

**BIOGEOGRAPHIC CONSIDERATIONS ON *COENAGRION HYLAS FREYI* (BILEK, 1954), BASED MAINLY ON THE KARYOTYPE FEATURES OF A POPULATION FROM NORTH TYROL, AUSTRIA (ZYGOPTERA: COENAGRIONIDAE)\***

B. KIAUTA and M. KIAUTA

S.I.O. Central Office, P.O. Box 256, NL-3720 AG Bilthoven,  
The Netherlands

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The chromosome cytology of the sp. ( $n\delta = 14$ , no  $m$ ;  $RI\delta = 26$ ) is compared with that prevailing in *odon. pioneer* spp., in spp. in the process of expanding their range (which is coupled with infraspeciation), and in those considered to represent Pleistocene ("glacial") faunal relics. While in *h. freyi* the chromosome number and the recombination index (RI) are stabilized at the modal adaptive level of the genus, this is not the case in the taxa referable to any of the 3 said groups. On the other hand, the karyotypic features of *h. freyi* do agree with those so far known in *odon. spp.* of trans-eurasian or holarctic distribution. The hitherto available information on its habitat requirements and behaviour is also taken into consideration, and it is preliminarily concluded that *h. freyi* is neither a pioneer sp., nor a recent introduction into the European fauna, but rather a trans-eurasian taxon, whose post-Pleistocene disjunction is the result of its specialized microhabitat requirements, associated with shallow, essentially stenothermic (sections of) subalpine lakes and ponds, characterized by a rather complex biotic community and by a climax *odon.* association. The paucity of the hitherto known localities in Europe is tentatively ascribed to the peculiar adult diurnal activity rhythm (which was hitherto unknown and, therefore, greatly reduced the chances of detection of a resident population), and to the rarity of the required type of habitats. — An annotated bibliography on the taxon is appended.

**INTRODUCTION**

Since the spectacular discovery of "*Agrion freyi*" in southern Bavaria (BILEK,

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1954), much has been discussed on its taxonomic status. Er. SCHMIDT (1956) was the first to point to the close affinities with the Asiatic *Coenagrion hylas* (Trybom), whose range is separated from the European localities by a gap of some 3000 km. The subject was also touched upon by BILEK (1957) and examined in considerable detail by LIEFTINCK (1964), who concluded that the two taxa are conspecific. HARZ (1978), on the other hand, attempted to show *freyi* as a clearly distinct species, though not all his arguments are convincing. DUMONT (1971) did not discuss the structural features of the two taxa, but advocated retaining the name *freyi* on geographic grounds, even if no clear structural distinctions between the Asiatic and the European individuals were to be found in the future. This suggestion was followed by DAVIES & TOBIN (1984), VANTOL & VERDONK (1988), BRIDGES (1991), TSUDA (1991) and by the 1988 and 1990 IUCN editions of the "Red list of threatened animals", referring to *freyi* as a subspecies of *hylas*. All other authors are refraining from a subspecific classification, adopting either *freyi* (JURZITZA, 1976; WELLS et al., 1983; COLLINS, 1985; d'AGUILAR et al., 1985; IUCN, 1986; BELL-MANN, 1987; COLLINS & WELLS, 1987; WENDLER & NÜSS, 1991), or *hylas* (BUCHHOLZ, 1967; LOHMANN, 1967, 1980; AGUESSE, 1968; HEIDEMANN, 1974; JURZITZA, 1978, 1988; Eb. SCHMIDT, 1977, 1978; TSUDA, 1986; ASKEW, 1988; SCHORR, 1990). A reliable study of the taxonomic status of these taxa is considerably hindered by several unfavourable circumstances. The appreciable individual variation in European material, particularly in the measurements and in the blue-black patterns, requires the study of longer series, which are generally and understandably not available. These are needed, since all the various Siberian infraspecific taxa in *hylas* are defined in terms of colour pattern distribution (e.g. BELYSHEV & HARITONOV, 1974). In addition, very few Asiatic *hylas* specimens are available in the collections outside the USSR. It is likely, therefore, that the controversy will remain unsettled for some time to come.

