

Systematic position of the *Hymenoptila* Chopard and notes on the geographic history of Gryllomorphinae (Orthoptera: Gryllidae)

Систематическое положение *Hymenoptila* Chopard и замечания по географической истории Gryllomorphinae (Orthoptera: Gryllidae)

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The former genus *Hymenoptila* Chopard, 1943 (of mainly African distribution) is placed in the genus *Gryllomorpha* Fieber, 1853 as its third subgenus (**stat. nov.**). The following hypothesis about the history of distribution of Gryllomorphinae is proposed: originally, two tribes of this subfamily were geographically isolated from each other by Tethys Ocean (Petaloptilini in South Europe and Asia Minor; Gryllomorphini in North Africa including Arabian Peninsula); later, after the arising of terrestrial contacts between Africa and Eurasia, the Gryllomorphini penetrated to more northern and more eastern territories (Europe and other parts of Southwest Asia) by two ways; but the Petaloptilini was probably not able to go beyond the limits of Europe, Asia Minor and some nearest islands.

Бывший (преимущественно африканский) род *Hymenoptila* Chopard, 1943 помещается в род *Gryllomorpha* Fieber, 1853 в качестве его третьего подрода (**stat. nov.**). Предложена гипотеза формирования современных ареалов Gryllomorphinae: первоначально, две трибы этого подсемейства были географически изолированы одна от другой древним океаном Тетис (Petaloptilini в Южной Европе и Малой Азии; Gryllomorphini в Северной Африке, включая Аравийский полуостров); позднее, после установления сухопутных контактов между Африкой и Евразией, Gryllomorphini заселили более северные и более восточные территории (Европа и другие части Юго-Западной Азии) двумя путями, а Petaloptilini, вероятно, оказались не способны выйти за пределы Европы, Малой Азии и некоторых ближайших островов.

Key words: crickets, taxonomy, geographic history, South Europe, North Africa, Southwest Asia, Orthoptera, Gryllidae, Gryllomorphinae, *Hymenoptila*

Ключевые слова: сверчки, таксономия, географическая история, Южная Европа, Северная Африка, Юго-Западная Азия, Orthoptera, Gryllidae, Gryllomorphinae, *Hymenoptila*

INTRODUCTION

The former genus *Hymenoptila* Chopard, 1943 was described for *Petaloptila panteli* Bolivar, 1914 and *P. rotundipennis* Chopard, 1939 (Figs 1–10, 15–18) with the latter species as its “génotype” (Chopard, 1943). Both these species were described from Morocco (Bolivar, 1914; Chopard, 1939). Then Baccetti (1960) included *Hymenoptila* to-

gether with some European genera (*Petaloptila* Pantel, 1890; *Discoptila* Pantel, 1890; *Acroneuroptila* Baccetti, 1960) in the taxon Petaloptilae, because males of all these genera have partly reduced tegmina. Gorochov (1984), based on the male genitalia structure, divided the subfamily Gryllomorphinae into two tribes: Petaloptilini Baccetti, 1960 and Gryllomorphini Saussure, 1877. The tribe Petaloptilini corresponded to

Petaloptilae sensu Baccetti in circumscription, but taxonomic position of *Hymenoptila* was questionable, because the male genitalia of its species were unstudied. The tribe Gryllomorphini contained only the genus *Gryllomorpha* Fieber, 1853 having the male genitalia strongly distinguished from those of Petaloptilini by the large sacculus and characteristic endoparameres (Figs 11–13, 19–21); all the specimens, included in *Gryllomorpha* in that time, lack tegmina.

Later, *Hymenoptila lanzarotensis* Kevan et Hsiung, 1992 was described from Canary Islands (Kevan & Hsiung, 1992), and the genus *Glandulosa* Harz, 1979, distributed in Asia Minor and originally not included in any tribe, was added to the tribe Petaloptilini (Otte, 1994). Recently Gorochov (2006) erected a new genus of Petaloptilini, *Ovaliptila* Gorochov, 2006, for numerous species from Balkan Peninsula and Asia Minor previously placed in *Discoptila* (which was synonymized with *Petaloptila* in the same paper). The same author (l.c.) suggested that *Gryllomorpha zernyi* Werner, 1934 from Morocco is possibly a member of *Hymenoptila* (Gorochov, 2006). The latter species was placed in the former genus *Discoptila* by Chopard (1943), who probably included it in this “genus” on the base of short tegmina in male, and later in *Petaloptila* s. str. by Eades et al. (2016); however, this species was probably described basing on nymphs of *Hymenoptila* and its name may be a junior synonym *H. rotundipennis*, because both nominal species were recorded by Chopard (1943) from the same locality (“Tachdirt”). Finally, Gorochov (2009) after study of the pictures of male genitalia of *H. lanzarotensis* in the original description also suggested that *Hymenoptila* belongs to Gryllomorphini. However, this suggestion required confirmation by more detailed study of the male genitalia.

