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NESTING BIOLOGY, MORPHOLOGICAL REMARKS, AND DESCRIPTION OF THE MATURE LARVA OF *MELLINUS ARVENSIS OBSCURUS* (HYMENOPTERA: CRABRONIDAE) IN NEPAL

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ABSTRACT

Recently re-named as a sub-species of *Mellinus arvensis*, *Mellinus arvensis obscurus* Handlirsch 1888 was investigated ecologically and morphologically in Nepal, in order to underline the most important differences with the well known *M. arvensis arvensis*. *Mellinus arvensis obscurus* females nested in clumped aggregations on inclined plains at high altitudes, both on sunny bare soil and on a shaded grassy one. Beginning of monsoon season probably interfered with wasp activity, and females performed few provisioning flights during the day. Prey consisted of a broad range of Diptera, except for one case of a spider. Many females were observed not provisioning a nest but floating on the nesting site, and many intraspecific interactions suggested a high degree of usurpation attempts. At least one species of flies and two of ants probably acted as natural enemies of the wasp. Morphological observations on females showed that the Nepal population shares more similarities (shape of tergite I, body punctation) with the European populations than with the closer Japanese population; melanization is strong, according to west-east and altitudinal cline. The mature larva of *M. arvensis obscurus* Handlirsch is described, illustrated, and compared with the other mature larva of the genus. The differences between both larvae mainly lie in the presence/absence, and number or differentiation of integumental structures. We conclude that morphological traits are more important than ecological and behavioral ones in distinguishing *M. arvensis obscurus* from *M. arvensis arvensis*.

Key Words: Hymenoptera, larva, *Mellinus arvensis*, morphological variation, nesting habits, subspecies character

RESUMEN

En el presente artículo se aportan los resultados y conclusiones de un estudio, llevado a cabo en Nepal, en el que se abordaron aspectos ecológicos, comportamentales y morfológicos (tanto del último estado de la fase larvaria como del adulto) de *Mellinus arvensis obscurus* Handlirsch 1888. El principal objetivo del estudio radicaba en mostrar las principales diferencias que separan a esta subespecie de la bien estudiada subespecie nominal. *Mellinus arvensis obscurus* nidifica a gran altitud, en terreno inclinado, con y sin vegetación, expuesto en mayor o menor medida al sol y en agregaciones muy compactas. Durante la estación lluviosa la hembras llevan a cabo pocos vuelos de aprovisonamiento. Las presas pertenecen al orden de los dípteros, aunque, en una ocasión se observó el aporte de una araña. Gran número de las interacciones intraespecíficas observadas sugieren un alto grado de intentos de usurpación de nidos. Los enemigos naturales más sobresalientes pertenecen al orden de los dípteros y a la familia de los formícidos. Del estudio morfológico del adulto, mencionaremos que la foma del terguito 1 y la escultura del cuerpo, en las hembras de las poblaciones del Nepal, son más semejantes a los de las hembras de las poblaciones europeas que no a los de las japonesas. De la fase larvaria se describe el último estado larvario, a la vez que se compara con la otra larva madura ya descrita del género. Las diferencias entre ambas larvas maduras radican en la presencia/ausencia, número o diferenciación de las estructuras tegumentarias. El estudio finaliza concluyendo que los rasgos morfológicos son más importantes, que los aspectos ecológicos y comportamentales, a la hora de establecer una separación entre las dos subespecies.

Translation provided by the authors.

The small genus *Mellinus* F. (13 spp. worldwide) includes solitary digger wasps that often nest gregariously (Bohart & Menke 1976). Morphologically, there is important inter-population variability, which is more evident in the two Palearctic, widely distributed species, *Mellinus crabro-*

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neus Thunberg, 1791 and *Mellinus arvensis* (L., 1758). Apart from the common European *Mellinus arvensis arvensis*, whose nesting habits have been studied in detail by many authors (Hamm & Richards 1930; Minkiewicz 1931; Bristowe 1948; Bonelli 1952; Grandi 1961; Ghazoul 2001), little is known about the biology of the genus. Only the mature larva of *Mellinus arvensis arvensis* (L., 1758) is known (Maneval 1939; Evans 1959). Scattered information on the nest, prey, mating behavior, and associate organisms has been offered for *Mellinus crabroneus* (Hamm & Richards 1930) and *Mellinus rufinodus* (Evans 1989).

