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A SOUTHERN CALIFORNIAN BOREUS, B. NOTOPERATES N. SP. I. COMPARATIVE MORPHOLOGY AND SYSTEMATICS (MECOPTERA: BOREIDAE)*

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Introduction

All but one of the 26 or so of the species of Boreus now known from Eurasia and North America (listed in Svensson 1972) are found chiefly within the bounds of north temperate or boreal forests where winters are cold. The northern margin of their distribution is roughly the o°C mean annual isotherm, in marked contrast to the more gentle climatic requirements of the vast majority of Mecoptera. Though distributional limits are now probably poorly known, the southmost regions from which Boreus have been reported have mean annual temperatures generally less than 12.8°C (55°F), and in all cases there is a winter period of snow cover. Because the adults are charming insects, bizarre and easily recognized but seen alive by but few, and are most often collected on the surface of snow, active and mating at temperatures below freezing, it is not surprising that a fairly large, markedly anecdotal literature has developed about them. Despite frequent notes and longer narratives (nowhere fully reviewed), there are few extensive accounts of their biology. Indeed Strübing's (1950) admirable study of Boreus hyemalis (L.) is the only substantial account available of the life history of a boreid.

My own experience with *Boreus* extends over many years. As others before me, I have always associated *Boreus* with cold, snow, fairly high annual precipitation (20 inches or more), and north temperate forest. It was with near disbelief that I found two female pupae of *Boreus*, on a very hot, dry autumn afternoon in an Upper Sonoran region of chaparral and yellow pine, in arid southern California. Not unexpectedly, this most southern of all *Boreus* proves to

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be new, and in a surprising number of ways it is the most specialized of all *Boreus*. In this account I describe *Boreus notoperates* n. sp., discuss its taxonomic relationships and specializations, offer reasons for disregarding *Euboreus* Lestage into which the new species would otherwise fall, and record the latitudinal dispersion of *Boreus* in the Holarctic. An account of the environment and discussion of host and habitat mosses, as well as other biological notes, will be the subjects of a second article.

DESCRIPTION

Boreus notoperates Cooper, n.sp.

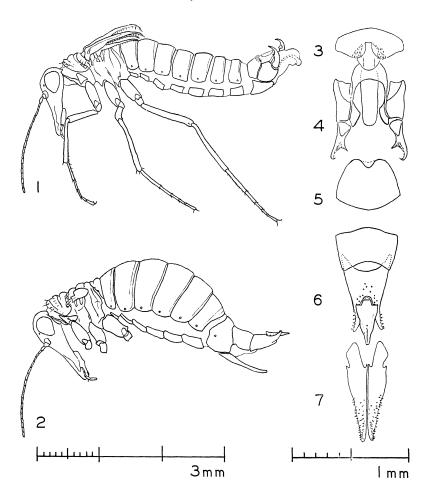
Diagnosis

Boreus notoperates n. sp. (figs. 1-2) may be separated from all other Boreus now known by the following combination of characters: male and female dark, with light wings; antennae 19-segmented, frons foveolate, no median ocellus, occipital foramen not divided by a sclerotized corporatentorium, hypostomal bridge very long; pronotum with 3 transverse folds; male: 2.7 mm long; forewing not spined on anterior margin; hindwing spined on posterior margin, without ventral brush; without tergal apophyses, 9th tergum with a glabrous, undivided, parallel-sided notch for styli; hypandrium emarginate; internal, submedian tooth of style simple, acute; female: 3.9 mm long; ovipositor short, cerci separated at tip, 10th tergum prolonged as a spined, upturned blade on each side of cerci; gonapophyses strongly spined laterally and ventrally.

Description

Coloration. Eyes plum-colored to brownish black; head, nota, procoxae and abdomen shining black with a bronze or greenish glint. Rostrum on sides, apically, and below, dark reddish brown. Flanks of thorax, meso- and metacoxae piceous or black, yet appearing ashen due to fine pubescence. Antennae and palps nearly black. Legs yellowish-brown to piceous, tarsi darker apically. Modified wings light brownish-yellow (sooty brown in one male) to yellow, those of male piceous apically, of female piceous at basal attachment. Gonocoxites and styli black, tips of styli flavescent. Ovipositor black; cerci black, flavescent or pallid laterally near tips.