Recently, the author of this paper received some additional material from Morocco which allows him to confirm the above-mentioned suggestion, to change the systematic position of *Hymenoptila* on the

base of detailed redescription of its type species, and to propose a hypothesis on the history of distribution of Gryllomorphinae. The material studied is deposited in the collection of the Zoological Institute, Russian Academy of Sciences, Saint Petersburg. All specimens were dried and pinned. The photographs of their morphological structures were made with a Leica M216 stereomicroscope.

TAXONOMIC PART

Subfamily **GRYLLOMORPHINAE**
Saussure, 1877

The subfamily considered here as consisting of only two tribes (Gryllomorphini and Petaloptilini) distributed mainly around Mediterranean Sea, but some of its species reach Canary Islands, territories around Black and Caspian Seas, and Central Asia.

Tribe **GRYLLOMORPHINI**
Saussure, 1877

The tribe includes a single widely distributed genus *Gryllomorpha* distributed almost as widely as the subfamily. Species of this tribe are usually apterous, but there males sometimes have small, lamellar and lobule-like tegmina (Figs 2, 3). The male genitalia are specialized and having some characters convergent to those of the subfamily Gryllinae: sacculus is large and with a characteristic transverse sclerite at the base; endoparameres are in the shape of a pair of elongate and strongly arcuate sclerites more or less fused in the median part (Figs 1–13, 15–17, 19–21).

Genus ***Gryllomorpha*** Fieber, 1853

The diagnostic characters as in Gryllomorphini. The genus is divided into three subgenera: *Gryllomorpha* s. str.; *Gryllomorphella* Gorochov, 1984; and *Hymenoptila* Chopard, 1943, **stat. nov.** All these subgenera are usually with a scalloped or looped

anterior part of the sacculus in the male genitalia (Figs 15–17, 19, 21), but some species and one group of species have a secondarily simplified (not scalloped and not looped) sacculus (Figs 11–13).

Gryllomorpha s. str. is characterized by a rather large body and the absence of wings in both sexes; the male genitalia with a rather weakly trifurcate rachis, sclerotized or semisclerotized longitudinal ribbons before the rachis (these ribbons may be more or less reduced), and usually large and widened (plate-like) apodemes of the endoparameres. This subgenus consists of several species-groups: the group of *G. dalmatina* includes species with the above-mentioned ribbons distinct, and the endoparameral apodemes clearly plate-like [*G. dalmatina* (Ocskay, 1832) as a type species and *G. longicauda* (Rambur, 1839); Figs 11–13, 19–21]; the group of *G. sovetica* contains species with these ribbons sometimes less distinct, and the endoparameral apodemes much narrower [*G. syriaca* Harz, 1979, *G. sovetica* Gorochov, 2009 and *G. occidentalis* Gorochov, 2009]; the other species included in *Gryllomorpha* s. str. by Gorochov (2009) possibly belong to its other species groups.

Gryllomorphella consists of rather small species completely lacking wings, with the male genitalia rather diverse but having more or less narrow endoparameral apodemes, strongly trifurcate rachis, and lacking sclerotized or semisclerotized ribbons before the rachis. This subgenus also contains several groups of species. The group of *G. miramae* has the male genitalia with a simple (not looped and not scalloped) sacculus and rather long ectoparameres (longer than the epiphallus) [*G. miramae* Medvedev, 1933 as a type species, *G. albanica* Ebner, 1910, and possibly *G. antalya* Gorochov, 2009]; the group of *G. uclensis* differs from previous one in a looped or scalloped sacculus and short ectoparameres (not longer than the epiphallus) [*G. uclensis* Pantel, 1890, *G. mira* Gorochov, 1993, and possibly *G. sternlichti* Chopard, 1963]; the group of *G. canariensis* is similar with the first group

in the shape of ectoparameres and with the second group, in the structure of sacculus [*G. canariensis* Chopard, 1940, *G. zonata* Bolivar, 1914, *G. robusta* Gorochov, 2009, and possibly *G. atlas* Gorochov, 2009]. The species *G. segregata* Gorochov, 2009 with a very long apical spine of the rachis may belong to another group of *Gryllomorphella*.