Mellinus wasps nest in sandy to compact soils and, unlike most solitary sphecoid wasps, often in grassy areas (Minkiewicz 1931; Bonelli 1952). Soil hardness seems to be an important factor for the occurrence of aggressive, competitive interactions between females (Ghazoul 2001). Nests are multicellular, including up to 20 cells 5-50 cm deep in the ground (Adlerz 1903; Minkiewicz 1931; Bonelli 1952) and which are provisioned with 3-15 flies (mainly Muscidae, Calliphoridae, Anthomyiidae, and Sarcophagidae) (Hamm & Richards 1930; Grandi 1961; Shaw & Pont 1972). Nests are left open during provisioning activity but brood cells are sealed when finished (Hamm & Richards 1930).

The biology of the subspecies observed in this study, the eastern Asiatic *Mellinus arvensis obscurus*, has been investigated only in Japan (Tsuneki 1946; Maruyama 1948). It had been considered as *Mellinus obscurus* Handlirsch 1888, a separate species, until very recently (Nemkov 2005).

In this paper we present behavioral and ecological information on nesting site, prey, and intraspecific and interspecific interactions of *M. arvensis obscurus* nesting in aggregations found in eastern Himalaya. In addition, we give an account of both adult female and larval morphological traits. All these biological and morphological data are compared with the available information for the much better known *M. arvensis arvensis*, in order to define which characters differentiate the two subspecies.

Materials and Methods

We studied *Mellinus arvensis obscurus* in the Sagarmatha National Park (Solu Khumbu district, Nepal; 27°45'-28°07'N, 86°28'-87°07'E). Two nesting sites were discovered in the western valley of the park along the path that links Namche Bazar and Thame. The area is characterized by monsoon rainfall from the middle of Jun to the end of Sep. Rain occurred everyday during the observation period, intermittently. The average temperature from Jun 22 to Jul 13 was 13.4 ± 1.11°C. Observations on the behavior of nesting females and their natural enemies were made at both sites, from Jun 25 to Jul 10, 2003; during this time we also collected prey from females coming back to their nests after provisioning flights. Thirteen h were spent for behavioral observations between 9.00 and 14.00 (solar hours). During 10 h, through 4 different days, we recorded individuals flying simultaneously on site 1, every 5 min. A two-dimensional lattice (1 m × 1 m mesh), was used to determine the coordinates of each nest entrance.

Seventeen adult females were collected for morphological analysis, and 2 mature larvae were extracted from the wasp nests for the same purpose. Non-parametric statistics (Kruskall-Wallis test) were used for behavioral and ecological data analysis. The spatial patterning of nests was investigated with the Clarke & Evans method (1954). In the text, average figures are given ± SD (standard deviation), except for nearest neighbor distances, which are given ± SE (standard error).

Specimens of *M. arvensis obscurus* and *M. arvensis arvensis* used in adult morphological comparisons came from our population and from the Universidad de Salamanca Collection (European and Japanese specimens). The methods and terminology of Evans (1987) were used in the preparation of the larvae and in the descriptions. The following abbreviations are used: d = diameter, l = length, and w = width. Adult and larval specimens are deposited in the Collection of the Área de Zoología, Universidad de Salamanca (Spain).

Results

Nesting Habits

One aggregation (site 1, 27°48.687'N-86°41.951'E) was situated along the main path at 3550 m a.s.l., facing south, while a second one (site 2, 27°49.146'N-86°41, 142'E) was placed in a flat area on the same slope, about 50 meters above the same path and around 1.5 km far from the first one. Both areas presented soil smoothed from heavy rain. Site 1 included 55 nests of *Mellinus arvensis obscurus* and 5 nests of *Crossocerus hingstoni* Leclercq in an area of 3 m × 2.5 m of bare soil, not covered by trees. Surroundings comprise a forest of *Abies spectabilis* and *Pinus wallichiana*. The nests of *M. arvensis obscurus* had an entrance diameter of 4.18 ± 0.75 mm (n = 55) while the 5 nests of *C. hingstoni* were 5 mm in diameter each. The aggregation had a nest density of 7.3 nests/m^2. The mean nearest-neighbor distance was 17.21 cm ± 1.70 (Rn = 0.03, c = 1.13, random distribution). In Nov 2003 two nests were excavated but it was not possible to analyze their whole structure, due to the wet and loose soil. We followed the main tunnel, almost vertical, for 23 cm and 28 cm.

