Article

"A Method for Comparison of Northern Fossil Insect Assemblages"

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A METHOD FOR COMPARISON OF NORTHERN FOSSIL INSECT ASSEMBLAGES

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ABSTRACT The paleoenvironmental resolving power of late Cenozoic Coleoptera fossils from arctic and subarctic sites is hindered by the fact that the fossil assemblages often differ greatly in taxonomic diversity and minimum number of individuals represented. In order to compare faunas of different age and from different sites, the fossil insect assemblages must first be normalized. One method of doing this is to group the fossils according to the ecological requirements of the taxa that they represent and then compare assemblages on the basis of the percentage of individual insects in each group. Eight such groups are defined in this paper and then used to compare fossil assemblages from the Yukon Territory, Alaska and eastern Siberia. Such comparisons reveal differences related to local site-of-deposition conditions but they also reflect the character of the regional late Pleistocene beetle fauna. The grouping procedure supports conclusions based on other information, such as taxonomic content, but it masks certain assemblage characteristics that may also be of paleoenvironmental significance. Thus grouping insect fossils as a means of normalizing the data for purposes of comparison should not be used in lieu of other analytical approaches.

RÉSUMÉ *Méthode de comparaison d'associations d'insectes fossiles nordiques.* Il est difficile de reconstituer les paléoenvironnements à partir des coléoptères fossiles du Cénozoïque supérieur provenant de sites de l'Arctique et du sub-Arctique, étant donné que les associations de fossiles ont souvent une grande diversité taxonomique et que le nombre d'individus représentés varie beaucoup. Afin de pouvoir comparer les faunes d'âges variés qui proviennent de sites différents, il faut d'abord normaliser les associations d'insectes fossiles. Une des méthodes consiste à regrouper les fossiles selon les exigences écologiques des taxons et comparer les associations en fonction du pourcentage d'individus dans chaque groupe. Le présent rapport définit huit de ces groupes et les utilise pour comparer des associations de de la Sibérie orientale. Ces comparaisons révèlent des différences qui sont liées aux conditions locales du lieu d'accumulation, mais elles reflètent aussi la nature des Coléoptères du Pléistocène supérieur. La méthode du regroupement appuie les conclusions fondées sur d'autres données comme le contenu taxonomique, mais masque certaines caractéristiques des associations qui pourraient également avoir une importance paléoenvironnementale. Le regroupement des insectes fossiles, en tant que méthode de normalisation des données à des fins de comparaison, ne doit pas être utilisé à la place d'autres méthodes analytiques.

ZUSAMMENFASSUNG *Eine Vergleichsmethode für nördliche Fossilinsekten Ansammlungen.* Es ist schwierig die Paleo-Umgebungen aus den fossilen Ansammlungen der Coleopter des Spätcenozoik zu erschliessen. Die Fossile von arktischen und subarktischen Forschungssitzen sind durch die Tatsache, dass sich die Fossilansammlungen oft durch grosse taxonomische Vielseitigkeit unterscheiden, sowie in der Mindestzahl ihrer repräsentierten Einzelwesen behindert. Um Faunen verschiedenen Alters und aus verschiedenen Forschungssitzen zu vergleichen, müssen die fossilen Insektenansammlungen zunächst normalisiert werden. Eine Methode um das zu tun, ist, sie nach den ökologischen Bedürfnissen der Taxa zu gruppieren und dann die Ansammlungen auf Grund des Prozentsatzes der einzelnen Insekten in jeder Gruppe zu vergleichen. Acht solcher Gruppen sind in dieser Forschungsarbeit behandelt und dann dazu gebraucht, sie mit fossilen Ansammlungen aus dem Yukon Territory, Alaska und dem östlichen Sibirien zu vergleichen. Solche Vergleiche zeigen Unterschiede die sich auf lokale Ansammlungs Verhältnisse beziehen, aber sie spiegeln auch den Karakter der regionalen, Spätpleistozän Insektenfauna wider. Die Reguppierrungprozedur unterstützt Konklusionen die aus anderen Informations bereichen, wie taxonomischer Inhalt, stammen, aber sie maskiert auch gewisse Ansammlungs Karaktere die auch einen Paleo-Umgebungs Wert haben können. Das Regruppieren von Insektfossilen als ein Mittel zur Normalisierung der Daten zum Zwecke von Vergleichen sollte nicht Anstelle anderen analytischen Materials verwendet werden.

INTRODUCTION

For the past several years, the author and his colleagues, working under the auspices of the Yukon Refugium project, have made a significant start in the study of Quaternary insect faunas from the northern Yukon. In addition, a number of Alaskan faunas have been studied (MATTHEWS, 1968, 1974; NELSON, 1982), and unpublished data exist for faunas from other Alaskan and Yukon sites.

Enough information is now available from the Alaska-Yukon area to warrant a regional synthesis (MORGAN et al., in press), but for several reasons northern fossil insect assemblages are difficult to compare. A common problem is that assemblages vary greatly in abundance and taxonomic diversity. In some samples fossils represent many taxa; whereas in others hundreds of specimens represent only a few taxa. Another common problem, one which is faced routinely by palynologists, is overrepresentation of local taxa. Fossil insect assemblages may also be biased by taphonomic effects and differential preservation (MORLAN and MATTHEWS, 1983). This means that assemblages from the same region, and possibly even the same local environment, may be quite different in taxonomic content.

Before fossil insect assemblages can be compared, one must acknowledge and deal with problems such as those mentioned above. One method the author has employed to do this is to group the fossils according to their broad habitat requirements or niche, then comparing the relative abundance of individual insects within each group (MATTHEWS, 1982; HUGHES et al., 1981). In this paper the group compositions of fossil insect assemblages from sites in the Yukon Territory, Alaska, and eastern Siberia are compared.

METHODS

Most of the samples discussed here were sieved with screens having a mesh size not exceeding .425 mm (40 mesh/inch), then processed by a kerosene flotation technique (COOPE, 1979) to further concentrate insect fossils. Percentage values are based on a sum of the minimum number of individuals (MNI)—an estimate of the number of insects of a taxon that are represented by fossils referred to it. The majority of such fossils are heads, pronota, and elytra of Coleoptera (beetles). Ideally, a count of any one of these anatomical elements of a taxon should yield the same MNI value, but differential preservation and taphonomic factors tend to bias the counts of certain elements (cf. MORLAN and MATTHEWS, 1983).

Although insect fossils often appear to be very abundant in Quaternary sediments, when the totals are cast in terms of MNI, the final values are often on the low side. This results in percentage diagrams that are based on very low MNI sums. My solution to this problem is to avoid presentation of the percentage values entirely and display instead the 95% confidence interval (cf. MAHER, 1972). This allows one to deal with small samples and still maintain the ability to recognize significant trends.