Irrespective of the true taxonomic status of the European populations, their biogeographic origin and nature are also subject to different opinions and speculations. DUMONT (1971) considers *freyi* a true glacial relic, while HEIDEMANN (1974) suggests *hylas* to have extended its range into Central Europe only in the last few decades, arguing that it is unlikely that it would not have been noticed there earlier, if present. Some workers (unpublished) are of the opinion that the European *hylas* is a "typical pioneer species".

Since the chromosome cytology of the Siberian and of the Japanese *hylas* is unknown, information on the karyotype morphology in Europe cannot lend any support to the clarification of the taxonomic status of the European population at this stage. In our opinion, however, it does provide some evidence towards understanding the biogeographic character of *C. hylas freyi*.

So far four populations of *freyi* were reported. The topotypical Zwingsee

population in Bavaria disappeared due to the destruction of the habitat (cf. DUMONT, 1971; SCHORR, 1990). The population at the locality discovered and described by HEIDEMANN (1974) in North Tyrol was said to have been small and to have completely ceased, without any apparent anthropogenic interference. We have seen the lake, but had no chance to look for *freyi*. The population in canton Berne, Switzerland, discovered in the 1970s by Miss I. Siegenthaler and Mr O. Strub (Thun), has never been documented by a single voucher specimen and, therefore, has always remained somewhat uncertain and a bit of a "puzzle". We have visited the locality in 1978, outside the adult season, and found its appearance almost identic with that of the other known localities (shallow, clear "lake", with *Carex* islands, fed by limnokrenic springs). Unfortunately, the habitat is said to have been destroyed through human impact some years ago. The fourth, and at present the sole known *freyi*-populated habitat is situated in the same general area as the "Heidemann locality".

Thanks to the courtesy of Dr Gerhard Lehmann (Kufstein, Austria) we were able to visit the spot in his company on July 18, and again, on our own, on July 22, 1991.

#### NOTES ON THE HABITAT<sup>1</sup>

The locality has been discovered on June 27, 1986, by Dr Jan T. Hermans (Linne, The Netherlands), at whose request the *hylas freyi* identification was confirmed by Dr Reinhard Jödicke (Nettetal, Germany).

The habitat is a large, shallow pond ("lake")<sup>2</sup> (ca 250x200 m; surface ca 1.3 ha), at an approximate altitude of 900 m. It is fed by several small to minute streams and by an unknown number of limnokrenic springs. Judging from the huge difference between the small volume of the inflowing surface tributaries and the amazingly large outflow, the limnokrenic springs seem to contribute most of the water.

Almost the entire shore area is swampy; reeds and/or other emergent and swamp vegetation (e.g. *Carex*, *Epipactis*, *Eriophorum*, *Menyanthes*, etc.) are abundant in various associations, here and there forming "islands" in the pond

<sup>1</sup> In accordance with the spirit of the recommendation by the IUCN Species Survival Commission/Odonata and in agreement with the responsible local odonatologist, the International Odonatological Society (S.I.O.) is disinclined to give information on the exact topographic position of the locality. This can be supplied solely to qualified workers and upon submission of an outline of the particular research project for which the visit to the area is required. For general "observations" and/or for the sole purpose of photographing the information cannot be provided. All workers to whom the locality is known have been requested to keep the information secret. Likewise, in publications the locality name should be replaced by a reference to its deposition in the S.I.O. Archives. — [Eds]

<sup>2</sup> Although in the German map reference the respective water body is called a "See" (= lake), this terminology hardly fits the case. Save for its somewhat deeper southern part, our locality rather has the hydrological features of a large pond: it is shallow enough to enable the vegetation to grow from the bottom, and the lacustrine thermic system is certainly lacking.



Fig. 1. *Coenagrion hylas freyi* (Bilek): the habitat in North Tyrol. (Photography by Rector J. Biedermann, July 18, 1991). — The peculiar habitat structure is essentially similar at all four hitherto known Alpine localities of the species.

(cf. Fig. 1). The surrounding coniferous forest reaches close to the "lake" in some places, elsewhere the distance amounts to anything between 50-300 m approx., with the intervening space being here and there dotted with solitary young spruce.

The minnow (*Phoxinus phoxinus*) is the most abundant vertebrate element in the "lake" and in the largest of its tributaries.