Site 2 comprised 104 nests of *M. obscurus* in an area of 5 m × 161 m, with a density of 0.1 nests/m^2. The area was partially covered with grass and dwarf shrubs of *Cotoneaster microphyllus* and *Rhododendron* spp. It seemed to be split into 2

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sections by some trees of *Betula utilis*, but some nests along the path appeared to join the main groups. Nest entrance was 4.204 ± 0.528 mm (n = 54) in diameter. Along the nesting area, 4 well separated nest aggregations with more than 10 nests were noticed (A = 15 nests, B = 17, C = 17, D = 12) where the ground was most suitable for nesting with bare soil, but the surface of B was partially covered with grass (23%). In B, we observed a few individuals of *C. hingstoni* nesting. The distances between these small aggregations of the site 2 were: A-B = 17 m, B-C = 100 m, C-D = 22 m. Mean neighbor distances revealed different aggregation patterns: NND_a (3 m × 3 m) = 27.246 ± 3.379 cm, Rn = 0.7, n = 15, c = -2.19, $P <$ 0.05, clustered; NND_b (4 m × 1.4 m) = 24.411 ± 2.712 cm, Rn = 0.85, n = 17, c = -1.78, ns, random; NND_c (2 m × 2 m) = 20.969 ± 2.453 cm, Rn = 0.017, n = 17, c = -1.07, ns, random).

Thirteen h were spent in behavioral observations between 9.00 and 14.00 (solar hours). Females did not provision their nest during rainfall. As rainfall occurred everyday, activity was generally low. During 10 h, through 4 different days, we recorded individuals flying simultaneously on site 1, every 5 min. The average number of observed wasps in these days was 1.19 ± 1.16 (n = 120 records) while occurrences in each day varied significantly (Kruskall-Wallis Test: H = 45.912, $P < 0.01$).

The highest average number of wasps was observed during light rain (2.5, precipitation = 3.8 mm) and the lowest during heavy rain (0.77, precipitation = 25.4 mm). Nineteen interactions between individuals were recorded. Usually (58% of the time), we observed 1 individual inside the nest putting its head out of the entrance in order to repel an individual getting close to the nest entrance. On 4 occasions, the individual inside the nest attacked the other one and a fight was observed, while twice 1 individual approaching the entrance of a nest was attacked by a flying individual. On 2 more occasions, 1 individual entered a nest while another was inside, and after 42 s and 38 s, 1 wasp came out from the nest, followed by the other, and flew away. Most of the interactions were probably nest usurpation attempts. We recorded no digging attempts, in spite of soil appearing easy to dig for wasps. That could be due to the critical weather condition and to the short time before heavy monsoon. We observed twice, at site 1, *M. arvensis obscurus* females attacking *C. hingstoni* females returning to their nests with prey (Diptera), and *C. hingstoni* females trying to enter *M. arvensis obscurus* nests but soon rejected by the owner wasp. Prey were collected directly from the individuals carrying them during provisioning flights. Flies belong to 3 families of Diptera: Sarcophagidae, *Ravinia* sp. (1 individual); Anthomyiidae, *Anthomyia* sp. (1); Muscidae, *Helina* sp. (1), *Thricops* sp (8), *Neomyia cornicina* (3), *Phaonia* sp. (2), and *Drymeia* sp. (3). On 1 occasion, a female was carrying a spider of the genus *Araniella*.