INSECT GROUPS

The insect groups described below deviate slightly in name and content from those discussed previously (MATTHEWS, 1982; see also HUGHES et al., 1981—Appendix B). The characteristics of the groups as used in this paper are as follows:

1. CRYOBIUS GROUP: Indicates mesic sites, especially mesic tundra. The group includes most members of the carabid subgenus Pterostichus (Cryobius) along with other carabids such as Carabus truncaticollis Eschz., Pterostichus haematopus Dej., and Trichocellus mannerheimi Mann. While most taxa in this group are carabids, Staphylinidae such as Eucnecosum (= Arpedium) are also included.

2. LEPIDOPHORUS-MORYCHUS GROUP: Beetles indicative of dry, scantily vegetated biotopes. The group includes taxa that occur at dry tundra sites far from water as well as those that occupy the driest areas of floodplains and shorelines. The weevil Lepidophorus lineaticollis Kby. and the byrrhid beetle Morychus are often the dominant members of this group, but it also includes carabid beetles such as Amara alpina Payk., a species of dry tundra, and Pterostichus sublaevis Sahlb.

The small staphylinid beetle, Micralymma, is also placed in the L-M Group. Micralymma is a rare beetle that has usually been collected near marine shorelines, but recently specimens of the genus have been collected at dry floodplain sites in the interior of the Yukon Territory.

Another occasional member of the L-M Group is the weevil, Vitavitus thulius Kiss. It is presently a very rare species and in the Yukon has only been collected at a single upland calcareous fell-field site.

3. HYGROPHILOUS AND AQUATIC GROUP: Includes inhabitants of ponds and lakes as well as wet shoreline and bog sites. Fossils of water beetles such as Dytiscidae and most Hydrophilidae are placed in this group, but it is often dominated by staphylinids such as Omalinae and Steninae that occur among the dense emergent plants of bogs and small ponds. Phytophagous taxa that are typically hygrophilous, such as Donacia, are placed in this group rather than "Miscellaneous and Phytophagous."

4. MISCELLANEOUS AND PHYTOPHAGOUS GROUP: Is largely a "catch all" category that includes fossils representing a variety of phytophagous beetles, except bark beetles (Scolytidae) and some hygrophilous types. Fossils of beetles, such as the lady-birds (fam. Coccinellidae), whose prey species are closely associated with plants, are also included.

5. FORMICID GROUP: This group differs from the others in that it is typified by ants (Formicidae) rather than beetles. Previously (in HUGHES *et al.*, 1981) I called it the "Scolytid Group" because scolytid or bark-beetles are often one of the common co-dominants. The group includes all taxa (like the bark-beetles and some weevils) that feed on trees plus those normally found within forested areas. Although ants are sometimes collected on tundra, they rarely occur far from regional treeline (GREGG, 1972). Thus the relative abundance of fossils of the Formicid Group is a crude index of the proximity of treeline.

6. TACHINUS GROUP: Includes all species of the genus *Tachinus*. In most assemblages the *apterus* species group is the only one represented. The ecological significance of this group is unknown. Nevertheless, *Tachinus* fossils form a distinctive component of some northern assemblages, and I suspect will be shown to have specific ecological implications when the habitat requirements of the *apterus* species group are better known.

7. SILPHID GROUP: Includes all taxa normally associated with carrion, such as certain species of the genus *Silpha* as well as fossils representing the families Cleridae and Nitidulidae. Silphid Group percentages only rise above background levels in those rare samples that are associated with mammalian carcasses.

8. APHODIUS GROUP: Includes beetles associated with dung and/or decaying vegetal matter. Fossils of the scarabaeid genus *Aphodius* usually dominate this group. However, not all species of *Aphodius* are dung feeders, and some species of *Tachinus* are also associated with various types of dung. The definition of this group, like that of the Tachinus Group, will probably change as we gain more information on the content and distribution of the northern coleopterous fauna.

In any assemblage of insect fossils there are some that defy placement in one of the above mentioned groups. Either the level of identification is too generalized, as in the case of fragments that can be identified only to the family or subfamily level, or the fossils represent undescribed species of unknown habitat requirements. Such fossils have the same status as the "indeterminate types" in fossil pollen spectra.

SAMPLE LOCALITIES

The fossil insect assemblages come from sites in the northern Yukon Territory, two regions of Alaska, and the Kolyma River valley of the U.S.S.R. (Fig. 1).

NORTHERN YUKON TERRITORY

In Figure 2 all samples, except HH75-9, come from the Old Crow Basin, one of several large lowland areas in the northern Yukon (HUGHES *et al.*, 1981). Most of the exposures in the Old Crow basin reveal two
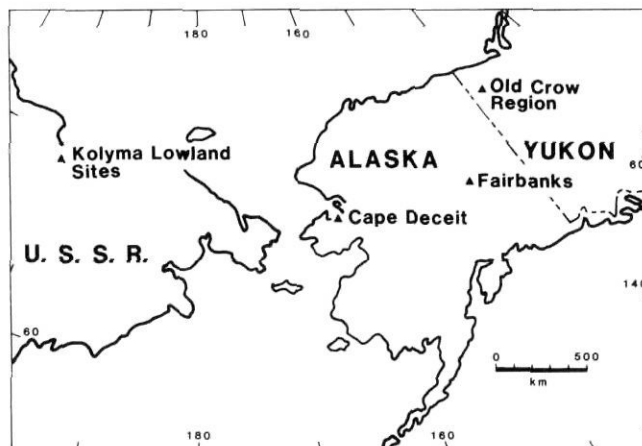

FIGURE 1. Localities mentioned in the text.
Localisation des sites mentionnés dans le texte.

lacustrine clay units separated by a thick sequence of alluvium and pond sediments. The age of the lower lacustrine unit is poorly known; the upper one formed between 25 000 and 12 000 years ago when the basins of the Northern Yukon filled with glacial meltwater that had been diverted by Laurentide ice impinging on the Richardson Mountains, near the eastern border of the Yukon Territory. The alluvial sediments immediately beneath the upper lake unit contain a major disconformity that is thought to have formed during a short, warm interval in the early part of Isotope stage 4 or late in stage 5 (MATTHEWS, 1980).