A detailed description of the habitat and of its odonate fauna is in preparation by Dr G. Lehmann and his associates, Dr H. Bellmann and Mr H. Heidemann, who are also conducting a systematic enquiry into the various aspects of *hylas freyi* autecology, behaviour and life history.

On July 18, 1991, the weather was generally fair, air temperature (at 12.30 h) 21°C, though a passing cloud would interfere sporadically with the sunshine for a couple of minutes. On July 22, the weather was splendid (at 11.00 h air temperature 19°C), with some eastern wind that did not seem to exercise any adverse impact on dragonfly activities. We were at the spot on July 18 between 11.30-14.30 h, and on July 22 between 10.00-15.30 h.

During our two visits, and in addition to the very numerous *C. h. freyi*, the following odonate species were recorded: *Enallagma cyathigerum* (few, mostly near the outflow, where no *freyi* were noticed, a single ♂ among *freyi* on the northern shore), *Pyrrhosoma nymphula* (everywhere, almost as common as *freyi*), *Aeshna cyanea* (1 ♂), *A. grandis* (1 ♂), *Anax imperator* (2 ♂), *Somatochlora arctica* (several in the swamps), *Libellula quadrimaculata* (common) and *Sympetrum danae* (1 ♂). — According to the information kindly provided by Dr Lehmann, *Coenagrion hastulatum*, *Lestes sponsa*, *Aeshna juncea*, *Somatochlora metallica*, *Leucorrhinia dubia* and *Libellula depressa* are among the species

evidenced from the "lake" earlier.

#### NOTES ON SOME BASIC BIOLOGICAL FEATURES OF *C. HYLAS FREYI*

While the Siberian *hylas* occurs in a variety of habitats, incl. deep and shallow, warm and cold, stagnant and running water sites (cf. BELYSHEV, 1973, p. 538), in the European Alps the species is strictly restricted to the shallow and essentially stenothermic (sections of) subalpine lakes or ponds, the features of which have been summarized by SCHORR (1990) and agree perfectly also with the general situation at the present locality.

As is apparent from the evidence published by LIEFTINCK (1964), LOHMANN (1967) and HEIDEMANN (1974), the adults are on the wing about the last decade of June into the first decade of August, though some local and annual variation in phenology, related to the altitude of a particular locality, water temperature, and to the particular weather conditions in a certain year, should be taken into account.

The zygopteran fauna, as recorded on our spot on July 18 and 22, 1991, consists of a large population of *Pyrrhosoma nymphula*, very few individuals of *Enallagma cyathigerum* and the *hylas freyi* population, which is at least as large as that of *P. nymphula*, if not larger. On a brief visit, without marking the individuals, it is difficult to reliably assess the strength of a zygopteran population. The abundance of *hylas* certainly resembles that of e.g. *E. cyathigerum* or *Coenagrion puella* at a similar lowland pond. On a shore stretch of about 150 m, which we kept under close observation, there were certainly more than 100 ♂ (and very few ♀!) on each of the two visits. Taking into account that not all sections are uniformly frequented by *hylas*, and that certainly some individuals were counted several times, one would still be inclined to assess the total annual population of the pond in terms of "hundreds" rather than "dozens" of individuals. Though this is at the moment the sole known *h. freyi* locality, it is most unlikely that some population would not exist in other similar habitats in the region, but the discovery of these is seriously hindered by the peculiar adult daily rhythm of our damselfly (cf. below).

The individual variation in the male blue-black abdominal pattern has been emphasised already by LIEFTINCK (1964) and occurs also in the present population. The individual size variation in males is in our population even larger than recorded by Lieftinck and LOHMANN (1967), viz. total length: 33-39 mm, abd. length: 25-30 mm. A similar, though considerably smaller size variation occurs in some alpine *Enallagma cyathigerum* populations, but we have never noticed it to this enormous extent in any other alpine damselfly. This is certainly related to the amount of food consumed at the larval stage. One might speculate whether the adult size could indicate the number of larval hibernations: one in the small, and two in the large individuals. (The local *P. nymphula* adults show very

little size variation, and we have seen too few *Enallagma* specimens to allow any assessment of the subject).

It is amazing that almost all adults observed along the shore were males. We have noticed only 4 solitary females, and slightly more than a dozen of tandems. No homeochromatic females, as described by LOHMANN (1967), were seen, and we are puzzled as to the whereabouts of the *h. freyi* female "population".