Four natural enemies were collected. *Amicia* sp. (Diptera: Sarcophagidae) was captured after shooting an egg in a nest where a wasp had entered with prey. It took 8 s, after landing on the entrance, to shoot the egg. The other, *Neomyia cornicina* (Diptera: Muscidae), was captured during its flights around the nests. It behaved like a satellite fly (i.e., following the wasp at a fixed distance in order to reach its nest). This fly followed individuals of *M. arvensis obscurus* flying on the aggregation 3 times, and was observed landing 2 times at a nest and waiting for 5 and 16 s, with the abdomen in contact with the nest entrance.

Site 1 had 2 nests of *Myrmica rupestris* Forel and *Aphaenogaster pachei* Forel (Hymenoptera: Formicidae). Both species entered the nests of *M. arvensis obscurus* several times looking for prey to feed larvae. We observed 3 prey obtained from ants during only 2 h of observations while they were carrying them to their nest.

Adult Morphology

Observations were made on female specimens from different European and Japanese sites, belonging to *M. arvensis arvensis* and the old-named *M. obscurus* and *M. tristis*. In the European populations, very small variation in morphology was noted, with exception of a certain variation in the extension of the medially ridged part of propodeum. Coloration is very variable, with melanization stronger in the northern populations across Europe. Our Nepal population differed from the European and Japanese ones for the finer sculptures on the whole body: head and scutum are shagreened (inconspicuously punctate), propodeal enclosure weakly sculptured (a median narrow sulcus only), petiole with short setae, and wing venation darker (including stigma). European specimens and Nepal specimens have a more similarly shaped tergite I and a more similar punctation comparing with the Japanese specimens. Melanization in the Nepal population is strong as in the Japanese one. In particular, Nepal females show the following few white-yellow parts: apical part of the clypeum, the lower half-part of the inner orbitae, mandibulae (at exception of the apex), forward face of scapo, two spots in the collar, inner face of the tibiae I, a small spot at the base of the tibiae II (eventually together with another one at the middle or at the apex), and two lateral spots on the tergite III (not always present). The metasoma is almost completely black.

Larval Morphology

General aspect (Figs. 1a, b, c)

Body (l = 5.5 mm, maximum w = 3 mm) hymenopteriform, broad, somewhat depressed, yel-

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lowish, weakly sclerotized, except for spinules, setae, spiracles, and mouthparts; each segment with a pair of similar conical prominences located dorsolaterally, except the apical abdominal segment, which is rounded. Anus (Fig. 2) ventral, preapical. Pleural lobes convex, prominent. Integument with sparse spinules (l = 5 µm) and setae (l = 20-25 µm) except: (a) on the tips of the pleural (Fig. 3) and dorso-lateral prominences of the first 11 segments, which are capped with a series of spinules (l = 5 µm) and scattered setae (l = 20-25 µm), (b) on the tips of the pleural and dorso-lateral prominences of the 12th and 13th abdominal segments, which are bare and smooth, and (c) on the apical third of the abdominal segment (Fig. 2), where there is a series of spinules (l = 5 µm) and scattered setae (l = 20-25 µm). Spiracles (Figs. 1b, 4) on prothorax, mesothorax, and first 8 abdominal segments; atria (d = 40 µm) goblet-shaped, walls lined with ridges forming small and irregular polygons; opening into subatria simple; subatria small, short.

Cranium (Fig. 5)

The w = 0.87 mm, h (height measured to apex of clypeus) = 0.68 mm, subcircular with sparse setae (l = 18-25 µm) and some punctations close to mandibular insertion; coronal suture and clypeolabral suture absent, parietal bands almost imperceptible; antennal orbits (36 × 54 µm) elliptical, with 3 sensilla. Clypeus with 6 punctations. The labrum (Fig. 6a) (maximum w = 300 µm; maximum h = 190 µm) is slightly bilobate; base smooth; each lobe surface with about 6 setae (l = 23 µm) and 7 sensilla (w = 5 µm); epipharynx (Fig. 6b) densely spinulose (l of spinules = 5 µm, basal w = 5 µm) apically and laterally, with 8 sensory pores (d = 5 µm) medially distributed in 2 epipharyngeal sensory areas, each with 4 pores.

