

**STUDIE O VYSOKOHORSKÝCH PÍDÁLKÁCH RODU PSODOS
TREITSCHKE 1828 SE ZŘETELEM K DRUHŮM V POHOŘÍCH
ČESKOSLOVENSKA A K OTÁZKÁM VZNIKU DRUHU
V HORSKÝCH OBLASTECH.**

**ON THE HIGH MOUNTAIN GEOMETRIDAE OF THE GENUS PSODOS
TREITSCHKE 1828 WITH REGARD TO THEIR SPECIES IN THE
MOUNTAINS OF CZECHOSLOVAKIA AND TO THE QUESTION OF
THE ORIGIN OF A SPECIES IN MOUNTAIN REGIONS.**

(LEPIDOPTERA — GEOMETRIDAE).

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I. Úvod — Introduction.

Vysokohorské píďalky rodu *Psodos* T r. jsou tvarově, ekologicky i vývojově jednou z nejzajímavějších skupin řádu Lepidoptera. Dosavadní práce však vytěžily při jejich studiu jistě méně závěrů, než bylo možno očekávat. Jako skupina s výrazně evropským těžištěm výskytu zajímaly nás tyto píďalky nejen z důvodů již uvedených, nýbrž také a zvláště proto, že jsou jednou z nejtypičtějších složek naší vysokohorské zvířeny a jejich biocenosa v Tatrách má všechny typické znaky stenoekní specifické zvířeny nejvyšších horských vrcholů střední Evropy. V této práci zveřejňujeme výsledky svého několikaletého studia této skupiny, jež je zejména v našich horských oblastech zcela nedostatečně prozkoumána. To se projevuje i v naší literatuře, neboť veškerá data o rodu *Psodos* T r. z Československa jsou vesměs uveřejněna v literatuře jiných národů a obsahují často mnoho chyb a nepřesností.

The high-mountain Geometridae of the genus *Psodos* Tr. are morphologically, ecologically and phylogenetically one of the most interesting groups of the order Lepidoptera, but the research done so far on them has certainly yielded fewer conclusions than might have been expected. As a group with a markedly European focus of occurrence these Geometridae interested us not only for the reason given above, but also—and especially—because they are one of the most typical components of our high-mountain fauna, and especially their biocenosis in the Tatra has all the typical features of a stenoec specific fauna of the highest mountain summits of Central Europe. In the present paper we give the results of our investigation, carried on for several years, of this group, which, especially in our mountain regions, has been quite insufficiently examined. This shows also in our literature, for all data on the genus *Psodos* Tr. from Czechoslovakia have been published in the literature of other nations and often contain many errors and inaccuracies.

II. Survey of the Main Publications on the Genus *Psodos* Tr.

The first to summarize the knowledge on the genus *Psodos* Tr. on a larger scale is Prout in Seitz (1915). Many of the forms described later are of course not included in his paper, but many of them have a very doubtful taxonomic value.

The study of Wehrli (1921) is of classical importance; he was the first author to work the known species in a larger monograph. Even though in Wehrli's conception there is to some extent an overdimensioning of the forms of the genus *Psodos* Tr., to many of which a taxonomic value was attributed which they do not deserve, as already Schwingenschuss (1923) pointed out correctly and others after him, yet Wehrli's conception is of fundamental importance for the further study of the genus *Psodos* Tr. In the intentions of static typology, which does not respect the phylogenetic system nor zoogeography, this genus was worked out by most of the later authors who—especially when describing new species—committed a number of mistakes (e. g. Schmidt 1930, Bartha 1933, Praviel 1938, a. o.). In so far as geographical races were described, especially from mountain groups outside the Alps, the mistakes are not so striking, as the spatial isolation led in this genus really always to the origin of subspecies. Wehrli (1953) himself concluded this period of the study of the genus *Psodos* Tr. with his conception of the genus in the work of Seitz; this working does not differ essentially from his earlier views. In the main he starts again from static typology, without following the deeper phylogenetic and zoogeographical points of view. Again a great number of forms appear whose taxonomic values are often unclear (ssp., var., ab., f. loc., etc.), and his position is not clear with regard to problematic forms. Also forms already described earlier are here described as new forms (*Ps. bentelii* ssp. *panticosea*, *Ps. noricana* ssp. *kusdasi*, gen. *Gnophopsodos*). Nevertheless his work is of lasting value, as it really accumulates material, whose further working will, however, in many cases demand a re-evaluation with regard to contents and form. The same cannot be said of other studies, which are confuse in every respect, and

which did not bring any progress in the investigation of the genus *Psodos* Tr. (e. g. Turati, Matsumura, a. o.).

We find faunistic data on the genus *Psodos* Tr. in almost all works dealing with the mountain fauna of Lepidoptera or with the faunistics of wider areas. On the genus *Psodos* Tr. in the Krkonoše we find a number of data summarised by Sterneck (1929), later Marschner (1934), and some other authors. Tykač (1949) gives quite confused data; thus he regards *Torula quadrifaria sudetica* Sterneck as boreoalpine species.

From the Králický Sněžník and Praděd we find faunistic data on *Ps. alpinata* Scop. in several authors. Skala (1912, 1931-32) took over these findings. The interesting findings of Stephan (1925) and Warnecke (1920) have to be specially mentioned.

Very inaccurate data on the fauna of the genus *Psodos* Tr. are published in the fauna Regni Hungariae (Aigner-Abafi, etc., 1918). The work of Husz (1881) is full of inaccuracies and fiction not only on the fauna of the genus *Psodos* Tr., but also on the other groups of Lepidoptera. Růžicka (1931) published reliable faunistic reports, but mentions also the certainly unfounded report of Albrecht on the occurrence of *Torula quadrifaria* Sulz. in the Vtáčník Mts. More recently Brčák (1951, 1952) published some remarks on *Psodos* Tr. in the Tatra. Further report gives Komárek (1953).

Quite considerable attention was devoted to the occurrence of members of the genus *Psodos* Tr. on the Polish side of the High Tatra (Prüfer 1923, Romaniszyn 1929, Niesiolowski 1929).

In the other parts of the Carpathians the research on this genus has an old tradition. In Transylvania it was studied by Czekelius (1898, 1922 till 1924, 1935), of course with some mistakes, and by Diószeghy (1930, 1935) and by Worrell (1951), and besides in the systematic-faunistic studies of Schmidt (l. c.) and Bartha (l. c.) already mentioned. Salay (1910) records some finds also from the Carpathians of Rumania.

From the mountains of the Balkan Peninsula, whose fauna is certainly very interesting and important, we have up till now only few accurate reports (Rebel-Zerny 1931, Bureš-Tuleškov 1937).

From the Alpine region there are sufficient faunistic works, of which we mention here at least the most important ones. Osthelder (1938) worked carefully the Bavarian Alps. Hellweger (1914) published the fauna of the genus *Psodos* Tr. of Northern Tyrol, the works of Kitschelt (1925) and Dannehl (1928) contain a number of records from Southern Tyrol. The Karavanks and Eastern Tyrol were worked by Thurner (1948); the occurrence of Lepidoptera in Styria had been published already earlier by Hoffmann & Klos (1914). From Lower Austria we have reports on the occurrence of members of the genus *Psodos* Tr. by Galvagni-Rebel-Zerny (1915) and Naufock (1912). The publications on the Swiss Alps are of very old date (e. g. Jäggi 1872, Frey 1880, Favre 1899, a. o.), and more recently Vorbrodt (1928, 1931) has dealt with this genus in some detail. In the French literature Oberthür (1913) and Culot (1919-20), and after them Lhomme (1923-35) have dealt with

the systematic-faunistic study of the genus *Psodos* Tr.; the last-named study gives a number of accurate reports.

The other numerous faunistic data are mostly scattered in papers of minor importance.

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III. Remarks to the Morphology and Taxonomy of the Genus *Psodos* Tr.

Wehrli (1921), the best expert on the genus *Psodos* Tr., provided for its investigation the exact scientific foundation in his well known classical study. As has already been said, his work imprinted its character on the whole later study of this genus. As Wehrli took in some cases subjective view of a species, he gave also some later authors the possibility to develop such views. Thus the later study of this group was governed all too distinctly by the endeavour to describe more and more new forms. As, however, these works often dealt insufficiently or superficially with questions of morphology, taxonomy and zoogeography, this conception was one-sided and often purely formal. The present state of knowledge of the genus can thus be compared to similar conditions in some other groups of insects which suffer from a systematic over-dimensioning, i. e. they contain an excessive number of species and forms described, which cannot maintain themselves when subjected to a critical investigation of their evolution, and which are often untenable also taxonomically.

Concerning the taxonomy of the genus *Psodos* Tr. and of the Lepidoptera in general we have to evaluate positively Wehrli's view of the taxonomic importance of the female outer genitalia and their chitinised parts. This fact has to be evaluated especially from the point of view of the time when this view was formulated, for we must remember that even today many experts completely underestimate the outer female genitalia as taxonomic criteria. The unscientific character of this view is especially due to the subconscious recognition and acceptance of the so-called preponderance principle; which is in this connection an almost generally accepted fact, though it is an ideologically incorrect conception arising from the generalisation of some of Darwin's ideas, therefore from a vulgarisation of Darwin. The opinion that only or mostly only the male genitalia have a taxonomic importance of the first order is an a priori simplification of the real data, which enable us in fact to distinguish in the Lepidoptera the following groups:

1. Groups in which the male and female genitalia are little specific or non-specific (e. g. some genera of the families *Lycaenidae*, *Pierididae*, etc.).

2. Groups in which the male outer (ectodermal) genitalia and their chitinised appendices show specific characters with an apparent uniformity of the female outer genitalia (e. g. the genus *Melitaea* F., etc.) or in which the specificity of the female organs is very indistinct.

3. Groups in which the female outer genitalia and their chitinised parts show good specific characters with a uniformity of the male outer genitalia (genus *Zygaena* F. and many others).

4. Groups where the males as well as the females show in the outer genitalia morphologically mutually corresponding characters which are specific.

Thus with regard to the taxonomic importance of the outer genitalia we observe in the Lepidoptera all possible categories, as it corresponds to the dialectic laws of specific differentiation. If nevertheless any generally applicable conclusions can be derived for the specificity of the outer genitalia of the Lepidoptera, they can be formulated as follows:

1. Most of the groups of *Lepidoptera* show distinct differences in the genitalia of the two sexes, which is entirely in natural agreement with the necessity of their mutual functional adaptation (principle of lock and key).

2. In each of the groups mentioned one can find cases which are in antithesis to the general morphological rule of the given group as far as its outer genitalia are concerned. Thus e. g. in broader groups, in which we find a uniformity of the male (female) outer genitalia, species can exist which on the contrary show good differences in the male (female) organs (e. g. genus *Lithocolletis* H b.).

3. The female outer genitalia show in most cases a smaller variability; they are thus in essence more specific than the male ones. The cause of this can be seen mainly in the morphological simplicity of their organs in comparison with the more complex organs of the males.

4. The morphological specificity of the outer genitalia is due to the quality and quantity of the agents which acted on the specific differentiation in the given group (origin of species by geographical isolation, physiological isolation, or its dependence on the phylogenetic age, natural plasticity and inner factors of the organism). This has to be taken in the sense that the conditions which cause the differentiation of the species in the different groups are qualitatively and quantitatively different, so that also the specific differences in the different groups are qualitatively and quantitatively different. Thus we know groups where the specific differences are evident already at first glance at the habit of an individual, whereas in other groups the habit does not offer any distinguishing specific character at all, while in the anatomy we find essential specific differences.

The genus *Psodos* Tr. is with regard to the configuration of the outer genitalia a defined group, in which the male and female organs show essentially equivalent specific differences. These differences can, however, be ascribed only to some formations especially of the male and to a lesser extent of the female organs. Because of the simplicity of the outer genitalia the females show, however, as already said, a lesser variability, and are therefore more specific than the males.

Generally speaking the outer genitalia of the genus *Psodos* Tr. do not at all deviate from the range of the family *Geometridae*, not even by presence of formations, which Poljanec (1899) and after him Wehrli (1921) and others call "innere Valven" mainly with a view to the function of these formations, but ontogenetically, as we shall show below not quite suitably. The formation of the base of this only organ, pairy only secondarily and under the influence of its function, in some species (e. g. *Torula quadrifaria* Sulz.), especially in *Orphne tenebraria* Esp. and related *Geometridae* of the genus *Gnophos* Tr. (also in *Gnophopsodos* Whli.), shows namely that it is ontogenetically a part of the ninth sternite, called juxta in the *Lepidoptera*. The juxta is preserved in a number of families as a triangular plate which is sometimes connected with the annellus through which the aedeagus penetrates. This plate is very striking, e. g. in some genera of the families *Tortricidae*, *Pyralidae* and *Gelechiidae*. But also many changes of this plate are known, which morphologically and functionally are reminiscent of the conditions in the genus *Psodos* Tr. These are especially the strikingly tongue-shaped formations of the genus *Pleurota* Hb., which ontogenetically are obviously of the same origin. The origin and connection of the "innere Valven" with the ninth sternite were thus correctly pointed out by Pierce (1914), who calls this formation "furca" in *Ps. coracina* Esp., as part of the juxta. More recently also Wehrli (1953) accepted this designation. The name "furca" is, however, in this connection also little suitable, as in anatomy this term is used for the special sclerites of the insect thorax. Thus Zander's (1903) view is certainly correct that these formations have as secondary appendices no direct connection with the valves, against which Wehrli (1921) polemised. Thus it has to be pointed out that though the furca attaches itself to the anterior base of the valves, it does so only by a narrow band, as we can see especially well in the species *Torula quadrifaria* Sulz., and *Orphne tenebraria* Esp., but it certainly is not directly connected with the valves. The connection with an ontogenetic origin of these shovel-shaped formations from the juxta are illustrated also generally by the state of the formation discussed in *O. tenebraria* Esp., i. e. in a species which, notwithstanding the generic difference, is yet obviously phylogenetically connected with the genus *Psodos* Tr. Though the form of the "furca" is here entirely different from that in *Psodos* Tr., much more primitive, yet its relation to the juxta is quite obvious. The further phylogenetic development of the furca and its specialisations ending with the origin of the "innere Valven" are further shown by the conditions in *Torula quadrifaria* Sulz., where especially the flatness of the basal, unpairy part indicates that it is a formation of the juxta, though "innere Valven" are here already distinctly developed. We find similarly in the Asian high-mountain genus *Gnophopsodos* Whli., from Tibet, which has also a relation to the genus *Gnophos* Tr., an indented juxta, whose two branches are, however, not yet separated or denticulated. This is a further proof that the modification described of the juxta as the sternal part of the ninth abdominal segment is in the gnophoid *Geometridae* a more general evolutionary tendency. The case of the branches of the juxta is most interesting from an evolutionary morphological and general biological point of view. It is a far-reaching and quite unusual ad-

aptation of the sternite to copulation purposes where the function calls forth such a profound change of the plate serving originally as a body cover that there arises from it a pairy organ not unsimilar to proper valves, that is to say to appendices derived from the gonopodes, from the original abdominal extremities. The term "innere Valven" is thus acceptable only in so far as it is taken functionally. As, however, in such cases we proceed rather from a homology than an analogy, we use for these appendices the term branches of the juxta.

The opinion of Poljanec that the two pairs of valves (i. e. the pair of branches of the juxta and the pair of valves) indicate the closeness of the genus *Psodos* Tr. to the *Orthoptera* (!) is of course quite erroneous. But in his endeavour to refute this incorrect opinion Wehrli (1921) vulgarises too much the term valve, by which we understand in the *Lepidoptera* always and unequivocally the gonopodes, i. e. formations which have in the close *Trichoptera* and *Mecopteroidea* still a coxal part. The characterisation of the different parts of the outer genitalia, given below, supplements and amplifies some points of view held up till now, especially as far as the taxonomic significance of their individual parts and appendices is concerned.

Uncus (Xth tergite): it is in most species of the genus *Psodos* Tr. pointedly beak-shaped, and, because of its uniformity, in essence so to say unspecific. Only in *Ps. alpinata* Scop. it is broadly rounded and specific.

Gnathos (Xth sternite): it is also in most species of the genus *Psodos* Tr. uniform, similar to the lower jaw of the beak. This formation is again strikingly specifically distinguished, i. e. broadly rounded, in *Ps. alpinata* Scop. *Torula quadrifaria* Sulz. has on the other hand a completely reduced gnathos and this together with the striking terminal narrowing of the valve and lack of the costal comb is quite certainly at least a subgeneric taxonomic quality, as the obvious closeness of this configuration to the conditions in *Orphne tenebraria* Esp. shows.

Tegumen (IXth tergite): it is of a triangular shape with differently deeply cut-out base, for instance with a shallowly cut-out one in *Ps. alpinata* Scop., a deeply cut-out in *Ps. noricana* Wgnr. But it is also subjected to considerable individual variability.