Pubescence. Of male, gray, except bristles which are yellow to brown; moderately sparse on abdomen, as long or longer than basal width of metatarsus; denser and a third or less as long on thoracic pleura. Occiput glabrous, vertex and frons with sparse hairs as long as width of scape; on each side a triangular patch of fine silvery



Figs. 1-7. Boreus notoperates n. sp. All specimens in fluid, under moderate pressure from above; camera lucida representations. — Fig. 1. Male, aedeagus everted. — Fig. 2. Female. — Fig. 3. Epandrium and proctiger, dorsal aspect. — Fig. 4. Gonocoxites, dististyles and elongated median plaque that overlies aedeagus, dorsal aspect. — Fig. 5. Hypandrium, dotted line across notch denotes limit of hyaline membrane present in teneral male, ventral aspect, apex above. — Fig. 6. Ninth and succeeding terga of ovipositor, dorsal aspect. — Fig. 7. Gonapophyses, ventral aspect, apex below.

pubescence in a depression running from ocellus to margin of antennal condyle; patch of 5-10 hairs at clypeal base, but no rostral subocular patch, only scattered hairs; few, fine hairs on stipes. Forewings with coarse, scattered, yellowish hairs. Long white hairs on anterior and posterior faces of pro- and meso-coxa, and anterior face of metacoxa. Abdominal pubescence somewhat longer, denser ventrally and toward sides; tergum I glabrous medially, as are t4 to t7 medially and, increasingly so, laterally.

Of female: much as in male, except pubescence appears yellowish, and everywhere somewhat shorter; patch at base of clypeus may be absent; but few long hairs on posterior surfaces of pro- and mesocoxae. Abdominal pubescence denser, posterior margins of terga polished, nearly glabrous, as are most of terga 8 and 9.

Head. Rostrum (from lower margin of eye to apex) ca. 2.1 times length of eye in male, 2.6 times in female; longer than protibia in female, slightly shorter in male. Eye slightly longer than broad, narrowed below. Antenna with 19 segments, condyle opposite lower margin of eye; scape much wider than long, pedicel swollen in apical third and shorter (by one-fifth) than the combined lengths of segments 3 and 4. Ocelli small, median ocellus lacking. Frons and sides of vertex coarsely foveolate. Occipital foramen single, not divided to an alaforamen and neuroforamen by a sclerotized corporatentorium. Hypostomal bridge (between occipital foramen and cardo) very long, longer than length of eye in female, somewhat less in male.

Thorax. Of male: pronotum polished, with occasional transverse wrinkles; strong anterior and posterior transverse grooves divide the pronotum into anterior, median and posterior transverse folds of widths roughly as 2:3:1; on each side: two or three long (and several shorter) bristles on anterior lobe, three or more shorter bristles on median fold, and two to four long bristles set in transverse, more or less confluent depressions along hind margin of posterior fold in front of wing base. Outer margin of forewing nearly straight in dorsal aspect, inner margin slightly concave behind basal third; hind margin with ca. 15 (range: 13-18) strong marginal spines below which are directed obliquely outwards; only vestiges of spines on front margin; hooked apex terminates in a pair of strong apical bristles. Hind wing shorter, glabrous, with ca. 16 (range 13-20) stout spines below, no ventral brush of fine pubescence; apex hooked, spatulate at tip. A dark spine at apex above each femoral anterior condule.

Of female: pronotum similar, but widths of pronotal folds roughly 3:4:1; bristles of posterior fold in shallow depressions. Forewing pad nearly twice as long as broad, without marginal spines, completely covering atrophied hindwing. Femoral spines as in male.

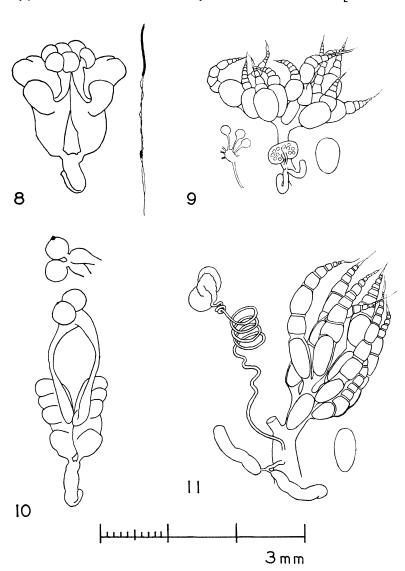
Genital Segments. Of male (figs. 3-5): eighth tergum and sternum, and 9t and 9s not fused at their respective pleural junctions; ninth tergum deeply infolded for reception of styles, the notch-like pocket with nearly parallel sides, glabrous within and not divided; a loose cluster of short spines (12-15±) externally on each lateral border of notch. Dististyles with a row of 15± short spines along apical one-third of inner margin; submedian internal tooth acute, not keel-like, relatively short; a membranous element lies within an ovate fenestra (or stylocavernula), broadest basally, on inner surface of each dististyle just distal to the submedian tooth. Hypandrium broad, strongly emarginate apically (emargination may be partially closed by a hyaline membrane which is lost or worn away in older individuals).