Hymenoptila includes a few species very similar to those of *Gryllomorpha* s. str. in the general appearance and male genitalia structure, but provided with small, lamellar and lobule-like tegmina in males having only slight traces of the venation and no traces of any stridulatory apparatus: *G. (H.) rotundipennis* (Chopard, 1939), **comb. nov.** (type species); *G. (H.) panteli* (Bolivar, 1914), **comb. nov.**; *G. (H.) lanzarotensis* (Kevan et Hsiung, 1992), **comb. nov.**; and possibly *G. (H.) zernyi* (Werner, 1934), **comb. nov.**, which is probably a synonym of *G. rotundipennis*. The male genitalia of *Hymenoptila* completely correspond to those of the group of *G. dalmatina* from subgenus *Gryllomorpha* s. str., and thus, *Hymenoptila* may be synonymized with the latter name. However, *Hymenoptila* is tentatively considered here as a separated subgenus of *Gryllomorpha* s. l., because it has an important primitive character, the presence of tegmina in male. The representatives of *Gryllomorpha* s. str. and *Gryllomorphella* may lose their tegmina independently and repeatedly.

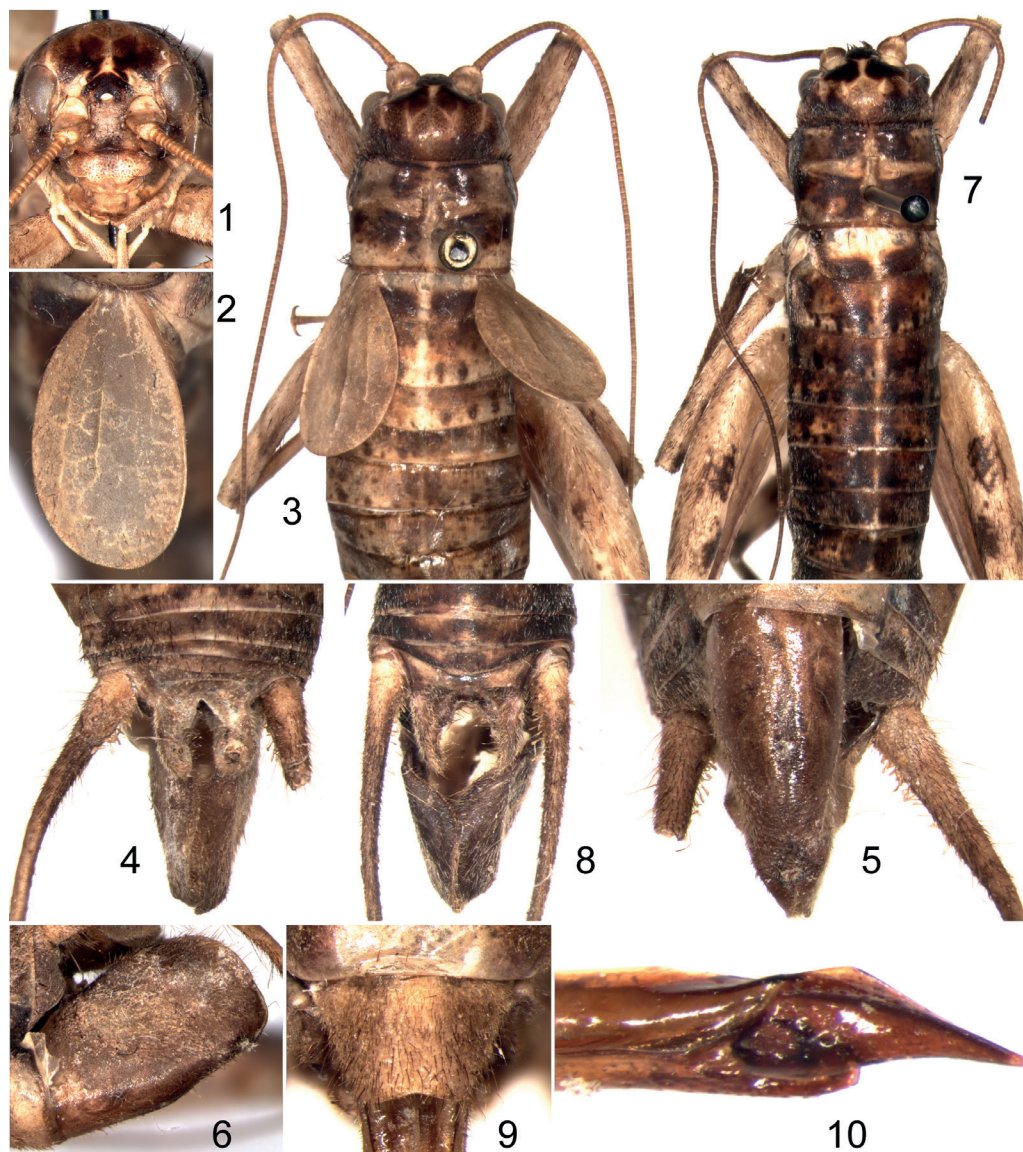
Gryllomorpha (Hymenoptila) rotundipennis (Chopard, 1939), **comb. nov.** (Figs 1–10, 15–18)

Petaloptila rotundipennis Chopard, 1939.