Saccus: this formation is the most variable part of the male organ. Though Wehrli pointed out this fact, yet in a number of cases he refers himself to the specificity of this organ. This did not prove fortunate so that the number of cases in which the shape of the saccus can have an (at least subordinate) taxonomic significance is in reality certainly smaller and has thus to be reduced.

Aedeagus: The configuration of the aedeagus carries few specific characters, but its general configuration is of a considerable importance for an understanding of the subgeneric phylogenetic relations. This fact, which is very important for a correct conception of the mutual relations between the different specific groups (sections) within the genus, was not appreciated by Wehrli so that his conception of these groups should be revised in many respects. This applies especially to the "*alticolaria* group", comprising species which have not much in common. *Ps. bentelii* Rtzr. and *Ps. noricana* Wgnr. form on the other hand obviously a natural group, as Wehrli

recognised correctly. But to these species we have certainly to place also *Ps. canaliculata* H o c h w. and the group of forms belonging to it, as indicated by the obvious similarity of their drawing, habit, and especially the configuration of the aedeagus, which by its s-shaped band excellently characterises this group of related species. The habit and configuration of the aedeagus indicate also a certain relation of *Ps. spitzi* R b l. to this group, as W e h r l i indicated, but without drawing from this any taxonomic conclusions. *Ps. alticola* M n. and the circle of forms close to it thus cannot be brought into a subgeneric connection with any of the other species of the genus *Psodos* T r., as even *Ps. wehrlii* V o r b r. has nothing in common with *Ps. alticola* M n. Also conditions in the species *Torula quadrifaria* S u l z. show the great subgeneric significance of the aedeagus. The configuration of the aedeagus, and especially the presence of spine-like cornuti, indicate the entirely isolated position of this species from the *Psodos* T r. proper or its obvious connection with the genus *Orphne* H b. with which it has in common also the reduction of the gnathos and the configuration of the valves. H ü b n e r's genus *Torula* for the species *quadrifaria* S u l z. has thus also for morphological reasons certainly a considerable justification.

Valves: The valves of the genus *Psodos* T r. are entire with a developed sacculus and a strongly chitinised costa which under the apex of the valve forms an elevation with a group of strong spines, and in certain species (i. e. *alticola*, *coracina*, *alpinata*, etc.) the apical end of the costa is differentiated into a club-shaped thickening bent into the valve and provided with strong spines (costal comb). The apex of the valve is auriculate, moderately cut-out in the slightly chitinised last third of the anterior margin. It is only in *Torula quadrifaria* S u l z. that the valve is distinguished more strikingly by its general habit from the valve of the other species by a distinct slimming towards the apex and the almost complete reduction of the costal comb. Thus it is very reminiscent of the valve of *Orphne tenebraria* E s p.

Branches of the juxta: This formation is specifically the most important of all parts of the male outer genitalia, as it enables us so to say at first glance to determine the species. It is obvious that the evolutionary agent which acted most on the specific differentiation in this genus manifested itself strongest by the morphological changes of this organ. This fact may be generalised for this genus in the sense that where we do not find essential differences in the shape of the branches of the juxta, we can hardly speak of good species. Abandoning this principle means to introduce chaos into the taxonomy of this genus, and to deny the evolutionary agents which acted in the differentiation of the different species, as it is an open declaration of the view that for each species in this genus we must introduce special and different taxonomic points of view which equals arbitrariness in systematics.

The female genitalia offer, as already said, very significant specific criteria, especially by the exceptional specialisation of the sternal region in the neighbourhood of the ostium bursae. W e h r l i pointed out correctly this very important fact, and used it also with considerable success. It applies of course also here that also the female genitalia are subjected to a certain variability, which of course cannot show itself to such an extent because of the lack of gonapophyses and gonopodes in the genital region.

As Wehrli's (1921) description of the female outer genitalia is rather detailed and adequate, we add only some supplementary remarks.

The bursa copulatrix can have taxonomically only a subordinate, i. e. supplementary significance for judging of the specificity. The signum is mostly strongly uniform; it is only in the species *Torula quadrifaria* Sulz. that its oval shape makes it possible unequivocally to identify the species, and this indicates of course just like a number of specificities already mentioned of this species that it is generically different from the *Psodos* Tr. proper. For the rest the signum is subjected, especially with regard to the extent and degree of chitination, interspecifically often to considerable deviations. The number of longitudinal lamellas ("Längslamellen") cannot be regarded as a specific criterium and the same applies to the general shape of the bursa, for both are strongly subjected to mechanical influences. The ductus bursae proper is usually only moderately chitinated and either narrow (when the general shape is spherical) or not essentially differentiated from the bursa (when the bursa is elongated bag-shaped). The proximal part of the ductus bursae usually widens in funnel-shape and is usually more strongly chitinated in the vagina, whose shape has rather a subgeneric significance. To the morphology of the circumostial formations we have only to add that the "vorderer Haftwulst" corresponds to the anterior part of the seventh sternite, whereas the "mittlerer Haftwulst", the "mamilläre Erhabenheiten" and the "freier Analwulst" with the "Uncuslücke" are the differentiated (mainly eight) sternite. The eight tergite is morphologically relatively uniform, but its measurements, especially the ratio of length to width, offer specific characters. The habit of the eight sternite, i. e. the circumostial region, is specific, but it is subjected on the other hand also to considerable individual deviations in the details, especially in the extent and shape of the "Haftwülste", as indeed the case of *Ps. alticolaria* M n. a. o., shows distinctly. The differences observed in the details, though significant, must therefore always be evaluated from the point of view of the existing variability so as not to lead to wrong conclusions.

Thus when we ask ourselves what morphological criteria we are to regard as specific in evaluating the specificity of the forms of the genus *Psodos* Tr., we arrive with Wehrli at the unequivocal conclusion that the branches of the juxta really offer objective specific distinguishing characters in the males, and taxonomically equivalent characters in the females are indubitably offered by the sternal formations in the neighbourhood of the ostium bursae. The other morphological characters have also an indubitable taxonomic significance, but have to be regarded as subordinate characters. In this connection we have to remark that the specific groups of the genus *Psodos* Tr. are thus quite distinctly objectively isolated from each other; phylogenetically they thus represent a group whose specific differentiation taking place in the Alps has in the main been terminated already for some time. Thus there can be no controversies about the species of the genus *Psodos* Tr. from a taxonomic point of view. But if we looked to the species of the genus *Psodos* Tr. for such objective criteria and if the result of our study is the conclusion that we find such objective morphological characters in the morphology of the outer genitalia, and when we thus come to the

opinion that the agent forming the species in this genus manifested itself objectively in the configuration of a certain body character, we have to respect such an opinion in judging every form of this genus. By the application of these points of view we thus arrive at the view that specificity cannot be attributed to the form "*chalybaeus*", for as will be shown below there are no objective morphological characters either in the male or in the female genitalia, or in the habitual characters by which this form would differ from "*alticolaria*". Wehrli partly acknowledges this fact, and this is all the more important as Zerny (1916) himself does not regard the form "*chalybaeus*" described by him as an independent species, certainly very rightly, as there exist absolutely indifferent individuals of a transition character between the two forms. The same is obvious not only from the expressed statement of Zerny: "Es kann daher von einer spezifischen Trennung keine Rede sein" (p. 114) but also from the citation given by Wehrli (1953) himself, and in which Zerny speaks expressly of forms whereas Wehrli speaks of independent species. To ascribe to this form specific independence is a subjective decision, which does not solve at all the real question. It is also of a subjective character in the same sense to ascribe specific independence to the Carpathian "*schwingenschussi*", which, notwithstanding certain deviations from the Alpine "*canaliculata*", cannot be objectively distinguished from it. The proof of this can most easily be given when we mix among preparations of male genitalia of the Carpathian "*schwingenschussi*" preparations of the Alpine "*canaliculata*" and then try to distinguish only morphologically the two forms from each other. Only by the study of a larger material do we arrive like Wehrli at the opinion that the asymmetry of the branches of the juxta is in the Carpathian form in most specimens smaller. But the females of both forms cannot be distinguished at all. Thus we have here obviously two geographical races of the same species. The same is also the case with *Ps. diószeghyi* Schmidt, which fits completely into the variation series of the species *Ps. coracina* Esp., when we study a larger material of different populations of this species throughout the area of its distribution. In this connection we wish to draw attention to the important fact that also within the populations of the same local form do we find in the configuration of the branches of the juxta often great differences within the range of the fluctuation variability, especially with regard to the spinosity. An example is *Ps. spitzi* Rbl. This species is an endemic form of Karavanks—it has thus the smallest known distribution of all species of the genus *Psodos* Tr.—and yet we find within this in the main one population living in a relatively small area distinct differences in the size and spinosity of the branches of the juxta. A similar case influenced still by geographical variability as a consequence of a greater geographical distribution can also be seen in the variability of the furcal branches of *Ps. coracina* Esp. It shows itself still more distinctly in the variability of the ostium bursae and its vicinity, which is unique also in the genus *Psodos* Tr., and which is obviously highly subject to the influence of the habitat. The geographical origin and partial morphological difference (of the subordinate characters) must thus be evaluated by the systematician always keeping in mind that a species is a collective of closely related organ-

isms, therefore a specific whole of living matter, whose individuals must, however, be able to react to similar yet in detail different conditions of the environment. The inability of an organism continuously to form and to react means that it is not able to live. When the systematist does not start from the assumption of variability he is always near mistakes.

Much clearer are those cases where it came to the description of new species while obviously ignoring the genus *Psodos* Tr. as a whole, so that such forms are then quite clear synonyms (e. g. *Ps. belzebuth* Praviel, *Ps. perlinii* Trti.).

We thus uphold consistently the view that the species is a form of existence of living matter, i. e. an objective reality of the living matter, that it represents a qualitative biological whole specifically completely differentiated morphologically and physiologically from other analogous qualitative wholes. The negation of this view, and especially the fundamental view of the species as of individual populations distinguished from each other by the number of average variants of an assemblage of characters whose plus and minus variants overlap however, so that no objective limit exists between them, leads the systematist astray. As an example may be given the impasse in which some systematists—narrow specialists—found themselves in the final evaluation of very laboriously collected material methodically often perfectly and uncontroversially and meritoriously analysed. The subjective conception as a result of an excessive narrowing of the problem leads them usually to the raising of populations to subspecies, of subspecies to species, of species to genera, or to the introduction of new taxonomic categories. The general acceptance of such views would gradually lead to the impossibility of any general recognition and determination of species, as it makes them dependent on the subjective opinion of the individual, and thus will manifest itself rather as an obscuring than as a solution of the question of what a species is. The acceptance of a specific independence of the forms *chalybaeus*, *schwingenschussi*, *diószeghyi*, *belzebuth* etc., which are not distinguished by any objective differences from species described already earlier, would necessarily lead to the raising of all forms, which have quite distinct differences in the shape of the branches of the juxta, to separate genera, and this would be absurd. Against such a conception speaks scientific taxonomy based on the consistent demand made by objective specific characters and supported also by zoogeographical and historical facts, therefore starting from evolutionary points of view.

IV. On the Question of the Genesis and Differentiation of the genus *Psodos* Tr.

As we can evaluate the conclusions on the differentiation of recent species with potential accuracy at most from the younger Tertiary, we can express ourselves also on the origin of the genus *Psodos* Tr. only with a certain probability. The present state of historical zoogeography admits in the main three working hypotheses on the origin of the genus *Psodos* Tr.

1. The first hypothesis starts from the assumption that the genus *Psodos* Tr. represents by its origin a group of Alpine origin, that we have thus here

species which differentiated essentially in the Alps after their upfolding. Their ancestor thus must have been a tropical or subtropical form which adapted itself to the mountain climate and gradually differentiated into the recent species.

2. The second hypothesis starts from the assumption that the genus *Psodos* Tr. is essentially of a northern origin as might be indicated by the present distribution of the forms of the coracina-group in the Eurasian tundra. *Ps. daisetsuzana* described by Matsumura from Japan certainly demands a further study, as the identification of the species is made very difficult by the insufficiency of the description and the confused geographical knowledge of the author (Cp. on this form also Wehrli 1953).

But according to this hypothesis the settlement of the high mountains of Central Europe by the genus *Psodos* Tr. would be historically relatively very late and certainly too short view of the present relatively rich and deep differentiation of this genus, quite apart from a number of further drawbacks of this hypothesis, which it would be difficult to account for.

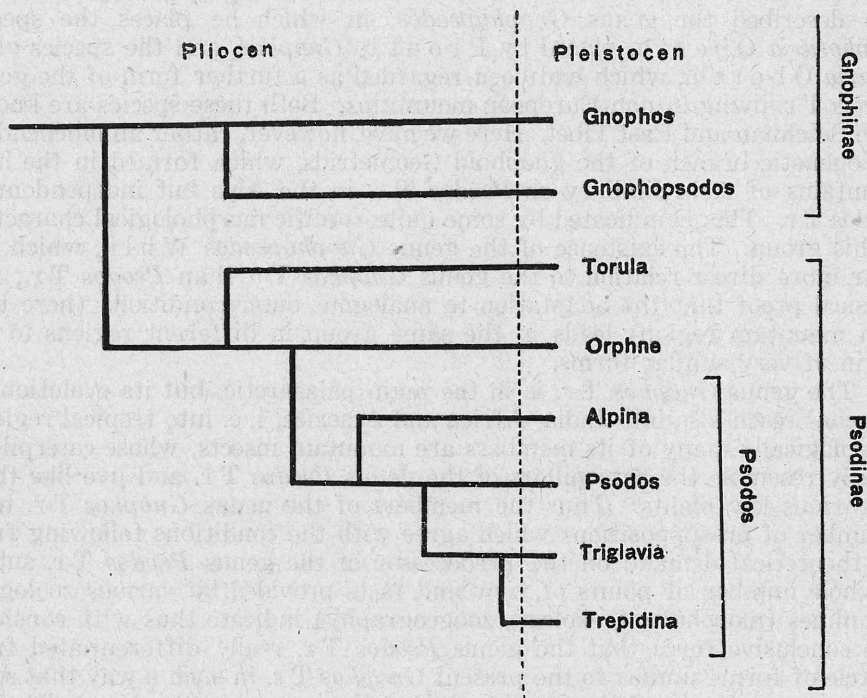
3. The third hypothesis starts from the assumption that the ancestors of the genus *Psodos* Tr. derive from the Tertiary Illyrian island in the area of present Dalmatia, whence after a connection had been effected it could penetrate into the Alps.

The results of our investigation lead us to uphold the first of these hypotheses, which can be supported by the greatest number of sufficiently heterogeneous facts:

The species of the genus *Psodos* Tr. are restricted to the European high mountains, where the greatest number of species is known from the Alps, where besides there live some strongly isolated, therefore obviously rather old, endemic species and forms (i. e. *spitzi* Rbl., *wehrlii* V or bro dt, etc.). The former view that *Psodos* Tr. lives also in the Asian high mountains has been refuted, for it has been shown that we have here an other generic group (*Gnophopsodos* Whli.). The other Asian species placed here up till now require still a solution (*Ps. daisetsuzana* Mats.). The Alpine species are most concentrated in the region of the high Swiss Alps, where we find with the exception of the species *Ps. spitzi* Rbl. practically all known species of *Psodos* Tr., while in the direction towards the margin of the Alpine area (e. g. in the Maritime Alps), where the species radiate to, locality morphs formed under changed conditions are living. The same conditions we observe also in the total area of the genus *Psodos* Tr., where the Alps are the centre with the greatest number of species. The fauna of the genus *Psodos* Tr. is in the other high mountain and mountain regions of the wider Central European area (the Pyrenees, Sudetes, Carpathians) specifically considerably poorer. Very important is the fact that none of these mountains has any more markedly differentiated endemic species. All species of the genus *Psodos* Tr. of the non-Alpine mountains have a very close affinity to Alpine species, from which they usually differ only by subordinate characters (vicariating forms) so that the differences throughout do not exceed the limits of subspecies (*canaliculata* — *schwingenschussi*, *noricana* — *carpathica*, *bentelii* — *retyetzatensis*, *coracina* — *diószeghyi*, *quadrifaria* — *pyrenaea*, *bentelii* — *panticosea*, etc.). The *Psodos*-fauna in the other European mountains is thus

in its present forms of relatively recent origin, for its stay there apparently does not reach back beyond the Würm glaciation.

The group of the forms of the species *coracina*, which penetrated the North European tundra (Scotland, Scandinavia) and thence far to the East whence two forms, obviously close to and apparently not more than subspecifically different from *Ps. coracina* E s p., are known from the Sajon Mountains, is apparently at the same stage of differentiation. Conditions farther



1. The theoretical phylogenetical systematics of *Psodinae*.

to the East are still unknown because the huge tundra of Western Asia has still been little investigated; also the Japanese "Psodoid form" described by Matsumura cannot be evaluated unequivocally, especially so long as the relations between the genera *Psodos* T r. and *Gnophos* T r. in Asia are not completely elucidated.

