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O PŮVODU HOLARKTICKÝCH DRUHŮ RODU AMARA BON.

THE ORIGIN OF THE HOLARTIC SPECIES OF THE GENUS AMARA BON

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O původu holarktických druhů rodu Amara BON.

О происхождении голарктических видов рода Amara BON.

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(22. příspěvek k poznání *Carabidů*. Contribution 22 to knowledge of *Carabidae* [Coleoptera].)

V anglické části textu se zabývám studiem původu holarktických druhů rodu *Amara* BON. Doposud bylo v literatuře uváděno 12 euroasijských druhů, vyskytujících se také v Severní Americe.

U tří druhů, a to u *A. aenea* DEG., *A. familiaris* DUFT. a *A. aulica* PANZ., byla identita severoamerických a euroasijských exemplářů prokázána jejich vzájemným srovnáním podle povrchových znaků (bez mikroskulptury) a snad tomu tak bylo i u dalších tří druhů, a to u *A. fulva* DEG., *A. lunicollis* SCHIÖDTE a *A. bifrons* GYLL. Z nich *A. aenea* DEG. je mi ze Severní Ameriky známa in natura a její identitu s euroasijskými populacemi jsem si ověřil podrobným srovnáním. Biologická a zoogeografická data nám potvrzují, že všech sedm druhů bylo do Severní Ameriky zavlečeno. Také *Amara anthobia* VILL. byla podle literatury v poslední době zavlečena do Severní Ameriky, identitu však bude nutno teprve ověřiti srovnáním s evropskými exempláři.

Amara brunnea GYLL., rozšířená po celé severnější části palearktické oblasti, je udávána i s Aljašky. Jsou-li skutečně severoamerické a euroasijské populace totožné, je zřejmo, že druh osídlil Severní Ameriku ze severovýchodní Sibiře přes Beringovu úžinu.

Přes Beringovu úžinu osídlila Severní Ameriku i *Amara erratica* DUFT., kterou podrobně studovali HOLDHAUS a LINDROTH (1939). Možná, že podobných vlastností je i *A. interstitialis* DÉJ., její výskyt v Severní Americe bude nutno teprve potvrditi.

Zcela neověřená totožnost severoamerických a evropských či euroasijských populací a nejasný původ byly u druhů *A. apricaria* PAYK. a *A. convexiuscula* MARSH. Oba druhy jsem podrobil důkladné morfologické revisi a poněvadž oba mají oedeagus stavěný na rozdíl od většiny ostatních druhů rodu *Amara* BON. poměrně komplikovaně, mohl jsem u nich dojíti k závěrům poměrně spolehlivým. Podle toho, i podle zoogeografických a biologických vlastností, jsou severoamerické populace druhu *A. apricaria* GYLL. zcela totožné s euroasijskými a byly zřejmě do Severní Ameriky zavlečeny.

Jinak je tomu u druhu *A. convexiuscula* MARSH. Severoamerické populace vykazují velmi subtilní, avšak konstantní diferenciaci od populací evropských (v Asii se druh nevyskytuje) a tato postihuje zvláště primární znaky (na oedeagu). Je proto zcela vyloučeno, aby druh byl do Severní Ameriky zavlečen. Přitom je diferenciace severoamerického vikarisujícího druhu tam malá, že — vzhledem k dosti velké plasticitě druhu *A. convexiuscula* MARSH. (vytváří v Evropě 2 rasy) — je nanejvýš nepravděpodobno, že by populace původního společného druhu přešly z Evropy do Severní Ameriky již ve starších třetihorách, kdy byly možné podle teorie posunu kontinentů větší výměny faun, protože oba kontinenty spolu ještě souvisely. Podle stupně diferenciace u původního druhu, z něhož se *Amara convexiuscula* MARSH. a její severoamerický vikariant diferencovali, se přechod z Evropy do Severní Ameriky udál patrně v mladších třetihorách, snad krátce před počátkem ledových období, nanejvýše však v nejstarších interglaciálech. Bez ohledu na to, zda je správná teorie posunu kontinentů či ODHNERova teorie smršťování (MALAISE, 1945), je však nejpravděpodobnější, že přechod druhu se nedál pouze po souši, nýbrž že druh překonával pasivním přeletem či anemohydrochorně i určité části moře, i když tato byla jistě menšího rozsahu nežli dnes v oněch místech. Lze tak usuzovati i z toho, že diferenciace, s jakou se setkáváme u komplexu vikariantů *A. convexiuscula* MARSH., je mezi *Carabidy* ojedinělá. Podrobněji se celým problémem zabývám v anglickém textu. Za jeho laskavý a pečlivý překlad děkuji paním Doc. Dr. J. Moschelesové a Dr. G. Hortové z přírodovědecké fakulty Karlovy university.

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В английской части работы подаю данные изучения голарктических видов рода *Amara* Bon. До сих пор в литературе приводится 12 евразийских видов, которые встречаются также и в Сев. Америке.

Идентичность трех видов из Северной Америки и Европы, *A. aenea* DEG., *A. familiaris* DUFT. и *A. aulica* PANZ., была установлена сравнением их внешних знаков (без изучения микроскопической скульптуры). и вероятно так это было и у следующих трех видов — *A. fulva* DEG., *A. lunicollis* SCHIÖDTE и *A. bifrons* GYLL. Из них *A. aenea* DEG., я наблюдал североамериканскую in natura, а в её идентичности с европейскими популяциями удостоверился подробным сравнением. Биологические и зоогеографические данные нас укрепляют во мнении, что всех семь видов в Сев. Америку были перенесены. И *Amara anthobia* VILL. по литературным сведениям последнего времени была также перенесена в Сев. Америку, но идентичность ещё необходимо установить сравнением с европейскими экземплярами.

Amara brunnea GYLL., распространенная во всей северной части палеарктической области была найдена и в Аляске. Являются ли действительно североамериканские и европейские популяции идентичными, то очевидно этот вид попал в Сев. Америку из северовосточной Сибири через Берингов пролив.

Через Берингов пролив перешла в Сев. Америку *Amara erratica* DUFT., подробно изученная HOLDHAUSom и LINDROTHom (1939). Возможно, что и *A. interstitialis* DÉJ. принадлежит к этим видам, но её нахождение в Северной Америке ещё необходимо установить.

Совершенно не была установлена идентичность североамериканских и евразийских популяций и уяснено происхождение видов *A. apricaria* PAYK. и *A. convexiuscula* MARSH. Я подверг оба вида основательному морфологическому сравнению а так как оба вида отличаются от остальных видов рода *Amara* Bon. сравнительно сложным копулятивным органом (oedeagus), мог притти к довольно надежным заключениям. По морфологическим, зоогеографическим и биологическим особенностям являются североамериканские а евразийские популяции вида *Amara apricaria* GYLL. вполне идентичными и были очевидно в Сев. Америку перенесены.

