два поколения в году. Зимовка второго поколения происходила на стадии предкуколки, отрождение имаго в 2022 г. наблюдали 12–19 июня у самцов и 17 июня–5 июля у самок. В качестве паразитоидов, уничтоживших лишь три ячейки, зарегистрированы *Melittobia acasta* (Walker, 1839) и неопределенный вид мухи-жужжала. Репродуктивный успех осы составил 65.2%; смертность потомства происходила, большей частью, по неизвестным причинам. Это первая находка *I. nigella* в Европе, за пределами первичного ареала. *Isodontia nigella* – второй инвазивный вид рода в Европе после *I. mexicana* (de Saussure, 1867) и пятый инвазивный вид семейства Sphecidae в Крыму.

INTRODUCTION

Species of the family Sphecidae are often reported to successfully colonize new territories outside their native ranges. This is the case of the genera which most representatives either nest in above-ground pre-existing cavities or make constructed aerial nests: *Chalybion* Dahlbom, 1843 and *Sceliphron* Klug, 1801 from the subfamily Sceliphrinae and *Isodontia* Patton, 1880 from the subfamily Sphecinae. A total of seven invasive species of these three genera have been reported to date from Europe: *Chalybion bengalense* (Dahlbom, 1845), *Ch. californicum* (de Saussure, 1867), *Ch. turanicum* (Gussakovskij, 1935), *Sceliphron* (*s. str.*) *caementarium* (Drury, 1773), *S. (Hensenia) curvatum* (F. Smith, 1870), *S. (Hensenia) deforme* (F. Smith, 1856), and *Isodontia mexicana* (de Saussure, 1867) (Schmid-Egger, 2005; Ćetković *et al.*, 2011, 2012; Mei *et al.*, 2012; Schmid-Egger & Herb, 2018; Bitsch *et al.*, 2020; Fateryga *et al.*, 2020).

The Crimea becomes one of the territories where invasions of Sphecidae are recorded. The first invasive sphecid wasp, collected from there for the first time in 2000, was an Oriental mud-dauber species *Sceliphron curvatum* (Shorenko, 2003; Fateryga & Kovblyuk, 2013). A Nearctic mud-dauber species *S. caementarium* was then recorded from the Crimea in 2007 (Shorenko, 2007). The third species was a Nearctic grass-carrying wasp *Isodontia mexicana* which nests were found there in 2012 (Fateryga *et al.*, 2014). The latter species has been, however, not recorded from the Crimea anymore but was then revealed further north-eastern in the city of Donetsk in 2015 (Amolin *et al.*, 2018). The fourth sphecid species found in the Crimea outside its native range was a Central Asian nest-renting wasp *Chalybion turanicum* recorded from there for the first time in 2019 (Mokrousov *et al.*, 2019; Fateryga *et al.*, 2020).

The genus *Isodontia* Patton, 1880 contains 62 described species (Pulawski, 2023) while only three species have been recorded from Europe to date. Besides the invasive *I. mexicana*, there are two native species: *I. paludosa* (Rossi, 1790) and *I. splendidula* (A. Costa, 1858). These Mediterranean species were never reported from the Crimea but both are known in Russia from the North Caucasus: *I. paludosa* from the Stavropol Territory (Danilov & Mokrousov, 2017) and *I. splendidula* from Dagestan (Mokrousov *et al.*, 2019).