Another important fact is that the genus *Psodos* T r. is not entirely isolated phylogenetically; the close genus *Torula* H b. attaches itself with the species *quadrifaria* quite obviously to another explicitly high-mountain Geometrid, *Orphne* (*Dasydia*) *tenebraria* E s p. which lives in the Alps, the Pyrenees and the Apennines at considerable altitudes (above 3000 m.), and has a visible relation to the piedmont genus *Gnophos* T r. For the relations between *T. quadrifaria* Sulz. and *O. tenebraria* E s p. speak, as already

said, e. g. the configuration of the aedeagus, especially the presence of needle-like cornuti in both species, also the already mentioned similarity of the branches of the juxta, whose shape in *T. quadrifaria* Sulz. is a connecting link between the *Psodos* Tr. proper and the genus *Orphne* Hb., further the reduction of the gnathos and the shape of the valves. The genus *Orphne* Hb. attaches itself (cp. Prout in Seitz) to some forms of the extensive Geometrid genus *Gnophos* Tr. The phylogenetic affinity between the genera *Psodos* Tr. and *Gnophos* Tr. has been also recently emphasised by Whli, who described the genus *Gnophopsodos*, in which he places the species *gnophosaria* Oberth. placed by Prout to *Gnophos*, and the species *altissimaria* Oberth., which had been regarded as a further form of the genus *Psodos* Tr. living in non-European mountains. Both these species are known from Setchuan and East Tibet. Here we have, however, rather an independent phylogenetic branch of the gnophoid Geometrids, which formed in the high mountains of Asia similarly as *Psodos* Tr. in the Alps but independent of *Psodos* Tr. This is indicated by some quite specific morphological characters of this group. The existence of the genus *Gnophopsodos* Whli., which has a far more direct relation to the genus *Gnophos* Tr. than *Psodos* Tr., is a classical proof that the adaptation to analogous outer conditions (here to a high mountain region) leads in the same group in different regions to the origin of very similar forms.

The genus *Gnophos* Tr. is in the main palaearctic, but its evolutionary branches reach also into India, Africa and America, i. e. into tropical regions. Chorologically many of its members are mountain insects, whose caterpillars greatly resemble the caterpillars of the genus *Psodos* Tr. and live like them on various low plants. Thus the members of the genus *Gnophos* Tr. have a number of presuppositions which agree with the conditions following from the theoretical demand on the predecessor of the genus *Psodos* Tr. sub 1. A whole number of points of view and facts provided by various zoological disciplines (morphology, ecology, zoogeography) indicate thus with considerable conclusive force that the genus *Psodos* Tr. really differentiated from a circle of forms similar to the present *Gnophos* Tr. in such a way that some of the parent forms of this group adapted themselves in the (late) Tertiary to the mountain climate of the upfolded Alps, where they further differentiated themselves in the interglacial periods into the present species *Psodos* Tr. The climatic upheavels of the Quaternary accompanied by the glaciation of the Alps pushed these mountain species into lower regions, in which they spread further during the ice ages under the conditions of the Arctic tundra steppe so that with the retreating glacier they not only returned to the Alps, but also to the other high mountain systems of Europe whose climatic conditions allowed them this, and one species (*Ps. coracina* Esp.) penetrated into the North European and North Asian tundra. Beirne (1947) who tried to study very exactly the history of the settlement of the British Isles by the Lepidoptera fauna in the last glacial period (Würm) regards *Ps. coracina* Esp. in the Scotch tundra as dating from the first Würm stadial (i. e. from about more than 100,000 years ago). *Ps. coracina* Esp. is thus a form of Alpine origin, whereas its present boreo-alpine character (as far as we consider its disjunctive area in Northern Europe) is obviously second-

ary. It is therefore just the contrary of most of the boreo-alpine fauna, which is mostly of a Northern origin and thus secondary in the European mountains. As far as *Psodos tundra* Whli. and *sajana* Whli. from the Sajan Mountains are concerned it will be necessary in evaluating their specific independence also to consider their possible age, which hardly reaches farther back then to the beginning of the Würm, and also their morphological characters, as Wehrli and especially Schmidt reports on them indicate rather their subspecific relations to *Ps. coracina* Es p.

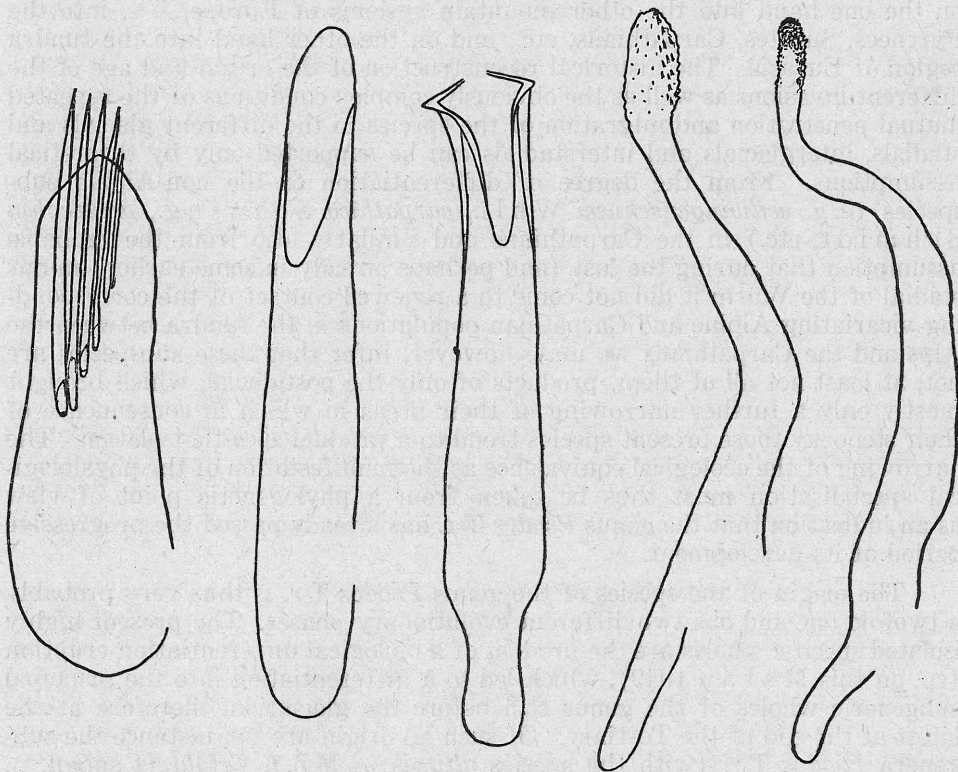
The other two hypotheses mentioned here have only a very slight foundation, and we shall therefore not deal further with them. The genus *Psodos* Tr. thus represents phylogenetically a very interesting group whose study enriches very essentially our views on the origin of insect species in mountain regions.

From a phylogenetic point of view the genus *Psodos* Tr. is thus a group of insects whose principal specific wholes certainly were sufficiently differentiated and isolated in the Alpine region at the latest to the beginning of the Pleistocene. The ice ages caused the penetration of these specific groups on the one hand into the other mountain systems of Europe, i. e. into the Pyrenees, Sudetes, Carpathians, etc., and on the other hand into the tundra region of Eurasia. The historical reconstruction of the origin and age of the different invasions as well as the obviously complex conditions of the repeated mutual penetration and migration of the species in the different glacials and stadials, interglacials and interstadials can be supported only by theoretical assumptions. From the degree of differentiation of the non-Alpine subspecies (e. g. *schwingenschussi* Whli., *carpathica* Schwing., *diószeghyi* Schmidt, etc.) in the Carpathians and similarly also from the probable assumption that during the last (and perhaps already in some earlier) minor stadial of the Würm it did not come to a renewed contact of the corresponding vicariating Alpine and Carpathian populations in the tundra between the Alps and the Carpathians we may, however, infer that these subspecies are not, at least not all of them, products of only the postglacial, which brought mostly only a further narrowing of their areas in which in consequence of their stenoeky these present species trend to a gradual specific isolation. The narrowing of the ecological equivalence as the manifestation of the physiological specialisation must thus be taken from a phylogenetic point of view as an indication that the genus *Psodos* Tr. has already passed the progressive period of its development.

The origin of the species of the genus *Psodos* Tr. is thus very probably a twofold one and has two different evolutionary phases. The present highly isolated specific wholes are the product of a biological differentiation eruption (cp. on this Mařan 1949), which led to a differentiation into the principal subgeneric wholes of the genus still before the glaciation, therefore at the latest at the end of the Tertiary. Of such an origin are for instance the subgenera *Psodos* Tr. (with the species *alticolaria* Mn.), *Triglavia* subgn. n. (*spitzi* Rbl.), *Trepidina* subgn. n. (*canaliculata* Hochw., *noricana* Wagner, *bentelii* Rtzr.), etc. Other forms (species) are distinctly of a younger origin, and arose apparently in a geographical way as the probable product

of areal isolation of the populations in the interglacials and interstadials of the Quaternary (e. g. *noricana*—*bentelii*, *alpinata*—*wehrlii*), for though specifically defined they show an obvious evolutionary connection and a common evolutionary basis. This process still continues under the present areal isolation of the different species and populations in the non-Alpine mountains.

In the Carpathian system the following species of the genus *Psodos* s. l. have thus been ascertained up till now: *quadrifaria*, *alpinata*, *noricana*, *canaliculata*, *coracina* and *bentelii*, which form there endemic geographical forms which may be evaluated taxonomically as subspecies arising in areal isolation, and which are at different stages of gradual differentiation into independent species.



2. Typi of aedeagus in the single groups of *Psodinæ*; from left to right; genus *Torula* (very closely related with *Orphne*), subgenus *Psodos* s. str., subgn. *Alpina*, subgn. *Trepidina*, subgn. *Triglavia*.

V. Systematic Part.

In this part are summarised the results of the investigation of the genus *Psodos* T r. after the material which was at our disposal and as far as they bring new points of view. The other data on the systematic of the psodoid *Geometridae* are contained in the literature given and were excerpted only as far as the completeness and clearness of this paper required it.

Genus **Orphne** Hübner 1826 (= *Dasydia* Guenée 1857).

The genus *Orphne* H b. shows in the exterior morphology (size, character of the pattern, configuration of the palpi, of the outer genitalia, habitus of the caterpillar, ecology, etc.) a number of characters which characterise it from the point of view of phylogenetic systematics as a pronounced transition from synthesising the characters of the genus *Psodos* s. l. and *Gnophos* s. l. This is indicated most markedly especially by the configuration of some parts of the male genitalia. They are especially the spine shaped cornuti of the aedeagus, which we find not only in the close genus *Torula* H b. but also in *Gnophos* T r. proper (e. g. *Gn. obscuraria* H b.), and especially the character of the branches of the juxta, in which the whole evolutionary descendance from the simple conditions in *Gn. myrtillata* T h n b g. via *Gn. obscuraria* H b., *Orphne* H b., *Torula* H b. to the genus *Psodos* T r. proper can be demonstrated. The furcal shovels show besides within the genus *Orphne* H b. a quite exceptional morphological variability. Also from the shape of the valve it is obvious that we have a morphological preliminary stage of the more specialised conditions in the genus *Psodos* T r., whereas the reduction of the gnathos which it shares with the closely related genus *Torula* H b. is rather a convergence (apomorphic character in the sense of Hennig, 1953; Kritische Bemerkungen zum phyllogenetischen System der Insekten; Beitr. zur Entomologie, 3: 1-85, Berlin). Though the systematic-phylogenetic, evolutionary and zoogeographical relations between the genera *Gnophos*, *Orphne*, *Torula*, *Psodos* and *Gnophopsodos* are not yet quite unequivocally solved, it is nevertheless clear that the road leads from *Gnophos* via *Orphne* and *Torula* to *Psodos* T r. Thus the genus *Orphne* H b. shows itself as a preliminary stage of the *Psodos* T r. proper, whereas *Gnophopsodos* Whli. is an independent evolutionary branch which is closely and more immediately connected with *Gnophos* T r. than with *Psodos* T r.

Orphne tenebraria Esper 1806.

O. tenebraria E s p. is a habitually and morphologically very plastic species, as is indicated by the number of individual and habitat forms (e. g. *wockearia* S t d g r., *septaria* G n., *innuptaria* H. - S.).

It occurs in the highest layers of the Alps, the Pyrenees and the Appennines, at altitudes approximately from 1600 to high above 3000 m. (imago and caterpillar). Trophically it is a strongly polyphagous species, as is indicated by a selection made at random of host plants: *Saxifraga caesia*, *Saxifraga oppositifolia*, *Silene acaulis*, *Ranunculus glacialis* and other herbaceous

plants of the high mountains. *O. tenebraria* Es p. is far distributed in its area. It occurs, however, mostly unabondantly and only here and there in a greater number. From the present known geographical distribution and from the relations to the genera *Gnophos* Tr. and *Psodos* Tr. it follows that it is genetically an Alpine endemite which because of its stenoeky penetrated only into the highest layers of the neighbouring high mountains, which it did in consequence of the glacial events.

Material studied:

Styria-Hochschwab 1 ♂, 26. 7. 11 (lgt. Dr. Schima); Styria-Hochschwab 2 ♂♂; Nordtirol 2 ♂♂, 1 ♀, 17. 7. 38; Groß Glockner 2 ♂♂; Tirol: Stilfser Joch 1 ♂; Ortler Gebiet 2200-2600 m ♂♀ (lgt. Pietzsch); Zillertaler Alpen 1 ♂; Tirol-Oetztal 2900 m, 1 ♂, 10. 8. 27 (lgt. Klimesch); Gleiwitzer Hütte 2200 m, 1 ♂, 24. 7. 25; Triglav 2500 m, 1 ♂, 7. 12. (lgt. Spitz), 2400 m, 2 ♂♂, 7. 29 (lgt. Bubacek); Helv.—Interlaken Umg. 1 ♂, Davos ♂♀, Umg. von Zermatt 1 ♂, 29. 7. 30 (lgt. Soffner); Stelvio 2500 m 3 ♂♂, sine loc. 15 ♂♂, 2 ♀♀.

Genus *Torula* Hübner 1826.

Torula quadrifaria Sulzer 1776.

Morphology and systematic position: Distinctly distinguished from the genus *Psodos* Tr. by the configuration of the aedeagus (in which are cornuti), by the reduction of gnathos, the costal comb of the valve, and the general character of the features of the first and second order (yellow spots on the wings). Monotypical genus.

Geographical distribution: Alps, Vosges (loc. typ.), Swiss Jura, Pyrenees, Sudetes and Carpathians, at altitudes above sea level from 900 (southern Bavaria) to 2600 m. (Glocknergebiet). It is thus characterised as an alpine form by a rather considerable hypsometrical valence.

Variability: In its area of distribution this species is characterised by a strong variability due on the one hand to the geographical isolation of some populations (ssp. *pyrenaea* O b e r t h.) and on the other hand to the strong hypsometrical valence of the species (in the Alpine-Bavarian-Carpathian region). Wehrli (1953) pointed out correctly that var. *sudetica* Sterneck does not differ at all in essence from the populations of the Swiss Jura and the Vosges, as it appears also from the figurings of Sulzer and Culot that these populations too have a broad yellowish band. Though the populations from the Austrian Alps, which Sterneck used for comparision in the description of var. *sudetica*, have a somewhat narrower yellowish band, the study of a larger material shows that the width of the band is strongly conditioned by the altitude above sea level of the locality, and thus it falls into the fluctuation variability. This state is shown e. g. by the conditions in the Slovak Carpathians whose populations have a very broad variability of the yellowish band so that beside specimens reminiscent of the form from the Sudetes there occur equally often also specimens with a much narrower band as we find it in the populations from the high layers of the Austrian Alps. A still more marked indication that the width of the yellow band is conditioned by altitude is that in the Alpine area *T. quadrifaria* Sulz. de-

velops a characteristic habitat morph with strikingly narrow yellow bands on the wings, and does so just at the greatest altitudes of the distribution of the species—*f. stenotaenia* Schwing. (loc. typ.: Glocknergebiet).

Ssp. *pyrenaea* Oberthür 1913 (loc. typ.: Pyrenees) is a very striking geographical form of the species, chiefly by its stateliness. The yellow bands are according to the description relatively narrow, so that the black border of the outer margin is strikingly broad. One of our specimens (Picada, 21. 7. 1908, ♂) has, however, broad bands, especially on the posterior wings. In the outer genitalia there is no essential difference from the nominate form. The ssp. *pyrenaea* Oberth. lives in the Pyrenees at an altitude of about 1500 m. a. s. l.

