

Systematic Reappraisal of the *Anopheles maculipennis* Complex

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Summary

The taxonomy and nomenclature of sibling species comprising the *Anopheles maculipennis* complex are discussed in relation to the newly described Russian species *A. beklemishevi*. Despite an editorial disclaimer appended to the type-description, the name *beklemishevi* is formally available, as published, for the first mosquito species ever to be named and described primarily from cytogenetic evidence. Although its anatomy is very similar to other sibling species, *beklemishevi* is a genetically independent member of the complex, with a more northerly distribution than that of *maculipennis* s. s. Published names which might take precedence over *beklemishevi* are *alexandraeschingarevi*, *lewisi* and *selengensis*; these names may apply instead to the widespread Eurasian species universally known as *messeae*. However, the original description of *messeae* seems actually to have been based on material of the Mediterranean species usually called *melanoon* (with its variety *subalpinus*). It is argued that the names *messeae* and *melanoon* should be preserved in their current sense, and that the name *beklemishevi* should be adopted while the names *alexandraeschingarevi*, *lewisi* and *selengensis* are suppressed.

Thirteen members of the *A. maculipennis* complex are recognized. These comprise 9 Palaearctic species: *atroparvus*, *beklemishevi*, *labranchiae*, *maculipennis*, *martinius*, *melanoon*, *messeae*, *sacharovi* and *sicaulti*, and 4 Nearctic species: *aztecus*, *earlei*, *freeborni* and *occidentalis*. This list includes two species (*martinius* and *sicaulti*) here resurrected on the basis of recent research.

Lectotypes are designated for *alexandraeschingarevi* (♂), *maculipennis* (♀), *martinius* (♀), and *sacharovi* (♂); a neotype ♀ is designated for *sicaulti*. It is pointed out that the name *typicus* (= *maculipennis* s.s.) was originally proposed by Hackett (1934), not by Hackett & Missiroli (1935), and that the original - and therefore correct - spelling of *labranchiae* and *messeae* is etymologically unsound. English translations are given for the type-description of *alexandraeschingarevi*, *maculipennis*, *martinius*, *sacharovi* and *sicaulti*.

Evolutionary relationships of the *maculipennis* complex are tentatively plotted from chromosomal evidence. Distribution maps and an identification key, largely based on egg and polytene chromosome characters, are given for all 13 recognized members of the Holarctic *maculipennis* complex.

Introduction

Publication of the type-description of *Anopheles beklemishevi* Stegnii & Kabanova, 1976, prompts some debate about the usage and validity of this and

other names proposed for members of the renowned *Anopheles maculipennis* complex. Another recent paper by Stegnii (1976) reported the existence of two fixed chromosomal inversion differences between "chromosomal races" of *Anopheles sacharovi*. Such karyologically distinct populations may also be regarded, at least provisionally, as a pair of genetically separate sibling species requiring different scientific names.

Proof that members of the *maculipennis* complex rank as separate biological species - not subspecies, races, biotypes, varieties or forms - has been amply demonstrated for the majority of taxa by means of hybridization tests and cytogenetical studies to confirm their genetical independence (Kitzmiller, Frizzi & Baker, 1967). The general taxonomic debate was effectively closed by Bates (1940) who argued convincingly that the complex comprises a group of species which may, and frequently do, exist as sympatric populations without undue introgression. Reviews of subsequent research on the *maculipennis* complex have been published by Frizzi (1952, 1953), Pratt (1952), Kitzmiller et al. (1967) and by Guy, Salières & Boesiger (1976). The ensuing notes should further clarify the nomenclature and systematics of these interesting and still important mosquitoes, the dead adults of which cannot be reliably identified as to species by any current approach.

Availability of the name *beklemishevi*

On the opening page (p. 192) of the paper in which *beklemishevi* was described in vol. 45 of *Meditinskaya Parazitologiya i Parazitarnye Bolezni*, there appeared an editorial footnote saying, in translation: "According to the International Code of Zoological Nomenclature, the proposed designation is unacceptable since, in this case, it does not fulfil the requirements of taxonomic publications, namely: no morphological description is given, no type-specimen or exact locality are indicated, nor is other necessary information provided. For the designation to become effective, the authors should comply strictly with the form of a taxonomic publication."

Needless to say, this editorial disclaimer cannot over-rule the formal availability of the proposed name *beklemishevi*, as published on p. 198, nor does it in any way retract the type-description of this newly recognised species. The proposal and description of *beklemishevi* by Stegnii and Kabanova appear to satisfy all mandatory Articles of the current Code (ICZN, 1964), though they fail to fulfil Recommendation 73A, that a type-specimen should be designated, and they give the known geographical range of the new species without citing an exact type-locality (cf Recommendations 72E and 73C.2).