Иное явление наблюдаем у вида *A. convexiuscula* MARSH. Североамериканские популяции отличаются от европейских видов (в Азии вид не встречается) очень тонкими, незначительными, но за то постоянными различиями в особенности по примарным признакам эдеагуса. Поэтому можно совершенно исключить завлечение этого вида в Сев. Америку. При этом различия североамериканского вида так малы, а вид *A. convexiuscula* MARSH., образующий в Европе 2 расы, так пластичен, что является совершенно невероятным переход популяций первоначально совместного вида из Европы в Сев. Америку ещё в раннем тритичном периоде, когда, согласно теории передвижения материков были возможны большие передвижения фауны, так как материки ещё не были отделены. По степени дифференциации первоначального вида от которого *Amara convexiuscula* MARSH. и её североамериканская вариация дифференцировали, переход из Европы в Сев. Америку вероятно произошел в младшем третичном периоде, или незадолго перед началом ледникового периода, возможно не позже самого старшего междуледникового периода.

Независимо от того правильна ли теория передвижения материков или теория сврашения ODHNERA (MALAISE, 1945) является наиболее вероятным предположение, что вид переходил не только по суше, но был и пасивно перенесен (анемогидрохорически) через определенные морские участки, которые в то время были в тех местах меньшими чем теперь. Это можно предполагать и потому что дифференциация с какой мы встречаемся у викарирующего вида *Amara convexiuscula* MARSH., является среди *Carabidae* исключительной.

Более подробный разбор явлений приведен в английском тексте.

The origin of the holartic species of the genus Amara Bon.

The investigation of the North American and European (Eurasian) faunas and their mutual relations yields much material which can help us to solve questions of paleozoogeography and evolution. Most authors, especially those of the last century, did not, however, deal with the study of these mutual relations as they worked only on one or the other of these two faunas. Thus it came about that a number of species occurring simultaneously in both continents, were known by one name in Europe and by another name in America. The name of the species, published later, had of course to be placed as synonym to the older name. Subsequently, however, morphological, and especially anatomical investigation proved that some of the combined species were really separate, usually vicariating species.

The task of this paper is therefore to elucidate the relations between the North American and European populations of some species of the genus *Amara* Bon. *(Coleoptera, Carabidae)*. Owing to lack of material I can only deal with the question of conspecifity, but am unfortunately unable to follow in detail the distribution of these species in North America. From the biological, morphological and zoogeographical data it is, however, possible to conclude to the origin of the North American populations.

Amara (Bradytus) fulva DEG.

This species occurs according to Lindroth (1945, pp. 132—134) only in the western part of the palearctic region, from Ireland and Southern Spain in the west to Western Siberia in the east, and from Mittle Sweden and the basin of the Pechora (USSR) in the north to Southern Italy, Bulgaria and Asia Minor in the south. Leng (1920, p. 60) recorded it with a question mark from New Foundland.

Brown (1940, 1950) records from North America a number of specimens from Quebec, New Brunswick, and New Foundland, where according to him the species was indubitably introduced. Already from this it is evident that it lives in the sand on the shores of rivers and of the sea and is able to fly.

Amara (Bradytus) apricaria PAYK.

The species *Amara apricaria* was described by Paykull (1798, p. 162) from Sweden; it is distributed through most of the palearctic region (Jakobson, 1905, p. 361; Lindroth, 1945, pp. 103—105); in North America it was not ascertained until 1896, by Wickham[1]) (1896, pp. 37 to 38), and it is reported from there also by Hayward (1908, pp. 41—42) and Casey (1918, pp. 237, 238). Not one of these authors proves, however,

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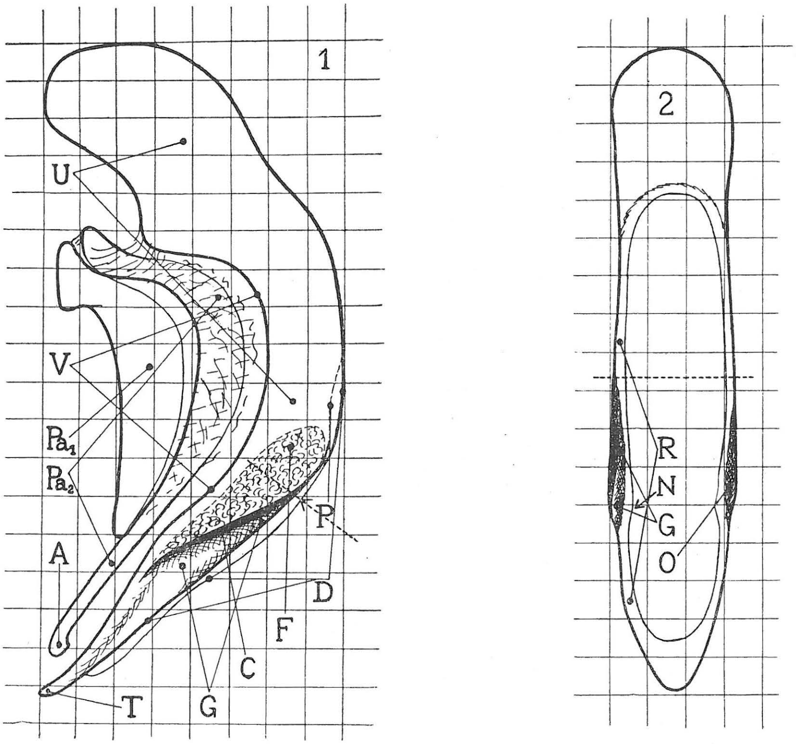
[1]) If of course *Amara Putzeysi* Horn. described already in 1875 after one female from New Foundland is not a synonym of *apricaria* Payk., as Wickman (l. c.) suspects.

the conspecifity by a detailed comparison of North American and European specimens, and thus I carry out here this comparison.

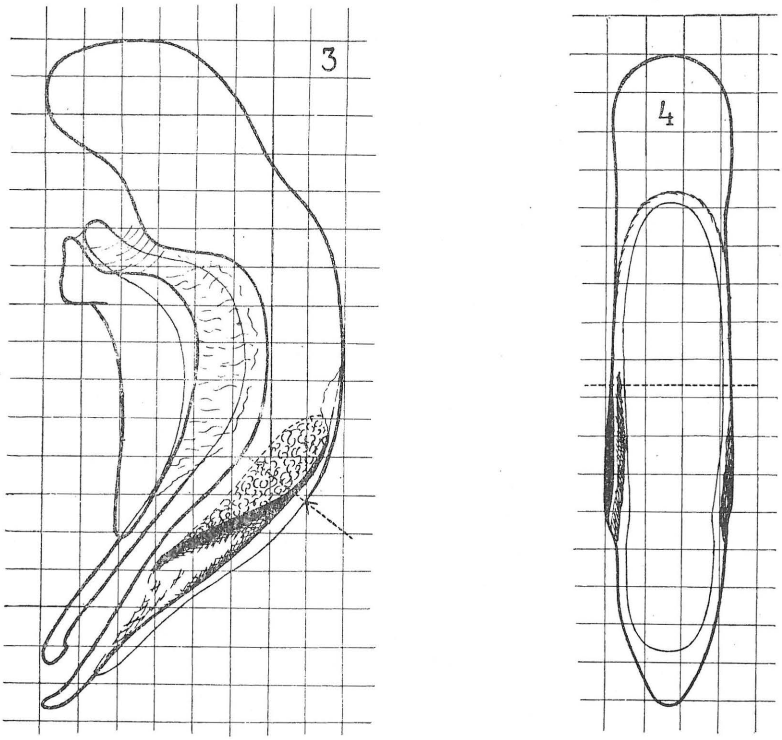
I obtained for my collection two males of this species from Canada (Sask., Redfield, V-VI 1948, leg. ?, ex coll. K. Kult) and compared them with specimens from Sweden (Abisko, Laponia, VIII 1948, leg. Tesař, in the collections of the Provincial Museum at Opava 2 ex., in my collection 1 ♂), with my specimens from the Baltic (Rügen, Sellin, VIII 1908, 2 ex.), from Central and Eastern Europe (a fairly large number of specimens from various localities), from the Caucasus (USSR, Teberda, leg. ?, 5 ex.), and from Siberia (USSR, Werchne Udinsk, leg. Biener, 1 ♀).