The subspecific differentiation thus indicates that the populations of *T. quadrifaria* Sulz. in the wider Central European region (Alpino-Bavarian and Sudeto-Carpathian system) belong in essence to one subspecies of the species. This is certainly to a large extent the result of a mutual mixing of the populations until fairly recent times, for their mutual isolation seems to be not older than 20,000 years. In contradistinction to this the considerable differentiation of ssp. *pyrenaea* Oberth. indicates that the populations there have been isolated in the Pyrenees for already a much longer time. The history of the European glaciation lets us surmise that the Alpine-Sudetic-Carpathian forms, as far as a taxonomic valence can be attributed to them, are apparently the product of an only postglacial isolation, whereas ssp. *pyrenaea* Oberth. is certainly at least of a lower Würm age.

Ecology: Ecologically *T. quadrifaria* Sulz. is a species of high mountain meadows with a fresh and rich vegetation, in which the imago hides. In the morning hours it uses also short sunshine for flying out; in the later hours of the day it flies rather only when disturbed. Often it occurs in a considerable number on smaller surfaces. Dännehl (1928) records that some specimens were caught also by light and one specimen even on bait. The author remarks correctly that it is certainly a chance occurrence. The caterpillars are polyphagous, for details on their mode of life see Vobrůdt (1914) and Hoffmann-Klos (1914).

In the Tatra *T. quadrifaria* Sulz. is flying very often common with *Ps. alpinata* Scop. and *Ps. canaliculata schwingenschussi* Whli., indeed, on many biotops the hypsometrical border between these three species cannot be fixed. Despite it is evident that *T. quadrifaria* Sulz. is the species of the mountain meadows of the plough-tail zone. This is demonstrated typically in the occurrence of this species in Belanské Tatry, for example. The ecological parallel with *Ps. alpinata* Scop. leads also to the hybridisation (hybr. *müller-rutzi* Whli. 1920). On the Pietros in the region of Hoverla Schwarz (1934) caught *T. quadrifaria* Sulz. on growth of *Rhododendron*.

In Czechoslovakia the following regions of occurrence are known: Krkonoše; Liptovské Hole; Nízke, Vysoké and Belanské Tatry; Fatra.

Material studied:

Ter.—Rotmoostal 3 ♂♂, 1 ♀, 18. 7. 28; Ter.—Seiser Alpe 1 ♂; Kärnten—Glockner-Gebiet 7 ♂♂; Schneeberg 3 ♂♂, 13. 6. 31; Groß-Glockner 2300 m., 1 ♂, 26. 7. 25; Styria—Hochschwab 1 ♂; Salisb.—Imbachhorn 2100 m., 6 ♂♂, 1 ♀; Schafberg 1700 m., 1 ♂, 14. 7. 23; Albulapaß 2300 m., 1 ♂,

14. 7. 21; Hirzbachalm 1 ♂, 21. 7. 23; Helv.—Zermatt 2 ♂♂, 8. 7. 35; Berner Oberl.—Grünwald 1 ♀; Carniola—Crna prst 2 ♂♂, 16. 7. 29; Feistritz 1 ♂, 29. 6. 09; Krkonoše—Studničná hora 1200 m., Sněžka 1500-1600 m., Obří Důl, Liščí hora, etc., 50 ♂♂, 12 ♀♀; Malá Fatra—Chleb 1300 m., 1 ♂, 5. 7. 33; Nízké Tatry: Dumbier 2000 m., 1 ♂, 28. 7. 51; Rovná Hora 3 ♂♂, 14. 7. 47; Prašivá 6 ♂♂; Liptovské Hole: Smutné Sedlo 1900 m., 3 ♂♂; Vysoké Tatry: Važecká dolina 1500-1700 m., 5 ♂♂; Furkotská dolina 1600-1800 m., 8 ♂♂, 5 ♀♀; Skok 6 ♂♂, 1 ♀; Sedielko 2 ♂♂, 3 ♀♀; Malá Studená dolina 2000 m., 6 ♂♂; Kopa 1 ♂; Kvačanská dolina 2 ♂♂, 1 ♀; Belanské Tatry: Rigliany potok 1500 m., 2 ♂♂, 1 ♀; Protěž, 1800 m., 2 ♂♂; Hlúpý 2000 m., 6 ♂♂; Košičany 2000 m., 1 ♂; Carp. or.—Hoverla 1 ♂; sine loc. 15 ♂♂, 5 ♀♀.

F. stoenotaenia Sch wingenschuss: 1 ♀ sine loc. (coll. Nickerl).

Ssp. pyrenaea O b e r t h.: Picada 1♂, 21. 7. 08; Gèdre 1 ♂, 2. 7. 24.

Genus *Psodos* T r e i s c h k e 1828.

Morphology and systematic position: The generically typical characters were given in modern time e. g. by P r o u t (1915), W e h r l i (1921, 1953), O b e r t h ü r (1913), C u l o t (1919-20), etc.

W e h r l i's (1953) generic diagnosis is quite confused in the description of the genitalia, as it is not clear whether it is taken generally (Aedeagus ohne Kornuti) or whether it applies only to the species *quadrifaria* S u l z., as seems indicated by the remark "...Gnathos fehlt...", and especially by the sentence which begins with the words "Beim Typus...". It is thus obvious that the species *quadrifaria* is generically different from *Psodos* T r., as shown by the reduction of the gnathos and the presence of cornuti, and by the general habitus of the species.

We have not been able to ascertain whether H ü b n e r's genus *Torula* is older than T r e i t s c h k e's *Psodos*. As it is, however, possible and because the species *quadrifaria* is the genotype of *Psodos*, the name *Psodos* T r. would be a synonym of *Torula* H b. But *Psodos* is certainly a nomen conservandum, and therefore we propose as genotype for *Psodos* T r. the species *Ps. alticola* M n.

The genus *Psodos* T r. represents obviously a strongly specialised (autapomorphic in the sense of H e n n i g, l. c.) group of the gnophoid branch of the family *Geometridae*. The genus obviously divides into several groups, which comprise the older species of the narrower Alpine region arising by specific differentiation soon after the origin of the genus. Other species are obviously of a younger origin and arose apparently by the immediate influence of the exterior conditions.

W e h r l i's (1921) division of the genus into sections is based on a purely typological point of view, which does little justice to the phylogenetic relations. Our own division is certainly not final, but it is indubitably better in keeping with the real conditions and the new evolutionary findings.

1. Subgenus *Psodos Treitschke*.Subgenotype: *Ps. alticolaria* Mann.

This monotypical subgenus contains one species—*Ps. alticolaria* Mn., restricted in its distribution to the highest layers of the Alps and Pyrenees (loc. typ.: Gamsgrube—Großglocknergebiet).

The fundamental type of the pattern in common to all members of the genus is preserved; typical for this species is the optical lustre of the front and reverse of the wings. Typical for the pattern are the striking shiny wavy lines at the outer margin of the reverse of the wings. Only *Ps. spitzi* Rbl. has a similar pattern, but this species seems to be without any direct closer relations to *Ps. alticolaria* Mn. (convergence). The outer genitalia are very characteristic. Aedeagus straight, apex almost rounded and smooth. Branches of the juxta relatively small and strongly variable. Costal comb strongly developed. Saccus glottal, also variable. Bursa copulatrix ovoid oval with a big signum. Sclerite of the "vorderer Haftwulst" strongly variable and morphologically unspecific.

Psodos alticolaria Mann 1853.

In its area of the distribution this species forms geographical, local and individual forms. The question of the taxonomic value of the form *chalybaeus* Zerny 1916 deserves the greatest attention. In our opinion it is obviously a local morph (not a good species as generally said), which apart from its classical locality (Stilfserjoch im Ortler-Gebiet) occurs still in Graubündner Alpen, Walliser and Waadter Alpen. Recently the occurrence of f. *chalybaeus* Zerny has been ascertained also in the French Alps so that it has a greater distribution than had been assumed at first (see also Wehrli 1953). Thus the areas of the two forms are not sharply isolated from each other.

In the anatomy of the male and female outer genitalia, which show in this genus so extraordinarily striking specific characters, the forms "*alticolaria*" and "*chalybaeus*" cannot be objectively distinguished at all from each other. In the configuration of the juxtal branches and "vorderer Haftwulst" we find on the contrary among the typical "*alticolaria*" a much greater variability than in "*chalybaeus*." But even in the habitual characters, in which the greatest difference between the two forms was seen, we do not find any fundamental qualitative difference, but only a different expressiveness of the wavy drawing of the wings. Also this drawing has in some individuals a pronouncedly indifferent character. As Zerny (1916) himself states (last paragraph on p. 114) that the form living on the Stilfser Joch does not differ specifically from *Ps. alticolaria* Mn. from the Gamsgrube (Großglocknergebiet), the later separation of these forms as good species must be pronounced unfounded. The differences given by Vorbrodt (1918) and Wehrli (1921) are entirely unspecific. The form "*chalybaeus*" is thus obviously a local morph, as is proved also by the unconnected area. This fact is also confirmed by the impossibility of distinguishing the caterpillars of the two forms (Ripper 1927, p. 114).

Variability: Two geographical races have been described up till now:

Ssp. gedrensis R o n d o u 1806-08.

Pyrenean form, which we do not know from autopsy; description apud O b e r t h ü r (1913, p. 324), W e h r l i (1921, 1953), a. o.

Ssp. frigidata V o r b r o d t 1919.

Subspecies described from the Swiss Alps, which according to the last opinion of A u b e r t (1953) differs only insignificantly from the nominate form. Thus a synonym.

The species is characterised by a considerable individual variability in the pattern as well as in genitalia. For the list of the (sometimes problematical) individual forms see apud S c h w i n g e n s c h u s s (1923) and W e h r l i (1953).

Material studied:

Ps. alticolaria M n.: Sonnblick-Gebiet, 24. 7. 36, 5 ex. (coll. Mus. Brno); Zentral-Alpen: Gemsgrube 2560-2600 m., 28. 7.-6. 8., 10 ex. (coll. Mus. Praha); sine loc. 2 ex. (coll. Mus. Praha).

F. chalybaeus Z e r n y: Ortler-Gebiet, 19. 7. 31, 2 ex. (coll. Mus. Praha); Ortler-Gebiet 2200-2600 m., 30. 7. 27 (lgt. W. Pietzsch, coll. Dr. Schulte, Kiel); Stilsfer Joch 2500 m., 4 ex. (coll. Staatssamml. München); Piz Umbrail, 3 ex. (lgt. Dr. Patzelt, coll. Mus. Praha); sine loc. 3 ex. (coll. Mus. Praha).

2. Subgenus *Triglavia* n. subgn.

Subgenotype: *Triglavia spitzi* R e b e l 1906.

Also the subgenus *Triglavia* n. is monotypical. The only species—*Triglavia spitzi* R b l.— is an isolated species, which of all the members of the genus *Psodos* T r. has the smallest area of distribution, occurring only on the Triglav, in the Karavanks, Kreuzberg and at Fassa.

The wavy drawing is typical by the presence of metallic blue-green shiny scales. On the reverse of the wings it is reminiscent of the drawing of the species *Ps. alticolaria* M n., though this seems to be due to convergence. The drawing on the front approaches the group of species of the following subgenus.

Aedeagus subapically inflected, costal comb reduced. The circumstrial sclerites for around the ostium bursae a plate of one piece; this is an entirely isolated case in the genus *Psodos* T r.

T. spitzi R b l. is a species very characteristic by the drawing, the configuration of the genitalia and the geographical distribution. Its occurrence is known up till now only in the Karavanks, where it is not abundant. This species belongs to the most notable elements of the European fauna.

Material studied:

Carniolia—Triglav 2400-2800 m., 6. 8. 29, 5 ex. (lgt. Bubaček et Kornič, coll. Mus. Praha et Dr. Schulte, Kiel).

W e h r l i (1953) placed in the close affinity of *T. spitzi* R b l. also *Ps. perlinii* T r t i. But T u r a t i's original description does not really elucidate what this form really is.

3. Subgenus *Trepidina* n. subgn.

Subgenotypus: *Trepidina canaliculata* Hochw.

This subgenus embraces the species of a comparatively young branch of the genus *Psodos* Tr., which contains highly specialised members of the genus.

The drawings are characteristic by the expressiveness of the wavy lines, the very close scales of the wings without any transparency; often slightly greenish or blue-green tones appear in the basic colour. Drawings and basic coloration are characterised by a considerable variability.

The aedeagus characterises this group quite unequivocally by the s-shaped bend and the scaly structure of the apex. The branches of the juxta attain their maximum measurements in the members of this subgenus. Ductus bursae often infundibuliform enlarged. The "mamilläre Erhabenheiten" just like the juxtal branches may be asymmetrical. All species of this subgenus are distributed also outside the Alpine region.

Trepidina canaliculata Hochenwarth 1785.

Syn.: *Psodos schwingenschussi* Whli., n. syn.

This species has in the genus *Psodos* Tr. a quite exceptional position because of the asymmetrical configuration of the juxtal branches, to which corresponds the asymmetry of the circumostial sclerites in the females. Thus also the Carpathian form *schwingenschussi* Whli. belongs quite unequivocally to this species. The differences recorded by Wehrli (1921) are not at all sufficient to attribute specific independence to this form. The main difference, which Wehrli sees in the mutual relation of the asymmetry of the juxtal branches, is only a quantitative variation of the same specific qualitative character. The extreme cases of the Alpine and Carpathian subspecies cannot be distinguished at all objectively from each other. The female organs are in both these populations completely identical. Thus the differences concern only subordinate characters, and also zoogeographically the Carpathian subspecies is obviously a derivation from the Alpine form. *T. canaliculata* Hochw. is characterised by a considerable geographical variability. The species has even in restricted localities a considerable tendency towards subspecific differentiation.

The Alpine form comprises obviously heterogenous populations whose uniform characterisation cannot be given. Often there occur here also more or less marked individual forms. The valence of a number of forms from here is, however, taxonomically doubtful.

Ssp. *schwingenschussi* Wehrli 1919 is the geographical form of the species in the Carpathian region (mountain vicariate); in this sense Brčák (1951) has to be corrected, according to whom it would be an endemic separate species of the Carpathians. This subspecies is characterised by its green-blue basic coloration without special changes in the pattern. The asymmetry of the juxtal branches is in most less marked than in the Alpine population. But this fact can be demonstrated only with the help of a rather large material so that the individual determination of ssp. *schwingenschussi* Whli.

after the genitalia is not possible. Also in the Carpathians a very strong tendency towards the formation of separate defined populations in rather narrow areas manifests itself, so that even under this point of view ssp. *schwingenschussi* Whli. cannot be characterised separately. Thus e. g. the population from the Belanské Tatry differs distinctly from specimens from the Kopa-Sedlo and the Květnica in Vysoké Tatry. Also the specimens from the Polish side of the Tatra (loc.: Skrajna Turnia) are distinctly differentiated from the other populations of these mountains. These locality morphs do not deserve in our opinion a special name as in the study of a large material it becomes evident that they fall within the general variability of the ssp. *schwingenschussi* Whli. This subspecies inhabits the higher layers (around 2000 m.), rocky biotops but with sufficient vegetation. The imagos appear in sunshine mainly in the morning hours and fly rather rapidly. The caterpillars hidden during the day under stones, where they pupate, live on herbaceous mountain plants.

In Czechoslovakia *T. canaliculata schwingenschussi* Whli. occurs only in the Liptovské Hole, Vysoké and Belanské Tatry.

T. canaliculata schwingenschussi Whli. is—in comparison with *T. quadri-faria* Sulz. and *Ps. alpinata* Scop.—very pretentious as for its hypsometrical claims. It is a typical species of the high mountain zones, flying in the Tatra in the layers of about 2000 m., mostly on biotops where the consistent growth is interrupted by the single stones, rocks and wreckage. Thus we find it mostly commonly with *Erebia pandrose roberti* Peschke and *Gelechia dzieduszyckii* Now. It prefers the habitats protected from the wind and exposed towards the sun, in which shine it is flying. The imagos are sitting upon the insolated stones. A little different is the character of the occurrence of the species in the Belanské Tatry. There *T. canaliculata schwingenschussi* Whli. is to be found mostly in the neighbourhood of the wreckage-channels in the slopes, flying also on places where is directly graze. The species does not occur in biotops typical for *T. noricana carpathica* Schwing. or it is very rare there.

Ssp. *weneri* Schawerda 1916. This subspecies is a representative of the genus *Psodos* Tr. in the Balkan Peninsula. Loc. typ.: Volujak; *T. canaliculata weneri* Schaw. occurs on the Pirin (El Tepe), Durmitor, etc. It is characterised by the strikingly black coloration.

Ssp. *pyrenaica* Schawerda 1919. Form from the Pyrenees described after specimens from the Pic du Midi.