Of female (figs. 6-7): ovipositor short, from base of tergum 10 to apices of cerci about two-thirds length of rostrum (from lower margin of eye to tip). Tenth tergum prolonged on each side as a pair of upwardly curved divergent blades bearing 4-6 strong spines above, tips of blades reach distal third of cerci; cerci separated apically; gonapophyses strongly spined laterally in apical halves.

Reproductive System. Of male (fig. 8): each testis consists of four lobes or "sperm tubes", each ensheathed in a rich russet-brown tunic, right testis slightly anterior to left, the apices of the two testes reaching only slightly cephalad of swollen main portion of vas deferens (that is, the "accessory gland"); calyx and efferent vas of each testis short, thick; vas deferens tapering markedly to juncture of accessory gland; accessory gland with 4 lobes, externally poorly delimited; lateral ejaculatory ducts barely demarcated; median ejaculatory duct strong, very muscular, U-shaped; fleshy aedeagus trilobed when everted. Spermatozoan (fig. 8) 87-96 μ long: head 22-26 μ long; tail with an "undulatory membrane".

Of female (fig. 9): Six ovarioles per ovary, each ovariole with 7-11 panoistic egg chambers conjoined apically to ovarian ligament which unites with that of other ovary; ovariolar pedicels irregularly conjoined to common ducts which merge to form a calyx; lateral oviducts short; common oviduct nearly as long as an ovary; spermatheca reniform, enclosing 24 sperm receptacles, 12 per side; spermathecal duct very short (less than short axis of spermatheca) arising

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from hilus of spermatheca, entering common oviduct at its caudal third; a pair of elongated, tubular accessory glands join oviduct by a very short common duct immediately posterior to entrance of spermathecal duct. Mature egg (fig. 9) buffy-white, from 0.53 \times 31 mm to 0.60 \times 30 mm, slightly narrowed at one end; chorion smooth.

Measurements (in millimeters; in each case ordered thus: mean of measurements, [range of measurements], number of examples measured.): Males, body length (in 70% isopropyl alcohol) — 2.7 [2.6-2.9] 5; body length (dry) — 1.9 [1.5-2.5] 9; antennal length — 1.66 [1.4-1.9] 13; rostral length (eye to tip) — 0.7 [0.6-0.8] 13; forewing length — 1.0 [0.9-1.1] 13.

Females, body length (in alcohol) — 3.9 [3.4-4.2] 6; body length (dry) — 3.0 [2.7-3.6] 5; antennal length — 1.7 [1.5-1.9] 10; rostral length — 0.9 [0.8-1.0] 10; forewing length — 0.3 [0.27-0.34] 10; ovipositor length (base of tergum 10 to tip) — 0.6 [0.56-0.64] 10.

Holotype. Male: 2.5 cm long (dry mount), collected 8 January 1972; Allotype, Female: 3.6 mm long (dry), collected 27 December 1970; 15 male and 12 female paratypes, collected 31 December 1971 to 22 January 1972. All specimens from Coldwater Canyon, ca 4400 ft altitude, below the town of Mountain Center (at 33° 42′ N/ 116° 44′ W), Mt. San Jacinto, Riverside Co., California; collected by Geoffrey, Tera, Ruth and K. W. Cooper.

Types and 2 paratypes are deposited in the Museum of Comparative Zoology at Harvard University where types of the majority of North American species are located. A pair of paratypes has been placed in each of the following collections: U. S. National Museum, California Academy of Sciences, Snow Entomological Museum (University of Kansas), and the University of California at Riverside. Dissections and remaining specimens are in my collection.

Figs. 8-11. Boreus, reproductive system. All figures in dorsal aspect; camera lucida representations.—Fig. 8. Male, B. notoperates n. sp., 4 lobes per testis; right testis lies anterior to left, tilt conceals 2 of the 4 lobes; to right, mature spermatozoan.—Fig. 9. Female, B. notoperates, 6 ovarioles per ovary; to left, spermathecal vesicles and connections to assembly-duct; to right, mature (laid) egg—the chorion is smooth.—Fig. 10. Male, B. nivoriundus Fitch, 1 lobe per testis, right testis anterior to left; above, testes from right side—note that a short efferent duct from each testis enters a common (fused) calyx; testes are mottled with an orange-brown pigmentation.—Fig. 11. Female, B. nivoriundus, 7 to 10 ovarioles per ovary; there are 8 ovarioles in the figured right ovary; to right, mature (laid) egg—the chorion is microscopically vermiculate.