Bionomics of the genus *Isodontia* were well summarized by Lin (1966), Bohart & Menke (1976), and Gess & Gess (1982). The data on the nesting of at least 15 species have been

published to date. Females of most species nest in above-ground preexisting cavities such as hollow stems, burrows of beetle larvae or carpenter bees in wood, burrows of other wasps and bees in vertical banks, stone crevices or even hollow leaves of an onion. Such nesting behavior favors the use of trap-nesting technology to attract nesting females and receiving a large amount of nests to study various aspects of the wasp life history (Piel, 1933; Tsuneki, 1963, 1964; Lin, 1966; Krombein, 1967; O'Neill & O'Neill, 2003, 2009; O'Neill *et al.*, 2007; Barthélémy, 2012; Barrett *et al.*, 2021). The exception is *I. simoni* (du Buysson, 1898) nesting in pre-existing vertical burrows in horizontal ground; this species was never introduced to trap nests (Gess & Gess, 1982, 2014). Most species of *Isodontia* are grass-carrying wasps, i.e., their females use fragments of grass stalks and blades as the building material to construct the partitions between the brood cells and the closing plug of the nest. The exceptions are some species which use various combinations of plant fluff, earth clods, and pieces of debris, such as *I. pelopoeiformis* (Dahlbom, 1845) and *I. simoni* (Gess & Gess, 1982, 2014). Females of most species do not construct lateral walls of the brood cell but *I. paludosa* sometimes constructs (Berland, 1960). In some species such as *I. nigella* (F. Smith, 1856), the partitions between two subsequent cells can be sometimes absent (Tsuneki, 1963) while such species as *I. auripes* (Fernald, 1906) and *I. harmandi* (Pérez, 1905) even construct communal cells with up to 14 progeny individuals in a single chamber (Tsuneki, 1963; Krombein, 1967; Barrett *et al.*, 2021). The prey of *Isodontia* wasps are orthopteran insects: usually tree crickets (Gryllidae: Oecanthinae) and katydids (Tettigoniidae) (Piel, 1933; Tsuneki, 1963, 1964; Lin, 1966; Krombein, 1967; Barthélémy, 2012; Četković *et al.*, 2012; Fateryga *et al.*, 2014; Gess & Gess, 1982, 2014).

Isodontia nigella is a species of grass-carrying wasps distributed in the Russian Far East, China, Korean Peninsula, Japan, India, and Australia (Danilov, 2017). Nests of this species were recorded in the Crimea in 2021. Thus, the purpose of the present contribution is to report the first record of *I. nigella* in Europe, as well as to describe briefly the structure and the composition of its nests in the conditions of the secondary range.

MATERIAL AND METHODS

A sheaf of reed canes (Poaceae: *Phragmites* sp.) was attached to a dead trunk of a recumbent tree in the Karadag Nature Reserve in the Crimea on 24 May 2021. The trap nest was inspected on 26 September when plugs made of fragments of grass stalks and blades were revealed closing a significant part of the canes (Fig. 1). The trap nest was removed and studied in the laboratory following the methods described earlier by Ivanov *et al.* (2019) except that the emerged wasps were not released. The reed canes containing nests were split open with a knife. A schematic drawing of the opened nest was made on an A4 sheet of paper. The size of the inner cavity of the reed cane (its length and greatest diameter) was measured with a vernier caliper and a ruler. The number of cells and their contents were documented. Cocoons of the wasps and other insects found in the nest cells were placed in short glass tubes tightly stopped at both ends with cotton wool and labeled with the nest and cell numbers. They were then kept in outdoor conditions. After emergence of adult wasps they were sexed, other insects were identified, and this information was added along with the dates of their emergence to the schematic drawings of the corresponding nests. Prey from the cells in which the wasp eggs died was collected, calculated, and identified. A total of 73 nests were revealed in the trap sheaf and studied. The imagines emerged in 2022 allowed the identification of the wasp as *Isodontia nigella*.



Fig. 1. A sheaf of reed canes with closing plugs of grass made by *Isodontia nigella* (F. Smith, 1856).

RESULTS

Isodontia nigella (F. Smith, 1856)

Figs 2–7

Sphex nigella F. Smith, 1856: 255, ♀ ♂ (type locality: “Shanghai” [China]; syntypes in the British Museum of Natural History, London, U.K.).

Sphex xanthognathus Pérez, 1905: 151, ♂ (type locality: “Yokohama” [Japan]; holotype or syntypes in the Muséum National d’Histoire Naturelle, Paris, France). Synonymized with *S. nigellus* by Berland, 1926: 283.