The four lower samples in Figure 2 come from the CRH-15 exposure (67°51.2'N; 139°49.6'W) on the Old Crow River (MORLAN, 1980; MORLAN and MATTHEWS, 1983) The lowest one is from sandy alluvium immediately above the lower lake clays. The three bracketed samples in the Figure 2 are all associated with the disconformity. The one labeled 78-48/50 is a pooled sample of the insects from three "peat balls" found at the same station and in the same stratigraphic position with respect to the disconformity. Their field relationship suggests that they are transported fragments of a nearby autochthonous peat. Samples 77-51 and 78-64 come from immediately above the contact of the disconformity in cross-bedded sands containing allochthonous organic detritus. See MORLAN and MATTHEWS (1983) for further details on sample provenance.

CRH-32 comes from the CRH-32 locality (68°03'N; 139°49'W) at a position immediately below the clays of the upper lake unit. Organics associated with the sample are dated at 31 300 ± 640 (GSC-1191; LOWDON and BLAKE, 1979). CRH-44, from the locality of the same name (68°13'N; 140°00'W), is from a Holocene peat above the upper lake clays. It represents organics that accumulated in a tundra pond 8460 ± 120 years ago (GSC-2605; LOWDON and BLAKE, 1979).

The only sample in Figure 2 not from the Old Crow Basin, HH75-9, comes from an exposure on the Porcu-
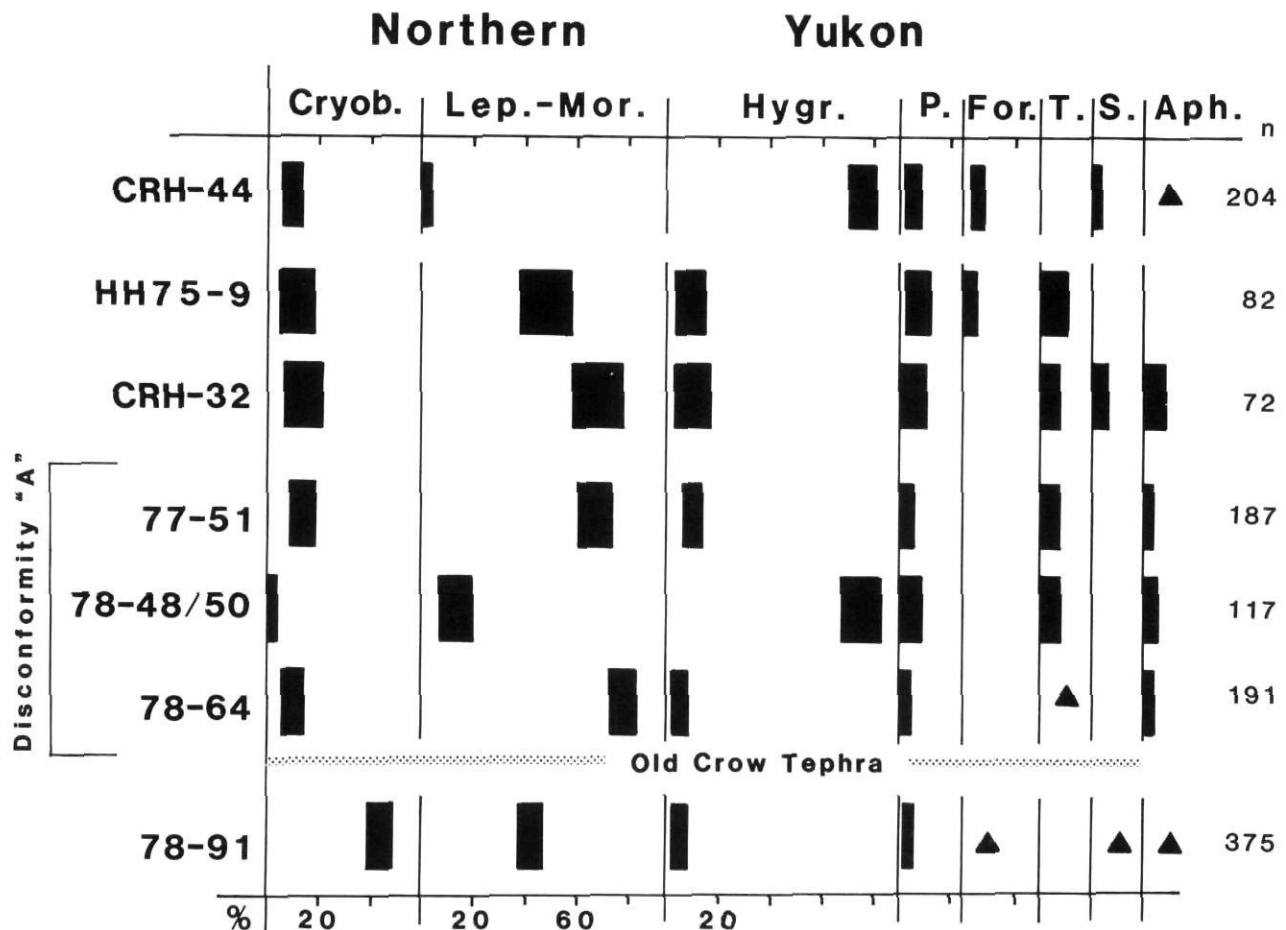
Northern   Yukon

FIGURE 2. Group comparison of insect assemblages from the Northern Yukon Territory. See text for details. Bars represent 95% confidence interval. Cryob. = Cryobius Group; Lep.-Mor. = Lepidophorus-Morychus Grp.; Hygr. = Hygrophilous-Aquatic Grp.; P = Phytophagous-Miscellaneous Grp.; For. = Formicid Grp.; T. = Tachinus Grp.; S. = Silphid Grp.; Aph. = Aphodius Grp.; ▲ indicates percentages of 2% or less. Samples within bracket come from approximaterly same horizon at CRH-15.

Comparaison de groupes d'association d'insectes provenant du Yukon septentrional. Les détails sont donnés dans le texte. Les traits déterminent des intervalles de confiance de 95%. Cryob. = groupe de Cryobius; Lep.-Mor. = groupe de Lepidophorus-Morychus; Hygr. = groupe hygrophile-aquatique; P. = groupe phytophage-divers; For. = groupe de Formicidés; T. = groupe de Tachinus; S. = groupe de Silphidés; Aph. = groupe de Aphodius; ▲ indique un pourcentage de 2 ou moins. Les échantillons entre parenthèses proviennent à peu près du même horizon que celui de CRH-15.

pine River in the Bell Basin (HUGHES *et al.*, 1981). Organics associated with the fossils are dated at 13 500 ± 310 years BP (GSC-2553; LOWDON and BLAKE, 1980).