Mouthparts

Mandibles (Fig. 5) (l = 430 µm, maximum w = 120 µm) robust, sclerotized; inner margin strongly excavate, beyond that point bidentate, the space between the teeth nearly straight. Maxillae (Fig. 7) with sparse lateral setae (l = 19 µm), mesally densely spinulose; maxillary palpi longer than wide (60 × 23 µm); galeae (l = 38 µm, w = 18 µm) similarly formed, with 1 apical sensillum. Labium (Fig. 8) with 4 setae (l = 38 µm) behind palpi and with its smooth margin; salivary orifices (l = 100 µm) slender and slightly pointed.

Discussion

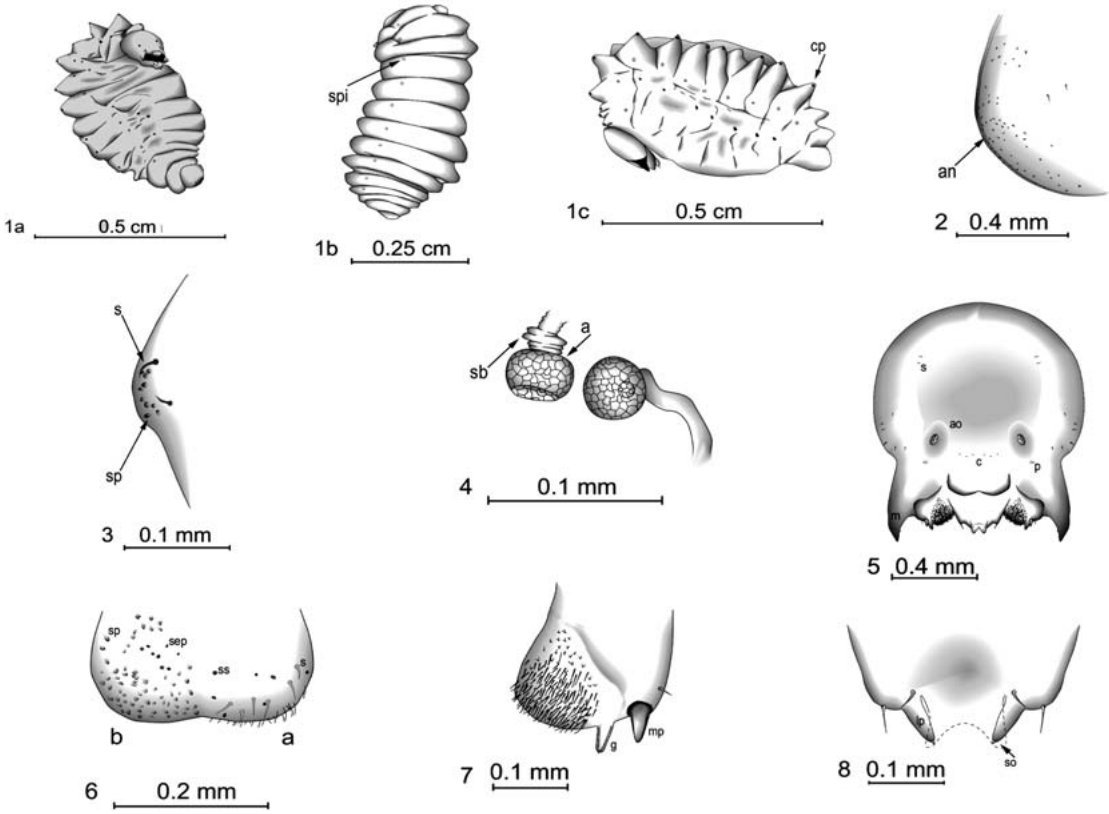
Nesting Habits

Mellinus arvensis obscurus nested at 3550 m a.s.l. The mean temperature in the study area was 13.4°C in Jun-Jul, and average maximum temperatures were being 14.9°C and 14.1°C in Jun and Jul, respectively, and 14.9°C and 12.5°C, respectively, in Aug and Sep. Total rainfall in Jun was 98.8 mm while from Jul to Sep rainfall was 603.6 mm. Judging from previous reports, this species seems to be commonly found in mountains, apparently co-adapted to their climatic conditions. It was observed nesting at 1700 m in Japan (Tottori Prefecture) in late Aug and Sep (Maruyama 1948). Temperatures during those observations ranged from 30 to 37°C around 12.00-13.00 PM. Grandi (1961) reported aggregations of *M. arvensis arvensis* around 1500 m in summer time in "Val di Genova" (Trentino Alto Adige County). In late Aug 1947 he found males and females breeding. Near that place, Bonelli (1952) observed an aggregation of *M. arvensis arvensis* at 1300 m from Jul to Oct in northern Italy (Cavalese). Between 1955 and 1960, during summer from Jul to Sep, maximum average temperature was 20.2°C while minimum one was 7.5°C. Moreover from 1950 to 1955 average rainfall from Jul to Sep was 268.9 mm. Both found evidence of its bivoltine cycle. Evans (1989) in Colorado, USA, found *M. rufinodus* nesting at 2300 m in late Aug-Sep, where mean temperatures in Aug ranged from 17.2 to 23.3°C (1994 to 2004) (data from www.contracostatimes.com).

The monsoon seems to have a great impact on *M. arvensis obscurus* activity in Nepal. In summer (till Sep) rainfalls are abundant and almost every day, sun light becomes low and temperatures still remain low during all summer. Our short observations, carried out under light rain in Jun-Jul when monsoon starts, could represent the last phase of the wasp annual cycle. We could assume that monsoon season acts as a treacherous barrier maybe forcing the species