MATERIAL EXAMINED. Crimea, Karadag, 44°54’48”N 35°12’06”E, from nests, 12.VI–5.VII 2022, 22 ♀, 81 ♂, leg. A. Fateryga.

DIAGNOSTIC CHARACTERS. *Isodontia nigella* can be easily distinguished from other European representatives of the genus. It differs from *I. splendidula* by the absence of a red pattern on the metasoma and from *I. mexicana* by the absence of a metallic shade of the body and the wings. *Isodontia nigella* differs from *I. paludosa* by a smaller body size and a longer and curved petiole of the metasoma (Figs 2, 4). Other diagnostic characters are illustrated in Figs 3, 5–7. In particular, the female propodeum is only slightly transversally wrinkled (Fig. 3) and the apical margin of the female clypeus has a remarkable narrow but deep incision at center (Fig. 6). The male clypeus is with indistinct incision at center of the apical margin (Fig. 7). The male genitalia are as in Fig. 5.

DISTRIBUTION. Russia: Crimea (new record), Primorsky Territory; China; Korean Peninsula; Japan; India; Australia.



Figs 2–7. *Isodontia nigella* (F. Smith, 1856), ♀ (2, 3, 6) and ♂ (4, 5, 7): 2, 4 – habitus, lateral view; 3 – scutellum, metanotum, and propodeum, dorsal view; 5 – genitalia, dorsal view; 6, 7 – head, frontal view. Scale bars = 1 mm.

BIONOMICS. The nests of *Isodontia nigella* were situated in reed canes with the length of 7.2–29.2 cm (17.9 ± 1.2 cm on average; $n = 73$) and the inner diameter of 7.4–13.1 mm (9.7 ± 0.3 mm on average; $n = 73$). The partitions between the cells as well as the closing plug

of the nest were made of packed fragments of grass stalks and blades (Fig. 8). There were from one to eight cells per nest (2.5 ± 0.3 on average; $n = 66$). Some partitions between pairs of subsequent cells were absent so that two wasp cocoons appeared together in a “communal cell” (Fig. 8: the first, the fourth, and the sixth nests from above). Such “communal cells” with two cocoons were counted as two cells because it was uncertain if a flimsy partition between the provisions stored for each egg had existed initially, before the larvae finished feeding and started cocooning.

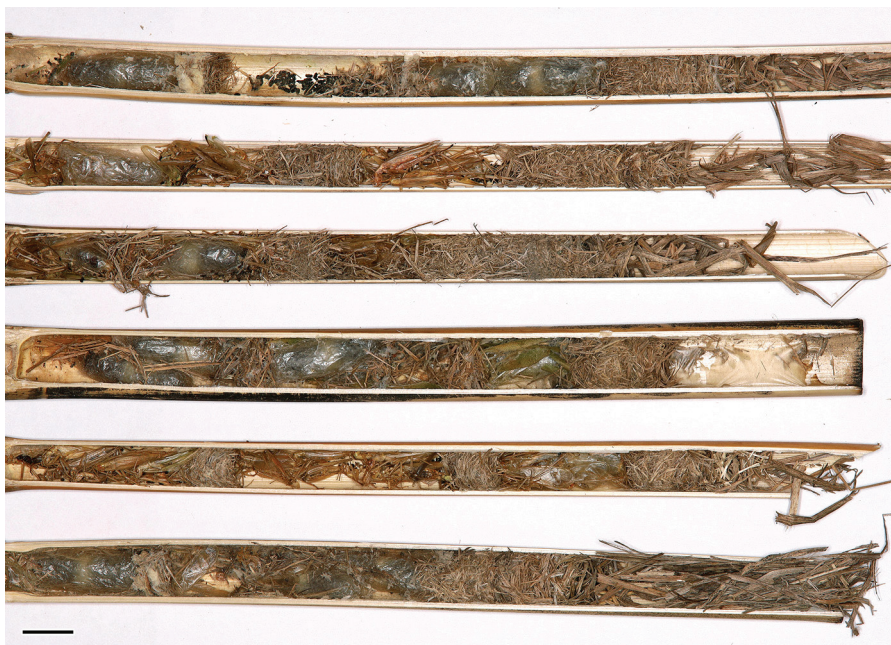


Fig. 8. Opened nests of *Isodontia nigella* (F. Smith, 1856) in reed canes. Scale bar = 1 cm.