Oedeagus of the species *Amara apricaria* PAYK. from Canada (Redfield, Sask.). — Fig. 1: View from above, with parameres. Fig. 2: View from the outer side (= dorsally), without parameres.
Thin lines are either outlines, hidden in a view from above, or weakly or inaccurately delimited contours, or contours of slightly chitinose parts. Magnification 50 × so that one square of the net corresponds to 0.01 sq. mm. The broken straight line in figs. 1 & 3 indicates the plane in which we observe the oedeagus in the view from the outer side in figs. 2 & 4. Other explanations in the text.

Though I examined in detail all characters which I give in the descriptions of the new species of the genus *Amara* BON. (e. g. FASSATI, 1949 b), I did not find one single character by which these two Canadian specimens would differ from the Eurasian ones. Also the microstructure of the elytra is completely the same.

When we compare the oedeagi of the Canadian specimen (see figs. 1 and 2) and of the specimen from Rügen (see figs. 3 and 4) we do not find any difference here either. From above size and shape are practically the same (figs. 1 and 3); this holds good for the shape of the oedeagus in a view from the outer side (figs. 2 and 4), for the shape of the tip (T) of the oedeagus, of the upper paramere (Pa_1), and for the apex (A) of the lower paramere (Pa_2). Both oedeagi also maintain completely the most characteristic features on the upper side (U) of the oedeagus. On the upper side there is developed at a distance of about one fifth of the length of the oedeagus from the tip (T) of the oedeagus a strongly chitinose carina (C), whose length is about one fourth of the length of the oedeagus, and which seen from above stretches across the flat upper surface of the oedeagus almost from the inner [= ventral (V)] to the outer [= dorsal (D)] margin. Between this carina (C) and the outer margin (D) (i. e. its upper part) of the oedeagus there is a distinct groove (G). This groove reaches into the



Oedeagus of the species *Amara apricaria* PAYK. from the island of Rügen (Germany). — Fig. 3: View from above, with parameres. Fig. 4: View from the outer side (= dorsally), without parameres. — Other explanations as in figs. 1 & 2.

rim (R) of the upper margin of the oedeagus, which is therefore in these places distinctly expanded (N). The underside of the oedeagus has also a similar groove (O) in an approximately similar position. The part (P) of the upper outer margin above the carina (C) is only slightly chitinose. From here in the direction obliquely downwards, i. e. apically, we can just see with an illumination and lighting-through of a certain intensity a tattered formation (F) looking as if studded with pits under the flat upper side of the oedeagus.

Also the oedeagi of the second male from Canada, of the male from Abisko and of the other specimens mentioned are conspecific with the two specimens just described and figured above, though it is often not possible to observe the tattered formation (F) in them.

From the comparison made it is therefore certain that *Amara apricaria* PAYK. really occurs in North America and obviously does not even form there a separate race. This striking morphological identity of the populations of North America and Eurasia strongly lessens the probability that *Amara apricaria* PAYK. could be a primary species in North America, and also the biological factors speak against this.

Amara apricaria PAYK. is a species which is very abundant in the whole of Northern and Central Europe; it is relatively euryoecal, living in culture steppes (steppicol, campicol), along roads, in loam-pits, in rubbish heaps (ruderally), etc. As stated by LINDROTH (1945, p. 104) *A. apricaria* PAYK. lives especially in the northern part of Scandinavia considerably synanthropically. It is a fully winged species, often observed in flight in light (e. g. LINDROTH l. c.; HORION, 1941, 269)[2]; also in daylight flights in quantities are recorded[3]) (e. g. LUTSHNIK, 1936, p. 141; LINDROTH, 1948, p. 846).

It can thus be taken as very probable that *A. apricaria* PAYK. was introduced into North America by boats from Europe, all the more so because its distribution in North America is according to WICKHAM (1896, p. 38), HAYWARD (1908, p. 42), and CASEY (1918, p. 238) confined to a broad strip of the Atlantic coast from New Jersey to the St. Lawrence Gulf and New Foundland, and to the Canadians Lakes. In these areas it obviously spread from one or more port centres and multiplied so as to be here according to CASEY (l. c.) an abundant species. Today it is apparently still more widely distributed, as may be seen from the locality of my specimens.

Some species of the genus *Amara* BON., especially the steppicol and xerophile species, have multipled strongly in Central Europe owing to the spread of culture steppes and the setting in of a dryer, more continental climate in the last two thousand years (so-called expansive species). Most of these species have a strong vagility, and therefore spread very quickly so that their advance into new territories can be followed in historical times and often directly in the present time.

An example of such an expansion is given by the palearctic species *Amara majuscula* CHAUD. which was described from Eastern Siberia

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[2]) At Ústí nad Labem 10 specimens flew 15—30 VIII 1951 into the flat of J. Strejček attracted by light.

[3]) I myself observed it in flight: Praha VII, 24 VIII 1949, hot afternoon.

and has been recorded also from Mongolia, China and Tibet (TSCHITSCHERINE, 1898, p. 214). This species lacks completely from Europe in old collections (LINDROTH, 1945, p. 150). In Fennoscandia this *Amara* was ascertained for the first time by LINDROTH (1943, pp. 50—52) according to one specimen caught in 1923 and several others of 1936 and later years. In recent years its occurrence in Fennoscandia is frequent (LINDROTH, 1948, pp. 623—625, 848); it was caught several times in flight towards light, by Ing. Makólski in Warsaw even in masses (LINDROTH, l. c.). It is still lacking in Norway. In Czechoslovakia it was first ascertained by KULT (1943—44, pp. 376, 378), who gives also localities from the European part of the USSR. Today it is known in Czechoslovakia already from several localities (KULT, 1948, pp. 27, 30; FASSATI, 1951, p. 13), the westernmost being Ústí nad Labem.[4]) In Germany it has not yet been ascertained, though it has surely already penetrated also to that country.

Some Czechoslovak specimens of the species *A. majuscula* CHAUD. were caught on loamy or loamy-clayey, disintegrating banks of fairly large rivers (Štúrovo—Parkáň, see FASSATI, l. c.; Čelákovice 9 VII 1944, leg. Kult et Fassati, cp. KULT, 1948) together with *Amara apricaria* PAYK., so that the ecology of the two species partly overlaps. Taxonomically *A. majuscula* CHAUD. belongs in the closest affinity of the species *A. apricaria* PAYK.

