Nesting behaviour and description of mature larva of *Lindenius albilabris* (Fabricius, 1793) (Hymenoptera: Crabronidae)

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Abstract
Nesting habits of the digger wasp *Lindenius albilabris* (Fabricius, 1793) at two localities in Poland were studied. The female hunts nymphs or adults of plant bugs *Lygus rugulipennis* Poppius, 1911 and *L. pratensis* (Linnaeus, 1758), depositing up to 10 individuals per cell, depending on their size. Nests are built in a wide variety of sandy habitats, on dirt roads, and in wastelands. The nest consists of a 10–12 cm long main burrow and one to three cells. Males are usually found on flowers of wild carrots *Achillea millefolium*, *Daucus carota*, *Psorospermum oroselinum*, *Pimpinella sp.* and *Tanacetum vulgare*. The nest kleptoparasite *Metopia argyrophylla* was recorded in nests of this species. The mature larva is first described in this study and its morphology is compared with other species of the genus.

Keywords: Behavioral ecology, digger wasps, predators, kleptoparasites, larva

Introduction
The genus *Lindenius* Lepeletier and Brullé, 1835 comprises 64 species, 57 of which occur in the Old World (Pulawski 2022). Representatives of this genus are small, stocky and black pigmented with widely spaced hind ocelli, which distinguishes them from the similar genus *Crossoecus* Lepeletier and Brullé, 1834. Miller and Kurczewski (1975) reviewed the world literature on the ethology of three Palaearctic species – *L. albilabris* (Fabricius, 1793), *L. panzeri* (Vander Linden, 1829) and *L. pygmaeus* (Rossi, 1794) – and added data on the nesting behaviour of *L. armaticeps* (Fox, 1895), *L. buccadentis* Mickel, 1916 and *L. columbianus errans* (Fox, 1895) from the Nearctic region. Bohart and Menke (1976) added at least partial information on the habits of three Nearctic species: *L. columbianus* (Kohl, 1892), *L. tecuya* Pate, 1947 and *L. tylotis* Court and Bohart, 1958.

Central European *Lindenius* usually nest in flat terrain, on both sandy and harder ground (Blösch 2000). The nest entrance is always surrounded by a prominent mound, and is not closed during the provisioning period, so that an approaching female with prey can easily get inside.

The prey is held belly up by the middle or hind legs or is impaled on the sting (Kazenas 2001). According to Kazenas (2001), nests can contain up to 24 cells and are usually built from the bottom up along the main channel, which can be 20 cm deep. Females prey on small insects from three orders: Diptera, Hemiptera and Hymenoptera (Lomholdt 1984). The egg is laid on one of the first prey individuals introduced into the cell and is placed under the head of the prey on the ventral side. The larva eats all prey within 1–5 days. The cocoon is covered with the remains of the prey. Adult digger wasps visit flowering plants from multiple families, e.g. Apiaceae, Lamiaceae, Asteraceae, Euphorbiaceae and many others (Kazenas 2001). Kleptoparasites are Miltogramminae (Sarcophagidae), *Myrmosa*...
Chloropidae and *Hedychridium* (Chrysidae) (Bohart & Menke 1976).

*Lindenius albilabris* is the most widespread species of *Lindenius* in the Palaeartic (Kohl 1915). Females of this species hunt prey belonging to two orders: Hemiptera – Miridae (Nielsen 1900; Bouwman 1911; Grönblom 1925; Hamm & Richards 1926; Minkiewicz 1931, 1933) and Diptera – Chloropidae (Hamm & Richards 1926), Empididae (Bristowe 1948), and Anthomyiidae (Hüsing & Jäger 1964).

The egg of this species is white and banana-shaped, attached to the prosternum obliquely (Minkiewicz 1931) or almost transversely (Adlerz 1910). Bonelli (1967) described the development of the larva and the cocoon construction. Interestingly, males of *L. albilabris* are able to dig a short burrow ending in a single cell in which they spend the night (Minkiewicz 1931). According to Bonelli (1967) under laboratory conditions, the larva reached maturity within four days and the cocoon is yellow-brown, covered with sand particles. Grönblom (1925) found smaller, darker cocoons in Finland and noticed that they were covered with prey remains, larvae droppings and gravel particles.