The individual forms described on the basis of the differences in the shape of saccus (f. *gracilis* Whli., f. *concava* Whli.) have—as in some other species of the genus *Psodos* Tr.—a problematic taxonomic value.

Material studied:

Südtirol 4 ex., Sellajoch 1 ex., Pforzheimerhütte 1 ex., Gornersgrat 1 ex., Oetztal 1 ex., Ortler 1 ex., Gr. Bösenstein (Styria) 2 ex., Großglockner-gebiet 10 ex., Glockner—Kärnten 2 ex., Appenzell 2 ex., Bormio 1 ex., Pasterze 2 ex., Zermatt 3 ex., Matrei 3 ex., Pitztal 3 ex., Gleiwitzer Hütte 1 ex., Zwing (Zentral-Alpen) 1 ex., Riffelberg 1 ex., sine loc. 3 ex.

Ssp. *schwingenschussi* Whli.: Liptovské hole: Plačlivo 3 ex.; Vysoké Tatry: Sedielko 12 ex., Furkotská dolina 16 ex., Květnica 4 ex., Kopa-Sedlo

3 ex., Mlýnica 1 ex., Skrajna Turnia 2 ex., Belanské Tatry: Košiary 8 ex., Ždiarská Vidla 1 ex., Bujačie 5 ex., Hlúpý 10 ex.; Southern Carpathians: Retezat-Mts. 4 ex.

***Trepidina noricana* W a g n e r 1898.**

This species is unequivocally characterised by habitual as well as by anatomical characters. The furcal shovels attain in this species a quite exceptional development, their spinosity is, however, strongly variable also in the members of one and the same population. *T. noricana* W a g n e r occurs in the Alps and in the Carpathians very locally and rarely. It gives obviously preference to limestone though the species is known also from mountains of primary rocks (Hohe Tauern, Gleiwitzer Hütte).

Nominate form described from Alps; in the Carpathians lives ssp. *carpathica* S c h w i n g e n s c h u s s 1915 (loc. typ.: Belanské Tatry—Bujačie). This locality is obviously identical with the locality "Beler Kalkalpen—Stirnberg". It is difficult to understand that W e h r l i still in 1953 maintained that the Belanské Tatry are in Hungary (Ungarn).

Like *T. canaliculata schwingenschussi* W h l i. is this subspecies characterised by the strong scaliness against the grayish tones from the Alpine region (Sonnblick, Hochschwab). Since the time of the first finding this species in the Belanské Tatry by S c h w i n g e n s c h u s s (1915), *T. noricana carpathica* has been captured in a few specimens by Novák in 1952: Košiary 2100 m. (5. 7. ♂), Ždiarská Vidla 2148 m. (4. and 5. 7. 2 ♂♂). In the second part of July 1954 a numerous series has been captured in the southern slopes of Bujačie (lgt. dr. Povolný). *T. noricana carpathica* S c h w i n g. is a species of the highest zones of Belanské Tatry (about 2000 m. a. s. l.) flying in the free gravel-ruins with scarce vegetation. In these habitats the species can be discovered abundantly. The imagos sitting on the stones in the sunshine are hunted by the spider *Acantholycosa tatrica* (Arachn., Lycosiidae det. Prof. dr. Miller). Outside its typical biotops only the single individuals can be occasionally captured. This insect belongs to the most notable members of the mountain fauna of the National Park of the Tatra.

The inaccessibility of the more extensive material from the non-Carpathian region prevents us from evaluating the valence of the other forms described of this species (e. g. ssp. *kusdasi* W e h r l i 1945, f. *furcata* W h l i., f. *variegata* S c h w i n g.).

Material studied:

f. nom.: Sonnblick — Hochschwab 1 ♂.

ssp. *carpathica* S c h w i n g.: Košiary 1 ♂, ždiarská Vidla 2 ♂♂ (lgt. I. Novák), Bujačie 13 ♂♂, 8 ♀♀ (lgt. dr. Povolný, coll. Mus. Brno); Bujačie (lgt. L. Schwingenschuss — Typus, coll. Mus. Budapest).

***Trepidina bentelii* R ä t z e r 1893.**

Loc. typ.: Mattmark. While the morphological basis is the same as in *T. noricana* W a g n e r, this good species is especially typical by the shape and spinosity of the branches of the juxta; in the females the broadly infundibuliform ductus bursae is characteristic.

Also *T. bentelii* R t z r. belongs among the local and rare forms. The geographical races ssp. *zermattensis* W e h r l i 1919, ssp. *panticosea* W e h r l i 1945, ssp. *alpmaritima* W e h r l i 1924, ssp. *retyezatensis* B a r t h a 1933 we have not been able to study more in detail because of the inaccessibility of the material. "*Ps. telekii*" B a r t h a 1933 is indubitably a malformed specimen, as R e b e l rightly pointed out. W e h r l i's conception (1953) of *Ps. telekii* B a r t h a as a subspecies is untenable in every respect, for it transpires even from W e h r l i's own description that it is at most an individual form. The occurrence of *T. bentelii* R t z r. in the uppermost layers of the Slovak Carpathians is not excluded as the species lives in the Ruman Carpathians.

Material studied: Zermatt ♀; Torla ♂ (4. 7. 28), ssp. *panticosea* W h l i.

Concerning *Ps. belzebuth* P r a v., this is a very problematical form so that after W e h r l i's (1953) unclear utterance its specific valence has still to be proved.

4. Subgenus *Alpina* n. subgn.

Subgenotypus: *Alpina coracina* E s p.

This subgenus comprises two species, one of which (*A. alpinata* S c o p.) occurs also in the subalpine zone as a typical companion of *Vaccinia*, and the second species (*A. coracina* E s p.) penetrates as the only member of the genus *Psodos* Tr. also far outside the mountain region into the North European and Asian tundra.

With the same morphological basis of the pattern these forms are habitually characterised by the quite extraordinary variability of the pattern and of the basis coloration (especially *A. coracina* E s p.).

The juxtal branches are not particularly characteristic, but here too a quite extraordinary variability is evident (see plate XIII.), especially in the spinosity. The aedeagus has at the apex on each side a slight spinal process. Also the circumostial sclerites of the females show a great morphological plasticity, often caused geographically.

Alpina coracina E s p e r 1786.

Of all the members of the genus this species has the greatest geographical distribution. Though of Alpine origin like the other species of the genus *Psodos* Tr., it has penetrated after the Pleistocene glaciation from the region of the glacial tundra of Central Europe with the retreating glacier far to the North, where it lives recently also in the tundras. It has thus explicitly a boreo-alpine distribution, though in contradistinction to most boreo-alpines it is of Alpine origine. In the high mountains of Europe as well as in the Eurasian tundra it forms a whole number of strongly defined geographical forms (many of which approach separate vicariating species). Nevertheless their common origin is obviously so that the attribution of specificity is to a considerable extent a matter of conception.

Juxtal branches and circumostial sclerites are characterised by a strong variability so that their taxonomic evaluation demands special carefulness.

Loc. typ.: Gipfel der Alpen des Juragebirges.

Ssp. pseudonoricana. It is one of the best defined subspecific circles of the species *A. coracina* Es p., and strongly approaches specific isolation, though it cannot be separated completely from *A. coracina* Es p. In contradistinction to all forms of the species *A. coracina* Es p. the juxtal branches are relatively long and narrow. The circumostial sclerites are strong and as if grown together into one disc-like formation. Habitually, however, it does not differ essentially, especially the female, from the other forms of the forma nominata, so that also after the habit the specific identification of this form is absolutely unequivocal.

This name (*pseudonoricana*) appeared for the first time with the photograph of a specimen apud Wehrli 1919, without any remark in the text. Later the same author (Wehrli 1921) regards Schwingenschuss in litt. (see also Wehrli 1953) as the author of this name, and states that it is not a form of the species "noricana" but a form of the group "coracina". Schwingenschuss (1923) does not define unequivocally his standpoint to the author's name *pseudonoricana*, and so it is very unclear which of the authors has created this name. Therefore we introduce for the typical population from the Triglav the name *Psodos (Alpina) coracina* ssp. *pseudonoricana* Povolný et Moucha, nomen emendatum.

Holotype: ♂ Carniolia—Triglav 1700-1900 m., Anfang VII. 1927., lgt. F. Daniel.

Allotype: ♀ (the same data).

Paratypes: 1 ♂ and 2 ♀♀ (the same data).

All specimens in coll. Musei Nationalis Pragae.

Topotypes: 16 ♂♂ and ♀♀ from the same locality in coll. Zoolog. Staatssammlung d. Bayer. Staates, München.

Ssp. transiens Wehrli 1921:

Geographical form from the Karwendel and Wettersteingebirge. A comparison with *T. noricana* Wagner (Osthelder 1938, p. 530) is quite unsuitable as it is a striking form of the species *A. coracina* Es p., which cannot be confused with another species.

Ssp. diószeghyi Schmidt 1930:

Geographical form of the Carpathian mountains group Reteyzat, which strongly approaches morphologically and habitually the North European ssp. *lappona* Whli. Description apud Schmidt 1930 and Barth 1933. Specificity certainly cannot be ascribed to this form as we have convinced ourselves by the study of the topotypes which Dr. L. Kovács (Budapest) sent us. The occurrence of this species also in other parts of the Carpathians cannot be excluded. But the occurrence announced from the Polish side of the Tatra (Prüfer 1923, a. o.) refers obviously to *T. canaliculata schwingenschussi* Whli.

Ssp. lappona Wehrli 1921:

North European tundra form with strongly darkened basic coloration. The morphological characters of the outer genitalia do not fall outside the range of the variability of the species.

Concerning the other geographical forms of the species *A. coracina* Es p. we have not succeeded in getting the necessary comparative material. As

far as we can see from the figurings apud Wehrli and Schmidt (l. c.) neither *Ps. tundrana* Whli. nor *Ps. sajana* Whli. (from the Asian tundras) fall outside the variability of the species *A. coracina* Esp., so that their possible specific independence has still to be studied. Even Wehrli's work of 1953 has not changed the uncertain position of these forms. With regard to *Ps. daisetsuzana* Mats. the relation of this form cannot be judged from the existing description even with regard to the genus *Psodos* Tr.

Material studied:

F. nom. (incl. ssp. *angustipennis* Whli. et var. *rectifasciata* Whli.): Zirbitz (Steiermark) 8 ♂♂ et ♀♀, Flücklapaß (Helv.) 20 ♂♂ et ♀♀, Ortler-Gebiet 6 ♂♂ et ♀♀, Ritterhorn (Bozen) 2 ♂♂, Albula (Helv.) 3 ♂♂ et ♀♀, Laugen (Ter. mer.) 3 ♂♂ et ♀♀, Brenner 1 ♂, Sonnblickgebiet 3 ♂♂ et ♀♀, Warscheneck 1 ♂, Schneeberg 1 ♂, N. Tauern 3 ♂♂ et ♀♀, Sallajoch (Ter. mer.) 1 ♂, Pitztal 3 ♂♂ et ♀♀, Stubaital 2 ♂♂, Ter. mer. 1 ♂, Gemsgrube 2 ♀♀, Interlaken 1 ♂, Gr. Pyhrngass 1 ♂.

Ssp. *transiens* Whli.: 22 ♂♂ and ♀♀ from the Karwendel region, Bayer. Alpen, Ammergauerge Berge, Rauheck—Allgäu, Nordtirol, Lobarger Hütte (coll. Zool. Staatsammlung d. Bayer. Staates, München et coll. Mus. Nat. Praha).

Ssp. *lappona* Whli.: Lapp. Finl. Enontekis 5 ex., Torne-Abisko 8 ex., Kilpisjärvi (Finl.) 1 ex. (coll. Mus. Nat. Praha et Dr. Schulte, Kiel).

Ssp. *diószeghyi* Schmidt: Zánoga-Retyezat, 4 ex. topotypes (coll. Nemzeti Múzeum, Budapest).

Alpina alpinata Scopoli 1763.

This is the most uniform species of the whole genus *Psodos* Tr., habitually as well as morphologically. The juxtal branches are morphologically so to say identical with those in *A. wehrlii* Vorbrodt. The configuration of the gnathos is very striking; it is broadly rounded, similiary as the uncus, which lacks the typical beak-shaped point. Apparently we have here a secondary change of these formations. The relation between *A. alpinata* Scop. and *A. wehrlii* Vorbr. certainly deserves attention as their morphological and habitual similarity is certainly not by chance. Even the possibility cannot be excluded that they may be altitude vicariants. The subgeneric positions of these two species would deserve further investigations.

A. alpinata Scop., similiary as *T. quadrifaria* Sulz. has the greatest hypsometrical valence in mountain regions. It lives at altitudes from 1000 to 3000 m.

In Czechoslovakia this species lives as the only representative of the genus *Psodos* Tr. also in the region of the Kralický Sněžník and of the Praděd. Here it is a typical inhabitant of *Vaccinia* growths. Besides it occurs in the Krkonoše and in the Slovak Carpathians, in latter region it rises high above 2000 m.

Material studied:

Schneeberg 2 ♂♂, 1 ♀; Dachstein 2500 m. 1 ♂, 13. 7. 23; Styria—Gamskogel ♂♀; Ter.—Rotmoostal 1 ♂, 18. 7. 27; Ter.—Oetztal 1200 m. 2 ♂♂; Pitztal 1 ♂, 4. 7. 28; Ortler-Gebiet 1 ♂, 4. 7. 33; Albulapaß 1 ♂,

25. 7. 14; Imbachhorn 2200 m., 1 ♂, 22. 7. 23; Simplon 1 ♀; 13. 7. 30; Zermatt-Schwarzseeweg 1 ♀, 15. 7. 36; Berner Oberland—Grünwald 1 ♀, 18. 7. 36; Krkonoše—Studničná hora 1200 m., Sněžka 1500-1600 m., Obří Důl, Liščí hora, etc., 47 ♂♂, 6 ♀♀; Silesia—Praděd 1450 m., 3 ♂♂, 2 ♀♀; Králický Sněžník 2 ♂♂, 2 ♀♀; Malá Fatra 1450 m., 1 ♂, 23. 7. 33; Nizké Tatry: Chopok 2000 m., 14 ♂♂, 1 ♀, 9. 7. 52; Ďumbier 2000 m., 3 ♂♂, 16. 7. 47; Prašivá 1700 m., 7 ♂♂, 1 ♀, 21. 7. 48; Královská Hola 1940 m., 4 ♂♂, 20. 7. 51; Liptovské Hole: Žiarská dolina 1400 m., 1 ♂, 1. 8. 51; Smutné Sedlo 1900 m., 1 ♂; Plačlivo 2000 m., ♂♀, 31. 7. 51; Vysoké Tatry: Važecká dolina, 1 ♂; Furkotská dolina 1600-1800 m., 11 ♂♂; Sediello 2 ♀♀; Kopa 1700 m., 2 ♂♂, 10. 7. 30; Malá Studená dolina 2000 m., 1 ♂, 17. 7. 25; Belanské Tatry: Košiary 2000 m., 8 ♂♂, 5. 7. 52; Hlúpy 2000 m., ♂♀; Ždiarská Vidla 2100 m., 1 ♂, 4. 7. 52; Carp. or.: Hoverla ♂♀, 7. 31; sine loc. 12 ♂.

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РЕЗЮМЕ.

К вопросам генезиса и дифференциации рода *Psodos* Tr.

Так как выводы о дифференциации рецентных видов мы можем с потенциальной точностью установить максимально от образования третичного периода, то о происхождении рода *Psodos* мы тоже можем говорить лишь с определенной правдоподобностью. Современное положение исторической зоогеографии допускает в основном три гипотезы о происхождении рода *Psodos*.

1. Первая гипотеза выходит из предположения, что род *Psodos* по своему происхождению является группой альпийского характера, что вопрос касается видов, которые по существу установились в Альпах после окончания орогенетического процесса. Их предком таким образом должна была быть форма тропическая или субтропическая, которая приспособилась горному климату и постепенно разделялась на существующие виды.
2. Вторая гипотеза выходит из предположения, что род *Psodos* является по существу северного происхождения, что могло бы свидетельствовать современное распространение форм группы *coracina* («*Coracina-group*») в евразийской тундре. *Psodos daisetsuzana* описанная Матсумурой в Японии требует во всяком случае дальнейшего исследования, так как сама идентификация вида очень затруднена недостатками в описании и неточными знаниями автора в области географии. См. об этом Wehrli 1953.

По этой гипотезе однако заселение средневропейских гор выше 2.500 м родом *Psodos* было исторически сравнительно очень позднего характера и безусловно чрезвычайно короткое вследствие к настоящей сравнительно богатой и глубокой дифференциации этого рода, несмотря на целый ряд дальнейших почти необоснованных недочётов этой гипотезы.

3. Третья гипотеза выходит из предположения, что предки рода *Psodos* происходят с динарского острова третичного периода в области современной Далмации, откуда после его присоединения смогли проникнуть в Альпы.