Especially owing to this close phylogenetic and biological affinity the example of the species *A. majuscula* CHAUD. thus explains and shows us that the spread of the species *A. apricaria* PAYK. over a large part of the Atlantic coast of North America and Canada from one or more centres of introduction and the strong multiplication of this species in these places could be really a question of only some decades.

A similar instance of a rapid spread on the Atlantic coast of North America is known also for two other species of the genus *Amara* BON., for *A. aenea* DEG. and *A. familiaris* DUFT.

Amara (s. str.) aenea DEG. and familiaris DUFT.

It was not until as late as 1918 that both species were described from North America by CASEY (1918, pp. 302, 307) under the names of *devincta* (= *aenea*) and *humilis* (= *familiaris*). DARLINGTON (1936) ascertained the conspecifity of CASEY's species with the European ones, and he arrived at the conclusion that both species had been introduced into North America from Eurasia. In the older American collections the two species are lacking. They were described from Connecticut, Rhode Island, and Long Island. In 1936 DARLINGTON knows both species from these states and from western Massachusetts where, as the author emphasises, they are so abundant as to be found alo in the streets.

Of the species *A. aenea* DEG. I obtained from North America 1 ♂ (Belcamp, Maryland, 10 V 1948, leg. F. A. Kinsel). A careful comparison

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[4]) I caught 1 ♀ at Lovosice (26 VIII 1951) on the sandy bank of the Elbe among sparse vegetation.

of all the characters, which I give in the descriptions of the new species of the genus *Amara* BON. (e. g. FASSATI, 1949 b), showed me that they do not differ at all from the large series of specimens from Central Europe in my collection in any character, nor in the shape and strength of the microsculpture of the elytra. The occurrence in Maryland shows that from the area it occupied in 1936 this species has spread in less than twenty years another 250—300 km. to the southwest, if of course there is not here a new centre of separate introduction.

The species *A. aenea* DEG. is the most abundant species of the genus *Amara* BON. in the greater part of Europe; it is distributed through the greater part of the palearctic region (LINDROTH, 1945, p. 99), and is explicitly xerophile and heliophile. Its vagility is great, it is fully winged, and in Central Europe it has often been observed in flight (LINDROTH, 1945, p. 100), also by me: Praha VII, in the street, 22 VII 1949, 2 p. m., hot sunny day, several specimens.

Thus the introduction of the species *A. aenea* DEG. into North America is obvious. BROWN (1950) lists it from further localities from New Scotland and from Ontario (Canada).

The species *Amara familiaris* DUFT. is not known to me from North America, but its introduction into North America is evident. HATCH (1949) described its spread. CASEY's oldest cotype from Long Island was found only in 1915, the first specimen on the Atlantic sea-board of North America not earlier than 1913. The same year the first specimen was found on the Pacific coast at Seattle, where the species was certainly introduced independently. Later the species spread from here according to HATCH (l. c.) over the whole northwestern part of the United States, where it is at present very abundant. BROWN (1950) knows this species also from British Columbia, where it was caught already in 1919, from New Scotland, New Brunswick, Quebec and New Foundland (all in Canada).

Amara (s. str.) anthobia VILL.

From North America the species is reported by HATCH (1949) from several localities in the state of Washington, where it was found in the years 1945—1947, and where it had been introduced according to HATCH from Europe. According to HORION (1941, p. 258) the species occurs here especially in the Mediterranean region; its most northern occurrences are in England and Brandenburg, its most eastern ones in the Caucasus.

The conspecifity of the North American and European specimens has not been confirmed by a comparison. Professor M. HATCH will make this comparison after specimens I have sent him.

Amara (s. str.) lunicollis SCHIÖDTE

LINDROTH (1945, pp. 146—148) records this species from almost the whole of northern Eurasia, from Ireland and the Shetland Islands in the west to the basin of the Lena and to Kamchatka in the east, and farthest south from Northern Spain, Bulgaria and Iran. It is winged rather eurytopic, but not expressly campicol (LINDROTH, l. c.).

BROWN (1950) gives under the name of A. vulgaris L. from North America three specimens caught in 1947 in New Brunswick at Dartmouth, and regards them rightly as introduced from Eurasia.

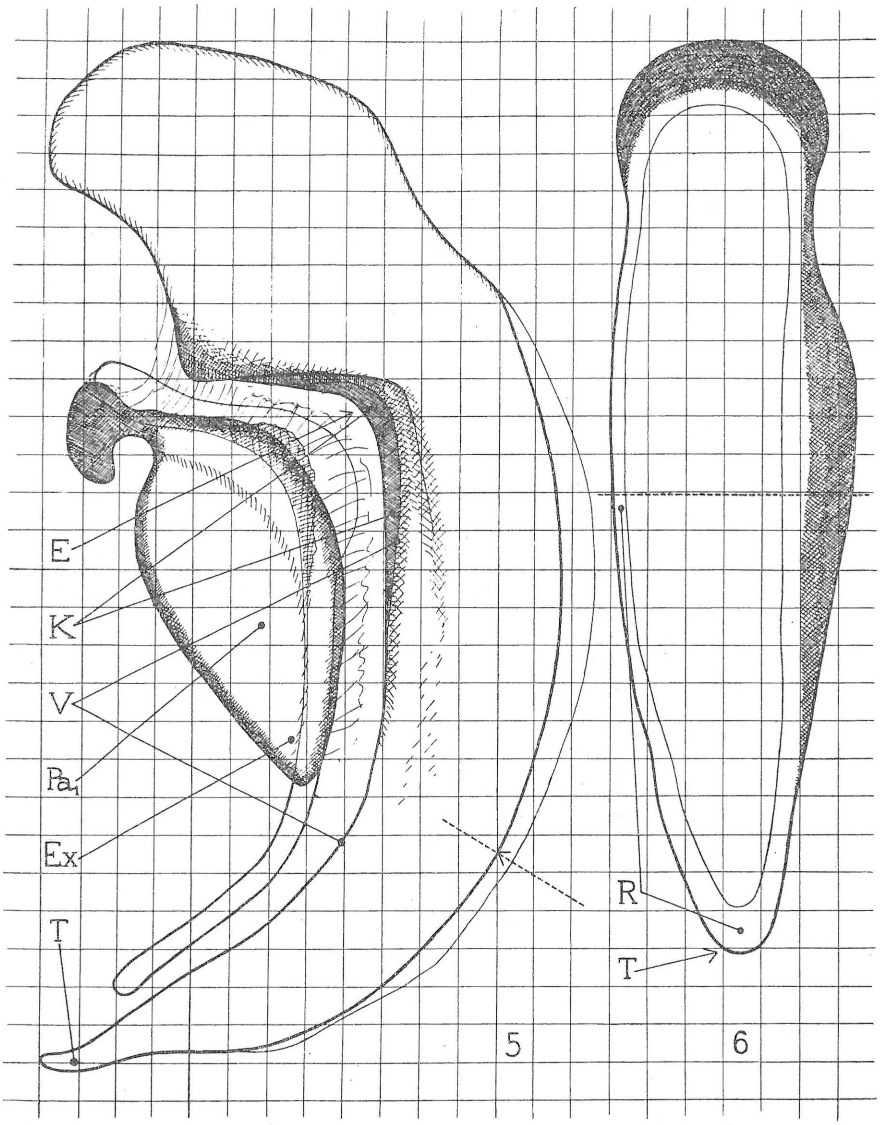
Amara (Cyrtonotus) convexiuscula MARSH.