The editorial assertion that "no morphological description is given" of *beklemishevi* ignores the fact that specific morphological characteristics of the egg-stage are well described and photographically depicted in comparison with the distinctly different egg of *maculipennis* s.s. This formal description of the taxonomic characters of the egg of *beklemishevi* is comparable in quality with the type-descriptions of several other sibling species in the *maculipennis* complex (viz: *labranchiae* Falleroni, *melanoon* Hackett, *messeae* Falleroni) for which the egg is the life-stage exhibiting the most reliable morphological characters for identification of the species. Moreover, for the strictly taxonomic purpose of separating sibling species, Stegnii and Kabanova's account of polytene

chromosome morphology in *beklemishevi* larval salivary glands has considerably more utility than any perfunctory description of the external structures of the larva, pupa and adults of both sexes. It is understood that the general morphology of *beklemishevi* is differentiated only by features of the egg and of the polytene karyotype. Through publication of a reasonably comprehensive account of the distinctive biological, autecological, cytogenetical and distributional characteristics of this newly studied species, and by naming it in conformity with essential Articles of the Code, particularly Article 13(a)(i) which demands no more than that the name proposed is "accompanied by a statement that purports to give characters differentiating the taxon", the name *beklemishevi* has been made formally available in zoological nomenclature.

Significance of the species *beklemishevi*

The detection and description of *Anopheles beklemishevi* comes as a logical development in a series of advanced entomological and genetical studies by Stegnii, Kabanova and their colleagues at the Institute of Biology and Biophysics, State University of Tomsk, and elsewhere in the U.S.S.R. They are continuing a programme of detailed investigations on the cytogenetics and population genetics of Russian anopheline mosquitoes (Kartashova & Kabanova, 1970; Kabanova et al., 1972a, 1972b, 1973; Stegnii, 1976; Stegnii & Kabanova, 1976; Stegnii et al., 1973, 1974, 1976a,b).

Frizzi's pioneering work on the cross-breeding relationships and chromosomes of various European *Anopheles* had previously clarified the status and relationships of certain sibling species in the *A. maculipennis* complex (Frizzi, 1952; Kitzmiller et al., 1967). However, Frizzi and his colleagues reported comparatively little intraspecific chromosomal inversion polymorphism in the species and populations studied (Frizzi, 1956a); their cytotaxonomic studies revealed only those species which had already been named and described on the basis of egg characteristics and other fine points of specific morphology. By contrast, Stegnii & Kabanova (1976) have reported up to 20% of inversion heterozygotes in *beklemishevi* and remarkable rates reaching 80% of inversion heterozygotes in the more widespread and abundant species which they identify as *messeae* (Stegnii, Kabanova, Novikov & Pleshkova, 1976).

The most notable outcome of the recent Russian work is that Stegnii & Kabanova (1976) have described, in advanced terms, the first new member of the *maculipennis* complex to have been reported since the heyday of malariology in Europe four decades ago. The idea that two allopatric and ecologically different sorts of zoophilic "*maculipennis*", both with barred eggs, are present in Eurasia had been appreciated by Hackett and co-workers in the days when the taxonomy of such mosquitoes depended on egg characteristics for separation of what were then considered to be varieties. Hackett & Missiroli (1935:33) expressed the point in these words: "*A. maculipennis* (type) is found breeding under two quite separate conditions throughout the range of the species. It is the characteristic race of the upland cold waters, but it is also found in sparse numbers at sea level, usually in connection with running water. There are places also, such as the Naples plain, where it is found in pure strain under sub-tropical conditions. It refuses to mate in captivity and it spends the winter in complete hibernation, which is proportionately shortened in southern latitudes."

To put this information in modern terms, we now know that *beklemishevi* and *maculipennis* s.s. are morphologically almost identical sibling species with superficially rather similar barred eggs that show micromorphological specific contrasts. The two species are allopatric, the former being endemic to cooler highlands and northern latitudes where it breeds in organically polluted stagnant water. The latter* is restricted to warmer lowlands and more southerly parts of Eurasia where it breeds in relatively cleaner water-courses. Both species are eurygamous and undergo complete winter diapause of a duration that is inversely correlated with photoperiod.

Thus the description of *beklemishevi*, with a preliminary account of its biology and geographical distribution, clarifies a matter of serious taxonomic misunderstanding in the past. Apparently *beklemishevi*, like *maculipennis*, is not particularly anthropophilic, so that neither species is specially significant as a potential malaria vector, although both could be of veterinary importance.