Результаты нашего изучения этого вопроса приводят нас к оправданию первой из приведенных гипотез, которую можно обосновать самым большим количеством разнообразных фактов:

Виды рода *Psodos* встречаются только в европейских горах выше 2.500 м, причем наибольшее количество видов известно из Альп, где помимо того живет несколько крайне изолированных, значит явно достаточно старых эндемических видов и форм (*spitzi*, *wehrlii* и другие). Мнение, с которым мы встречались раньше, что *Psodos* живет в азиатских горах выше 2.500 м, уже устарело, так как оказалось, что вопрос касался иных родовых групп (*Gnophopsodos*). Иные азиатские виды, которые до настоящего времени сюда включались, требуют еще нового рассмотрения («*Psodos daisetsuzana*»). Альпийские виды больше всего концентри-

руются в области высоких Альп швейцарских, где мы практически встречаемся за исключением вида *T. spitzi* со всеми известными видами *Psodos*, в то время как в направлении на край альпийского ареала (например в Приморских Альпах), куда виды расширяются, при измененных условиях создаются местные морфы. Это мы наблюдаем и на общем ареале рода *Psodos*, где Альпы являются центром с самым большим количеством видов.

Фауна рода *Psodos* в остальных средневропейских горных областях выше и ниже 2.500 м (Пиренеи, Судеты, Карпаты) является, что касается видов, значительно беднее. Весьма существенным обстоятельством является еще то, что ни одна из этих гористых областей не имеет ни одного выразительно дифференцированного эндемического вида. Все виды рода *Psodos* из мимеоальпийской гористой области имеют повсеместно очень узкие родственные отношения к альпийским видам, от которых обычно различаются только второстепенными знаками (викарирующие формы), так что различия ни в одном случае не перешли границу субспеций (*canaliculata*—*schwingenschussi*, *noricana*—*carpathica*, *bentelii* — *retyezatensis*, *coracina* — *dioszéghyi*, *quadrifaria* — *pyrenaea*, *bentelii* — *panticosea* и т. п.).

Фауна *Psodos* в остальных европейских горных областях является таким образом в их современных формах сравнительно недавнего происхождения, так как фауна её существования там повидимому не идёт дальше чем до вюрмского ледникового периода.

Приблизительно на одинаковом уровне дифференциации находится группа форм вида *Psodos*, который проник в североевропейские тундры (Шотландия, Скандинавия) и оттуда далеко на восток, откуда нам известны две формы, явно близкие и повидимому не более чем как подвид отличающиеся от *coracina* из саянских гор. Обстоятельства далее на восток из-за недостаточного исследования огромной тундры в западной Азии до настоящего времени не известны, тоже японскую псодоидную форму («*Psodoidform*») описанную Матсумурой нельзя точно оценить, особенно потому, что до сих пор не выяснены отношения между родом *Psodos* и *Gnophos* в Азии.

Дальнейшим важным фактом является то, что род *Psodos* до сих пор совсем не изолирован в своём развитии; близкий к нему *Torula* Hb. навазывает видом *quadrifaria* совершенно ясно на другую высокогорную пяденицу *Orphne* (*Dasydia*) *tenebraria*, которая живет в Альпах, Пиренеях и Аппенинах, а именно в значительных высотах (более 3.000 м) и имеет явное отношение к подгорному роду *Gnophos*. О родственности между *Torula quadrifaria* и *Orphne tenebraria* свидетельствует, как мы уже сказали, например формирование эдеага, в особенности наличие игольчатых *cornuti* у обоих видов; тоже приведенное подобие лопаток юксты, форма которых у *quadrifaria* является соединительным звеном между собственным *Psodos* и родом *Orphne*, далее редукция гнатога и форма вальв. Род *Orphne* затем навазывает (см. Prout in Seitz) на некоторые формы распространенного рода пядениц *Gnophos*. Родственность развития родов *Psodos* и *Gnophos* была однако опять подчеркнута

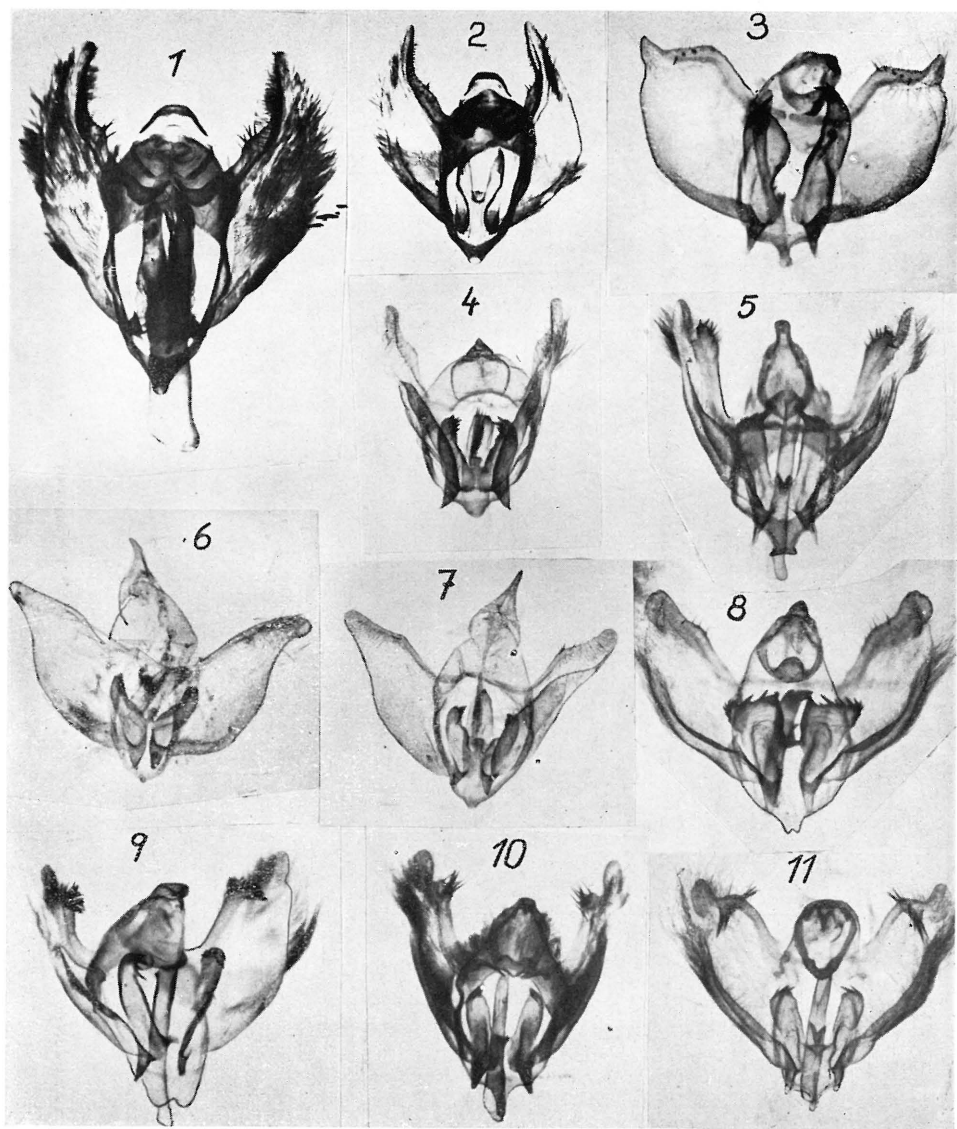


Plate I. — the male genitalia

- 1-2. *Orphne tenebraria* (sine loc.).
3. *Ps. (Trepidina) canaliculata schwingenschussi* — Liptovské Hole: Plačlivo, 1. 8. 1951.
4. *Torula quadrifaria* — Krkonoše: Studničná hora, 14. 6. 1930.
5. *Ps. (Alpina) coracina pseudonoricana* — Carniolia: Triglav, 7. 1927.
6. *Torula quadrifaria* — Kärnten: Glocknergebiet.
7. *Torula quadrifaria pyrenaea* — Pyrenees: Picada, 21. 7. 1928.
8. *Ps. (Triglavia) spitzi* — Carniolia: Triglav, 9. 8. 1927.
9. *Ps. (Alpina) alpinata* — Großglockner, 27. 7. 1923.
10. *Ps. (Alticola) alticolaria chalybaeus* — Ortler Gebiet, 19. 7. 1931.
11. *Ps. (Alticola) alticolaria* — Großglockner, 5. 8. 1927.

Plate II. — the male genitalia

1. *Ps. (Alpina) alpinata* — Krkonoše, 1. 7. 1929.
2. *Ps. (Alpina) alpinata* (terat. asym.) — Gleiwitzerhütte, 22. 7. 1923.
3. *Ps. (Trepidina) bentelii* — Torla, 4. 7. 1923.
4. *Ps. (Alpina) alpinata* — Schweizerische Schneealpen.
5. *Ps. (Alpina) alpinata* — Helv.: Simplon, 13. 7. 1930.
6. *Ps. (Trepidina) noricana carpathica* — Belanské Tatry: Ždiarská Vidla 4. 7. 1952.
7. *Ps. (Trepidina) schwingenschussi* — Vysoké Tatry: Mlýnica, 20. 7. 1925.
8. *Ps. (Trepidina) noricana* — Hochschwab, 7. 1906.
9. *Ps. (Trepidina) canaliculata* — Zentralalpen, Teur Zwing, 5. 6. 1923.
10. *Ps. (Trepidina) canaliculata* — Sonnblickgebiet, 27. 7. 1933.
11. *Ps. (Alpina) coracina lappona* — Enontekis, 27. 6. 1920.
12. *Ps. (Alpina) coracina dioszeghyi* — Carp.: Retyezat, 28. 7. 1916.

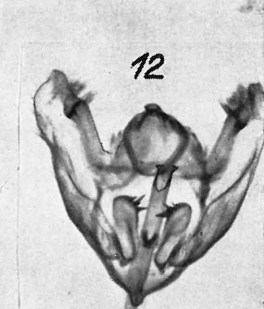
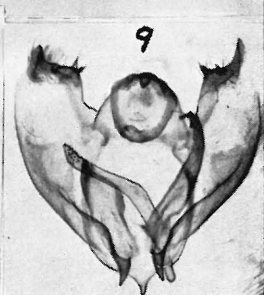
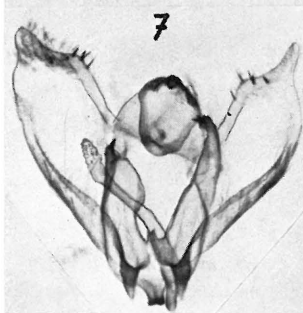
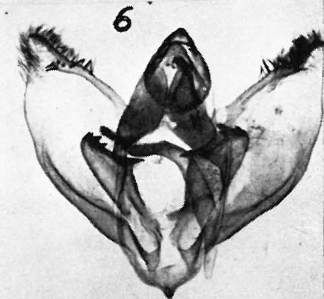
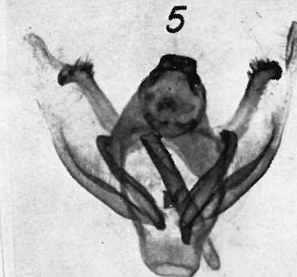
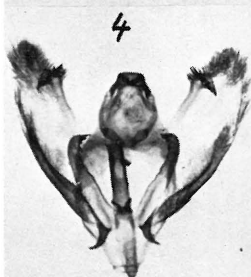
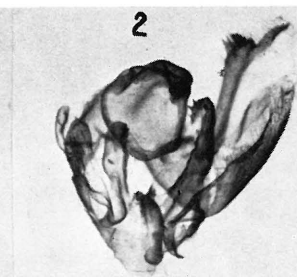


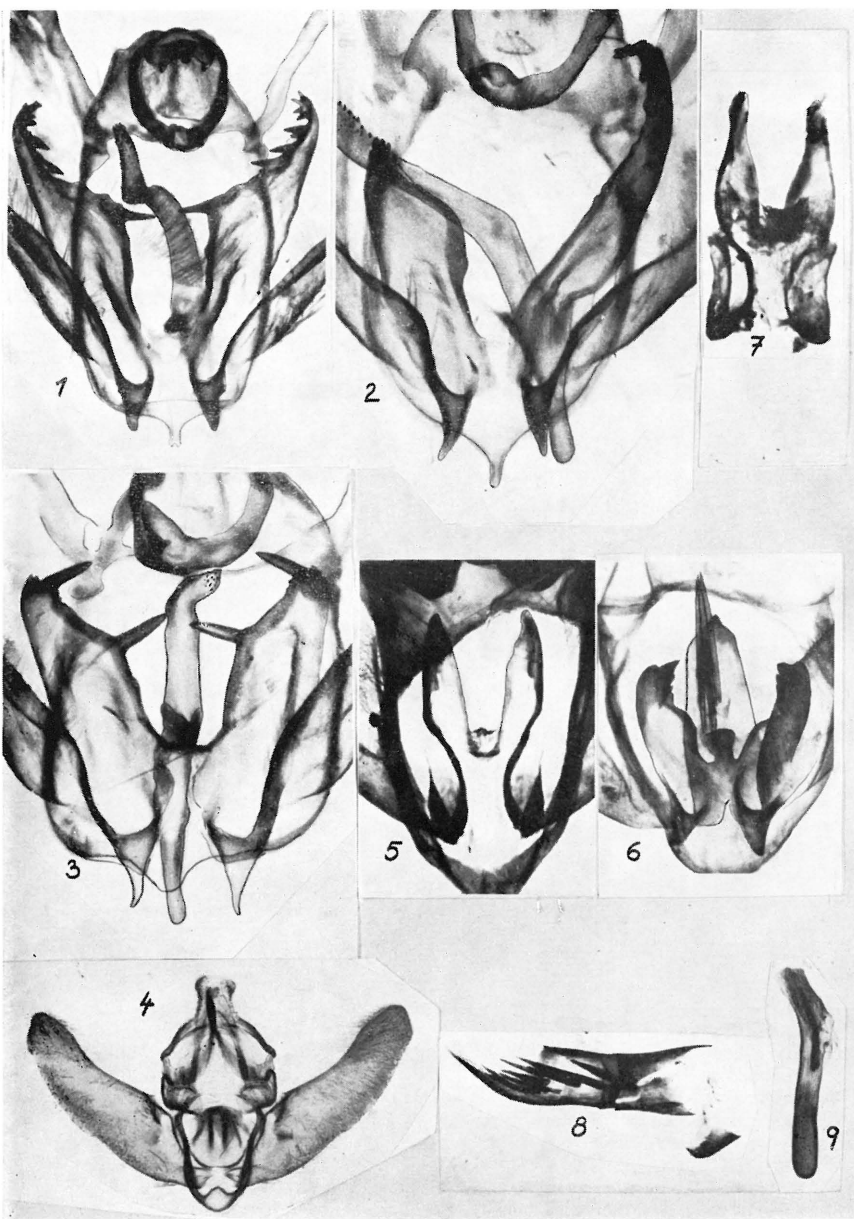
Plate III. — the female genitalia

1. *Ps. alticolaria* f. *chalybaeus* — Ortler Gebiet, 19. 7. 1931.
2. *Ps. (Trepidina) canaliculata schwingenschussi* — Vysoké Tatry: Sedielko, 27. 7. 1951.
3. *Torula quadrifaria* — Vysoké Tatry: Mengušovská dolina, 3. 7. 1928.
4. *Ps. (Triglavia) spitzi* — Carniolia: Triglav, 6. 8. 1929.
5. *Ps. alticolaria* — Sonnblickgebiet.
6. *Ps. alticolaria* — Pic Umbrail, 1895.
7. *Orphne tenebraria* (sine loc.).
8. *Torula quadrifaria* — Umg. von Bern, 18. 7. 1936.
9. *Ps. (Alpina) coracina* — Pyrenees: Gedre, 7. 7. 1907.
10. *Ps. alticolaria* (segm. VIII., IX., X.) — Sonnblickgebiet, 7. 1936.
11. *Ps. alticolaria* — Sonnblickgebiet, 24. 7. 1936.
12. *Ps. (Alpina) coracina pseudonoricana* — Carniolia: Triglav, Anf. 7. 1927.
13. *Ps. (Alpina) coracina* — Umg. von Innsbruck, 5. 7. 1937.
14. *Ps. (Trepidina) canaliculata canaliculata* — Pitztal, 15. 7. 1928.
15. *Ps. (Trepidina) bentelii* — Zermatt, 22. 7. 1930.
16. *Ps. (Alpina) alpinata* — Krkonoše, 9. 7. 1933.



Plate IV.