Amara convexiuscula MARSH. was reported from the northern part of North America by KIRBY (1837, p. 35).

In fact my three specimens of the sg. *Cyrtonotus* STEPH. from Canada (Redfield, Sask., V-VI 1948, leg. ?, ex. coll. K. Kult) resemble so much the typical race of ssp. *convexiuscula* MARSH. from the coast of the North Sea and the Baltic that KIRBY's point of view seems to me quite understandable. For comparison I had the following specimens of the typical race: 1 ♂ from England, cotype, lent from Marsham's collection in the British Museum in London. — Göteborg, leg. Sudin, in coll. Ing. Kouřil, 1 ex. — Lübeck, coll. Obenberger in coll. Mus. Nat. Praha, 1 ex. — Kopenhagen, (leg.) Leonhard, in my collection 2 ex. — Turku, leg. A. Merisuo, in my collection 5 ex. — Of ssp. *bohemica m.* I had for comparison many tens of specimens listed in the original description (FASSATI, 1943—44) and in my 16th contribution (FASSATI, 1949 a).

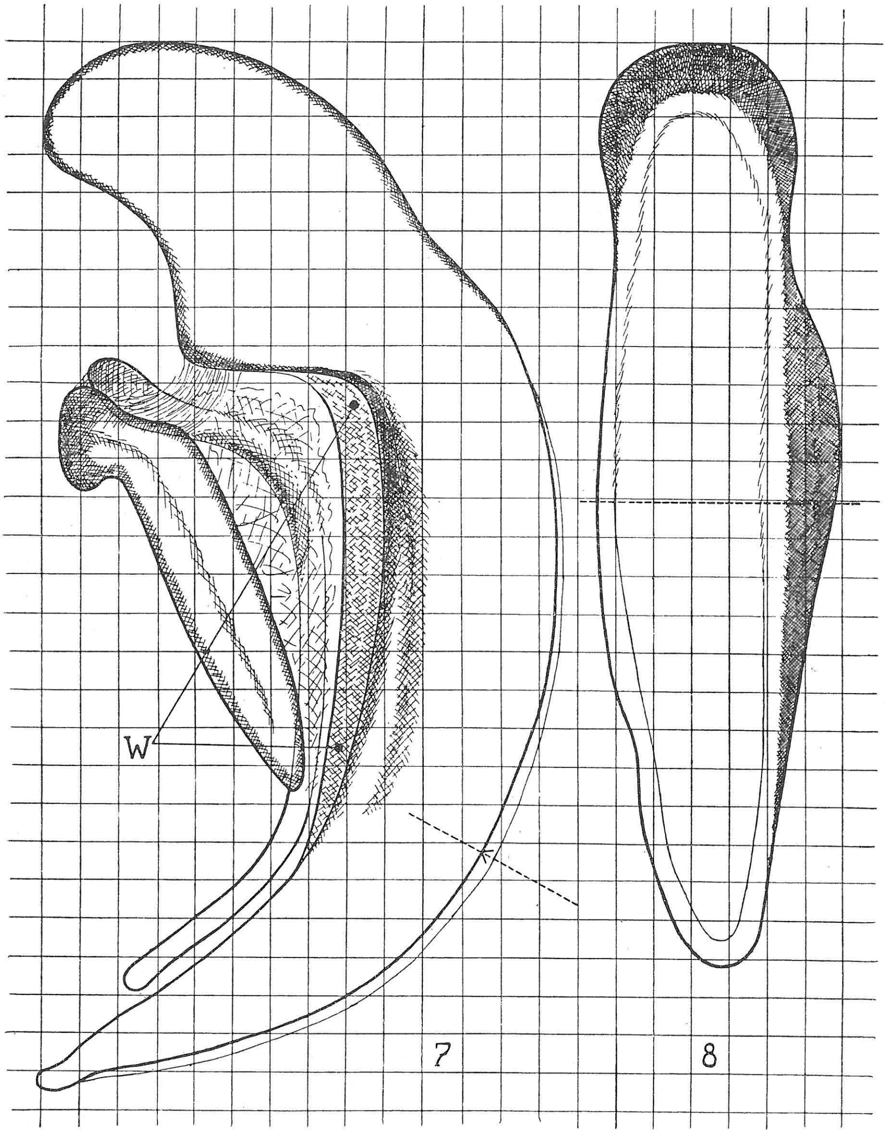
A. convexiuscula MARSH. forms two races in Europe as far as we know. The first, halobiontic or at least halophile race, ssp. *convexiuscula* MARSH. is distributed along the Atlantic coast of France, Belgium and the Netherlands (JEANNEL, 1942 a, p. 948), in England and on the coast of the North Sea and Baltic to the south from approximately 62° N (LINDROTH, 1945, pp. 116—118). The second race, ssp. *bohemica m.*, lives in clay, ruderally or at most halophile, and is distributed in Bavaria, Czechoslovakia, Austria and Hungary. As I recorded in the original description (1943—44), ssp. *bohemica m.* differs from ssp. *convexiuscula* MARSH. especially by having the striate of the elytra more coarsely punctured, and this puncturing spreading also to the apical part of the elytra. When in the course of time I obtained a larger comparative material, I could verify the applicability of still two further characters: Ssp. *bohemica m.* has the tip of the oedeagus seen from the outer side (see fig. 13) more pointed than ssp. *convexiuscula* MARSH. (see figs. 11 and 12). Further ssp. *bohemica m.* has as a rule a straight, not emarginate base of the thorax, and the hind angles of the thorax are as a rule not prominent, usually obtuse or rectangular, while in ssp. *convexiuscula* MARSH. the base of the thorax is mostly emarginate and the hind angles are usually prominent, and are acute.

The very detailed comparison of all characters, which I give in the descriptions of the new species of the genus *Amara Bon.* (e. g. FASSATI, 1949 b), showed me, however, that the Canadian specimens differ after all from the European *A. convexiuscula* MARSH. The difference can be observed especially in the oedeagus. The Canadian and European specimens have almost the same size and shape of the oedeagus (see



Oedeagus of the species *Amara* sp. propria *Amara convexiusculae* MARSH. from Canada (Redfield, Sask.). — Fig. 5: View from above, with parameres. Fig. 6: View from the outer side (= dorsally), without parameres. — Other explanations as in figs. 1—4.