Etymology. The name notoperates derives from the Greek: notos, masc., south, and perates, masc., wanderer, alluding to the remarkable extension by this species of the range of Boreus to the south.

RELATIONSHIPS

Males of Boreus notoperates will classify as B. isolatus Carpenter when Carpenter's keys (1935, 1936) for North American Boreus are used. However, they strikingly differ from that species by their considerably longer rostrum (ca 2.1 × eye-length; "scarcely longer than the eye" in B. isolatus). Females of the new species will be excluded at couplet 7 (revised key, Carpenter 1936) because the ovipositor of B. notoperates is but two-thirds the length of the rostrum.

The only known North American form with which B. notoperates might be confused is the closely related B. brevicaudus Byers (1961). These two are markedly alike by having a reduced number of antennal segments (most Boreus have 21 or more), condules of antennae opposite lower margins of eyes, no median ocellus, a long hypostomal bridge, no epandrial "hood", and the 10th tergum of the female is abruptly narrowed on each side to form a pair of spined terminal blades. However they are readily distinguished in both sexes, for B. notoperates has 19-segmented antennae (18 in B. brevicaudus), the frons more conspicuously foveate, a more heavily and richly spined area to each side of the epandrial notch, a very much shorter, inconspicuous submedian tooth of the dististyle, an emarginate hypandrium (entire in B. brevicaudus), a relatively longer forewing in the female (L/W = 1.7 \times ; 1.3 \times in B. brevicaudus) which lacks subapical spines, a relatively longer ovipositer (0.67 × rostrum versus 0.5 ×) with more coarsely and extensively spined gonapophyses and apical blades, and the apical blades are divergent. Though color differences are often of little weight, the males of these two species have the color patterns of their genital segments and dististyles reversed; what is dark in the one is light in the other, possibly continuing a distinction important at a time that their progenitors were sympatric.

At least four of the twelve recognized Eurasiatic forms share with B. notoperates (and B. brevicaudus) the following set of characters: a reduced number of antennal segments (21 or less), a relatively short ovipositer, a male having the forewing narrow at base and no (or nearly no) apophyses on abdominal terga 2 and 3, namely B. chadzhi-gireji Pliginsky (1915) and B. vlasovi Martynova (1954),

each with 19 antennal segments, B. navasi Pliginsky (1915) (20 segs.), and B. bey-bienkoi Tarbinsky (1962) (21 segs.). To these may perhaps be added B. aktijari Pliginsky (1915), described from a single female said by Pliginsky to have 19-segmented antennae and to be very like his B. chadzhi-gireji¹. Nevertheless large differences separate each of these species from B. notoperates and B. brevicaudus. None of the Eurasiatic species have the apex of tergum-10 abruptly modified as a blade on each side; B. chadzhi-gireji and B. vlasovi have the 9th tergum of the male fused laterally with its sternite (Martynova, 1954) (a free suture is present in both American forms)2; and males of B. navasi and B. bey-bienkoi have apical brushes of fine pubescence on the under surfaces of the hind wings (absent in the two American forms). It is likely that all 5 of the Eurasiatic species have short hypostomal bridges, like most Boreus but unlike B. notoperates and B. brevicaudus; regrettably this is definitely known to be so only for B. chadzhi-gireji (see Pliginsky, 1915, fig. 9).

STATUS OF EUBOREUS

I have not used the generic name Euboreus (genotype Boreus nivoriundus Fitch) which Lestage (1940-41) proposed for all boreids of which the males lack transverse apophyses on abdominal terga 2 and 3. Lestage would restrict Boreus (genotype Boreus hyemalis

²Mickoleit (1971b) has briefly discussed the fusion of the 8th abdominal tergum and sternum in male Boreus. The condition of the 8th (and 9th) abdominal segments in male Boreus, however, is more complicated than he knew. Symbolizing such fusion with +, we have for the palearctic species: Boreus orientalis (8+, 9+), B. chadzhi-gireji (0, +), B. semenovi (0, +), B. vlasovi (0, +), B. hyemalis (+, 0), and B. westwoodi (+, 0) (see Martynova 1954); for the nearctic species: B. borealis (+, 0), B. californicus (+, 0), B. coloradensis (+, 0), B. brevicaudus (0, 0), B. brumalis (0, 0), B. nivoriundus (0, 0), and B. notoperates (0, 0). It seems that such fusions have little to tell of the larger affinities of Boreus that Mickoleit discusses, yet it seems clear that these fusion-patterns must feature importantly in any world-wide taxonomic revision of Boreus as now constituted.