A point of additional and historical interest is that *beklemishevi* is the first mosquito species the discovery, description and naming of which have depended essentially on chromosomal evidence. The latest work by Stegnii (1976) on chromosomally distinct populations of "*sacharovi*" seems to indicate that more members of the *maculipennis* complex may yet be found in the same way.

Validity of the name *beklemishevi*

According to the Law of Priority, *beklemishevi* can only be regarded as the valid name for the taxon described by Stegnii & Kabanova (1976) if no other available names have been proposed previously for the same species. As the separation of *beklemishevi* from other members of the *maculipennis* complex depends at present upon examination of characters on the eggs or chromosomes, it is difficult to determine the specific identity of dead adult specimens of *maculipennis* s. l. collected in the past from places in the extensive range where *beklemishevi* is sympatric with other sibling species, particularly with populations known as *messeae*.

Some of the places where *beklemishevi* occurs are close to the type-localities pertaining to three older names that have long been treated as junior synonyms in the nomenclature of the *maculipennis* complex. Any of these available names might have been based on specimens of the species described by Stegnii and Kabanova, in which case its valid name could not be *beklemishevi*.

In order to decide upon the validity of *beklemishevi*, it will be necessary to consider most of the names proposed for members of the *maculipennis* complex.

Interpretation of the name *alexandraeschingarevi*

Anopheles (Anopheles) alexandrae schingarevi Shingarev, 1928, was proposed as the name for a species described from adults of both sexes collected by Dr.

*The nomen nudum *caucasicus* Shtakel'berg, 1937, was apparently intended for this nominotypical member of the complex (see further footnote p. 27).

E. M. Orlov at Vladimir (180km ENE of Moscow) and by N. G. Saikin at Penza (550km SE of Moscow). The taxon was described quite well (see below) and was said to differ from *maculipennis* only in male hypopygial characteristics, as illustrated. The compound name must be conjoined in accordance with Article 26 of the Code, so the corrected specific epithet is *alexandraeschingarevi*.

Tarwid (1933) reported specimens resembling *alexandraeschingarevi* from Poland, but found sufficient variation of the hypopygial bristles to interpret the taxon as being identical with *maculipennis*, as it was then understood. After re-examining the *alexandraeschingarevi* type-material, Zhelokhovitzev (1937) endorsed its synonymy with *maculipennis* (though the provenance of his *maculipennis* is uncertain; the material may well have been *beklemishevi* in fact). The only other author to have employed Shingarev's name for this taxon was Martini (1931: 163) who published a German translation of the type-description and placed it under the heading "Anopheles maculipennis Alexandrae [Shingarevi]". Thus the available name *alexandraeschingarevi*, which was incorrectly hyphenated as *alexandrae-schingarevi* by Edwards (1932), Knight & Stone (1977) and elsewhere, has consistently been associated with *maculipennis* and is usually regarded as a junior synonym.

The two type-localities of *alexandraeschingarevi* appear to lie in the geographical range of *beklemishevi*, rather than that of *maculipennis* s.s. To be precise, one *beklemishevi* locality at Cheboksary is 350km NNE and 400km E, respectively, of the *alexandraeschingarevi* type-localities at Penza and Vladimir. Stegnii & Kabanova (1976) mention that Hackett & Barber (1935) found *beklemishevi*-like eggs at many places in the Volga River basin, as far west as Orekhovo-Zuyevo (90km E of Moscow). Thus *beklemishevi* has been recorded on three sides of the *alexandraeschingarevi* type-localities, making it fair to infer that these two names could be synonymical. On the other hand, *alexandraeschingarevi* can no longer be regarded as synonymous with *maculipennis* (cf Zhelokhovitzev, 1937; Stone, Knight & Starcke, 1959), since the latter has a more southerly distribution. But the interpretation of *alexandraeschingarevi* remains equivocal because the species known as *messeae* is nearly everywhere sympatric with the newly described *beklemishevi*. So, without a morphological method of distinguishing the types of *alexandraeschingarevi*, it remains impossible to know for which sibling species this name has priority. On distributional evidence alone, therefore, we could apply *alexandraeschingarevi* to either of the species otherwise known as *messeae* or *beklemishevi*, perhaps preferring the former because it usually predominates.

Description of the species *alexandraeschingarevi*

For purposes of international discussion, it helps to have English translations of the type-descriptions pertaining to all names proposed for members of the *maculipennis* complex. The type-description of *alexandraeschingarevi* is here translated from the Russian original text. A German translation was given by Martini (1931).

"Anopheles (Anopheles) alexandrae schingarevi sp. n.