We have no personal evidence on the oviposition mode. In the single case recorded and photographed by LIEFTINCK (1964, pl. 19), it takes place under male attendance and not submerged.

In the sunshine at the waterside the adults fly in the usual *Coenagrion* manner, close above the vegetation, seldom higher than 60 cm, but usually as low as the vegetation permits. They never appear at any distance over the open water surface, crossing the water table solely from one to another close-by located vegetation spot, usually some 20 cm above the water. The speed and "determination" of their flight at the waterside do not very significantly deviate from those of other *Coenagrion* species, though they do belong to the better fliers among the congenics. If undisturbed by another individual or by a *Pyrrhosoma*, they usually cover stretches of some 5-7 m, whereupon they settle on the vegetation for anything like 10-30 s.

The diurnal activity pattern of *C. h. freyi* is greatly peculiar. The adults are active at the waterside explicitly in bright sunshine and solely between about 11.00 and 14.15 h. They appear and disappear suddenly, almost simultaneously, though the first solitary male was seen on July 22 at 10.45 h (air temperature 19°C), and the last at about 14.30 h. The females appear considerably later, the first tandem (and a solitary ♀) were seen at 12.15 h, and the last tandem, on July 18, at 14.30 h, and on July 22 at 14.40 h. After that moment, adult dragonfly life at the "lake" continues as usual, *Pyrrhosoma* greatly prevails, but there is not a single *h. freyi* individual at the waterside any more. Consequently, a casual visitor would be unable to detect the species, no matter how much time he/she spent on the shore after the said hour. This peculiar habit of *h. freyi* certainly is responsible for the difficulties in discovering resident populations.

*C. hylas freyi* is also exceptionally sensitive to sunshine; a passing cloud triggers the disappearance from the waterside of the complete "population", within a minute. They will reappear just as fast, as soon as the sun reappears.

We had the opportunity to watch several individuals taking off from the waterside at the end of their day. On the northern bank, where some young, solitary spruces stand about 10 m off the shoreline, they took into the trees, spent there some 10-30 s at about 1-2 m height, and then continued in the direction of a line of mature spruce, some 40 m behind the intermediate resting spot. We were unable to establish whether or where they landed. At the western bank, the forest is at some distance from the water. We had seen a male crossing rapidly, in horizontal flight, across the intervening swamp, at a height of hardly 50 cm.

When it had reached the shadow line of the forest, it landed exactly on the line, rested for less than 10 s, and then continued into the shady woods, where we could not follow it.

The flight off the waterside during passing of a cloud was on the northern shore identical to that described above. On the southern shore, however, where the woods almost reach the bank, we have watched several males and a tandem pair taking off for nearby tree crowns (height ca 8-10 m), in a straight, rapid flight, at an angle of about 70°. Whether they stayed there or continued inland we were unable to ascertain.

As apparent from the above, the adults spend their "inactive" periods away from water, but we had no chance to try and find their whereabouts. It is interesting that BELYSHV (1973) does not refer to this peculiar behaviour in the Siberian *hylas*, but he does emphasize that the adults are often found at a considerable distance from water.

#### MATERIAL AND METHODS

About 8 hours after collection, 6 ♂ were dissected and aceto-carmin squash preparations made. Figure 2 is drawn from fresh preparations, with phase-contrast optics, with the use of a Zeiss 45° drawing prism.

The specimens are in the authors' collection.

In addition, and "under embargo" of the locality data, 2 ♂ each were/are to be deposited in the collections of the International Odonata Research Institute (Gainesville, Florida, USA), British Museum (Natural History) (London), and in those of the Museum National d'Histoire Naturelle (Paris).