Hymenoptila rotundipennis: Chopard, 1943.

Material studied. **Morocco**, Grand Atlas: 2 males, 2 females, “nr. Imlil stlm, 31°08′41.5″N, 0.07°54′25.0″W, 17–21.IX.2013, D. Gapon” (ZIN); 1 nymph (male), “Atlas, Arround, 1950 m, 24–25.VI.30, Ebner”, “*Discoptila zernyi* Werner”, “topotypus” (ZIN); 1 nymph (female), “Atlas, Tashdirt, 2450 m, 26.VI.30, Ebner”, “*Discoptila zernyi* Werner”, “topotypus” (ZIN).

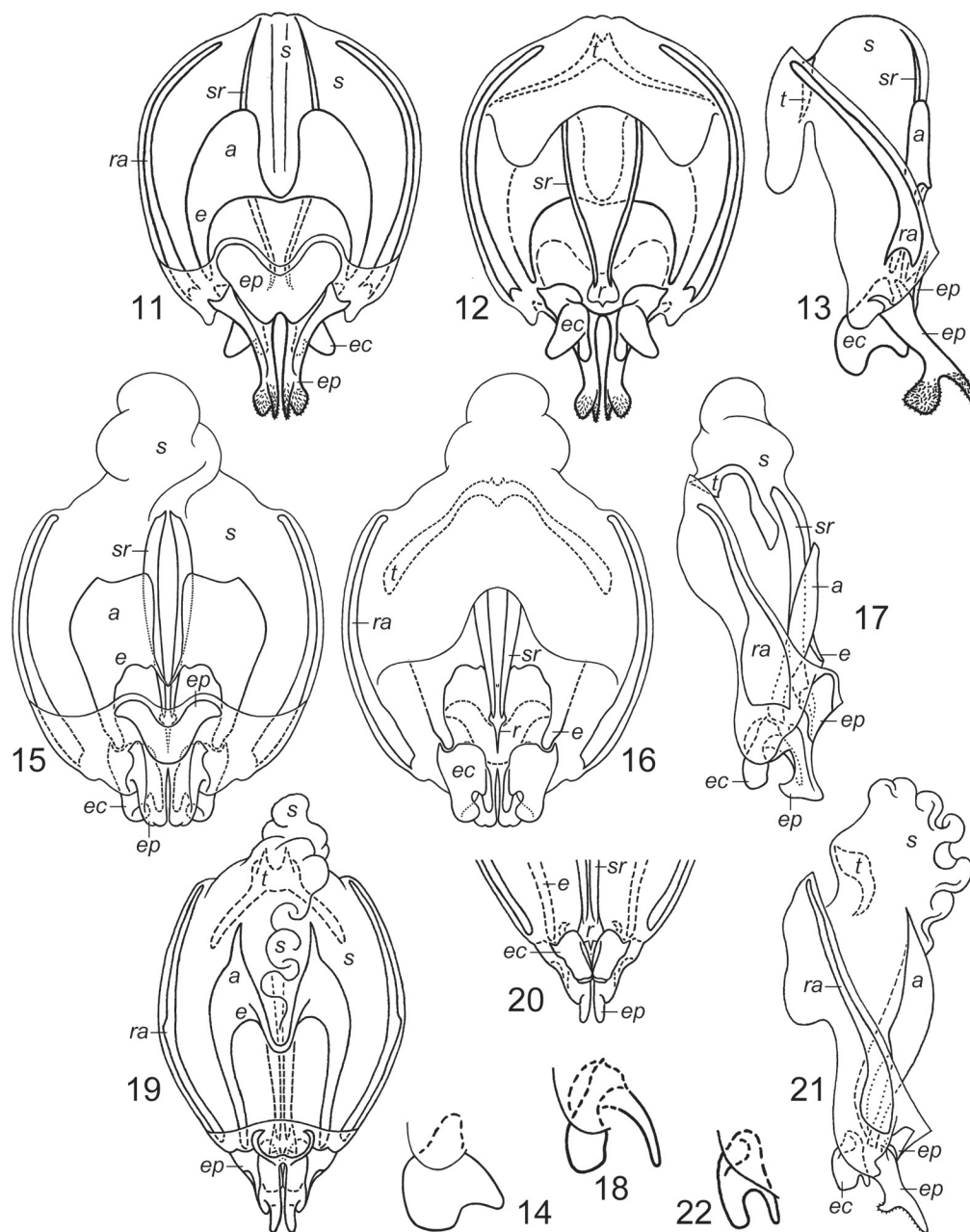
Redescription. Male. General appearance very similar to that of *G. dalmatina*, but