Dark mosquitoes of medium size (male lighter than female), externally very little distinguished from the dark forms of *A. maculipennis* Mg., but the sexual apparatus of ♂♂ enables one to establish the independence of this species.

Proboscis black, palpi of ♀♀ black, palpi of ♂♂ brown, third segment with thick tuft of long golden yellow hair. Antennae of ♀♀ black with rosettes of short black hairs. Antennae of ♂♂ light brown, and covered by long brown hair, except for the last two segments, which are covered by short brown hair and dark pubescence. Head dark brown, covered above with black protruding fork-like scales, admixed with black bristles near the eyes. The section adjoining the clypeus is covered with decumbent white sickle-shaped scales. Mesonotum with pale light-grey stripe in middle. In its posterior part (near scutellum) and in the anterior part (near head) with dark brown narrow stripes in the middle. Lateral sections of the mesonotum are black, but some parts adjacent to the sternum are dark brown. In the frontal part of the mesonotum clusters (2) of white scales are arranged along the sides of the dark stripe. The hairy covering of the mesonotum is of a pale golden colour. Sides of the thorax brown, with some light grey stripes. Scutellum grey, darker towards the sides and covered with long dark brown bristles and short golden hairs. The halteres are of light brown colour. The wing membrane has slight yellowish shade. Veins very thickly covered with dark brown almost black scales. The spots on the wings are situated in the same way as in *A. maculipennis* Mg., but are larger, and darker especially at the bases $R_2 + R_3$ and $M_{1+2} + M_3$. The feet are dark brown but somewhat paler inwardly, tarsi black. Tips of femora and tibiae with pale spots. Abdomen black. Abdomen in ♂♂ with light triangular markings. The abdomen is covered with long golden yellow hair. Hypopygium (Fig.) has one simple spine near the middle of the internal edge of the basal segment of the valvae, it is situated on a tubercle of medium size - it is thick and short. The next spine after it is slightly thinner and twice as long. This spine is situated on a small tubercle, adjacent to the first. And, finally, the third spine is even thinner and situated at the base of the first tubercle. Its size is shorter than the second, but longer than the first; all spines are simple. Claspettes three-lobed; the exterior lobe has two spines on the top, very near to each other, but not joined together. The middle lobe has two spines standing separately on top, and the internal lobe is covered with hair and has one spine near the top. Aedeagus narrow and long, with six leaf-like appendages, the middle pair of leaves is comparatively large and long, and the other two pairs considerably smaller and shorter. The ninth tergite is very strongly chitinized, with long slightly widened valves at the end.

The larva is unknown.

Geographical distribution: Vladimir and Penza governments (Collected by Dr. E. M. Orlov, Vladimir malaria station and coll. N. G. Zaikin, Penza malaria station)."

According to Zhelochovtsev (1937), the type-series was in the collection of the Martsinovskiy Institute of Medical Parasitology and Tropical Medicine in Moscow. The hypopygia of two males were prepared on slides, one being that illustrated by Shingarev (1928; Plate 1, Fig. 2) and by Martini (1931; p. 163, Fig. 191). I hereby designate the depicted male as lectotype and have requested Dr. V. N. Danilov of the Martsinovskiy Institute to label it accordingly.

Interpretation of the names *lewisi* and *seleniumensis*

Ludlow (1920) described *Anopheles lewisi* (8♀♀ and 14♂♂ syntypes) and *Anopheles seleniumensis* (2♀♀ syntypes) from collections made by Surgeons of an

American Expeditionary Force in July 1919 at Selenga and at Upper Udinsk, Siberia. These two localities are a little to the east and west, respectively, of Lake Baikal.

Aitken (1945) re-examined the type-series of *lewisi* and *selengensis* which remain in the United States National Museum. Although familiar with the refined standards of morphological evaluation appropriate to adults of the *maculipennis* complex, he discerned no appreciable differences between the two syntypic series, so interpreted *lewisi* as a synonym of *selengensis*, the former being accorded priority apparently by page precedence. Aitken's paper included a male lectotype designation for *lewisi*, as clarified by Stone & Knight (1956:278) who further designated a female lectotype of *selengensis*.

In debating the relationship of *lewisi* (= *selengensis*) to other members of the *maculipennis* complex, Aitken (1945) noted that *messeae* was the only form reported from the Lake Baikal area (cf Beklemishev & Zhelochovtzev, 1937; Beklemishev, 1944), the southern end of which lies between the two type-localities of *lewisi*. On that basis he concluded that *lewisi* and *messeae* probably represent a single species, the former name having seniority. Pending more detailed information, however, Aitken chose not to assert this synonymy.