FAIRBANKS DISTRICT, ALASKA

The assemblages plotted in Figure 3 come from the organic silts or "mucks" (retransported loess) exposed at two adjacent placer gold mines near Fairbanks, Alaska. The sample labeled R-B (MATTHEWS, 1982, HUGHES *et al.*, 1981) is from the base of the Holocene Ready Bullion Formation which caps the Ready Bullion Bench section. Although the sample yielding the insects is not dated, it was collected at the same level and the same station as a piece of wood previously dated at 8080 ± 165 (PIC-5) (PÉWÉ, 1975) Remaining samples in Figure 3 were collected at the Eva Creek exposure (MATTHEWS, 1968, 1970; PÉWÉ, 1975 p. 9). 3-1A, 3-3B, and 3-3C are discussed in MATTHEWS (1968). The last two come from the Wisconsinan Goldstream Formation.

Wood associated with 3-3C is dated at 24 400 ± 650 yrs BP (I-2116). Sample 3-1A is from the Eva Formation, a woody horizon resting on an unconformity that represents a period of regional thawing and slumping. Wood from the Eva Formation has yielded a date of > 56 900 years (Hv-1328). Assemblages 1 and 2 in Figure 3 are unpublished. Both come from the upper part of the Gold Hill Loess Formation (PÉWÉ, 1975) which is probably early to mid Wisconsinan in age (MATTHEWS, 1979; J.A. Westgate pers. comm., 1983). Sample 1 comes from the 20 cm interval immediately below the mid-Wisconsinan Dome tephra[1] (J.A. Westgate, pers.

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1. Note added in proof: The tephra exposed at the Eva Creek exposure is now known to be different from the one found at the Dome Creek locality (J.A. Westgate, pers comm., 1983); hence it is incorrect to refer to the tephra at Eva Creek as the "Dome tephra". Nevertheless, the tephra at Eva Creek is older than 56 900 years and of mid Wisconsinan to early Wisconsinan Age (J.V.M., Jr.).
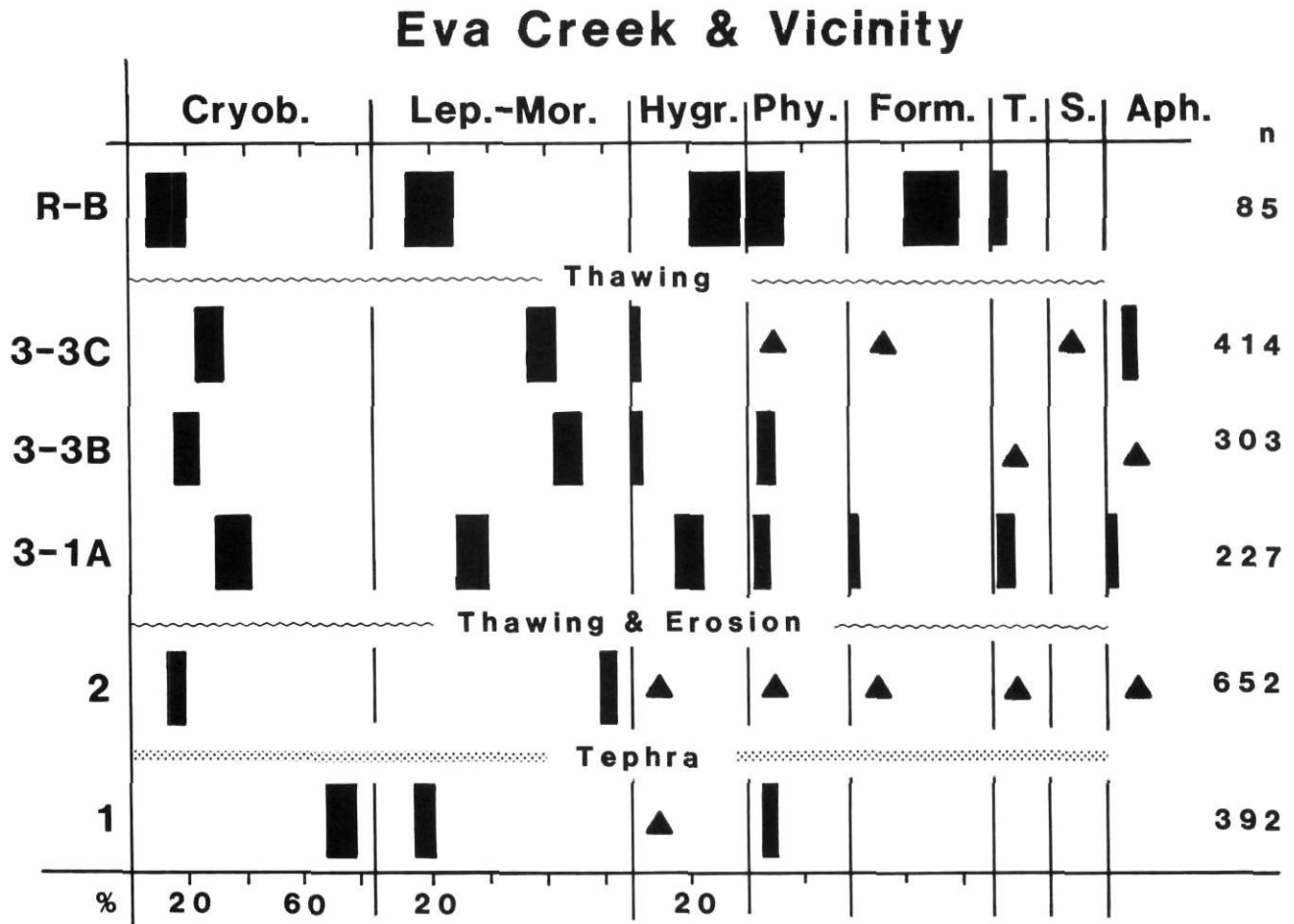
Eva Creek & Vicinity

FIGURE 3. Group comparison of insect assemblages from Eva Creek and other exposures in the Fairbanks region, Alaska. See text for details. Bars represent 95% confidence interval. Cryob. = Cryobus Group; Lep.-Mor. = Lepidophorus-Morychus Grp.; Hygr. = Hygrophilous-Aquatic Grp.; Phy. = Phytophagous-Miscellaneous Grp.; Form. = Formicid Grp.; T. = Tachinus Grp.; S. = Silphid Grp.; Adp. = Aphodius Grp.; ▲ indicates percentages of 2% or less.

Comparaison de groupes d'associations d'insectes provenant de Eva Creek et d'autres sites de la région de Fairbanks, Alaska. Les détails sont données dans le texte. Les traits délimitent des intervalles de confiance de 95%. Cryob. = groupe de Cryobius; Lep.-Mor. = groupe de Lepidophorus-Morychus; Hygr. = groupe hygrophile-aquatique; Phy. = groupe phytophage-divers; Form. = groupe de Formicidés; T. = groupe de Tachinus; S. = groupe de Silphidés; Aph. = groupe de Aphodius; ▲ indique un pourcentage de 2 ou moins.

comm. 1983); and 2 was collected above the Dome tephra and immediately beneath the disconformity that forms the base of the Eva Formation.