Figs 1–10. *Gryllomorpha (Hymenoptila) rotundipennis* (Chop.). 1–6, male with normal tegmina; 7, 8, male with small proximal parts of tegmina only; 9, 10, female. Head in front (1); right tegmen (2); body of male without distal part (3, 7); male abdominal apex from above (4, 8) and from below (5); male genital plate from side (6); female genital plate from below (9); distal part of ovipositor from side (10).

body with tegmina or small proximal remnants of tegmina (most part of tegmina torn off). Colouration yellowish with following pattern: epicranium with large brown or dark brown spot (between antennal cavities and anterior halves of eyes) crossed by light stripes along sutures and along dorsal

edges of these cavities (latter stripes including lateral ocelli), with dark or light greyish brown median spot near clypeus completely or partly fused with previous spot on rostrum (Fig. 1), with brown transverse band on posterior part of dorsum (this band with two or four longitudinal lateral stripes



Figs 11–22. *Gryllomorpha*, male: 11–13, *G. (Gryllomorpha) dalmatina dalmatina* (Ocsk.), Crimea. 14, *G. (G.) dalmatina* subsp., Montenegro; 15–18, *G. (Hymenoptila) rotundipennis* (Chop.), Morocco; 19–21, *G. (G.) longicauda longicauda* (Ramb.), Spain; 22, *G. (G.) longicauda adspersa* Bol., Morocco. Genitalia from above (11, 15, 19), from below (12, 16), and from side (13, 17, 21); lateral view of ectoparamere with membranous fold covering its proximal part, sclerotized parts of epiphallus not pictured (14, 18, 22); distal part of genitalia from below (20). *a* – apodeme of endoparamere; *e* – endoparamere; *ec* – ectoparamere; *ep* – epiphallus; *r* – rachis (= guiding rod); *ra* – ramus; *s* – sacculus (= spermatophore sac); *sr* – sclerotized ribbon before rachis; *t* – transverse sclerite (?= formula). 11–14, 19–22, after Gorochov (2009) with modifications.

crossing light area between this band and previous large spot), with brown spot between each eye and subgena, and sometimes with darkish stripe along posterior edge of each gena; antennae with very light brown or light greyish brown flagellum and sometimes with darkish medial mark on scape; mouthparts with brown or light brown small median spot on upper part of clypeus and with brown anterior (medial) parts of mandibles and small lateral parts of clypeus; pronotum with disc as in Figs 3 and 7, and with lower half of each lateral lobe brown or dark brown but having small yellowish longitudinal spot near anterior half of ventral edge; other tergites also spotted (their general coloration varied from slightly lighter to slightly darker; Figs 3, 7); tegmina uniformly light yellowish grey (Figs 2, 3), but their remnants in one male darkened (Fig. 7); legs with very sparse brown or light brown spots on fore and middle femora, with somewhat more numerous dark brown or brown marks on hind femur, and sometimes with almost uniformly light greyish brown tibiae and tarsi; abdominal apex with light brown or greyish brown anal and genital plates, and with greyish brown cerci having light proximal part (Figs 4–6, 8). External structure of body also similar to that of *G. dalmatina*: head semiglobular (not high and not flattened), with rostrum between antennal cavities slightly narrower than scape (Fig. 1), and with palpi moderately long and thin (apical segment of maxillary palpi clearly longer than their other segments); pronotum distinctly transverse, with almost parallel lateral sides (Figs 3, 7), with more or less straight anterior and posterior edges of disc, and with almost not oblique ventral edges of lateral lobes; tergites of pterothorax and of abdomen without traces of specialized gland (any glandular area with strong pubescence on these tergites also absent; Figs 3, 7); tegmina (if they not torn off) reaching apex of second abdominal tergite, elongately oval (with narrow basal part and practically without lateral field), lamellar, coriaceous, poorly pubescent dorsally and ventrally,