1. *Ps. (Trepidina) noricana*: scapulæ juxtæ et aedeagus.
2. *Ps. (Trepidina) canaliculata*: idem.
3. *Ps. (Trepidina) bentelii*: idem.
4. *Cledeobia moldavica*: genitalia externa cum juxta.
5. *Orphne tenebraria*: scapulæ juxtæ.
6. *Torula quadrifaria*: scapulæ juxtæ et aedeagus.
7. *Orphne tenebraria*: typus differens scapularum juxtæ.
8. *Orphne tenebraria*: aedagus.
9. *Cledeobia moldavica*: idem.



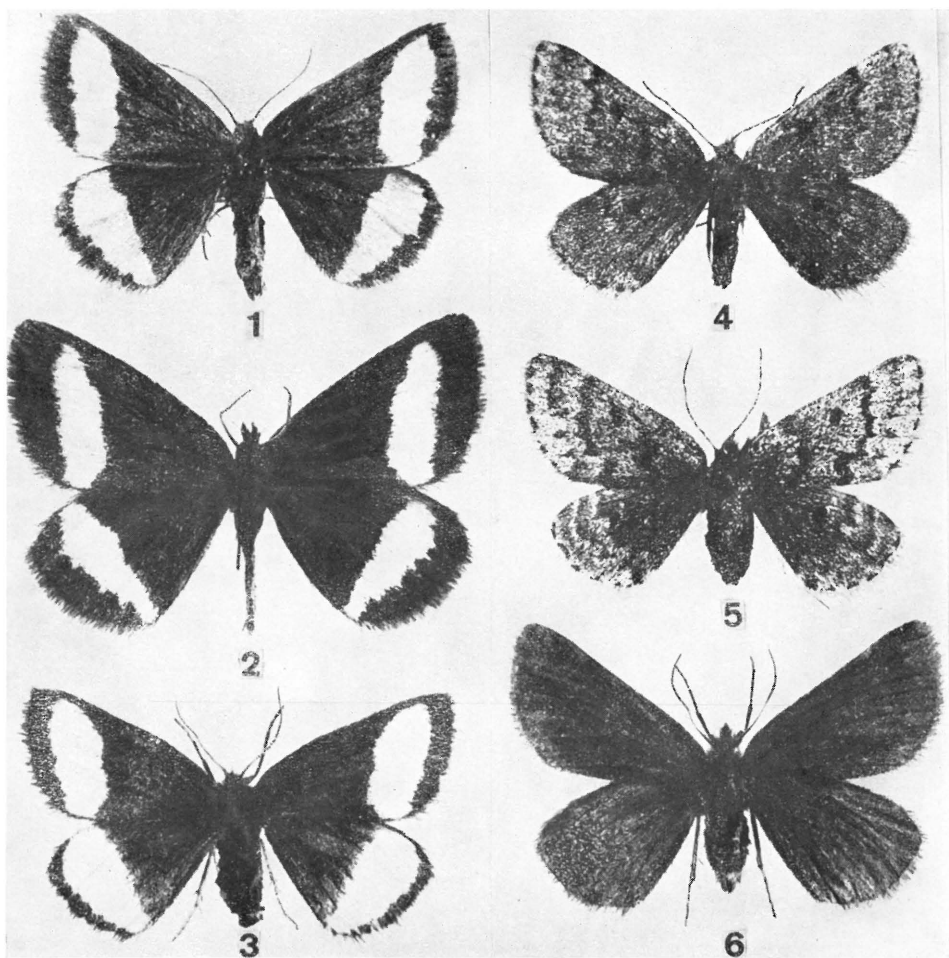


Plate V.

1. *T. quadrifaria* Sulz. ♂, — Vysoké Tatry: Malá Studená dolina 2000 m, 17. 7. 1925, lgt. Silbernagel.
2. *T. quadrifaria pyrenaea* Obth. ♂ — Hautes Pyrenées: Barèges, 10. 7, 24, lgt. ?
3. *T. quadrifaria* Sulz. ♀, Krkonoše, 15. 6. 30, lgt. Soffner.
4. *Ps. coracina pseudonoricana* nom. emend. ♂, Triglav 1700—1900 m, 7. 1927, lgt. Daniel (Holotypus).
5. *Ps. coracina pseudonoricana* nom. emend. ♀, the same data (Allotypus).
6. *Ps. alpinata* Scop. ♀, Krkonoše, 1. 7. 29, lgt. Soffner.

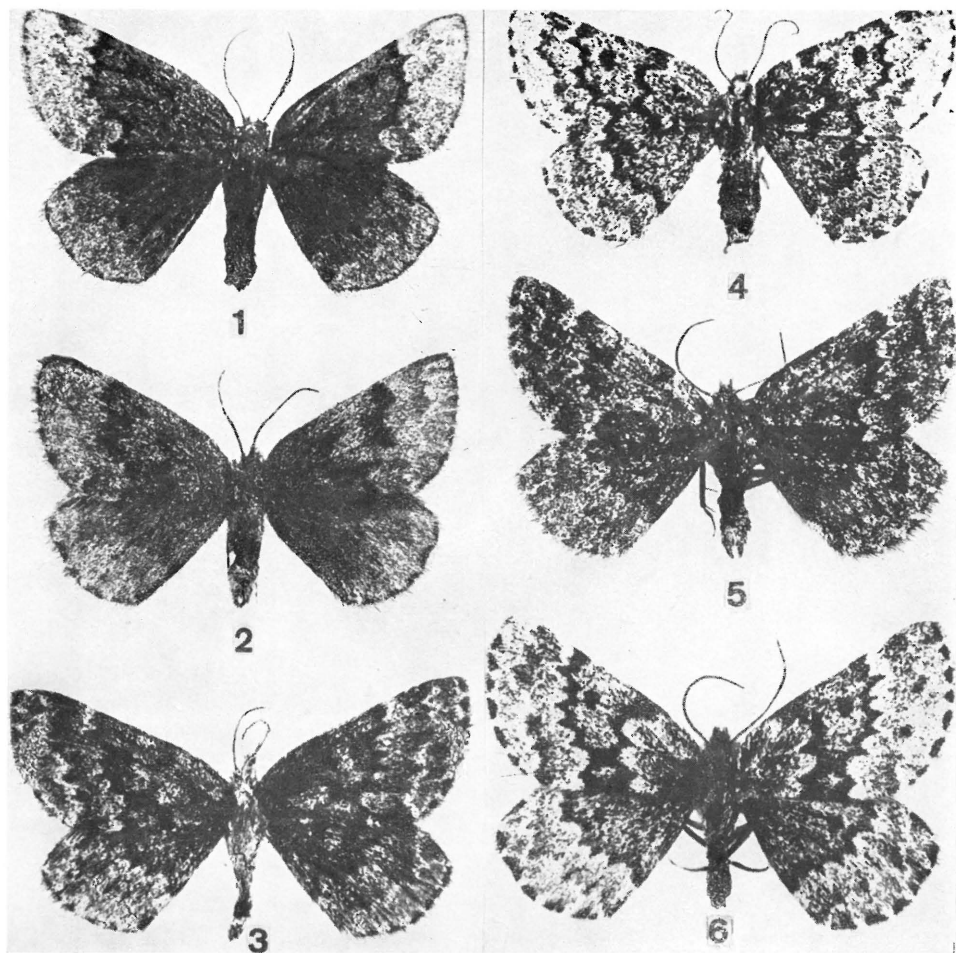


Plate VI.

1. *Ps. benteli panticosea* Whrli. ♂, Torla, 4. 7. 28, lgt. ?
2. *Ps. noricana carpathica* Schwing. ♂, Belanské Tatry: Košiary 2000 m, 5. 7. 52, lgt. Novák.
3. *Ps. canaliculata schwingenschussi* Whrli. ♂ (the same data).
4. *Ps. canaliculata schwingenschussi* Whrli. ♀, Vysoké Tatry: Furkotská dolina 1700 m, 7. 7. 50, lgt. Novák.
5. *Ps. canaliculata schwingenschussi* Whrli. ♂, Vysoké Tatry: Sediello, 8. 1951, lgt. Povolný.
6. *Ps. canaliculata schwingenschussi* Whrli. ♂, Vysoké Tatry: Skrajna Turnia, 15. 7. 1927, lgt. Niesiolowski.



Plate VII.

1. High Tatra: Mengušovská dolina — valey with the peak of Rysy (2503 m — upper left) and the peak of Velká Vysoká (2565 m — upper right) with typical biotops of *Psodos* in the Tatra. The consistent plough-tail zone with single meadows is typical for *T. quadrifaria*, rising up to the interrupted plough-tail zone together with *Ps. alpinata*, whereas *Ps. canaliculata schwingenschussi* appears as soon as in the zone of the lakes visible under the peak of Rysy.
2. A. detailed view of a meadow with *Pinus mugo* — a typical habitat of *T. quadrifaria* (Belanské Tatry).



Plate VIII.

1. A typical biotop of *Ps. canaliculata schwingenschussi*, *Erebia pandrose roberti* and *Gelechia dzieduszyckii* in the valley of Květnica (High Tatra — Vysoké Tatry, about 2150 m).
2. The same, a detailed view.



Plate IX.

1. The free gravel-ruins with scarce vegetation in the slopes of Bujačie (Belanské Tatry) — a typical habitat of *Ps. noricana carpathica*.
2. A total view on the biotopes of *Psodos* in Belanské Tatry (the slopes of Murán). The under part with *Pinus mugo* — a habitat of *T. quadrifaria*. The lower layer of the rocks with typical flora of the high mountain limestone is the floating place of *Ps. canaliculata schwingenschussi*, whereas the upper layer of rocks and the ruins under themselves are typical habitats of *Ps. noricana carpathica*.

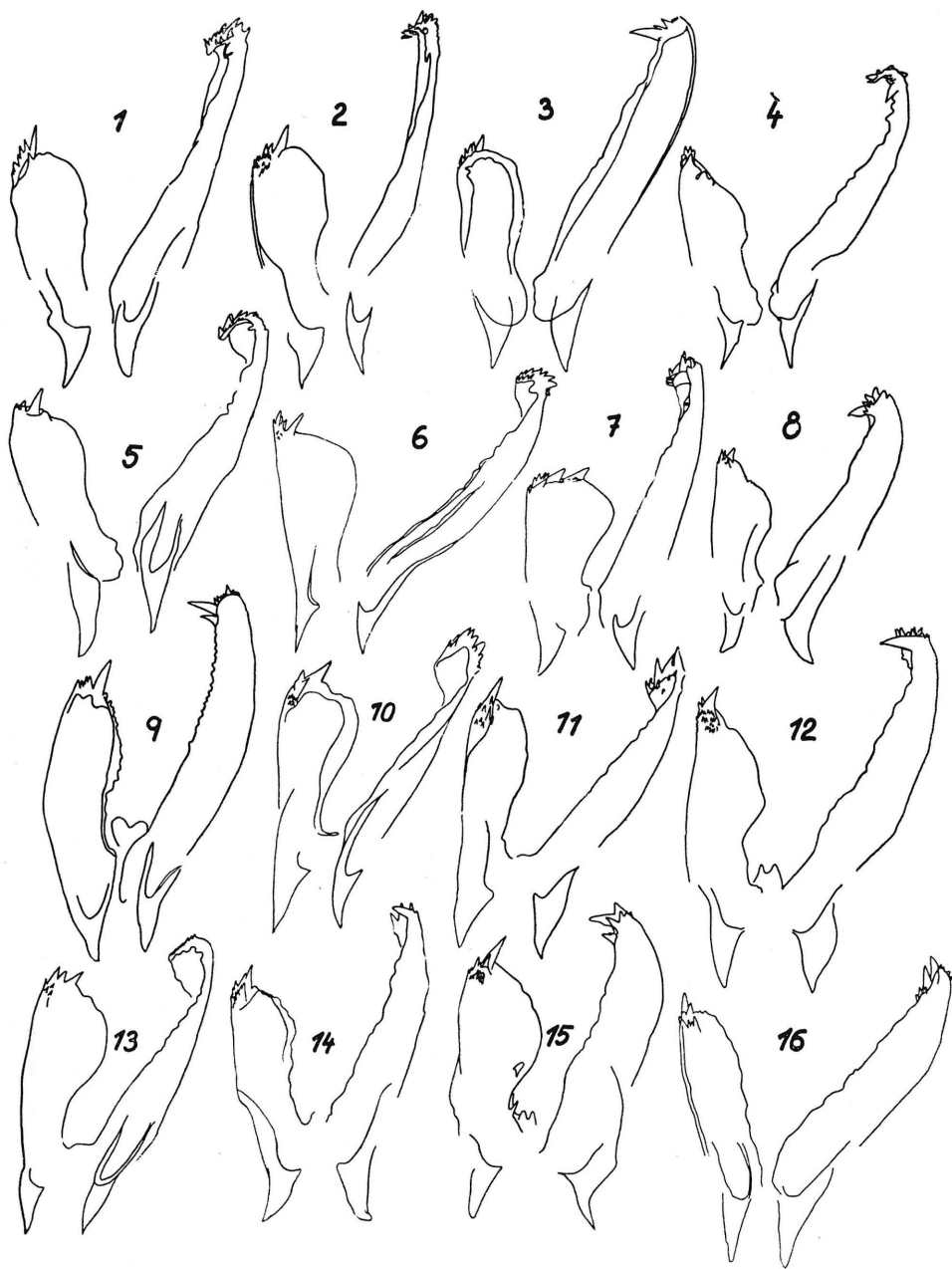


Plate X.

Ps. (Trepidina) canaliculata, forma scapularum juxtæ in variis formis geographicis speciei.
 1. Sonnblickgebiet, 24. 7. 1936; 2. Geisbergthal, 27. 7. 1927; 3. Großglockner, 28. 7. 1924;
 4. Zentralalpen — Teur Zwing, 5. 6. 1923; 5. Ter. mer. — Pforzheimer Hütte, 2. 8. 1903;
 6. Matri (sine dato); 7. Zermatt (sine dato); 8. Alp. mer. — Gornergrat, 30. 7. 1929,
 ssp. *schwingenschussi*; 9. Tatry — Skrojna Turnia, 15. 7. 1927; 10. Carp. mer. — Retyezat,
 28. 7. 1916; 11. Retyezat — Zanoga, 28. 7. 1932; 12. Vysoké Tatry — Mlýnica, 20. 7. 1925;
 13. Vysoké Tatry — Sediello, 7. 8. 1951; 14. Retyezat, 28. 7. 1916; 15. Liptovské Hole —
 Plačlivo, 1. 8. 1951; 16. Retyezat, 16. 7. 1928.

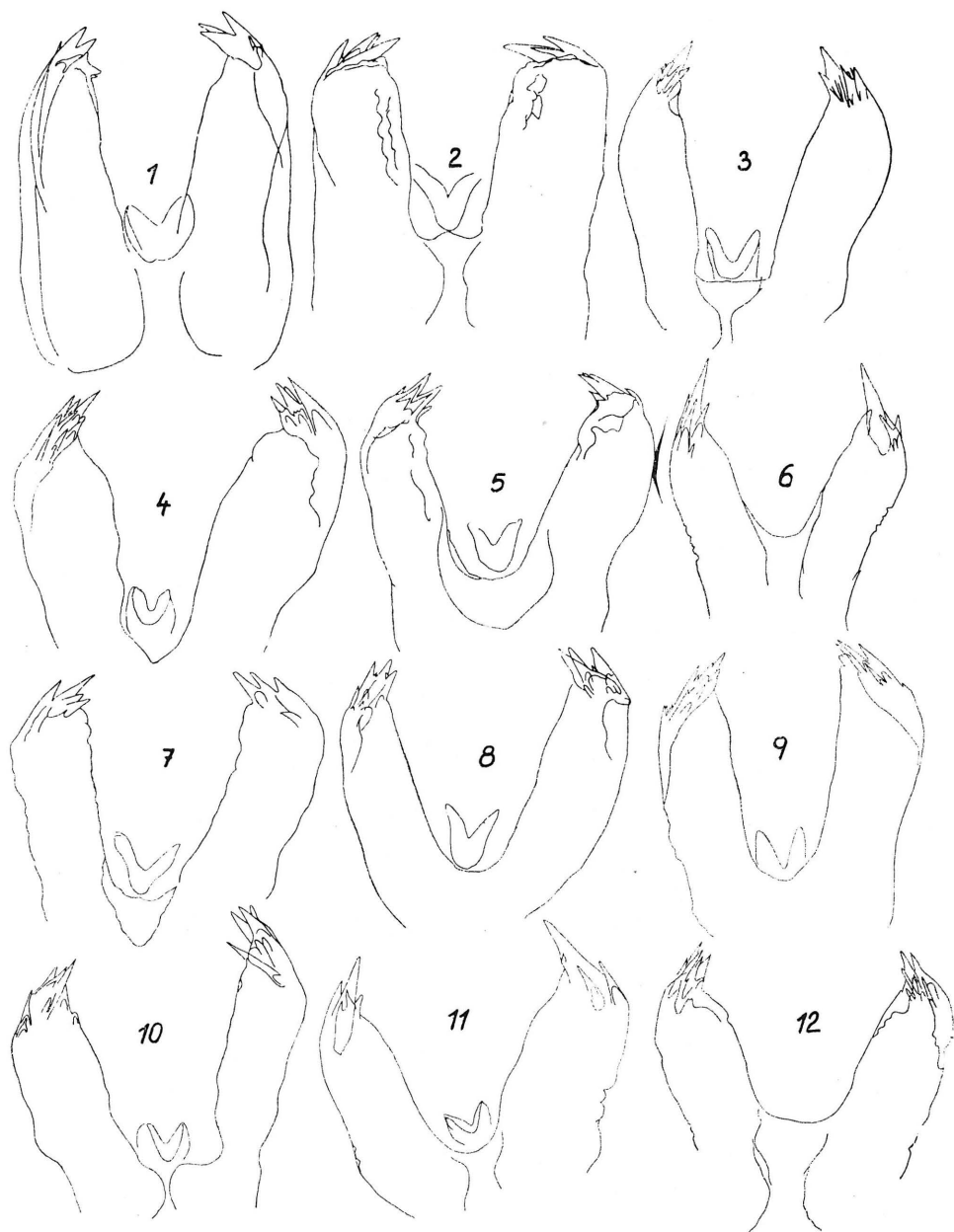


Plate XI.