The objective of the study is to provide information on the nesting habits of *L. albilabris*, such as: (1) nest construction, including number of cells, length and diameter of the main burrow and transport of prey to the nest; (2) larval food, including species composition and the number of individuals per cell; (3) description of the mature larva; and (4) kleptoparasites.

**Materials and methods**

The research on *L. albilabris* was carried out in the town of Kowalewo Pomorskie (53°10′05.7″N, 18°52′15.5″E) and the village of Sierakowo (53°10′19.0″N, 18°52′21.7″E) both in Poland, from early June to late September in 2020 and 2021 in insignificantly varying weather conditions of sunny and warm days (with a temperature of at least 18°C) and in comparable timed samples (Table 1). The site in Kowalewo Pomorskie was an agricultural wasteland overgrown with segetal and ruderal vegetation, dominated by *Tanacetum vulgare* L., *Taraxacum officinale* F.H. Wigg., *Geranium pusillum* L., *Trifolium arvense* L., *Lactuca serriola* L., *Cerastium holosteoides* Fr. em. Hyl., *Berteroa incana* (L.) DC., *Artemisia vulgaris* L., *Achillea millefolium* L., *Daucus carota* L. and *Potentilla anserina* L. This site partly covered the same area that was described in our papers on nesting biology of *Dryudella stigma* (Olszewski et al. 2021a), *Oxybelus variegatus* (Olszewski et al. 2021b) and *Alysson spinosus* (Olszewski et al. 2022). The second site, in Sierakowo, was described in the paper on nesting biology of *A. spinosus* (Olszewski et al. 2022) and consisted of sandy loam, dominated by *Helichrysum arenarium* (L.), *Peucedanum oregelimum* (L.), *Sedum spp.* and *Seneio vernalis* Waldst. et Kit. The surroundings of the studied sites included an agricultural landscape dominated by the cultivation of maize, cereals and potatoes. Nesting activity (i.e. nest digging and prey transportation) was analysed based on direct observations and on-site notes. Photographs were taken with a Canon EOS M50 camera; an additional Raynox M-250 macroscopic lens was also used. The foraging range was determined by nest inspection. The structure of the nest was analysed by unearthing it. During the females’ activity (from late June to late September), their nests were dug out and larvae were collected for analysis. Larvae and pupae of kleptoparasitic wasps were grown in Eppendorf tubes. The larvae were fixed in Pampel’s solution.

To describe the larval specimens, we transferred some of the larvae into Pampel solution (30 volumes of distilled water, 15 volumes of 96% ethanol, 6 volumes of formaldehyde and 4 volumes of glacial acetic acid) as described by Švácha and Danilevsky (1987). After taking photographs of the intact larvae, we examined their sclerotised parts. For this purpose, we placed the larvae into a 10% solution of hot (60°C) KOH for 12 h to dilute all body parts except the integument. We then coloured the integument in 5% Chlorazol Black E (Sigma Aldrich) for 2 s and then moved it into 96% ethanol. To observe the species-specific characteristics, we placed the integument into glycerol and separately observed the head, mouthparts, spiracles and other parts under a light microscope. We used the same specimens to study small structures such as setae, sensilla or mouthparts. We drew figures of (1) the head, with a focus on the clypeus, labrum, maxillae and labium; (2) mandibles, in anterior view; and (3) spiracles of larvae. Specimens of kleptoparasitic flies and prey are deposited in the first author’s collection.

**Table 1. Number of 30 minute observation samples per month in 2020 and 2021.**

| Month     | 2020 | 2021 |
|-----------|------|------|
| June      | 5    | 4    |
| July      | 6    | 5    |
| August    | 4    | 4    |
| September | 3    | 4    |
Results

Environmental preferences

Adult individuals were observed from early June to late September 2020 and 2021, with females (Figure 1(b–f)) most frequently observed carrying prey to the nest (Figure 1(e,f)) or accompanied by a male (Figure 1(a)), on plants such as *Achillea millefolium*, *Daucus carota*, *Peucedanum oreoselinum*, *Pimpinella* sp. and *Tanacetum vulgare*. A total of 12 nests were found during the research, of which four nests (two in sandy loam and two in agricultural wasteland) were inspected. The area with nests in the wasteland area was strongly hardened, surrounded by rich segetal and ruderal vegetation. In Sierakowo, nests were built in bare ground surrounded by rich ther- mophilic vegetation. The nests were usually built as single structures, or rarely in pairs in close proximity to each other (Figure 2(b–d)), with the nearest distance between the channel entrances being 10 cm (N = 4). The circular nest entrance, with a diameter of 3–4 mm, was surrounded by a mound (which, depending on the site, may have been blown away by the wind) approximately 25 mm wide × 5 mm

Figure 1. Adult *Lindenius albilabris*. (a) Male; (b–f) female.
high. Provisioning females usually entered directly into the main canal while still in flight (by diving). Females in flight transported their prey impaled on the sting or supported it with their middle legs.