to shift its cycle backward some months. *Mellinus arvensis obscurus* nested in sunny and inclined slopes as previously reported for the species *M arvensis obscurus* by Maruyama (1948) and *M. arvensis arvensis* by Bonelli (1952) but not in compact soil. Hamm & Richards (1930) and Bonelli (1952) found *M. arvensis arvensis* in sandy areas while Minkiewicz (1931) and Maruyama (1948) found it in compact soil with sparse grass; sometimes it was found nesting under vegetation (Bonelli 1952).

Nearest-neighbor analysis showed different patterns of dispersion of nests. When bare soil was detected we noticed a clustered pattern in group a of Site 2 but a random one in Site 1. When vegetation was present, distribution of nests resulted always random (b and c of 2), furthermore in site C the nests seemed to follow, accurately, its presence. Site 1 was protected from wind while site 2 was not. Moreover, nearest neighbor distances observed were much higher than those in aggregations studied at sea level in UK, ranging from 4.47 ± 0.14 cm to 13.50 ± 1.17 cm and with a much higher number of nests (Ghazoul 2001). Other factors, if any (e.g., soil hardness), could in-

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Figs 1-8. Mature larva of *Mellinus arvensis obscurus*: (1a, b, c): general aspect: a and c (lateroventral view); b (dorsal view). (2) anal segment. (3) tip of pleural prominence. (4) spiracle (atrium, subatrium, and tracheal trunk): dorsal and lateral view. (5) cranium (frontal view). (6a) labrum; (6b) epipharynx; (7) left maxilla; (8) labium. Abbreviations used: antennal orbit (ao), anus (an), atrium (a), clypeus (c), conical prominences (cp), galea (g), labial palpus (lp), mandible (m), maxillary palpus (mp), punctation (p), seta (s), salivary orifice (so), sensillum (ss), sensory pore (sep), spinule (sp), spiracles (spi), subatrium (sb).

terfere with wasps' nest settlement choice. In Dec, we were able to dig 2 nests to a depth of 23 cm and 28 cm, respectively. About the end of the second burrow we found the content of a cell with a mature larva of *Mellinus arvensis obscurus*. Similar depths have been reported for *M. arvensis* nests (Ghazoul 2001).

Constant presence of wasps flying as typical "nest searchers" could indicate a habit to use occupied or unoccupied burrows and thus possible nest usurpation attempts, as found or *M. arvensis arvensis* by Ghazoul (2001), who stated that wasps were able to distinguish occupied and unoccupied nests.