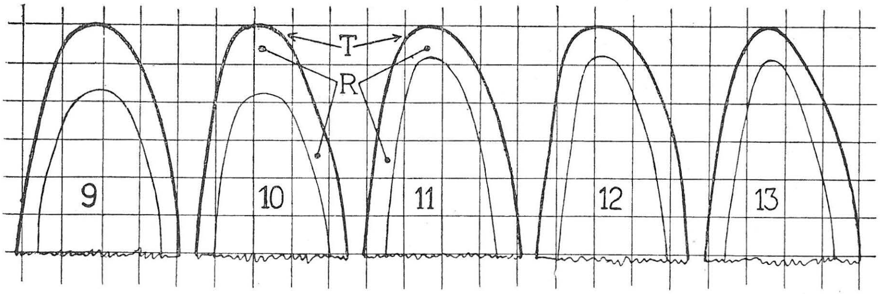
figs. 5—8). In all specimens the oedeagus is on the ventral side obliquely compressed from above and on the dorsal side obliquely compressed from below so that in cross-section it forms approximately a parallelogram whose acute angles form the lower ventral edge and upper dorsal edge of the oedeagus. The lower ventral edge (V) extends in all European



Oedeagus of the species *Amara convexiuscula* MARSH. s. str., cotypo collatum, from Finland (Turku). Fig. 7: View from above, with parameres. — Fig. 8: View from the outer side (= dorsally), without parameres. — Other explanations as in figs. 1—4. The upper parameres (Pa$_1$) in figs. 5 and 7 cannot de compared with each other, as they are placed differently obliquely in each figure.

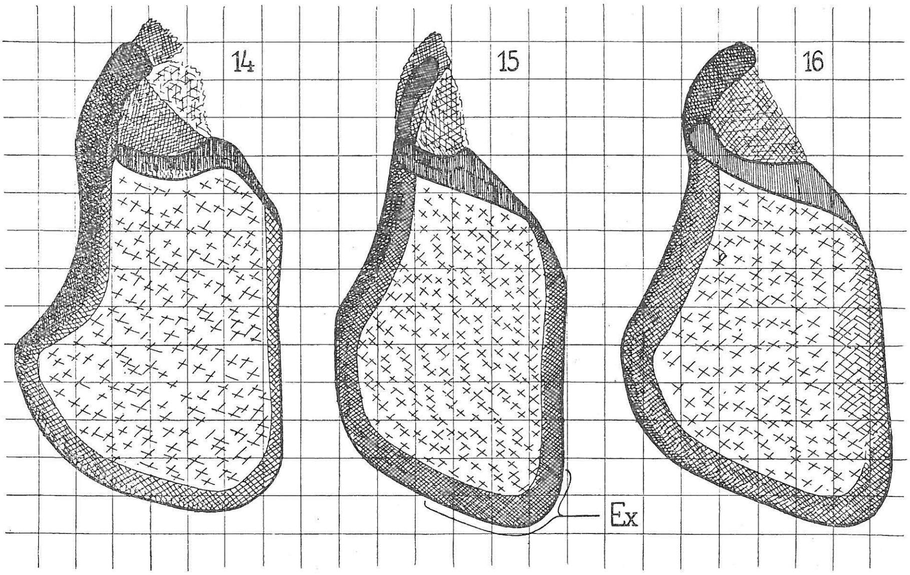
specimens (see fig. 7) from the emargination (E) under the parameres for a length of about two thirds (i. e. about 1.1 mm.) of the ventral margin of the oedeagus in a ventral direction as a fairly thin and therefore rather translucent wedge (W), 0.08—0.10 mm. wide. In both Canadian males (see fig. 5) the lower ventral edge is extended only in a smaller, strongly chitinose and therefore little translucent keel (K) and only in the wider vicinity of the emargination (E). The second differentiating character is the width of the rim (R) of the dorsal face of the oedeagus delimiting the opening for the inner sac (i. e. the "rim of the opening for the inner sac") at the tip of the oedeagus seen from the outer side: Whereas in all European specimens (see figs. 11—13) the rim (R) is at the tip (T) of the oedeagus more or less as wide as on the sides anterior to the tip, i. e. 0.07—0.09 mm., it expands in the two Canadian specimens considerably at the tip so that it is here 0.17—0.18 mm. wide. Certain differences are found in the shape of the upper paramere (Pa_1) (see figs. 14—16). This character, which can be observed directly, without preparing the paramere, is the best to use for distinguishing between them. The extremity (Ex) of the paramere is in the Canadian specimens (fig. 14) blunter and more rounded than is ssp. *convexiuscula* MARSH. (see fig. 15), and somewhat also in ssp. *bohemica* m. (see fig. 16).

There are hardly any differences in the superficial characters between the Canadian specimens and ssp. *convexiuscula* MARSH. Even the characters serving to differentiate ssp. *convexiuscula* MARSH. from ssp. *bohemica* m. (see above) are in the main the same and fall entirely within the limits of individual variability. The Canadian specimens can be distinguished with certainty from *A. convexiuscula* MARSH. only according to the epipleurae of the elytra. In the Canadian specimens (see fig. 17) they are somewhat less abruptly crossed[5]) and in a lateral view they are in the apical part, especially posteriorly to the crossing (Cr), broader than in *A. convexiuscula* MARSH. (see fig. 18). This width is in the Canadian specimens approximately 0.21 mm, in *A. convexiuscula* MARSH. approximately 0.13 mm. The anterior angles of the thorax



Tips of oedeagi seen from the outer side of the oedeagus, always perpendicularly to the plane of the tip. Fig. 9: *Amara* sp. propr. *A. convexiusculae* MARSH. from Canada (Redfield, Sask.), second male. — Fig. 10: The same specimen from Canada as in figs. 5 and 6. — Fig. 11: *A. convexiuscula* MARSH. s. str., typo collatum, from Turku (Finland). — Fig. 12: *A. convexiuscula* MARSH. s. str. from Kopenhagen (Denmark). — Fig. 13: *A. convexiuscula* ssp. *bohemica* m., holotype, from Prague (Bohemia).

Magnification 50 × so that one square of the net corresponds to 0.01 sq. mm. Figs. 9—13 cannot be compared with the tips in figs. 6 and 8, where the tips are observed obliquely and thus are distorted.



Upper parameres of the oedeagi seen from below. Fig. 14: *Amara* sp. propria *A. convexiusculae* Marsh., from Canada (Redfield, Sask.), second male. — Fig. 15: *A. convexiuscula* Marsh. s. str., from Turku; the same specimen as in figs. 7 and 8. — Fig. 16: *A. convexiuscula* ssp. *bohemica* m., from Prague, cotype no. 8. Magnification 50 ×, so that one square of the net corresponds to 0.01 sq. mm. Explanations in the text.

project in the Canadian specimens very slightly beyond the level of the anterior margin (= apex) of the thorax[6]) (in the European specimens they do not project), and the eyes are very slightly flatter than in the European species. In most cases the lateral margin of the prothorax is in the Canadian specimens a little more elevated than in *A. convexiuscula* Marsh.[5]) The Canadian female has distinctly shorter antennae (by about the length of 1½ joints) than the two Canadian males. In ssp. *convexiuscula* Marsh. the females have shorter antennae than the males only by the length of ½—1 joint; in ssp. *bohemica* m. this difference is on an average even a little smaller.

In most cases it is very difficult and often impossible to determine the phylogenetic relations between the different species of the genus *Amara* Bon. or the evolutionary age of these species. There are several reasons for this. Most of the species resemble each other very much in habitus, their mutual distinction is restriceted to a small number of characters; these characters are mostly relatively fine and often also fairly variable. Also the shape and outer structure of the male copulation organs are in most species considerably uniform and simple, and in the inner structure (= inner sac) of the oedeagus the chitinose parts are lacking.