Ps. alticolaria, forma scapularum juxtæ et variabilitas subspecifica.

1. Groß Glockner, 6. 8. 1927; 2. Ortler Gebiet, 19. 7. 1931; 3. Gemsgrube, 30. 7. 1935;
4. Groß Glockner, 28. 7. 1927; 5. Groß Glockner, 28. 7. 1927; 6. Sonnblickgebiet, 24. 7. 1936;
7. Piz Umbrail, 1895; 8. Groß Glockner, 26. 7. 1925 (*f. chalybaeus*); 9. Groß Glockner,
28. 7. 1924; 10. Stilfser Joch, 11. 7. 1922 (*f. chalybaeus*); 11. Sonnblickgebiet, 24. 7. 1936;
12. Groß Glockner, 5. 8. 1927.

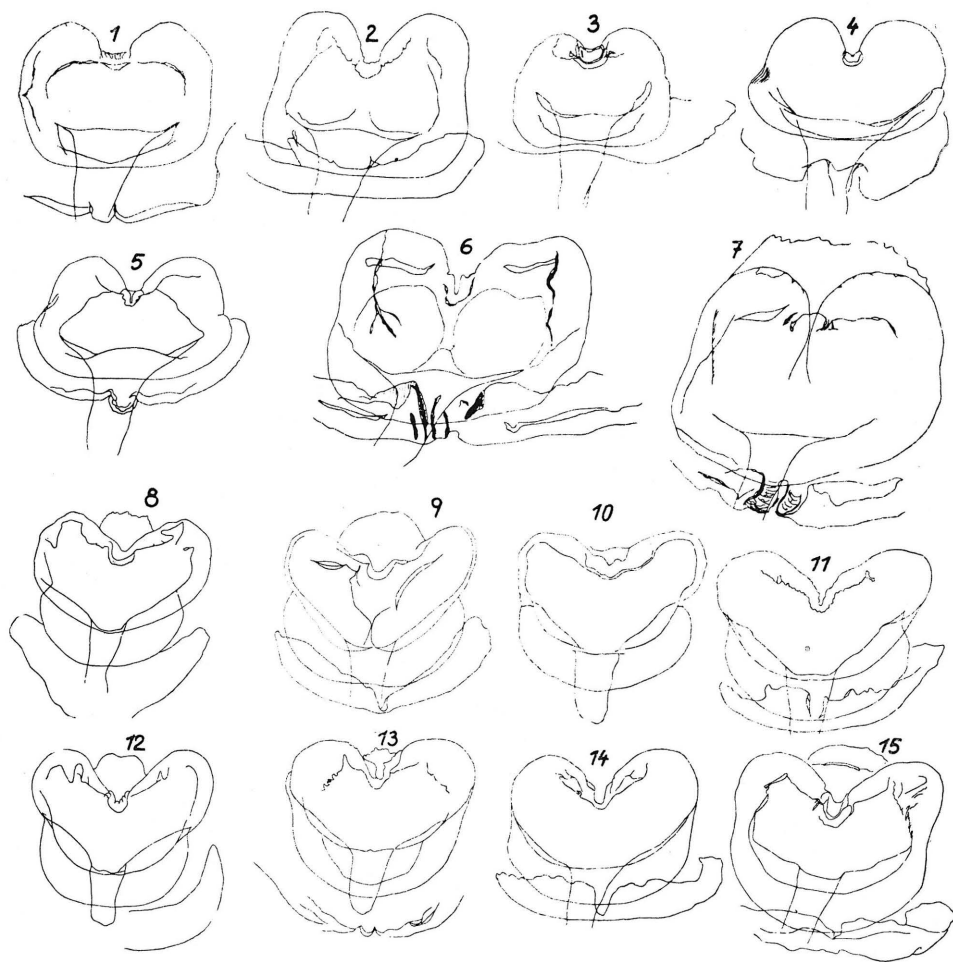


Plate XII.

Ps. (Alpina) coracina, ostium bursae in variis individuís et formis geographicis:

1. Hoher Innsbruck, 5. 7. 1937; 2. Hoher Innsbruck, 5. 7. 1937; 3. Retzevat, 26. 7. 1929;
4. Gedre, 7. 7. 1901; 5. St. Ulrich, 7. 1911; 6. Triglav, 7. 1927 (ssp. *pseudonoricana*);
7. Triglav, 7. 1927 (ssp. *pseudonoricana*).

Ps. alticolaria, variabilitas subspecifica ostii bursae:

8. Gemsgrube, 8. 1927; 9. Sonnblickgebiet, 4. 7. 1936; 10. Ortler, 19. 7. 1931 (*f. chalybaeus*);
11. Stilfser Joch, 10. 7. 1923 (*f. chalybaeus*); 12. Groß Glockner, 31. 7. 1927; 13. Piz
- Umbrail, 1895; 14. Alpen (sine dato); 15. Sonnblickgebiet, 24. 7. 1936.

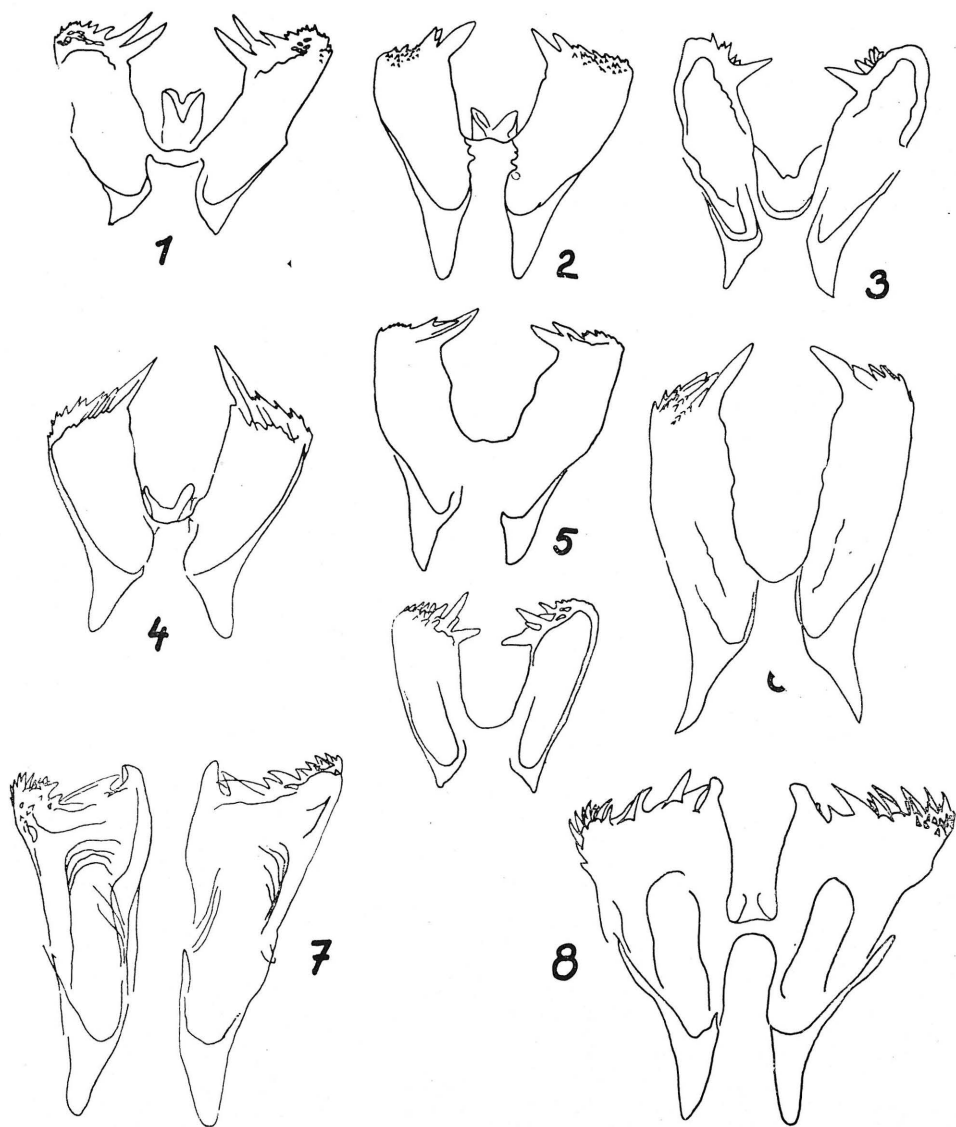


Plate XIII.

Ps. (Alpina) coracina, forma scapularum juxtae in variis formis geographicis speciei:
 1. Karwendel, 29. 7. 1934 (ssp. *transiens*); 2. Enontekis, 27. 6. 1920 (ssp. *lappona*);
 3. Retyezat, 26. 7. 1929 (ssp. *diószeghyi*); 4. Sonnblickgebiet, 27. 7. 1933; 5. Sonnblick-
 gebiet, 27. 7. 1933; 6. Triglav, 7. 1927 (ssp. *pseudonoricana*); 7. Enontekis, 27. 6. 1920
 (ssp. *lappona*).

Ps. (Trepidina) spitzi, forma varia scapularum juxtae:

8. Triglav, 6. 8. 1929; 9. Triglav, 9. 8. 1927.

Верли (Wehrli), который установил род *Gnophopsodos*, к которому присоединяет вид *gnophosaria* Oberth., включенный Проутом к *Gnophos* и вид *altissimaria* Oberthür, который был рассматриваемый как дальнейшая форма рода *Psodos* живущего в мимоевропейских горах. Оба эти виды известны из Тибета (Seévan, Ta-cien-lou).

В этом случае вопрос касается самостоятельной линии развития гнофойдных падениц, которая возникла в азийских горах выше 2.500 м, одинаково как *Psodos* в Альпах, но в общем независимая на *Psodos*. Об этом свидетельствуют некоторые совершенно специфические знаки форм этой группы. Существование рода *Gnophopsodos*, который имеет к роду *Gnophos* более непосредственное отношение чем *Psodos*, является классическим доказательством, что приспособливание аналогическим внешним условиям (в этом случае высокогорным областям) приводит у той же группы в различных областях к возникновению весьма подобных форм.

Род *Gnophos* по существу палеарктический, но его линии развития достигают тоже Индии, Африки и Америки, т. е. тропических областей. Хорологически являются многие его члены существами горными, гусеницы которых очень похожи на гусеницы рода *Psodos* и подобно как они живут на различных низких растениях. Таким образом члены рода *Gnophos* имеют ряд предположений, которые отвечают условиям, вытекающим из теоретического требования к предшественникам рода *Psodos* sub 1. Ряд мнений и фактов, которые приводят разные зоологические науки (морфология, экология, зоогеография) свидетельствуют таким образом со значительной документацией, что род *Psodos* действительно возник из округа форм подобных сегодняшним *Gnophos* а именно тем, что некоторые из основных форм этой группы в позднем третичном периоде приспособились горному климату Альп после окончания орогенетического процесса, где они в интерглатциалах далее развивались в виды *Psodos* настоящего времени. Климатические сотрясения следующего периода, сопровождаемые обледенением Альп, вытеснили эти виды в более низкие местоположения, в которых в течение глатциалов в условиях арктической тундровой степи далее расширялись и с отступающими ледниками возвращались не только обратно в Альпы, но также в остальные высокогорные области европейские, климатические условия которых им это позволяли, и один вид (*Ps. coracina*) проник в североευропейские и североазиатские тундры. Beirne, который старался очень точно изучить историю заселения британских островов фауной *Lepidoptera* в последнем (вюрмском) глатциале, считает *Ps. coracina* в шотландской тундре происходящем из первого вюрмского стадиала), т. е. приблизительно 100.000 лет тому назад). Таким образом *Psodos coracina* является нам формой альпийского происхождения, в то время как её современный бореоальпийский характер, принимаем ли во внимание её дисъюнктивный ареал североευропейский, является видом явно вторичным. Таким образом это является прямой противоположностью большинства бореоальпийской фауны, которую в большинстве случаев нужно считать скандинавского происхождения, и таким обра-

зом вторичной в европейских горах. Что касается *Psodos tundrana* и *sajana*, описанных Верли из Саянских гор, потребуется при определении их специфической самостоятельности принять во внимание и их возможное время существования, которое едва ли идёт дальше чем к началам Вюрма, а также их знаки форм, как о них пишет Верли а в особенности Шмит, свидетельствуют скорее о их отношении к *Psodos coracina*.

Другие две приведенные гипотезы являются мало существенными, и поэтому не будем в дальнейшем их затрагивать. Род *Psodos* представляет собою в смысле развития очень интересную группу, изучение которой в значительной мере обогащает наши взгляды на возникновение видов насекомых в горных областях.

С точки зрения развития является таким образом род *Psodos* группой насекомых, главное специфическое целое которых достаточно разрознилось и изолировалось в альпийской области самое позднее до начала плеистоцена. Причиной проникновения этих специфических групп с одной стороны в остальные горные европейские системы, а именно в Пиренеи, Судеты, Карпаты и др., а с другой стороны в тундровые области евразийские были глациалы. Историческая реконструкция происхождения и времени отдельных инвазий как и явственно сложных условий повторного перемешивания и миграции видов в отдельных глациалах эвентуально в интерглациалах, может опираться только на теоретические предположения. По степени дифференциации мимеоальпийских субспеций (например *schwingenschussi*, *carpathica*, *diószeghyi* и др.) в Карпатах и на основании правдоподобного предположения, что при последнем (возможно что и в некотором более раннем) стадиале вюрмском не произошло вторичное сношение себе отвечающих викаризирующих популяций альпийских и карпатских, в тундре между Альпами и Карпатами. Однако мы можем предполагать, что эти субспеции (хотя не все) не являются продуктом только лишь постглациала, который в большинстве случаев принёс с собою дальнейшее сужение их ареалов, в которых из-за своей стеноэкии идут эти сегодняшние субспеции по-степенно к изоляции видов. Суживание экологической валентности, как проявление физиологической специализации, нужно с точки зрения развития считать как доказательство, что род *Psodos* уже преодолел прогрессивный период своего развития.

Возникновение видов рода *Psodos* является таким образом по всей вероятности двойного происхождения и имеет два разных фазиса развития. Настоящие, весьма изолированные специфические группы, являются продуктом дифференциальной биологической эрупции (см. об этом Маѳап 1945), которая вела к разделению на главные субгенерические группы рода ещё перед обледенением, т. е. самое позднее в конце третичного периода. Такого происхождения является например подрод *Trepidina* (с видом *canaliculata*, *bentelii*, *noricana*), *Triglavia* (с видом *spitzi*), *Psodos* (с видом *alticola*) и др. Другие формы (виды) — явственно более младшего происхождения и повидимому возникали географическим путём как правдоподобный продукт областной изоля-

ции популяций в интерглатциалах и интерстадиалах четвертного периода (напр. *noricana* — *bentelii*, *alpinata* — *wehrlii*) так как, хотя они и специфически оформлены, показывают ясную связь в развитии и общее основание развития. Этот процесс продолжается далее областной изоляцией настоящего времени отдельных видов и популяций в мимеоальпийских горах.

В карпатской системе были таким образом установлены до настоящего времени виды рода *Psodos* s. l.: *quadrifaria*, *alpinata*, *noricana*, *canaliculata*, *coracina* и *bentelii*, которые там образуют эндемические географические формы, которые можно таксономически оценить как субспеции, возникшие местной изоляцией и находящиеся на различной степени постепенной дифференциации на самостоятельные виды.