Prey collected proved once more a generalist hunting behavior for this species. *Anthomyia*, *Helina*, and *Phaonia* had been reported as prey by Bonelli (1952), Hamm & Richards (1930), and Shaw & Pont (1972). *Thricops*, *Neomyia*, and *Drymeia* appear to be new records for the species. All these new genera belong not surprisingly to Muscidae, very common prey among the species (Hamm & Richards 1930), with the exception of *Anthomyia* (Anthomyiidae). Maruyama (1948) found *M. arvensis obscurus* carrying *Halictus* sp. as prey (Hymenoptera: Halictidae). A spider (*Araniella* sp.) as prey suggests possible mistakes occurring during hunting.

Adult Morphology

M. arvensis populations exhibit important morphological variation, which has led to the description of several species and subspecies (Pérez 1905; Yasumatsu 1943) that only recently have been considered synonymous. In spite of these synonymies, populations of *Mellinus arvensis* have been assigned to different varieties (*Mellinus arvensis* var. *alpinus* Handlirsch, 1888 and *Mellinus arvensis* var. *ibericus* Dusmet & Alonso, 1931) in case of close distributional ranges and, recently, to different subspecies (*Mellinus arvensis arvensis* and *M. arvensis obscurus*) in case of distant populations (Nemkov et al. 1995).

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In general, in the genus *Mellinus*, the greatest difference between the Nearctic/Neotropical species (New World) and the Palearctic ones are in the sculpture of propodeal enclosure: shagreened in the former and more or less medially ridged in the latter (Siri & Bohart 1974). Our findings agree with this pattern. However, in the same species variation of some characters is not strictly linked to a given subspecies. For example, we found more similarity concerning punctation patterns and shape of the tergite I between the Nepal and the European populations (belonging to 2 subspecies) than between the Nepal and the Japanese populations (belonging to a single subspecies). However, other characters divide clearly the 2 subspecies. The strong melanization found in the Nepal specimens is common in the Asiatic populations of *M. arvensis*, and it seems to be a character linked someway to a latitudinal and an altitudinal cline. Other species of *Mellinus* were found to be melanic in the Neotropics (Menke 1996).

Larval Morphology

The description of the mature larva of *M. arvensis obscurus* is in reasonable agreement with the description of the only mature larva of the genus described: *M. arvensis arvensis* (Maneval 1939; Evans 1959). Nevertheless, there are some differences between the 2 subspecies: (a) *M. arvensis obscurus*: integument with spinules and setae/*M. arvensis arvensis*: integument smooth, bare, except on the tips of the pleural and dorso-lateral prominences, (b) *M. arvensis obscurus*: tips of the pleural and dorso-lateral prominences of the 12th and 13th abdominal segments bare and smooth/*M. arvensis arvensis*: tips of the pleural and dorsolateral prominences of the 12th and 13th abdominal segments with a series of spinules and scattered setae, (c) *M. arvensis obscurus*: apical third of the abdominal segment with a series of spinules and scattered setae/*M. arvensis arvensis*: apical third of the abdominal segment bare, without setae or spinules, (d) *M. arvensis obscurus*: top and sides of the cranium with conspicuous convexities/*M. arvensis arvensis*: top and sides of the cranium without conspicuous convexities, (e) *M. arvensis obscurus*: labrum slightly bilobate/*M. arvensis arvensis*: labrum strongly bilobate, (f) *M. arvensis obscurus*: maxillae with sparse lateral setae/*M. arvensis arvensis*: maxillae with numerous lateral setae, (g) *M. arvensis obscurus*: labium with 4 setae behind palpi/*M. arvensis arvensis*: labium with 2 setae behind palpi, and (h) *M. arvensis obscurus*: salivary orifices slightly pointed. *M. arvensis arvensis*: salivary orifices pointed.

Conclusions

From the behavioral and morphological data we can conclude that adult morphology, and more notably larval morphology, vary considerably between the subspecies (with a possible geographical cline, with the adult habitus of *M. arvensis arvensis*, closer to *M. arvensis obscurus* in Nepal than to *M. arvensis obscurus* in Japan). This variation is stronger than the behavioral (nesting biology, kind of prey) and ecological (preference of high altitude nesting sites) traits.

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