¹According to Martynova (1954), Pliginsky's types of B. navasi and B. aktijari cannot be found, but his specimens of B. chadzhi-gireji were studied by her. She states that the tergal apophyses are almost (pochti) absent in the males of B. chadzhi-gireji. Pliginsky (1915) did not describe the male of this species, but merely observed, in his commentary in German (there is an obvious misprint in the corresponding text in Russian), that it differs from that of his B. navasi only by having 19 antennal segments; but the male of B. navasi is pointedly stated by him (p. 365) to be without apophyses on abdominal terga 2 and 3.

(L.)) to include only those species having such apophyses, an assemblage of species geographically restricted to western Eurasia which he believes to represent a derivative, more highly evolved, endemic palearctic lineage. So far as now known, Lestage's Boreus would include only four or five species: B. hyemalis (L.), B. westwoodi Hagen, B. lokayi Klapalék, B. kratochvili Mayer, and B. chadzhi-gireji to judge from Martynova's (1954) remarks. If recognized, Euboreus would encompass all, or nearly all, of the remainder, some 15 North American species and at least 5 of the Eurasiatic forms: B. navasi, B. semenovi, B. orientalis Martynova, B. vlasovi, and B. bey-bienkoi (no males are known for either B. aktijari or B. sjoestedti Navás, 1926). In Lestage's view, the species falling into Euboreus represent "un type paléoendémique primitif", an important notion (were it true) which features prominently in his evolutionary explanation of boreid zoogeography.

One test of the degree to which Lestage's two genera are useful concepts is to enquire whether other characters, not ordinarily employed in taxonomics, independently suggest that these aggregates do reflect important phyletic distinctions even though main, externally visible characters traditionally used in diagnosis are shared by certain members in each of Lestage's two genera. Certainly it would seem to be so if forms placed in *Euboreus* share as a group important internal and cytological dissimilarities from the members of Lestage's *Boreus*.

There is not much information to draw upon, but what there is The reproductive systems of Boreus hvemalis seems conclusive. (Steiner 1937; Potter 1938) and "Euboreus" brumalis (Cooper 1940) are strikingly dissimilar in lobulation of testis, testicular calyx, and spermatheca, as well as in their sex chromosomal complements. I have found that B. hyemalis has an XO (male) - XX (female) sex determination. "Euboreus" brumalis, however, has X_1X_2Y — males and $X_1X_1X_2X_2$ females (Cooper 1951). Nothing is known of the chromosomes of "E." notoperates, nor have others described the chromosomes of additional species. But the genital systems of "E." notoperates (figs. 8-9), though peculiar by possession of a very short vas deferens, one less lobe per testis, and a distinctively organized spermatheca which has a duct of negligible length, are not as unlike those of "E." brumalis as they are those of B. hvemalis. Indeed the chief distinctions shown by "E." notoperates may be viewed as larger departures along the same paths as those by which "E." brumalis differs from B. hyemalis, and thus wholly consistent with Lestage's views.

However, I find that the genotypic species of Euboreus, namely B. nivoriundus, has XO (male) — XX (female) sex determination and genitalia that are extremely similar to those of B. hyemalis; thus the testes are single lobed and have fused calyces (fig. 10), and there is an extremely elongated spermathecal duct in the female (fig. 11) that is "coiled like a watch spring", just as Potter (1938) described it for B. hyemalis. Interestingly, XO-XX male heterogamety is the general mode of sex determination for the Mecoptera so far studied (Panorpa, Ullerich 1961; Bittacus, Matthey 1950; Chorista, Bush 1967; and Merope, Cooper, unpublished)³, and is most probably primitive; primitive also is the very elongated spermathecal duct, a condition which Potter (1938) places among the five "most striking of the typically Mecopterous characters of the order".