CAPE DECEIT, ALASKA

All the samples in Figure 4 come from the Cape Deceit exposure in western Alaska (MATTHEWS, 1974). Assemblage S-10-67 comes from finely laminated, organic silts in the early Pleistocene Cape Deceit Formation. S-1 is from buff-colored, relatively inorganic silts of probable early Wisconsinan age (*cf.* Hopkins' Deering Interval: HOPKINS, 1982); and S-5 from peat nodules (Peat 5) >39 900 years old (I-4099) that are within a unit thought to be early Wisconsinan (HOPKINS, 1982; GITERMAN et al., 1982) or (less likely) Sangamon in age (MATTHEWS, 1974). Assemblage S-6 (12 420 ± 180 yrs BP; I-4781) is from late Wisconsinan pond sediments in the upper part of the Deering Formation (MATTHEWS, 1974).

KOLYMA LOWLAND, U.S.S.R.

Sergei Kiselyov (Moscow) has studied a number of insect faunas from the Quaternary exposures in the Kolyma Lowland of the far-eastern sector of the USSR (SHER et al., 1979; KISELYOV, 1981; GITERMAN et al., 1982). Sample K-66 in Figure 5 is from the early Pleistocene sediments of the Olyor Suite at the Krestovka exposure (Unit IIIa). DY-3 comes from sediments of possible thermokarst origin near the base of the Duvannyy Yar exposure on the Kolyma River. An associated radiocarbon date on wood (37 600 ± 1100 yrs BP; MGU-468) from the same level shows that DY-3 is of Karginsk (mid Wisconsinan) age (SHER et al., 1979; GITERMAN et al., 1982). K-68 represents the base of late Pleistocene sands of Unit IV at Krestovka. Al-102 is from the base of a late Sartan (late Wisconsinan) dune-sand complex at the Alyoshkina Zaimka section; and Dy 13-16 is from Holocene "alass" deposits at
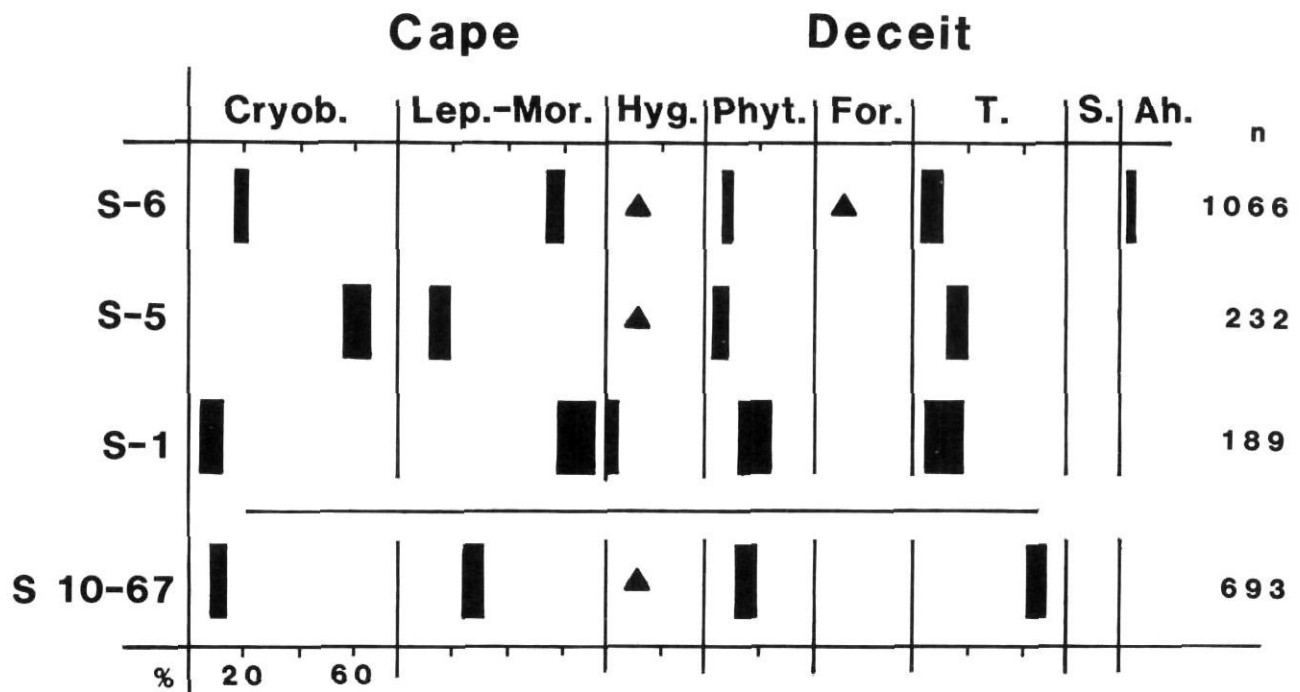
FIGURE 4. Group comparison of insect assemblages from Cape Deceit, Alaska. See text for details. Bars represent 95% confidence interval. Cryob. = Cryobius Group; Lep.-Mor. = Lepidophorus-Morychus Grp.; Hyg. = Hygrophilous-Aquatic Grp.; Phyt. = Phytophagous-Miscellaneous Grp.; For. = Formicid Grp.; T. = Tachinus Grp.; S. = Silphid Grp.; Ah. = Aphodius Grp.; ▲ indicates percentages of 2% or less. Horizontal line separates sample from Cape Deceit Formation and those from Deering Formation.

Comparaison de groupes d'associations d'insectes provenant de Cape Deceit, Alaska. Les détails sont donnés dans le texte. Les traits déterminent des intervalles de confiance de 95%. Cryob. = groupe de Cryobius; Lep.-Mor. = groupe de Lepidophorus-Morychus; Hyg. = groupe hygrophile-aquatique; Phyt. = groupe phytophage-divers; For. = groupe de Formicidés; T. = groupe de Tachinus; S. = groupe de Silphidés; Ah. = groupe de Aphodius; ▲ indique un pourcentage de 2 ou moins. La ligne horizontale distingue les échantillons de la Formation de Cape Deceit de ceux de la Formation de Deering.

Duvannyy Yar. For more information on the stratigraphy of the Krestovka and Duvannyy Yar exposures and the provenance of the samples see SHER et al., 1979 and GITERMAN et al., 1982.