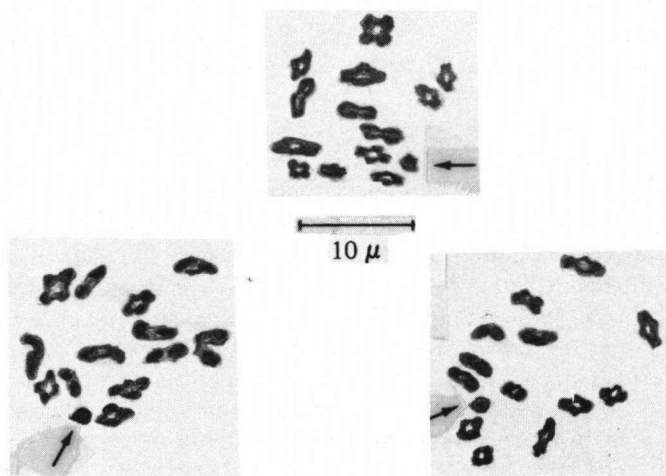


Fig. 2. *Coenagrion hylas freyi* (Bilek): early primary spermatocyte metaphase; arrows indicate the unpaired sex element. — [Aceto-carmin squash; 45° drawing prism]

## THE KARYOTYPE

Nothing is known on the adult longevity of *C. hylas freyi*; the cytologically examined individuals were taken at the moment assumed to coincide with the approximate peak of the adult season of the local population. They were mature, but not old; on our two visits we were unable to find a single freshly emerged or teneral individual. As it appears, meiotic activity in *h. freyi* is brief, secondary spermatocytes prevailed; only in 2 individuals were some metaphase-I stages encountered.

The chromosome complement,  $n\delta = 14$ , is of the usual *Coenagrion* type, there are no *m*-chromosomes, and the unpaired X is the smallest element of the metaphase-I set. A single chiasma occurs per bivalent, resulting in what is considered the usual recombination index ( $RI\delta = 26$ ) in the genus (cf. Fig. 2).

## DISCUSSION

The *Coenagrion hylas freyi* karyotype ( $n = 14$ ) and the recombination potential of the species ( $RI\delta = 26$ ) appear stabilized at the usual *Coenagrion* level. Since an increased RI promotes flexibility, i.e. the ability of a genotype to vary and adapt itself to changing conditions, while a reduced RI promotes fitness, i.e. the survival value and the reproductive capability of a genotype as compared with the average of the population or the other genotypes in it, it is of some interest to review the *h. freyi* situation in the light of cytological conditions prevailing in pioneer species, in the range expanding taxa, in holarctic and trans-eurasian species ranging from eastern Asia to western Europe, and in the stationary relics.

## CYTOLOGY OF THE ODONATE PIONEER SPECIES

In dragonflies, by "pioneer taxa" are understood species able to successfully invade habitats that are at the initial stage of the biotic community succession (e.g. freshly made artificial ponds), or to survive and reproduce in habitats where the normal community succession is precluded by adverse climatic or other microenvironmental conditions (e.g. high-altitude alpine sites)<sup>3</sup>. In the first case the occupation may be temporal and the species might disappear when the development of the biotic community (viz. vegetation, etc.) will have reached a more advanced (or climax) stage, but in the second case the occupation is

<sup>3</sup> The term "pioneer species" comes from botany. Although it is often used with reference to animal communities, its applicability in zoology is questionable, and it can be solely used within a modified definition. While the pioneer plant species are the first settlers in a given new habitat, preparing the latter for a more complex climax vegetation, the animals are only associated with a pioneer vegetation for reasons of their microclimatic and/or trophic requirements, but do not play any essential role in the "preparation" of the habitat for a more advanced animal community.

permanent, as the microenvironmental conditions, such as e.g. the climate conditioned by the altitude, preclude the "normal" succession. Apart from various, usually not easily recognizable physiological and life history adaptations, mobility, i.e. the capability to detect such new habitats, is one of the basic requirements for pioneer species.

In the alpine regions of Central Europe much attention has been given to faunal succession in man-made habitats (e.g. WILDERMUTH & KREBS, 1983); *Ischnura pumilio* and *Libellula depressa* appear pioneer species par excellence, the former occurring also in some high altitude environments. In the case of *Libellula*, no words are needed with reference to its adult mobility, while in *I. pumilio* the ability to utilize thermal air currents for rapid long-distance travel has been recently discovered and described by FOX (1989). Catching the uplifting air current is performed by *I. pumilio* in rapid, steeply upward active flight, not unlike that described above for *C. h. freyi* when flying rapidly towards the crowns of the trees close behind the shore line, though in the latter species the air thermics is certainly not utilized, and the damselflies return to the waterside immediately after the sun reappears, or else the next day at the usual time.