It now appears likely that *beklemishevi* is also endemic to the type-localities of *lewisi* and *selengensis* with the corollary that *beklemishevi*, rather than *messeae*, could fall in their synonymy. The easternmost locality at which Stegnii & Kabanova (1976) actually found *beklemishevi* was Krasnoyarsk, approximately 350km and 1050km, respectively, to the west of the *lewisi* type-localities. Their statement "in the east, it may be found beyond Krasnoyarsk" suggests that they saw no obvious reason why *beklemishevi* should be limited by the edge of the West Siberian Plain, implying that it may well spread eastwards through Transbaikalia as indicated in Figure 1 of this paper. Without reliable morphological characters for the identification of the old dead type-specimens, therefore, it remains impossible to decide to which of the species otherwise termed *messeae* and *beklemishevi* the name *lewisi* (probably with *selengensis* as a junior synonym) should be applied as the valid name.

Interpretation of *messeae*, *melanoon* and *subalpinus*

A fundamental problem with usage of the name *Anopheles messeae* Falleroni, 1926, is that the northern Eurasian species to which this name is customarily applied does not occur as far south as the *messeae* type-locality in Italy; this was restricted to the Pontine marshes, west of Rome, by Bates (1940:352). Falleroni described *messeae* as having characteristically dark eggs, with larger floats than those of *labranchiae*, and with variable amounts of grey barring on the deck (Missiroli, 1939:1628, provided an abridged English translation of the *messeae* type-description). Detailed illustrations given with Falleroni's highly original publication showed the darker and paler extremes of variation he observed in the pattern on the decks of *messeae* eggs. So far as can be ascertained, no type-material of *messeae* (or of *basili* and *labranchiae*, the other names proposed by Falleroni) has been kept.

Because workers in the Netherlands (Swellengrebel & De Buck, 1933) and elsewhere mistakenly adopted the name *messeae* for a more northerly species with more

strongly barred eggs (but not so strongly barred as the eggs of *maculipennis* s.s.), the name *melanoon* Hackett, 1934, was proposed subsequently for the Italian species with dark eggs. This left open to doubt the identity and taxonomic status of barred eggs of the sort which Falleroni had regarded merely as a variation of the *messeae* dark egg phenotype. Accordingly, populations producing dark or barred eggs with large floats, all of which Falleroni would have called *messeae*, were investigated in various places around the Mediterranean and it is paradoxical that the term 'Italian *messeae*' was adopted to keep a distinction from 'Dutch *messeae*' which only Diemer & Van Thiel (1936) realized was being wrongly accepted as the standard (cf Christophers et al., 1934; De Buck, Schoute & Swellengrebel, 1934; Hackett & Missiroli, 1935).

The terminological need to name the barred egg variant of true *messeae* was eventually satisfied by the description of *Anopheles maculipennis subalpinus* Hackett & Lewis, 1935, from Albanian populations producing barred eggs and not the darker *melanoon*-type eggs. Advanced genetical studies (Frizzi, 1952; 1953; Kitzmiller et al., 1967) and widespread surveys (eg Bates, Beklemishev & La Face, 1949; Frizzi, 1956b) have shown that *melanoon* is a species fully distinct from *maculipennis*, but that *subalpinus* merely represents an alternative egg phenotype of *melanoon*, the two forms of egg apparently being intergrading conspecific varieties that occur as pure populations in limited geographical areas.

Strictly according to the Code, *melanoon* should be placed as a junior synonym of *messeae* in its true and original sense, though by usage the name *messeae* of authors might fall instead under the priority of any or all of the names *alexandraeschingarevi*, *lewisi* and *selengaensis* (vide supra). This nomenclatural conundrum will be worked out in the discussion below.

Spelling of the names *messeae* and *labbranchiae*

Falleroni (1926) described *messeae* and *labbranchiae* as varieties of *Anopheles claviger*, the name customarily misapplied to *A. maculipennis* s.l. by Italian authors prior to the revision by Edwards (1932). The two patronymics were proposed in honour of Dr. A. Messea (Director General) and Dr. A. Labranca (Division Chief) of the Public Health Service. Since these officials were both undoubtedly male, proper latinization of the specific epithets would be *messeai* and *labrancai*. Earlier editions of the Code required emendation of these spellings, but Article 32 of the current Code (ICZN, 1964) accepts the original spellings as correct for purposes of nomenclature, regardless of their etymological faults.