with distinct traces of five almost straight longitudinal veins and barely visible traces of transverse venation (Figs 2, 3); legs typical of *Gryllomorpha* s. str., i. e. with tympana absent, and with hind basitarsus rather long, slender and straight; anal plate with rather long posterolateral lobules and deep notch between them (Figs 4, 8); genital plate elongate, longer than anal one, more or less vertical (somewhat laterally compressed), with roundly truncate apical part in profile but having narrow and rather deep crevice-like posteromedian notch (Figs 4–6, 8). Genitalia intermediate between those of *G. dalmatina* and *G. longicauda* (for comparison see Figs 11–22): epiphallus as in *G. longicauda* in length (shorter than in *G. dalmatina*), with posterolateral lobes somewhat wider than in both these species, and with medial plate large (almost as in *G. dalmatina* but much larger than in *G. longicauda*); endoparameres as in *G. dalmatina* but with almost truncate (not rounded) anterior parts of apodemes (in *G. longicauda*, endoparameres shorter and with spine-like anterior projection on each apodeme); sacculus somewhat looped in anterior part (in *G. longicauda*, this part strongly scalloped, but in *G. dalmatina*, sacculus in shape of simple sac); rachis with rather long apical spine and a pair of much shorter and rounded lateral lobules (in both above-mentioned species, this apical spine short, not longer than lateral lobules of rachis); sclerotized longitudinal ribbons of sacculus located before rachis similar to those of *G. longicauda* but with more distinct (more sclerotized) anterior parts (these ribbons similar also to those of *G. dalmatina* but somewhat wider and shorter); ectoparameres in these three species somewhat different in shape but having similar dorsal process directed more or less backwards (in profile, this process longer than in *G. longicauda* and *G. dalmatina*, and narrower than in latter species; see Figs 14, 18, 22).

Female. Coloration and structure of body as in males, but tegmina completely absent, anal plate almost square with widely

rounded posterior part, and last abdominal sternite in both females studied distinctly longer than all other abdominal sternites; genital plate clearly smaller (shorter and narrower) than last sternite, and distinctly narrowing to slightly notched apex (this notch varied from roundly angular but not deep one to almost absent; in latter case, apex of genital plate almost truncate; Fig. 9); ovipositor thin and straight, about 1.3 times as long as hind femur, and with distal part as in Fig. 10.

Length, in mm. Body: male 17.5–18, female 17–19; pronotum: male 2.6–2.9, female 2.8–3; tegmina, male 4.6; hind femora: male 11–12, female 12–12.5; ovipositor 15–16.

Note. One of two males has only very small basal parts of the tegmina (Fig. 7). This male and all the females studied are almost identical to the representatives of the group of *G. dalmatina* (*Gryllomorpha* s. str.) in general appearance and might be determined as one or another species of this group, or described as a separate species of *Gryllomorpha* by the previous authors. Possibly the male tegmina contain an attractive secret and are eaten by female during copulation (this action is useful for her fixation in the copulatory position); this assumption is also supported by the absence of any distinct gland or glandular area with remarkable pubescence on the dorsum of pterothoracic and abdominal tergites as well as on the tegmina.

This species, rather widely distributed in the central part of Morocco, differs from *G. panteli* (southwest part of Morocco: Agadir) in longer male tegmina and ovipositor (in *G. rotundipennis*, hind femur is 2–2.5 times as long as tegmen, and ovipositor is 1.3–1.5 times as long as hind femur; in *G. panteli*, these ratios are about 3.6 and 1.2, respectively). From *G. lanzarotensis* (Canary Islands), it is distinguished by the male genitalia with a distinctly deeper posteromedian notch of the epiphallus and probably a somewhat different shape of the ectoparameres, endoparameres and transverse sclerite (these structures do not seem very cor-

rectly depicted by Kevan & Hsiung), as well as a clearly less deep posteromedian notch of the female genital plate (in *G. lanzarotensis*, the above-mentioned ratios for hind femur, tegmen and ovipositor are similar to those of *G. rotundipennis*: about 2.3 and 1.3, respectively). Differences between *G. zernyi* (central part of Morocco) and the congener redescribed are unknown; the above-mentioned nymphs, determined by Ebner as “*Discoptila zernyi*”, are very similar to *G. rotundipennis* and seem to be identical to the original description by Werner (1936); thus, these names may be synonymous.

NOTES ON THE GEOGRAPHIC HISTORY OF GRYLLOMORPHINAE

Inclusion of *Hymenoptila* in the tribe Gryllomorphini limited the area of distribution of the tribe Petaloptilini to the regions of Europe and Asia Minor around Mediterranean Sea and Black Sea only. Each large peninsula in Northern Mediterranean has an endemic genus or subgenus (see Fig. 23). In Iberian Peninsula, *Petaloptila* s. l. is represented with two subgenera (*Petaloptila* s. str. and *Zapetaloptila* Gorochov et Llorente, 1993) and numerous species. In Apennine Peninsula, *Italoptila* Gorochov et Llorente, 1993 (as a subgenus of *Petaloptila* s. l. or a separate genus) with one or several species is known (male genitalia for all the species are unstudied). In Balkan Peninsula, in the territory between Adriatic and Black Sea (including Crimea), and in the western and central parts of Asia Minor, *Ovaliptila* with numerous species and subspecies is common. In the central and eastern parts of Asia Minor, *Glandulosa* with a few species is presented. It is interesting to note that this genus was not found to the west from Antalya City, but it is very usual to the east from this city (Gorochov & Unal, 2012). Thus, central part of Asia Minor is possibly a unique territory where two genera of Petaloptilini are sympatric. In some islands of Northern Mediterranean, this tribe is also presented: in Sardinia, by the endemic