Neither of the two pioneer species possesses an RI stabilized at the modal adaptive level of the respective group (family, genus) to which it belongs. In *I. pumilio* it is increased and invariably stabilized at  $RI \text{ ♂} = 28$  ( $n \text{ ♂} = 15$ ) (KIAUTA, 1979), while in *L. depressa* the RI and  $n$  vary even within the cells of one same individual, based on male haploid complements of 12, 13 and 14 (FRANKOVIĆ, 1987).

From the above it seems that increased genetic flexibility is among the requirements of pioneer species. In *C. hylas freyi* any such increase appears lacking.

#### ODONATE SPECIES EXPANDING THEIR RANGE

With reference to *C. hylas*, HEIDEMANN (1974) stated: "Da nicht anzunehmen ist, dass sie in dem gut erforschten Mitteleuropa hundert Jahre lang übersehen wurde, halte ich für möglich, dass sie sich in den letzten Jahrzehnten von Osten her nach Mitteleuropa ausgebreitet hat. . . dabei könnten vor allem Gebirge, etwa die Karpathen, Zwischenstationen sein", but he did not elaborate further on this theory.

It goes without saying that due to the ever increasing interest in odonate mapping, some localities are likely to be brought on record whose topographic position lies outside the previously known ranges of the taxa concerned. Even so, it should be emphasized that *Sympetrum pedemontanum* is probably the only species that in Europe shows some trends towards a local westward range expansion, similar to the recent eastward expansion of *Gomphus pulchellus* in Central Europe (cf. GÄCHTER, 1988, with references). On the other hand, a systematic northward range expansion was recorded in several species, for most

of which various stages in this process (i.e. the geographic latitude reached) can be even approximately dated. This applies e.g. in North America to *Enallagma basidens* (CANNINGS, 1989), and in Europe to *Brachythemis leucosticta* (CRUCITTI et al., 1981), *Trithemis annulata* (TERZANI, 1991), *Libellula depressa* (DOLMEN, 1989), *Somatochlora flavomaculata* (OLSVIK, 1990), etc. — to mention just a few examples. In all these and other similar cases on record, the northward range expansion is systematical, progresses gradually over relatively short geographic distances, but it is amazingly rapid in terms of years needed to cover a certain stretch. Cytologically, most, though not all of these taxa were examined from one or more localities. With the exception of the above described situation in *L. depressa*, none shows any significant karyotypic variability, their chromosome numbers and recombination potentials are modal for the respective higher taxa and, needless to say, there is no infraspeciation within the territory concerned.

Whatever the infraspecific status of *C. hylas freyi*, its modal chromosome complement is inconclusive in this category, the hitherto still unbridged gap of 3000 km is too large for any speculation, and considering its extremely brief diurnal activity (cf. above) it is more than likely the species could escape the notice of collectors even in well explored areas such as Central Europe. A person visiting its breeding site after, say, 14.00 h, will record a rich dragonfly fauna, but will be unable to sight a single *h. freyi* individual!

Although the habit of a rapid flight off the habitat, as demonstrated by *h. freyi* (cf. above), could be speculated to be an "initial evolutionary stage" in achieving migratory ability as described by FOX (1989) in *Ischnura pumilio*, there is so far no firm evidence that this technique is being applied by our damselfly in locating new habitats at any geographically significant distance from the original breeding site. It could, however, be tentatively assumed that this behaviour enables the species to detect new adequate habitats in the immediate environment.

#### CYTOLOGY OF THE GENUS/SPECIES RANGE EXPANSION, COUPLED WITH SPECIATION/INFRASPECIATION

The phenomenon has been described by KIAUTA (1984) in Chlorocyphidae, and by KIAUTA (1983) in the *Crocothemis servilia* complex (Libellulidae). In both cases, range expansion is coupled with (infra)speciation and with pronounced cytological modifications of the original karyotype in the derived taxa. In view of the modal type of the *h. freyi* karyotype, the same situation does not obtain in this case.