Description of the species *maculipennis*

As the original description of *Anopheles maculipennis* Meigen, 1818, was published so long ago in Gothic German script, it seems worth giving here, apparently for the first time, an English translation of the type-description. "An. maculipennis. Hoffmgg. Wings with five brown spots. (Plate 1. Fig. 17 female, Fig. 13 section of the wing). Mesonotum ash-grey with a brown lateral stripe and two dark, inconspicuous longitudinal stripes along the middle. Abdomen brownish; hind margins of the segments darker, a blackish line along the middle; anus of the female with two curved hooks (Fig. 16). Legs brown, with yellowish bases to the femora. Halteres dirty yellowish brown. Wings with five brown spots which have the same position as in *Culex annulatus* [= *Culiseta annulata*

(Schrank)]. In the male, the antennal hairs are brown, the tip of the last two palpal segments shades into rusty yellow. - I collected the female a few times in Spring in boggy areas; I received the male from Mr. Wiedemann. - 3 lines [= 1/4 inch]."

Meigen's attribution of the specific epithet to Hoffmannsegg presumably refers to his use of *maculipennis* as a manuscript name, perhaps attached to the male which Wiedemann supplied possibly from the Hoffmannsegg collection in Berlin (cf Steyskal, 1974:84). As the description and illustration concentrate on the female, it is reasonable to assume that the species was essentially based on material collected by Meigen himself in the vicinity of his home near Aachen (= Aix-la-Chapelle). The species *maculipennis* s.s. and that known as *messeae* were both found at Aachen in July 1934 by Diemer and Van Thiel (1936), who identified specimens from egg characters. Thus it is appropriate here to restrict the type-locality of *A. maculipennis* Meigen to Aachen in the Federal Republic of Germany.

By courtesy of Dr. L. Matile, Dipterist at the Entomology Laboratory, Muséum National d'Histoire Naturelle, Paris, I was able in August 1977 to examine the syntypes of *A. maculipennis* in the Meigen collection. The type-series was found to comprise 1♂ and 1♀, without collection data. The female is hereby designated as lectotype and has been so marked; assuming that the paralectotype male is actually the one supplied by Wiedemann, it would be of less definite geographical origin.

Interpretation of *sacharovi* and names hitherto placed in its synonymy

After describing *Anopheles elutus* Edwards, 1921, from specimens collected at Kishon [=Quishon River] and elsewhere in Israel, Edwards (1926, 1932) followed Shingarev (1926) who sank this name as a synonym of *Anopheles sacharovi* Favre, 1903, the type-locality of which is at Yevlakh in Yelizavetpol District of the Georgian Republic, USSR. The species concerned is well known as a widespread and common malaria vector in the Balkans, Caucasus, Asia Minor, Middle East and some southern parts of the Soviet Union.

Eastwards, Gutsevich et al. (1974) gave "Middle East . . . Afghanistan, West China" as the geographical range of populations to which have been given the names *martinius* Shingarev, 1926 (type-locality: near Tashkent in Uzbekistan), *relictus* Shingarev, 1928 (type-locality: Chikmek near Samarkand in Uzbekistan) and *elutior* Martini, 1930 (type-locality; Tashkent in Uzbekistan). These three names have been generally treated as synonyms of *sacharovi* although several authorities, notably Martini (1931:144) and Bates (1940:354), kept in mind the possibility that Asia-oriental populations might not be taxonomically identical with true *sacharovi* from the west.

Now that Stegnii (1976) has detected clear cytotaxonomic distinctions between Transcaucasian *sacharovi* and the form in central Asia, the name *martinius* should be reinstated as the valid name for the eastern taxon hitherto confused with *sacharovi*. Stegnii's studies on what can therefore be called *martinius* employed material from Tashauz in Turkmeniya and from Urgench in Uzbekistan. These two towns are only 70km apart and approximately 200km to the south of the Aral; they are also 700-800km to the west of the *martinius* type-locality (Figure 2). Presumably the names *relictus* and *elutior*, the types of which are apparently lost, should be transferred from the synonymy of *sacharovi* to that of the resurrected *martinius* on geographical grounds.

According to Stegnii (1976), evidence that *martinius* is less involved than *sacharovi* in malaria transmission has been provided by Beklemishev (1944).

Description of the species *sacharovi*

The type-description of *sacharovi* was published in a rare Russian book by Favre (1903) which I have been unable to find in England. Shingarev [= Shingarev] (1926:897) provided a French translation of the type-description, and I have now been fortunate to obtain the following English translation (by R. Ericson) of the original text (Favre 1903:189), by courtesy of the Medical Entomology Project at the U.S.N.M. in Washington. "Besides the usual representative of the species *Anopheles claviger* [i.e. *A. maculipennis*], which were the same both for central and southern Russia and for the Caucasus, I found in Yelizavetpol district a species which was similar to *A. claviger* in many respects but differed perceptibly from it in others. I saw a great many of these mosquitoes at a station on the Transcaucasian railway, Evlaxe [= Yevlakh, where the Tbilisi-Baku railway crosses the Kura River], in Yelizavetpol district, and found them among mosquitoes sent to me from Aresch district.