COMPARISONS

Figures 2 to 5 compare the percentage of individuals in each group from samples at the sites described above. All but the one showing the Kolyma Basin series display the percentages as the range for 95% confidence limit. This was not possible in the case of the Kolyma samples because of groups used by Kiselyov (in SHER et al., 1979) are not exact counterparts to those used in this paper. Nevertheless, it should be obvious that samples with few individuals, such as DY 13-16 and DY-3, would have large confidence intervals compared to the others in Figure 5.

NORTHERN YUKON

The samples in Figure 2 form three distinct classes. CRH-44 and 78-48/50 both show a dominance of the Hygrophilous-Aquatic Group and low frequencies of Lepidophorus-Morychus; 78-91 displays co-dominance of the Cryobius and Lepidophorus-Morychus groups; while the remaining samples (HH75-9, CRH-32, 77-51, and 78-64) are all dominated by the Lepidophorus-

Morychus Group. Except for HH75-9, the Lepidophorus-Morychus Group in this last named cluster of samples consists mostly of the species Lepidophorus lineaticollis Kby. Excellent preservation of the L. lineaticollis fossils, particularly in 75-51 and 78-64, suggests that the species resided at the site of deposition (MORLAN and MATTHEWS, 1983); hence, its fossils are undoubtedly over-represented. The species L. lineaticollis is common today on sandy floodplains, that being the type of local depositional environment for both 75-51 and 78-64. Although sample 78-91 also represents such a flood-plain community, it contains nearly equal percentages of the Cryobius and Lepidophorus-Morychus groups. It also differs by its taxonomic content (MORLAN and MATTHEWS, 1983). The reason for these distinctions is not clear, but fossil insect assemblages with similar characteristics occur above the lower lake unit at other Old Crow exposures (MATTHEWS, 1975).

The organics in both samples 78-48/50 and CRH-44 are autochthonous or nearly so, and this probably accounts for their group similarity. Dominance of the Hygrophilous-Aquatic Group suggests that both samples were deposited at poorly drained, peat-forming sites well removed from the active floodplain. For CRH-44 this conclusion is supported by associated fossils and in particular by the diversity of species in the Hygro-
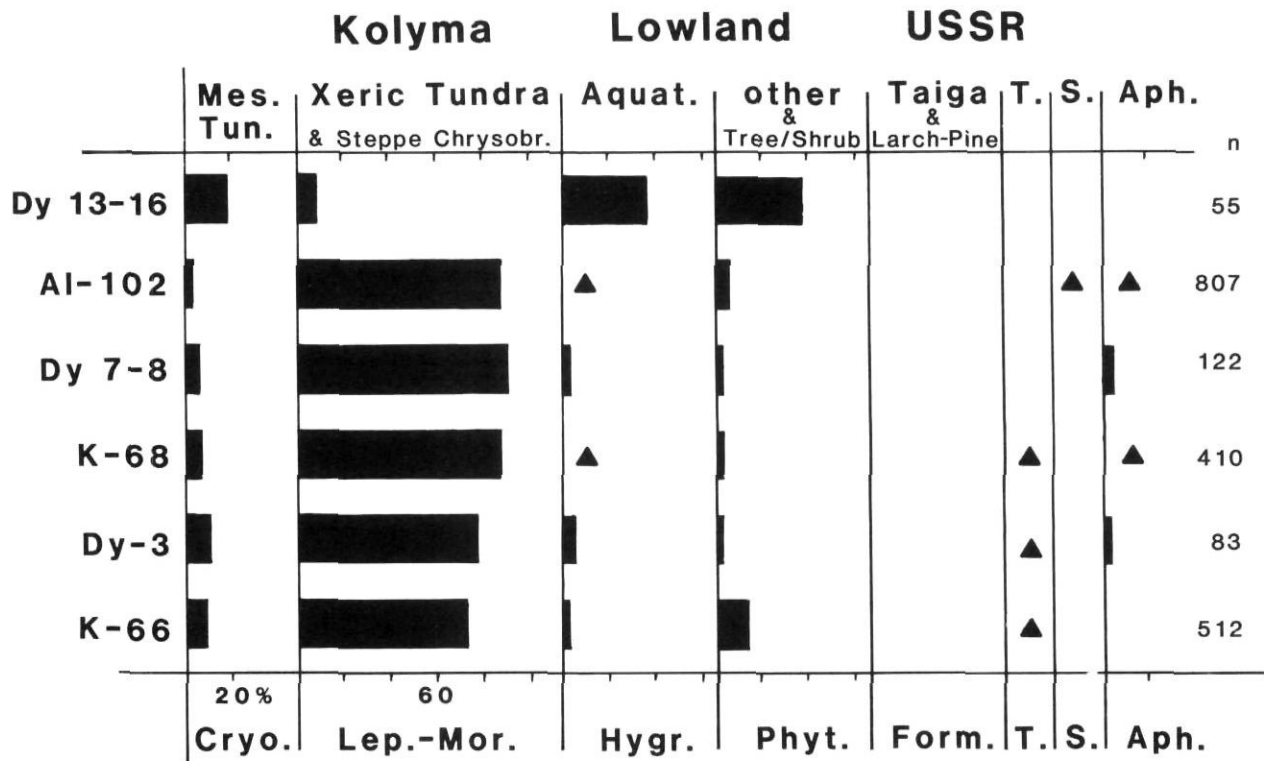
FIGURE 5. Group comparison of insect assemblages from the Kolyma Lowland, U.S.S.R. Headings at top of columns are the groups used by Kiselyov (see SHER et al., 1979). Headings at bottom of columns are the groups used in this paper. Cryo. = Cryobius Group; Lep.-Mor. = Lepidophorus-Morychus Grp.; Hygr. ≈ Hygrophilous-Aquatic Grp.; Phyt. = Phytophagous-Miscellaneous Grp.; Form. = Formicid Grp.; T. = Tachinus Grp.; S. = Silphid Grp.; Aph. = Aphodius Grp.; ▲ indicates percentages of 2% or less.

Comparaison de groupes d'associations d'insectes des basses terres de Kolyma, U.R.S.S. Les rubriques au-dessus des colonnes identifient les groupes utilisés par Kiselyov (voir SHER et al., 1979). Les rubriques au bas des colonnes représentent les groupes utilisés dans cette étude. Cryo. = groupe de Cryobius; Lep.-Mor. = groupe de Lepidophorus-Morychus; Hygr. = groupe hygrophile-aquatique; Phyt. = groupe phytophage-divers; Form. = groupe de Formicidés; T. = groupe de Tachinus; S. = groupe de Silphidés; Aph. = groupe de Aphodius; ▲ indique un pourcentage de 2 ou moins.

philous-Aquatic Group. Hygrophilous-Aquatic Group diversity is much lower in sample 78-48/50, but the character of the host sediments also implies deposition at a well vegetated, peat-forming site.