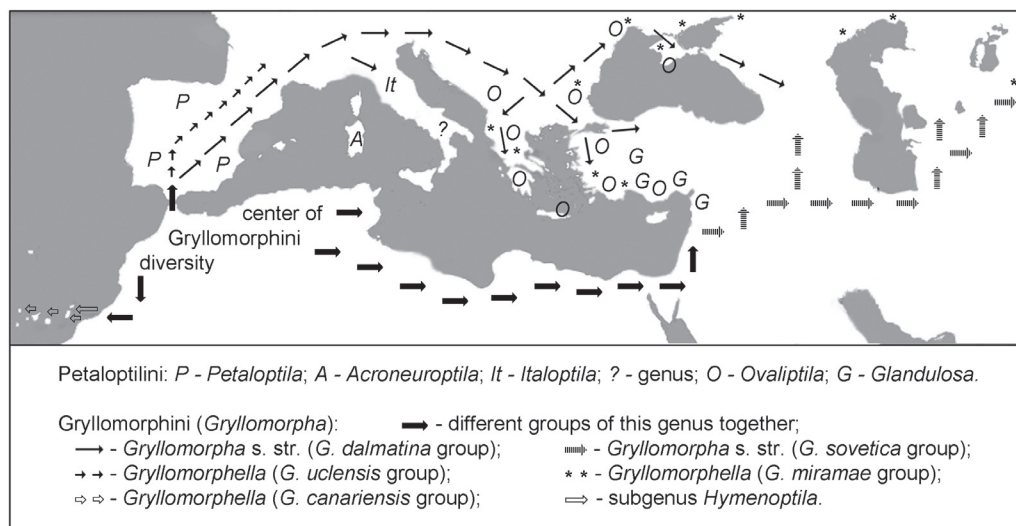


Fig. 23. Recent distribution of Gryllomorphinae with hypothetical reconstruction of migratory ways for some groups of *Gryllomorpha*.

genus *Acroneuroptila* with two species; in Greek Islands, by *Ovaliptila* with several species. In the other large islands of Mediterranean Sea, this tribe is unknown. The representatives of Petaloptilini are mainly inhabitants of forest floor near water reservoirs, but some of them live in crevices of rocks near water or in caves. Thus, they are adapted to more or less humid climate and are not found in more arid conditions.

Gryllomorpha s. l. (the only genus of Gryllomorphini) as well as two its subgenera (*Gryllomorpha* s. str. and *Gryllomorphella*) has much wider distribution: all the regions around Mediterranean Sea and around Black Sea, and the enormous arid territories in Southwest Asia and in Central Asia (Fig. 23). These data indicate that representatives of *Gryllomorpha* from these subgenera have much more pronounced ability to migrate than representatives of Petaloptilini. Climatic preferences in representatives of *Gryllomorpha* are also more diverse. The greatest number of species of Gryllomorphini inhabits Atlas Mountains, especially their Moroccan part (Chopard, 1943; Gorochov, 2009). This region has a more humid climate than all other regions of North Africa and Arabian Peninsula. In

the latter regions, many species of Gryllomorphinae may live only in the narrow stripes along sea banks or along rare rivers and lakes, but some (probably not numerous) species are adapted to live in the burrows of rodents and reptiles in arid lands (in the steppes and semideserts). All the species of Gryllomorphini, distributed in the enormous arid territories of Eurasia, are inhabitants of burrows. They are presented by only a few species belonging to two groups: group of *G. sovetica* from *Gryllomorpha* s. str.; group of *G. miramae* from *Gryllomorphella* (Fig. 23). In the forest zone of South Europe (more conducive to the life of *Gryllomorpha* s. l.), this genus is also presented by a few species of two groups: group of *G. dalmatina* from *Gryllomorpha* s. str.; group of *G. uclensis* from *Gryllomorphella* (Fig. 23). Moreover, majority of these European species are distributed only in the western part of Europe (Portugal, Spain, France), and possibly only one species (*G. dalmatina* with several subspecies) is distributed also in forests of Eastern Europe and of Asia Minor. Such poverty of the European fauna of Gryllomorphini compared to Moroccan one suggests the hypothesis of its African origin. This hypothesis is discussed below.