The provisioning flights took place with varying intensity, mainly between 9.30a.m. and 4.30p.m., from late June to late September. The highest density of active females was observed in the afternoon from 12.00p.m. to 4.00p.m. The female did not leave the main burrow at night or during unfavourable weather conditions. The kleptoparasitic sarcophagid fly *Metopia argyrocephala* (Meigen, 1824) was spotted entering the nest during the absence of the female (Figure 4).

**Nest structure**

During the excavation of four nests, pupae of *M. argyrocephala* and two larvae of *L. albilabris* were excavated (Figure 3(a, b); Table II). No eggs were recorded and no larvae of *L. albilabris* were reared. The nest consisted of a nearly vertical main tunnel about 10–12 cm long (3–4 mm in diameter). From half of the tunnel depth to the kink there were one to three cells, then the tunnel curved horizontally (about 2 cm) and ended with another cell (Figure 2(a)). A single brood cell contained up to 10 dead specimens paralysed or dead plant bugs (Figure 3(c)).

Figure 2. Nest of *Lindenius albilabris*. (a) Lateral view of nest and brood cells; (b–d) top view of the nest entrance.
Figure 3. (a, b) Larvae of *Lindenius albilabris*; (c) nymphs of *Lygus* spp., prey of *L. albilabris*.

Figure 4. *Metopia argyrocephala*. (a) Fly; (b) puparium.
Table II. Nests of Lindenius albilabris.

| Site          | Nest | Cell |    |    |    |    | Prey | Larva | Pupa |
|---------------|------|------|----|----|----|----|------|-------|------|
|               |      |      | 1 | 2  | 3  | 4  |      |       |      |
| Sierakowo     | Prey | L2   | 7.5 mm | L2 | L8 | L10| 22   | 2     | 0    |
|               | Larva| Lr6  | 0    | 0  |    |    | 6    | 0     | 0    |
| Kowalewo     | Prey | Lr2, 1.5 | L1, Lp3| 0  | 0  |    | 11   | 0     | 0    |
| Pomorskie     | Prey | L3   | 1*   |    | 0  |    | 8    | 0     | 1*   |
|               | Larva/Pupa | L5 |      | 0  |    |    | 47   | 2     |      |

Abbreviations: Lr – Lygus rugulipennis (imagines); Lp – Lygus pratensis (imagines); L – Lygus sp. (nymph); * – pupa of kleptoparasitic fly.

**Description of larva**

**Material examined.** Two larvae, Sierakowo, 29 August 2021.

**Diagnosis.** The larva of *L. albilabris* is similar in most details to those of *L. pygmaeus* and *L. tylotis*. The main difference is the size, *L. albilabris* being larger than the other two. Grandi (1928, 1961) described the mature larva of *L. pygmaeus*. According to him, the mandible of that species has three teeth as opposed to the four in *L. albilabris* and *L. tylotis*. However, one tooth is lateral and may have not been taken into account by the author. The mandible of *L. albilabris*, however, is more massive, with a length-to-width ratio of 10:6, and the teeth are more rounded. The shape and measurements of the mandible were not mentioned in the short description of mature larva of *L. tylotis* by Evans (1959), so we cannot make any comparison. Additionally, the

![Figure 5. Larva of Lindenius albilabris.](image-url)

(a) Body, lateral view; (b) mandible, frontal view; (c) spiracle; (d) head, frontal view.
diameter of the basal ring of the antenna is about 1/5 the distance from the closest point of the ring to the centre of the anterior tentorial pit, so it is larger than that of L. pygmaeus. In all other characters, the mature larva of L. albilabris generally agrees with those of L. pygmaeus and L. tyloites.