FAIRBANKS REGION

Fossil insect assemblages from the Fairbanks region (Fig. 3) exhibit much more variability than those from the Northern Yukon. The confidence limits of the Hygrophilous-Aquatic and Tachinus groups just overlap for samples R-B and 3-1A. In the former, however, the Formicid Group is better represented, and when their taxonomic content is compared, the two appear even more dissimilar. R-B represents a taiga environment. 3-1A, on the other hand, was evidently deposited in tundra or an open forest-tundra environment (MATTHEWS, 1970).

Statistical tests show that 3-3C and 3-3B are taxonomically more similar to one another than either is to 3-1A (MATTHEWS, 1968). In the Cryobius Group, for example, 3-1A differs from the other two samples by its abundance of fossils of Pterostichus (Cryobius) nivalis Sahlb., a beetle that often occurs in thickly vegetated

tundra regions. In contrast, the Cryobius Group in 3-3B and 3-3C is comprised of species characteristic of drier tundra in which vegetation is more scattered. These taxonomic deviations are reflected by group percentages (Fig. 3), for even through there is overlap of the Cryobius Group percentages among 3-1A, 3-3C and 3-3B, the latter two stand apart by their higher percentages of the Lepidophorus-Morychus Group.

The insect fossils in sample 2 are poorly preserved. Many of the beetle pronota and elytra possess a type of pitting that often occurs on fossils from well aerated sediments (MORLAN and MATTHEWS, 1983. The fossils come from sediments immediately beneath a major disconformity that formed at a time of deep thawing. Thus it is possible that differential preservation has favored certain species within the Lepidophorus-Morychus Group, thereby inflating its percentage. Lepidophorus lineaticollis fossils dominate the group, and of all northern species it is one expected to suffer least in the face of chemical and soil biological degradation. But this is clearly not the entire explanation for the high percentage of the Lepidophorus-Morychus Group in sample 2 because the representation of

the different types of *Lepidophorus* fossils is also skewed. *L. lineaticollis* elytra in sample 2 represent 522 individuals, while pronota and heads only 269 and 39 respectively. The reason for such deviations is not entirely known, but may be due to differential buoyancy of the various fragments. In any event, it is clear from this example that such potentially significant information is totally obscured by the grouping procedure used to construct Figure 3. Thus, the grouping procedure should not be used to the exclusion of other more traditional types of analyses.

Sample 1 from Eva Creek is puzzling. The values for the Cryobius Group are extremely high and virtually all of the fossils in the group are from species of the subgenus *Cryobius*. The other groups contain a total of less than seven taxa. Individuals of various *Cryobius* species are abundant in existing mesic tundra, but never to the exclusion of the other taxa normally placed in the Cryobius Group.

CAPE DECEIT, ALASKA

The most obvious departure of the Cape Deceit samples from nearly all others is in their high values for the Tachinus Group. It is most pronounced in the early Pleistocene sample, S-10-67. Many of the *Tachinus* fossils were partially articulated which suggests that they represent individual insects living at the site of deposition.

Sample 10-67 contains more than 20% Lepidophorus-Morychus; however, none of the fossils are *Lepidophorus*. This illustrates the fact that the groups do not merely express the abundance of the taxa for which they are named, and it also shows the danger of ignoring taxonomic comparisons of fossil assemblages.

The S-1 assemblage is one of those that carry a significant number of fossils that cannot at present be placed in any particular group. For example, 43 individuals represent a staphylinid beetle (Staphylinidae) that I formerly referred (incorrectly!) to the genus *Subhaida* (MATTHEWS, 1974). Fossils of this same beetle occur in other Alaskan samples (NELSON, 1982), and they may represent an undescribed genus recently collected at relatively dry biotopes in Idaho (J.M. Campbell, pers. comm., 1982). If so, the 43 individuals in S-1 would be placed in the Lepidophorus-Morychus Group, further emphasizing its already dominant status (Fig. 4).

Cape Deceit sample S-5 stands apart from all the others in Figure 4 by its abundance of the Cryobius Group. The group is dominated by the species *P. (Cryobius) nivalis*, which as indicated above, favors tundra sites with a rich vegetation cover. Pollen and plant macrofossils from S-5 also call for such an environment.

In terms of its group composition sample S-6 is similar to S-1. The only differences concern the Aphodius Group, and to a lesser extent the Miscellaneous-Phytophagous Group. The group similarities of these two samples, however, mask important taxonomic differences: S-6 lacks many of the species in the Lepidophorus-Morychus Group of sample S-1, and instead contains, like some of the Yukon samples, abundant fossils of the pill beetle, *Morychus*.

KOLYMA LOWLAND, U.S.S.R.

Kiselyov (in SHER *et al.*, 1979) presents tables that compare percentages of insect individuals in various ecological classes for samples from key exposures in the Kolyma Lowland. Figure 5 is an attempt to compare the group composition of several assemblages in terms of his classification system (column headings at top) and those used in this paper (column headings at bottom). The two classification schemes are not identical and Figure 5 involves some assumptions that might not prove acceptable to one more familiar with the east Siberian fauna.

The most striking feature of the Kolyma diagram is that all samples except the one of Holocene age (Dy 13-16) display markedly high percentages of the Lepidophorus-Morychus Group. In North America few samples show such a dominance of the Lepidophorus-Morychus Group; in eastern Siberia it is apparently a common feature of Pleistocene insect assemblages. What is not evident in Figure 5 is that the Lepidophorus-Morychus Group in Siberian samples does not contain *Lepidophorus* (currently a rare beetle in Siberia). Instead the majority of the insects in the group represent the pill beetle, *Chrysobyrrhulus*, which is probably congeneric with *Morychus*. Kiselyov's explanation for the dominance of *Chrysobyrrhulus* and other insects that I include in the Lepidophorus-Morychus Group is that they indicate tundra-steppe environments.

The Holocene sample Dy 13-16 is quite distinct. Soviet palynologists and paleoecologists often stress the uniqueness of the Holocene environment, and this is clearly shown by the group composition of Dy 13-16 compared to the others in the series.

REGIONAL COMPARISONS

To this point comparisons have dealt mainly with the analyses of trends revealed by samples from the same site or region. Figure 6 compares sample pairs from different regions.

Late Wisconsinan (Sartan) samples from east Siberia and the northern Yukon are shown in Figure 6-1. The two are similar except for the greater frequency of the Lepidophorus-Morychus Group in the Siberian sample (Al-102). This distinction, though subtle, is a reflection of important taxonomic differences between the two assemblages.