There are, therefore, no grounds at present for viewing Lestage's Euboreus as a useful taxonomic set, or even for attributing to its members as a group the emphasis which Lestage gave them as more primitive forms. Quite to the contrary, "E." notoperates indeed seems to be the least primitive among all the Boreus known. Its "advanced" characters include the long hypostomal bridge, loss of the median ocellus and the corporatentorial bridge⁴, loss of the brush of fine pubescence on the hind wing, the unparalleled reduction of the submedian tooth-complex of the dististyles, the peculiar apicolateral blades of the 10th tergum of the female, and the distinctive spermatheca with its very short duct — all exceptional departures from the usual conditions in the Boreidae. Except for the marked reduction of the submedian complex of the dististyles, B. brevicaudus shares all of the external peculiarities with B. notoperates, and quite likely it possesses most or all of the remaining anatomical departures as well. These two Boreus, then, are the most specialized boreids known. Conversely, members of Lestage's "Boreus" have a quite generalized morphology, and should the tergal apophyses of their males prove to be vestiges of notal appendages homologous to those of Notiothaumids, Panorpids, and Panorpodids (Crampton 1931; Mickoleit 1971a), they are evidently the most "primitive" forms known (but see ftnt. 2). At best they comprise a species-group within Boreus as now defined, namely the hyemalis-group.

³Also see Atchley and Jackson (1970).

^{*}Boreus nivoriundus (Otanes 1922), B. hyemalis (Slais 1947), B. unicolor and B. californicus (Hepburn 1969), and as I have found for B. brumalis, have 3 ocelli and a divided occipital foramen. At present the Boreidae is the only family of Mecoptera within which the number of ocelli varies, and in which the occipital foramen occurs in both states: divided and undivided (see Hepburn's fine study).

EXTENT OF THE LATITUDINAL RANGE OF BOREUS

Boreus notoperates now provides the southmost record (33.7°N) of all known species of Boreus. Nevertheless, in eastern North America, B. nivoriundus and B. brumalis extend nearly as far south. Both range from Jackson, New Hampshire (Dohanian, 1915) and Ellsworth, Maine to Tennessee, in the Great Smoky Mountains at 4000 ft (Carpenter 1931, 1939; Cole and Gillespie 1950), namely from 44.8°N to a latitude perhaps as low as 35.4°N. In the far West B. californicus Hine has a comparable range: from Kaslo, British Columbia (Carpenter 1931) to Hobart Mills, Nevada Co., California (new record), or from about 49.9°N to about 39.4°N. In the West, only B. notoperates has been found south of 39°N. The total latitudinal range of *Boreus* in North America is therefore from the vicinity of McCarthy and Kennicott (ca 61.5°N in Alaska, B. intermedius Carpenter and B. gracilis Carpenter; Carpenter 1935. 1936) to Mt. San Jacinto (33.7°N) in California, a total range of nearly 28° of latitude, or about 1900 miles.

Were Lestage's (1940, p. 16; 1941, p. 119) listing of Persia a valid record for the range of *B. lokayi* Klapálek, it would perhaps provide the most southern outpost of *Boreus* in Eurasia. It is an error evidently originating from Enderlein's (1910) rendering of the type locality⁵, which had been cited simply as *Sedmihrad* by Klapálek (1901). Now "Sedmihrad" is Czech for Siebenbürgen (Transylvania, now in Rumania), and Klapálek (1903) leaves no doubt for he says he has many specimens of *B. lokayi* that were collected by Lokay "in Buczecz in Siebenbürgen".

Nevertheless it is an odd coincidence that *Boreus* has been found just across the northern border of Iran, providing the southmost record in Eurasia. It is that for *B. vlasovi* from Ashkhabad, Turkmen S. S. R. (ca 37.9°N) (Martynova 1954). The northmost record is that of *B. westwoodi* from the island of Kil'din (69.3°N), slightly NE of Murmansk, U.S.S.R. (Tarbinsky 1962). Although *Boreus* ranges nearly 8° farther to the north, it has a known latitudinal range in Eurasia not quite 4° greater (about 250 miles)

⁵". . Boreus lokayi Klap. 1903 (Persien, Sedmihrad) . ." thus, Enderlein (1910, p. 394). Perhaps Enderlein refers to the Muntii Persani of the Sedmihrad that, near Brasov, run north from the southern Carpathians of which the Bucsecs (Buczecz, M. Bucegi) is a member. If so, it may represent a valid, otherwise unrecorded locality of capture, in addition to the type locality. The most recent record for B. lokayi appears to be that of Miller and Povolny (1950): High Tatra Mountains, about 1600 m, Czechoslovakia.

than that in North America — a datum of considerable ecologic and zoogeographic interest.

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