**Description**

**Body.** Body length 7.5 and 8.7 mm (N = 2) (Figure 5(a)). Body covered with densely distributed short spicules, and with several slender, pale setae, tapering to fine points, arising from small but distinct alveoli; setae not elongate. Several setae on mouthparts, mandibles, area around mandibular condyli and maxillary and labial palpi brownish, remaining body whitish. Other body parts with only several setae, except last three metasomal segments more setose. Body of postdefecating larva fusiform and only very slightly dorsoventrally flattened, robust; body segments similarly wide along whole length. Paired body tubercles present and well developed on all mesosomal and metasomal segments except T10, tubercles similarly large on all segments but most conspicuous on mesothorax and metathorax and on T7–T9. Dorsal tubercles wide, flat and well developed on all three thoracic segments, most conspicuous on T4–T5. In predefecating larva, T3–T6 have the greatest diameter in lateral outline. Abdominal segment 9 more hirsute than previous ones, segment 10 attached to middle of segment 9 in lateral view; anus positioned medially and transverse. Spiracles unpigmented, subequal in diameter; atrium globular, slightly wider than deep (Figure 5(c)), projecting little above body wall, with rim; atrial opening diameter vs. peritreme width ratio 1:4; atrial inner surface with rows of wrinkles concentric with primary tracheal opening; primary tracheal opening without collar; subatrium short, with about 10 chambers of approximately equal size except one or two next to atrium slightly larger in diameter. Sex characters unknown.

**Head.** Head moderately small in relation to body size; oriented in normal, hypognathous position relative to thorax. Setae long but sparse on upper part of head capsule; those of maxillary and labial apices large, straight and conspicuous (Figure 5(d)). Head capsule unpigmented except at points of articulations with mandibles; mandible conspicuously pigmented; labrum and maxillary sclerites faintly pigmented; salivary lips projecting but unpigmented; maxillary and labial palpi all uniformly moderately pigmented. Coronal and postoccipital ridges absent. Tentorium mostly absent because of impending ecdisis. Parietal bands absent. In lateral view, clypeus globularly projecting beyond frons, antenna arising from ill-developed prominence, and labrum extending beyond clypeus. Diameter of basal ring of antenna about 1/5 distance from closest point on ring to centre of anterior tentorial pit; antennal papilla only slightly pigmented, very small and not elongate, bearing two sensillus apically. Frontal area between antennae with two groups of five setae and many spinules. Parietal region with many setae – three setae from pleurostomal ridge to front tentorial pit and multiple sensillus on the sides. Clypeus wide with ill-developed basal and apical margins, with two sensillus basally on sides and three small sensillus more medially on each side. Labrum not emarginated apically in the middle, with a group of nine conspicuous setae and several smaller sensillus on each side subapically; labral sclerite not defined and only poorly pigmented. Epipharynx simple with large spinulea on the whole surface. Mandible moderately robust; darkly pigmented, with apical tooth longest and moderately blunt, conspicuous lateral tooth, and with one sub-basal and two subapical tubercles; outer mandibular surface without setae (Figure 5(b)). Maxillary apex strongly bent mesad in frontal view, maxillary palpus subapical, with many small elongated setae. Cardo distinct, posterior end directed towards posterior tentorial pit; stipes weakly sclerotised; maxillary palpi elongate, more than three times basal diameter, both pigmented. Stipes with five conspicuous setae. Labium not divided into prementum and postmentum; apex moderately narrow in frontal view, with three setae on each side. Spinneret transversal and well visible, with inner surface bearing parallel longitudinal grooves; lip width slightly more than double width of maxillary palpus. Labial palpus elongate, with two sensillus in middle.