#### CYTOLOGY OF THE HOLARCTIC AND TRANS-EURASIATIC ODONATE SPECIES

Not considering the *Cordulia aenea/shurtleffi* complex, and *Crocothemis*

*servilia*, recently imported to the United States, 4 species are conspecific in the Old and New World, viz. *Lestes dryas*, *Enallagma cyathigerum*, *Libellula quadrimaculata* and *Sympetrum danae*, while *Aeshna juncea* and *A. subarctica* are infraspecifically distinct. All were studied cytologically, either from one or from both sides of the Atlantic/Pacific. In *E. cyathigerum* and in both *Aeshna* species the karyotypes are not (entirely) stabilized at the modal generic level, but they do seem to be so in the other species.

In the numerous trans-eurasian species, whose ranges extend from western Europe to eastern Asia, and several of which are considered infra-specifically distinct in different geographic regions, the chromosome numbers are identical throughout the species range, but there may occur more or less significant minor differences in karyotypic morphology between geographically distant populations of some species, notably so in the occurrence and size of *m*-chromosomes (e.g. KIAUTA, 1968a; KIAUTA & KIAUTA, 1984).

*Coenagrion hylas* falls within the latter group. Considering its broader ecological tolerance in Siberia (as compared with the European populations) which probably can be assumed from the brief note on the subject by BELYSHEV (1973, p. 538), and the supposed infraspeciation in eastern Asia (cf. BELYSHEV, 1973; BELYSHEV & HARITONOV, 1974), the origin and radiation centre of the species must be located somewhere in the eastern Palearctic. In this respect, the species appears similar to the *Calopteryx virgo* complex, which is also believed to be of Angaran (= Siberian) primary origin. It is interesting to note, therefore, that neither in the European *h. freyi* nor in the European *v. virgo* there are any significantly smaller autosomes, while a very distinct and minute *m*-pair occurs in the Japanese member of the *virgo* complex (KIAUTA, 1968b). Though without knowing the cytology of the Asiatic *hylas* this evidence is inconclusive, it certainly does not contradict the speculation on the Angaran origin of *hylas*.

#### CYTOLOGY OF THE PLEISTOCENE RELICS IN THE EUROPEAN ODONATE FAUNA

*Aeshna caerulea* and *Somatochlora alpestris* are considered by some, mainly after ST. QUENTIN (1938), to be the sole "true glacial relics" in the European odonate fauna, though it goes without saying that the distributional patterns of a number of other taxa are also notably influenced by the Pleistocene glaciation history (e.g. *Macromia splendens*; cf. DUMONT, 1971). Their recombination indices and chromosome numbers are not stabilized at the usual level of the respective genera (cf. resp. OKSALA, 1943; KIAUTA & KIAUTA, 1980). Though in itself possibly inconclusive, this evidence does not support the suggestion of a "glacial relic" character of *C. hylas freyi*, but it gains in significance if coupled with the ecological requirements of the three taxa. While *A. caerulea* and *S. alpestris* in Central Europe are mainly restricted to biocoenologically "primi-

tive" alpine peatbog habitats, *C. h. freyi* occurs at lower elevations and in much more complex biotic communities.

### PRELIMINARY CONCLUSION

Until more information on habitat requirements, autecology, behaviour and structural peculiarities of *hylas* populations throughout the species range will have become available, we are inclined to tentatively assume that *h. freyi* is a westernmost form of a trans-eurasian species, whose post-Pleistocene disjunction is due to its specific habitat requirements and to the scarcity of adequate water bodies. It is neither a pioneer species, nor a recent element in the Central European fauna, and lacks most of the features of the European "glacial relic" dragonflies.

Apart from the fact that the population at the Tyrolean locality studied is very large, we are confident that more localities will become known if searched for systematically, with due consideration for the species' phenology and its peculiar daily activity rhythm, and provided the absurd "species conservation" legislation in a steadily increasing number of countries will not preclude adequate taxonomic identification. The larva has already been bred in captivity, and it is hoped that its description is soon to be published. This, of course, will immensely facilitate the search for new resident populations, and extend detection possibilities to all ice-free months and to all hours of the day.

The places to look for the species are shallow stenothermic, largely limnocranically fed ponds and similar sections of small subalpine lakes, with clear water, with *Carex* and similar vegetation, and situated at approximate elevations of 800-1200 m, in the valleys of the Northern Alps, in Austria, Germany and Switzerland. Certainly worthwhile to explore are also similar situations in the East European mountain systems.

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