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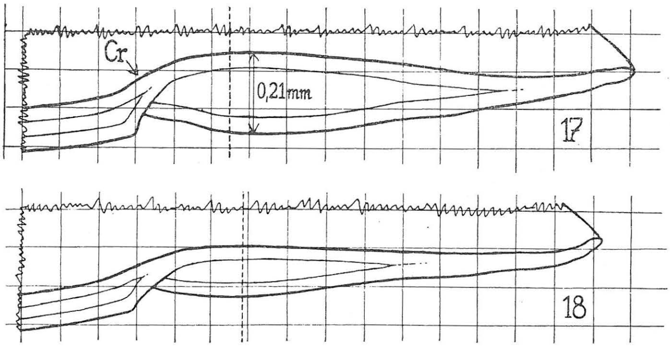
[5]) I wish to thank Dr. C. H. Lindroth for having drawn my attention to these characters.

[6]) We have to look perpendicularly from above so that the anterior margin of the thorax forms a straight line.



Epipleurae of the left elytron in its apical part in a horizontal view obliquely from behind. — Fig. 17: *Amara* sp. propr. *A. convexiusculae* MARSH. from Canada (Redfield, Sask.), male. — Fig. 18: *A. convexiuscula* MARSH. s. str. from Finland (Turku), male.
Magnification 50 ×, so that one square of the net corresponds to 0.01 sq. mm. The broken straight lines indicate the place in which we observe the object. Explanations in the text.

Thus we cannot follow the arrangement of the inner formations and use them as the most essential characters for distinguishing and for determining the affinity (SZÉKESSY, 1934, 1936). Therefore we have usually no possibility to distinguish between primary phylogenetic characters and characters of functional adaptation.7) To this comes further that the great majority of *Amara* does not form geographical races and that there are also very few endemic species. This is due also partly to the considerable vagility of many species which have almost all fully developed wings, and thus some species probably formed by way of ecological differentiation (e. g. the complex of species *communis* PANZ., *Pulpáni* KULT and *Mülleri* MAKÓLSKI i. l.).

Amara convexiuscula MARSH. is an exception; its phylogeny can be followed. The subspecies *bohemica* m. differs from the typical race by secondary superficial characters, with transitions existing between them. Also the pointing of the oedeagus, in which there is on the copulation organ the only definable difference, is the first to be subjected to the variability in all characters of the oedeagus. The Canadian specimens differ from ssp. *convexiuscula* MARSH. on the whole by more subtle characters than ssp. *bohemica* m. differs from ssp. *convexiuscula* MARSH., but these characters are clearly more primary. Thus it may be assumed that the Canadian population is of an older origin than ssp. *bohemica* m., and it is excluded that it could have been introduced, however early, into North America as a population of the species *A. convexiuscula* MARSH. and differentiated from it in the course of some centuries. Thus it has to be admitted that the Canadian population is primary

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7) Also some subgenera of the genus *Amara* BON. are phylogenetically heterogeneous, as obviously sg. *Zezea* CS.: The thickened trifide apical spur of the anterior tibiae served the beetle to hold on to grasses. It developed in species which specialised in eating the grains from the ears of still standing stalks, and is thus a character of functional adaptation. — Inhomogeneous are also sg. *Bradytus* ZIMM. and *Pseudobradytus* CS.

in North America. From the material examined it is evident that the differences given between the Canadian and the European populations are relatively constant, and therefore the Canadian specimens must be regarded as a separate species. The affinity according to the copulation organs is, however, so obvious that they are certainly **vicariating** species.

As I pointed out in 1943—44, *A. convexiuscula* MARSH. is distributed only in parts of Europe and has not yet been ascertained in the whole of Asia, where it is evidently lacking. The old determinations refer to related species, especially to *A. intermedia* MOTS., which is presumably a vicariating species to *A. convexiuscula* MARSH., but with a considerably looser affinity. It is thus most probable that the settling of North America by the original common population of the present species *A. convexiuscula* MARSH. and of the Canadian species could not take place via northeastern Siberia and the northwestern part of North America[8]), but went via northwestern Europe, perhaps also via Iceland and Greenland to New Foundland and Labrador.

According to KÖPPEN and WEGENER (1924) the former continents Laurentia (in the main present-day North America) and Angaria (in the main present-day Eurasia) were last connected in their northern part in the Lower Tertiary (Paleogene). At that time, especially in the Montian and Oligocene, there was an extensive exchange of faunas between the two continents (JEANNEL, 1942 b, pp. 457—462). In the course of the Upper Tertiary Laurentia gradually detached itself from the south from Angaria. It is in this period that we place the beginning of the differentiation of many present North American vicariating species.

The Canadian species vicariating for *A. convexiuscula* MARSH. is, however, so little differentiated from the latter that it more probably originated in younger geological periods; this is all the more likely as the species *A. convexiuscula* MARSH. has not a lesser plasticity than the other species of the subgenus. On the contrary it is the only species of the subgenus in Europe which here forms a race.

When we investigate whether there was according to the continental drift theory any possibility of at any rate at least a small exchange of the faunas between the two continents, we see that there were two such possibilities.

(1) As it was only gradually that the continents split and drifted apart, it is obvious that the disance between Ireland and New Foundland was relatively small in the Neogene. Therefore we can assume that as far as species which fly well and often are concerned there was at any rate the possibility of a passive crossing by air, and that as far as coastal forms such as the present-day *A. convexiuscula* MARSH. are concerned there was also the possibility of a transport by rafts or by an anemo-hydrochoral manner (PALMÉN, 1944). This type of migration plays a

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[8]) From the distribution and number of species in the two continents we can conclude that sg. *Cyrtonotus* STEPH. is of Angarian origin. The centre of distribution with the greatest number of species is approximately in the more eastern part of Siberia and in Mongolia. From here as a rule it came to an immigration into North America, where even today a considerable part of the species is distributed only in Alaska or on the Pacific coast.

much more important part in the spread of insects than was accepted until recently, and thus may well have acted also in the large gulf of the Atlantic Ocean, closed to the north by Greenland.

(^{2}) There is also the possibility according to the continental drift theory that the species migrated from Europe to North America via Scotland, Iceland, Greenland and Labrador either in the youngest Tertiary or in the oldest Quaternary when all these islands and Labrador were still completely or almost completely connected. We have of course to take into consideration that the climate at the time and in these regions was—if not outright glacial—then at any rate so cold as to be supportable only by artic or strongly coldloving species; but at the same time we must not forget that it is not excluded that very cold periods alternated with somewhat warmer ones (cp. e. g. MILANKOWITSCH's temperature curve, or REINIG's (1937) opinion on the shifting of the pole during the Ice Ages), and if so it would be quite feasible for less cold-loving species such as *A. convexiuscula* MARSH. to effect the crossing from Europe to North America in these warmer periods.