**Discussion**

The biology of *Lindenius* species is incompletely known; the available information is mainly limited to the food base of larvae, plants as a source of nectar for adults, and environmental preferences for several Palaeartic and New World species (Bohart & Menke 1976). Our data on *L. albilabris*, including the description of the adult larva, nesting habits, time of nest construction, and food of larvae, mostly agree with previously reported observations (Nielsen 1900; Adlerz 1910; Minkiewicz 1931, 1933; Bristowe 1948; Bonelli 1967). The varying number of cells in individual nests may depend on the abundance and size of food or the type of substrate.
In this study, the food base from two orders (Hemiptera and Diptera) for larvae of *L. albilabris* was not confirmed. Minkiewicz (1931) emphasised the homogeneity of *Lygus pratensis* (L.) prey carried by the female into the cells. During our research, we have confirmed the homogeneity of prey with respect to the genus *Lygus* (Table II). During this study, *L. rugulipennis* is reported for the first time as prey of *L. albilabris*. It seems that the choice of both *L. pratensis* and *L. rugulipennis* as prey results from their common availability near the nesting site. Both species are broadly distributed throughout Poland and Europe, being the most numerous and widespread representatives of the genus (Gorczyca & Wolski 2011), with the vast majority being nymphs. Besides the relative availability of these heteropterans, the habitats selected by *L. albilabris* largely overlap with those occupied by *Lygus pratensis* and *L. rugulipennis*: crop lands and grasslands. In such habitats, *L. rugulipennis* and *L. pratensis* are among the most numerous true-bug species (Holopainen & Varis 1991, Gorczyca & Wolski 2011).

Plant bugs of the genus *Lygus* feed on various cultivated species – trees, vegetables and cereals – and are among the most important pest on a wide range of crops in Europe (Wheeler 2000). Thus, *L. albilabris* feeds the brood in such habitats exclusively with *Lygus*, and plays a hitherto undiscovered and highly advantageous role as a natural enemy of these pests (Wheeler 2001).

The egg of *L. albilabris* is attached to the proctum obliquely (Minkiewicz 1931) or almost transversely (Adlerz 1910). No rearing of larvae of *L. albilabris* was conducted in this study. Breeding results were presented by Bonelli (1967), who described the cocoon as yellow-brown covered with sand particles. Interestingly, Grönblom (1925) found smaller, darker cocoons in Finland and noticed that they were covered with prey remains, larvae droppings and gravel particles. Lomholdt (1984) reported two ecophenotypes, one of which, as mentioned above, uses Hemiptera as food for larvae, while the other, apparently a more southern type, uses smaller flies. According to Adlerz (1910), both types are represented in Sweden but they are not sympatric. Adlerz (1910) additionally described a population that uses both flies and plant bugs for larval provisioning. The issue of *L. albilabris* species identity certainly requires examination of the material of both ecophenotypes by molecular tests to clarify their status.

*Lindenius pygmaeus* also preys on a wide spectrum of prey, which includes insects from two orders: Hymenoptera (Bracidae, Formicidae, Ophionininae, Pteromalidae) and Diptera (Ceratopogonidae and Sciaridae) (Miller & Kurczewski 1975). On the other hand, *L. panzeri* seems to choose only Diptera (Chloropidae, Milichiidae, Simuliidae, Tephritidae) (Miller & Kurczewski 1975).

To date, the morphology of the larvae of only two species of *Lindenius* is known. Grandi (1928, 1961) provided a description of *L. pygmaeus* larvae, while Evans (1959) provided a description of *L. tylotis* larvae. The larva of *L. albilabris* is mostly similar to the larvae of the two already known species, but is generally larger. However, the available data show that all known larvae are morphologically very similar, and it is hard to compare anything with the short description of Evans (1959). Features such as eyes naked, mandibles without ventral emargination, and short galeae are known in all three species identified so far and can be used to distinguish *Lindenius* from related genera.

Conclusions

Reviewing the nesting biology of *L. albilabris*, we can conclude that nests are usually built as single structures, or rarely in pairs within a short distance of each other. Entrances, surrounded by a mound of earth, were open all the time during the provisioning period. Provisioning females were usually falling directly into the main canal while still in flight. The female collects up to 6–10 nymphs or imagines of *L. rugulipennis* or *L. pratensis* per cell, depending on their size. Females transported their prey in flight impaled on the sting or supported with their middle legs. Provisioning flights took place with varying intensity, mainly between 9.30 a.m. and 4.30 p.m. The nest consisted of an almost vertical main channel and, from mid-depth down, one to three cells. There were on average six paralysed or dead plant bugs in each cell, belonging to two species: *L. rugulipennis* and *L. pratensis*. The larva of this species is larger in size compared to other known larvae of this genus. It differs in having more rounded and stronger mandibles. In addition, the diameter of the basal antennal ring is about 1/5 of the distance from the closest point on the ring to the centre of the anterior tentorial pit.

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Disclosure statement

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