The differences of the two Holocene samples in Figure 6-2 support conclusions drawn on the basis of comparison of their respective taxonomic components. CRH-44 represents a poorly drained, shrub tundra site, hence the high percentage of the Hygrophilous-Aquatic
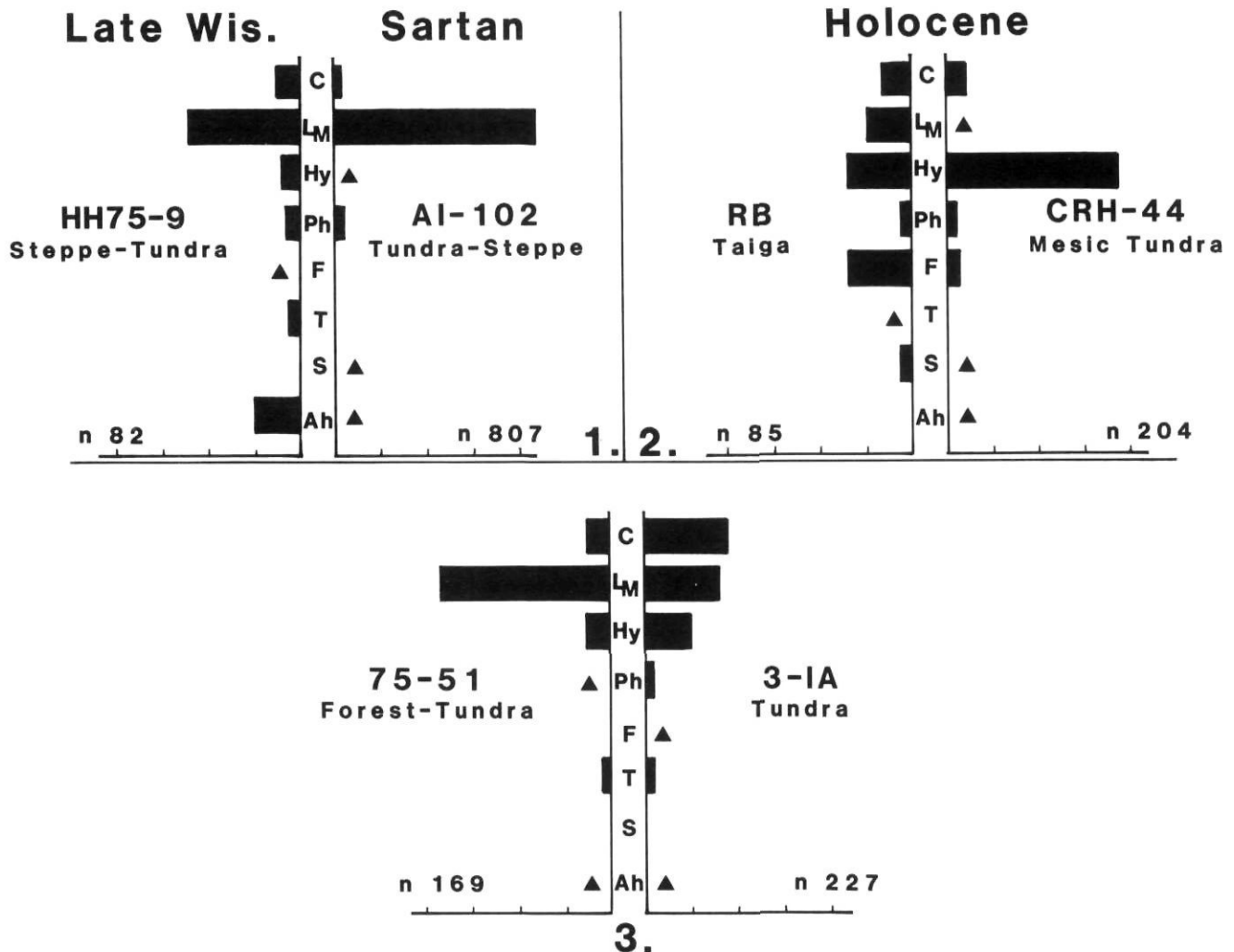
FIGURE 6. Comparison of assemblage pairs but from different regions of Alaska-Yukon and Siberia. See Figures 2-5 for details. C = Cryobius Group; LM = Lepidophorus-Morychus Grp.; Hy = Hygrophilous-Aquatic Grp.; Ph. = Phytophagous-Miscellaneous Grp.; F = Formicid Grp.; T = Tachinus Grp.; S = Silphid Grp.; Ah = Aphodius Grp.; ▲ indicates percentages of 2% or less.

Comparison de paires d'associations provenant de différentes régions en Alaska, au Yukon et en Sibérie. Les détails sont donnés aux figures 2 à 5. C = groupe de Cryobius; LM = groupe de Lepidophorus-Morychus; Hy = groupe hygrophile-aquatique; Ph = groupe phytophage-divers; F = groupe de Formicidés; T = groupe de Tachinus; S = groupe de Silphidés; Ah = groupe de Aphodius; ▲ indique un pourcentage de 2 ou moins.

Group. On the other hand, the R-B assemblage represents forested conditions (note the Formicid Group) and slightly drier substrata.

The two early Wisconsinan samples (Fig. 6-3) are quite dissimilar, but this is probably due to overrepresentation of *Lepidophorus lineaticollis* in 75-51 (see also MORLAN and MATTHEWS, 1983).

DISCUSSION

The prime objective of the grouping procedure is to make the interpretation of insect faunas easier. The method should also be of value for analysis of regional trends in insect assemblages from different sites and regions. I believe that the comparisons discussed above show that these objectives are attainable. None of the group comparisons lead to conclusions that are opposite to those derived from study of the taxonomic content of the assemblages. In some cases grouping the fossils opens the way for comparisons that could not have been made otherwise (MORLAN and MATTHEWS, 1983). On the other hand, it has been shown above that the group comparisons may conceal important taxonomic differences between assemblages. Consequently, the method should not be used as a replacement for other types of fossil insect analysis. It should also be obvious from the examples discussed above that the composition of the groups in some samples will change as our understanding of the northern fauna grows. This contingency is especially likely in samples containing a large component of fossils that cannot be placed in any group. Finally, I acknowledge

that the simple analytical measures used here will no doubt be replaced at some future time by more rigorous statistical tests. At present, however, the data do not justify such an approach.

A simple typesetter's lapse would render the "grouping procedure" described here as the "groping procedure". While not exactly the blind search that such a misprint would imply, this report is obviously not a final statement. Nevertheless, I do believe it shows that the grouping procedure, as a means for comparing fossil insect assemblages of greatly different size and/or taxonomic character, merits further testing and refinement.

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