Not yet having determined whether I had to do here with a separate species, or with a variety of *A. claviger*, I am provisionally calling it *Anopheles sacharovi* because I have not found a description of the said mosquito that is suitable for determination. The difference of *sacharovi* from *claviger* consists in size, colour and wing marking. First of all, this mosquito is perceptibly smaller than *A. claviger*, its length together with the "sting" is from 6 to 8mm, length of wing 4.5mm. Colouring light brownish yellow; scutellum and wings covered with yellowish scales, of the same colour are the "sting", palpi and legs; only the ends of the tibiae are dark. Abdomen with yellow hairs. The wings at first sight apparently without spots, and only with a lens is it possible to observe traces of spots in those places where they are found in *Anopheles claviger*. For the rest, *Anopheles sacharovi* resembles *Anopheles claviger*."

According to Zhelochovtsev (1937), the *sacharovi* type-series was in the Zoological Museum of the Moscow [Lomonosov State] University, and comprised 9♂♂ and 3♀♀ syntypes. Better accounts of this taxon have been provided by Edwards (1921, 1926) and Martini (1931), under the synonym *elutus*, and by Gutsevich et al. (1974). For comparability with the holotype male of *elutus*, I have requested Dr. V. N. Danilov to mark the best preserved *sacharovi* male specimen as the lectotype.

Description of the species *martinius*

An English translation of the unillustrated type-description of *martinius* as given by Shingarev (1926:47) is as follows: "*Anopheles (anopheles) martinius* sp.n. Small mosquito of dark colour. Palps distinctly shorter than proboscis (1/2 - 1mm). Proboscis curved inwards; white patch of hairs and scales on frons, like that on *A. maculipennis*, absent. Forked head scales all of dark brown colour. Spots on wings distributed in the same pattern as in *A. maculipennis*, being conspicuous only under a lens. Two females forwarded by Dr. Lubchenko from Tashkent district."

When he looked later for the *martinius* type-series in the collection at the Martsinovskiy Institute in Moscow, Zhelochovtsev (1937) reported locating only one female specimen, being headless, with rubbed wings and with the body darkened by engorged blood, together with a male hypopygium preparation. The female should be regarded as lectotype, and I have asked Dr. V. N. Danilov to so mark it. Labels bearing the name *martinius* and the collection dates (8.vii.1925 for the male; 25.viii.1925 for the female) are apparently in Shingarev's handwriting, making it difficult to doubt the authenticity of the male which was unmentioned in the type-description. Martini (1931:164) gave a German translation of the type-description; the only other authors to have mentioned *martinius* were Enikolopov (1930), who reported it with *sacharovi* and other species from the Caucasus, and Zaitzev (1934) who doubted that record. Zhelochovtsev (1937:709) relegated *martinius* to the synonymy of *sacharovi*, where it has remained until the present.

Other members of the *maculipennis* complex and their names

Several North American mosquitoes clearly belong to the *Anopheles maculipennis* complex and certain others have frequently been included on the basis of their karyological, more than morphological, resemblances (Kitzmilller et al., 1967; Guy, Salières & Boesiger, 1976). It is probably best to regard *aztecus* Hoffman, *earlei* Vargas, *freeborni* Aitken and *occidentalis* Dyar & Knab as the only Nearctic species to be grouped with Palaearctic taxa in the sibling species cluster that comprises the Holarctic *A. maculipennis* complex (Pratt, 1952; Kitzmilller, 1977). Taxonomy and nomenclature of these four Nearctic members of the complex are not in any question.

Palaearctic members of the complex include the stenogamous *atroparvus* Van Thiel, 1927, and the eurygamous *labranchiae* Falleroni, 1926. These were classified formerly as a pair of allopatric subspecies, but their independent specific status had recently been demonstrated by Bianchi (1968) and by Coluzzi & Coluzzi (1970). According to Bates (1940), the names *fallax* Roubaud, 1934, and *cambournaci* Roubaud & Treillard, 1936, should fall as junior synonyms of *atroparvus* and this has been generally accepted (Stone et al., 1959; Knight & Stone, 1977), except by Senevet & Andarelli (1956). As regards *labranchiae*, Missiroli (in Bates, 1940:352) himself decided that *pergusae* Missiroli, 1935, is synonymous. Bates (1940:354) also placed the name *sicaulti* Roubaud, 1935, as a questionable synonym of *labranchiae*. However, the original description, based on material from Rabat, Morocco, mentions and illustrates several distinctive attributes of the egg, larva and adults, permitting differentiation of *sicaulti* from *labranchiae* and other members of the *maculipennis* complex. Roubaud was particularly emphatic that Moroccan *sicaulti* differed from Algerian *labranchiae*, while he considered the latter to be the same as *labranchiae* from Spain and Italy.