The prey of *Isodontia nigella* consisted of three species of orthopteran insects. They were found mainly in cells with dead wasp eggs (see below). In a few nests there were also “false cells” containing the provision only, without the wasp progeny. A total of 288 specimens of the prey were collected from 37 cells (including the four “false cells”). Among them, a tree cricket *Oecanthus pellucens* (Scopoli, 1763) (Gryllidae: Oecanthinae) predominated with 238 imagines and 36 juveniles (95.1% of all identified specimens). The second prey species was a leaf katydid *Phaneroptera nana* Fieber, 1853 (Tettigoniidae: Phaneropterinae) with two imagines and 11 juveniles and the third was *Anadrymadusa retowskii* (Adelung, 1907) (Tettigoniidae: Tettigoniinae) with one juvenile specimen. There were from three to 15 victims stored per cell (8.6 ± 0.8 on average; $n = 33$).

Among 73 nests, there were seven nests of the first generation with empty cocoons from which the wasps of the second generation had already emerged before 26 September 2021. The remaining 66 nests represented the nests of the second generation with the prepupae hibernating in the cocoons. Thus, the species had two generations per year. The progeny

emerged from the nests of the second generation in 2022: males on 12–19 June, females on 17 June–5 July (Fig. 9). A total of 103 specimens emerged: 22 females and 81 males. Thus, the sex ratio was strongly male-biased, about 1♀:4♂. There were 51 nests from which at least one wasp emerged. Among them, nine nests produced females only, 11 nests produced imagines of both sexes, and 31 nests produced males only. In the nests with mixed progeny, females usually emerged from the inner cells while males emerged from the outer ones. There was the only exception in the largest nest with eight cells and the following sequences of sexes: ♂♀♂♂♂♂♂♂ (from the innermost cell to the outermost one).

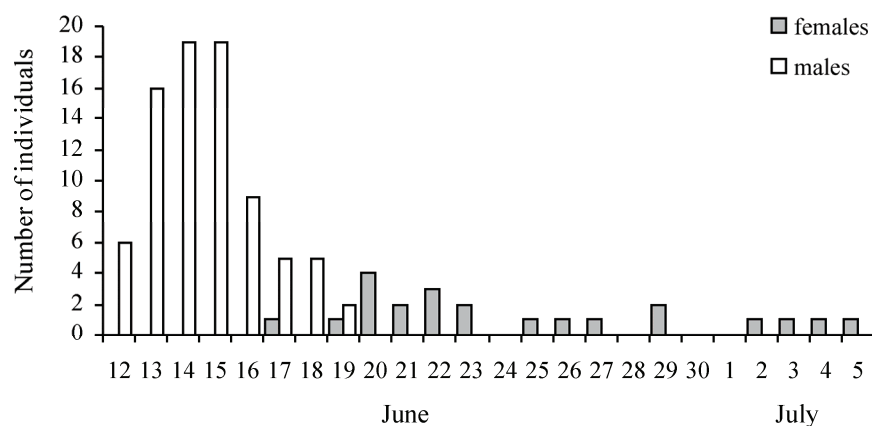


Fig. 9. Dynamics of emergence of *Isodontia nigella* (F. Smith, 1856) imagines from the cocoons in 2022.