However, ODHNER's Constriction Theory (MALAISE, 1945) appears to be even more relevant than either of the above possibilities. According to ODHNER the shallow sea bottom between Scotland, the Shetland Islands, the Faroe Islands, Iceland, Greenland and North America was either entirely or for the larger part above sea level still during certain periods of the Pleistocene. Thus *A. convexiuscula* MARSH. can have crossed here to North America, according to the present differentiation most probably in the younger Tertiary, perhaps shortly before the beginning of the Ice Age, or at the latest in the oldest interglacial periods (pre-Günz?- cf. MALAISE, 1945, p. 31). A migration in the younger Interglacials and especially in the Riss-Würm Interglacial is improbable, as at the time the North Atlantic bridge was already interrupted to a larger extent. This is indicated by the fact that most species which settled in Iceland in the Riss-Würm Interglacial have not yet differentiated here even racially (LINDROTH, 1931).

Among the species of the genus *Amara* BON. and also among the other species of the *Carabids* the differentiation of the cold-shuning amphiatlantic elements, which we find in the complex of vicariants of *A. convexiuscula* MARSH., is very sporadic.

Ssp. *bohemica* m. seems to have differentiated in the course of the Ice Ages, but any more accurate determination will be difficult.

We have still to establish the name of the Canadian species. When we determine it after HAYWARD's key (1908, pp. 18—20) we come to the group no. 8 as it has the "thorax wider at base than apex" in the ratio of about 76:67. Here, however, the descriptions of all three species are different, already in size (the Canadian species measures 12,5—13.0 mm.). There remains the possibility of regarding the "thorax as wide at base as apex", and then we come to the group of species no. 6, and in it to the species *adstricta* PUTZ., *laticollis* LEC., *carinata* LEC., and *rufimana Kirby*. The latter has, however, the "elytra twice as long as wide", so that it is excluded as my species has the elytra only about 1.77 × as long as wide. Of the remaining three species the best seems to be *laticollis* LEC., to which HAYWARD (l. c., p. 60) really places the species *A. convexiuscula* KIRBY as synonym. But the name cannot be used, as it is pre-occupied by STEPHENS, and CSIKI (1929, p. 459) places it as synonym to *adstricta* PUTZEYS (1866, p. 238).[9]) But in the original description the author compares *A. adstricta* PUTZ. with *A. aulica* PANZ., not with *A. convexiuscula* MARSH. Further, *A. adstricta* PUTZ. is said to have as acute posterior angles of the thorax as *A. aulica* PANZ., i. e. of about 65—70°, whereas all my three Canadian specimens have anterior angles of the thorax of 75—85°. PUTZEYS does not mention either that the width of the elytra would be different in *aulica* PANZ. and *adstricta* PUTZ., this being a striking difference between *aulica* PANZ. and my species (and also *convexiuscula* MARSH.). Thus I cannot conclude from the description that my species is *A. adstricta* PUTZ.

I do not know the original description of the species *A. carinata* LEC., but according to HAYWARD's characterisation (1908, p. 19) *A. carinata* LEC. has a "thorax with the sides strongly rounded, rather feebly sinuate in front of the hind angles, which are rectangular", which again does not agree with my three Canadian specimens.

Dr. C. H. Lindroth was so kind as to tell me that my species is determined in America as *A. laticollis* LEC.

The question of nomenclature and synonymy can only by solved on the basis of the classic material.

Amara (Cyrtonotus) aulica PANZ.

The species is indigenous in the western part of the palearctic region (LINDROTH, 1945, pp. 105—108), where it lives also campicolly and ruderally; it can also fly. In 1929 FALL (1934) collected one specimen of this species at Louisburg in Nova Scotia (Canada), where it had been introduced. The specimen was revised by Ing. Jedlička, who confirmed its conspecifity with the European specimens. Later the species was introduced also into New Foundland, where according to BROWN (1950) it was caught in 1949. Thus its recent distribution is amphiatlantic.

Amara (celia) bifrons GYLL.

Until recently this species was known only from the western part of the palearctic region, from the Shetland Islands and Ireland to Kazakhstan and Uzbekistan SSR, and from the northern part of Scandinavia to Portugal, Middle Italy, Bulgaria and the Caucasus (LINDROTH, 1945, pp. 108, 109). In Scandinavia the species lives according to LINDROTH in a way similar to that of A. fulva DEG., in Central Europe according to my observations rather eurytopically, partly ruderally, sometimes also steppicol or campicol. It is fully winged.

According to BROWN (1950 A. bifrons GYLL. was introduced into New Scotland and New Foundland (Canada), where it was caught in 1947 and the following years; its recent distribution is therefore amphiatlantic.

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[9]) Not p. 283 as given by CSIKI (l. c.)

Amara (Celia) erratica DUFT. and interstitialis DÉJ.

A. erratica DUFT. and perhaps also *interstitialis* DÉJ. are circumpolar species (LINDROTH, 1945, pp. 124—126, 140—443).

A. erratica DUFT. was studied in detail by HOLDHAUS and LINDROTH (1939), and with full right these authors (p. 235) regard it as a primary species in North America. According to these authors *A. erratica* DUFT. (like *A. interstitialis* DÉJ.) is lacking in Iceland and in Greenland, and it is thus evident that it came to North America via northeastern Siberia and Alaska (the opposite way is improbable already because of its recent distribution in Eurasia). In Europe this species is boreo-alpine, but in the various isolated mountain areas it tends already to form races, as MAŘAN (1945, p. 47) reports. JEANNEL (1942 a, pp. 927, 928) even describes two races from the western Alps and the Pyrenees. Thus it will have to be ascertained whether the North American populations are not geographically variable. The geographical variability of the species *A. erratica* DUFT. in Europe has obviously its origin in the Postglacial, at the earliest in the Riss-Würm interglacial period. If the geographical variability of the North American population is not greater than that of the European ones, and if it were HOLDHAUS and LINDROTH (1939) would certainly have pointed it out, it is difficult to assume that the immigration of the species *A. erratica* DUFT. into North America should have taken place earlier than in the last two Interglacial or Glacial periods.

The occurrence of the species *A. interstitialis* DÉJ. in North America is doubtful according to LINDROTH (1945, p. 142).

Amara (Acrodon) brunnea GYLL.

The species is known from almost the whole northern part of the palearctic region, from Scandinavia to the basin of the Lena (LINDROTH 1945, pp. 109—111). LENG (1920, p. 60) records it from Alaska and with a query from Br. Columbia and Colorado. MINSK and HATCH (1939) described in 1939 from the state of Washington (USA) the species *A. exalinae*, very closely related to the species *A. brunnea* GYLL. Thus it is possible that the North American specimens of "*A. brunnea*", especially those from Colorado and Br. Columbia, belong really to the species *A. exalinae* MINSK & HATCH. If, however, *A. brunnea* GYLL. really occurs in Alaska or farther south along the Pacific coast of North America, then its spread is amphipacific, as the species is lacking in the more eastern parts of North America and in the islands between Europe and America. From this distribution it is clear that the species migrated into North America via the Bering Bridge. When this happened in the case of the species *A. brunnea* GYLL., and whether it happened at all, can be ascertained only by a detailed revision of the North American and East Asian populations, or by determining the degree of their differentiation.

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