Most likely, the formation of two tribes of Gryllomorphinae took place in conditions of prolonged isolation of Africa from Eurasia. The tribe Petaloptilini was formed to the north of Tethys, and the Gryllomorphini was formed to the south of this ocean. In Late Caenozoic, Europe and Africa endured climatic cooling and aridization. Under these conditions, the area of thermophilic and moisture-loving species in Europe could be reduced to a few isolated southern spots on almost each large peninsula (island) of Mediterranean Sea, and the evolution of Petaloptilini was connected with the formation of some separate genera in each of these spots. In warmer Africa, these climatic processes could lead to a narrowing of the area of Gryllomorphini up to a large refugium in Atlas Mountains, to a dramatic impoverishment of its fauna in more dry lowland regions, and to the appearance of adaptations to life in vertebrate burrows on arid territories. Numerous small climatic fluctuations (humidization-aridization) in Africa could serve as a stimulus to the development of migratory adaptations in *Gryllomorpha* s. l. and eventually to the development of greater ability to migrate than in Petaloptilini. Thus, it is very possible that most part of North Africa repeatedly populated by some species of this genus from the Atlas refugium (Fig. 23). Migration of *Gryllomorpha* s. l. to the north probably could start after the appearance of permanent land contact of Africa with Eurasia in the Miocene. It is impossible to establish the time of this penetration; moreover, different species and groups of species could migrate in Eurasia in different epochs and at least by two ways.

The western migratory way was from Morocco to Iberian Peninsula (Fig. 23). This way was used by two groups of species: the group of *G. dalmatina* (*Gryllomorpha* s. str.) with *G. dalmatina* and *G. longicauda*; and *G. uclensis* from the group of *G. uclensis* (*Gryllomorphella*). The group of *G. dalmatina* is characteristic for comparatively humid ecosystems presented

both in the northern Moroccan coast and in Iberian Peninsula. One species, *G. longicauda*, penetrated into Spain and Portugal and diverged into two subspecies: Moroccan and Iberian ones (Figs 21, 22). The second species, *G. dalmatina*, spread over Apennine and Balkan Peninsulas, all the regions around Black Sea, Asia Minor and many islands of Mediterranean Sea (Fig. 23) and formed several subspecies in these regions (Figs 13, 14); however it is recorded also from the Moroccan refugium, Algeria and Tunisia (Chopard, 1943). The group of *G. uclensis* penetrated into Iberian Peninsula and France (Fig. 23), and formed several subspecies in North Africa. The penetration of all these species from Africa to Europe is probably late (subrecent), because during the time of their residence in Europe, they were able to diverge into subspecies only.

The eastern migratory way was from Africa and Arabian Peninsula to Southwest Asia along the Mediterranean coast (Fig. 23). This way was probably used by the group of *G. sovetica* from *Gryllomorpha* s. str. This group consists of at least three species: *G. syriaca* from Syria, *G. sovetica* from Armenia, Azerbaijan, North Iran and Kazakhstan (from Caspian Sea to Balkhash Lake; Fig. 23), and *G. occidentalis* from Morocco. These species are very similar in the general appearance; they are probably inhabitants of vertebrate burrows in semidesert landscapes. Their migration to these regions was possibly also rather late: in these regions, this group diverged into a few closely related species only. Somewhat earlier migration possibly had place in the group of *G. miramae* from *Gryllomorphella*. This group is unknown in Africa and Arabian Peninsula; all its representatives live in vertebrate burrows on the steppe-like and semidesert territories: *G. albanica* from the northern part of Balkan Peninsula; *G. miramae* with two subspecies distributed from Greece to Western Turkey, Uzbekistan, Eastern and Northern Kazakhstan, and the regions near Black Sea; and possibly *G. antalya* which is known only from one locality

in Southern Turkey (Fig. 23). If this group formed in Eurasia, the arrival of its ancestors from Africa may be earlier than in the other groups of *Gryllomorpha* s. l., but the way of their penetration in Eurasia remains unknown; there is no information about presence of this group near the western or eastern passes. Nevertheless, the eastern way for migration of the latter group from Africa to Eurasia seems more possible, because this group has adaptations to life in more or less arid landscapes which are much less distributed in the western half of Europe.

Finally, it is reasonable to mention another way of migration of *Gryllomorpha* s. l. leading to its penetration into Canary Islands. It was used by at least two groups of this genus, the group of *G. canariensis* from *Gryllomorphella* with one species (*G. canariensis*) and by the subgenus *Hymenoptila* with also one species (*G. lanzarotensis*). Both species seem to be not adapted or almost not adapted to life in arid landscapes, and their method of overcoming maritime straits is unclear. Each of group has an endemic species distributed in some of these islands and few related species in North Africa (Morocco) which suggests that their arrival from Africa could be somewhat earlier than for the Western European species.

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