Besides 103 successful cells (65.2% of a total of 158 cells in the nests of the second generation, without taking into account the “false cells”), there were 55 cells in which the progeny died. Two species of parasitoids were revealed in the nests: *Melittobia acasta* (Walker, 1839) (Hymenoptera: Eulophidae) in one cell and an unidentified bee fly (Diptera: Bombyliidae) in two cells. Most mortality cases were, however, for unknown cause, especially at the egg stage (Table 1).

Table 1. Mortality of *Isodontia nigella* (F. Smith, 1856) progeny due to parasitoids and other factors

Parasitoid species or other mortality factor	Number of cells	Proportion of cells, %
<i>Melittobia acasta</i> (Walker, 1839)	1	0.6
Bombyliidae gen. sp.	2	1.3
Death of egg for unknown cause	33	20.9
Death of larva for unknown cause	3	1.9
Death of prepupa for unknown cause	11	7.0
Death of pupa for unknown cause	2	1.3
Cells destroyed by an unknown predator	3	1.9
Total	55	34.8

DISCUSSION

The record of *Isodontia nigella* from the Crimea is the first case of its introduction into Europe. This is the second invasive species of the genus *Isodontia* after *I. mexicana* which became established first in France in the early 1960s and finally reached Eastern Europe in 2000s and 2010s (Četković *et al.*, 2012; Fateryga *et al.*, 2014; Amolin *et al.*, 2018). *Isodontia nigella* is the fifth invasive species of Sphecidae in the Crimea and the eighth in Europe (see Schmid-Egger & Herb, 2018; Bitsch *et al.*, 2020; Fateryga *et al.*, 2020).

The results of the presented study of the nests of *Isodontia nigella* are largely consistent with the previously published data on this species (Piel, 1933; Tsuneki, 1963, 1964; Barthélémy, 2012). Particularly, the prey of the genera *Oecanthus* Serville, 1831 and *Phaneroptera* Serville, 1831 were reported for this species from Japan (Tsuneki, 1963). The same is true for the presence of several generations per year (Tsuneki, 1963). A male-biased sex ratio in *I. nigella* was known in both Japan, 1♀:2.4♂ (Tsuneki, 1964) and China, 1♀:3♂ (Barthélémy, 2012). It is of note that a male-biased sex ratio is typical of other species of *Isodontia* as well (Barrett *et al.*, 2021) while some species have rather equal sex ratio (O'Neill & O'Neill, 2009).

Unusual cells with two cocoons have been also already recorded for *Isodontia nigella* by Tsuneki (1963). It is interesting that Gess & Gess (1982) reported cannibalism in the cells of *I. pelopoeiformis* in which two eggs had been deposited close to each other. It seems that a larva having devoured its first victim actively seeks out any conspecific larva in the cell and kills it. In the case of the presence of at least a flimsy partition between the provisions stored for each egg, the larvae are well separated spatially and cannibalism does not happen. In the case of *I. nigella* it was uncertain if a flimsy partition between the provisions stored for each egg had existed initially because both us and Tsuneki (1963) recorded “communal cells” at the cocoon stage only. It is possible that such partitions existed but were damaged by cocooning larvae. It is of note that Krombein (1967) speculated the evolution of the nest structure of the grass-carrying wasps from nests with substantial partitions between all cells, such as in *I. elegans* (F. Smith, 1856), through nests with flimsy partitions, such as in *I. mexicana*, to nests with true communal brood chambers, such as in *I. auripes*. Obviously, *I. nigella* belongs to the second evolutionary stage, according to the Krombein's (1967) hypothesis.

It is also of note that the reproductive success of *Isodontia nigella* in our study was relatively high in comparison with most native species of Sphecidae which usually had 28–49% of successfully emerged progeny (Weaving, 1995; Fateryga & Kovblyuk, 2014; Barrett *et al.*, 2021). Invasive species often have a higher reproductive success, about 64–67% (Fateryga & Kovblyuk, 2013; Fateryga *et al.*, 2020) that is similar to *I. nigella*. A high reproductive success of 62% was, however, reported for a native population of this species as well (Barthélémy, 2012).

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