After not having been recognized for nearly four decades, *sicaulti* seems to have been rediscovered recently in the form of samples collected in 1973 in Morocco by Bailly-Choumara and Ramsdale (pers.comms) and subsequently investigated by Coluzzi (Anon., 1974). This Moroccan *labranchiae*-like material produced pale eggs resembling the *sicaulti* originals depicted photographically by Roubaud (1935, Plate 1, Fig. 1). By examining broods of eggs obtained from *labranchiae*-like adults captured widely in Morocco and Algeria, Ramsdale (pers. comm.) found that true *labranchiae*, identified by its eggs, seemed to be geographically separated from the pale egg *sicaulti* populations by the Moroccan Atlas

Mountains which run northwards into the Mediterranean Sea between Tangiers and Mellila. According to Coluzzi, when "Moroccan *labranchiae*" (ie *sicaulti*) was crossed with Italian *atroparvus* the pattern of F_1 infertility differed from that of the crosses between Italian *labranchiae* and *atroparvus*. This incomplete evidence certainly makes it desirable to uphold the name *sicaulti*, giving it provisional specific rank, pending further genetical evaluation of this poorly known taxon which has been confused for so long with normal *labranchiae*, supposedly the prevalent anopheline of Morocco (Benmansour, Laaziri & Mouki, 1972).

Only two synonyms of *maculipennis* itself remain to be mentioned. These are *basilii* Falleroni, 1932, and *typicus* Hackett, 1934.* Both of these names (and perhaps the nomen nudum *caucasicus* Shtackel'berg, 1937) were proposed for the nominotypical member of the complex in the days before the present state of taxonomic understanding and relative nomenclatural stability had been attained.

Description of the species *sicaulti*

For convenience, an abridged English translation of the type-description of *Anopheles sicaulti* Roubaud, 1935, follows. The description is based on a strain from Rabat region of Morocco, as supplied by "Monsieur Sicault". Senevet & Andarelli (1956) seem to be the only subsequent authors to have recognized this taxon, which they treated as a subspecies at a time when it was customary to rank members of the complex no higher. "*Anopheles maculipennis sicaulti*"
 I. Adults. - White fringe spot on the wing tip generally smaller than in *labranchiae*; it extends scarcely from the end of the fore-branch of the first forked vein to that of vein 3. Black wing spots and dark lateral bands of the scutum well marked. On the male hypopygium (Fig.) the harpago spines are all sharp, the external spines sometimes double, sometimes single, of roughly the same dimensions as in *labranchiae*. Maxillary index: [abridged] paucidentate, usually not above 14; average 13.7. II. Eggs. - Compact, dumpy, more rounded at the tips than in *labranchiae* (Figs). Light grey colour never observed. The general appearance is dull with only, under favourable illumination, an ash-grey or iron-grey sheen in the middle third [of the deck], grading into the two darker terminal thirds. Both poles darken progressively without showing the distinctly delimited dark cap of the *labranchiae* egg. The black, cuneiform spots are poorly differentiated, large and irregular (Fig.), much fewer and less pronounced than in *labranchiae*. The plain middle area has a frosted appearance, as in *labranchiae*. The large columellae with irregular contours, described as being characteristic of the latter species by De Buck & Swellengrebel (1934), are present but less numerous and distributed chiefly on the middle part of the egg. The small columellae rarely have a dark central spot. The float is small, of the *labranchiae* type, with a rough intercostal membrane (Fig.). Float index approximately 0.3. III. Larvae. - Seta No. 1 of segment II not palmate, with filiform branches (Fig.). These hairs contrast with the really palmate ones of *labranchiae* (Fig.). The antepalmate hair of segments IV and V has less than 9 branches, generally 2 to 6 in full-grown larvae.

*This name appears to have been published first as *typicus* Hackett, 1934:114, although Bates (1940:353) and the World Catalog of Mosquitoes (Stone et al., 1959; Knight & Stone, 1977) attributed it to Hackett & Missiroli (1935:45). Furthermore, the type-specimens and type-locality of *typicus* must be, by implication, the same as for *maculipennis* s.s., although this has not been stated before.

Biological characters [abridged]: Very similar to *labranchiae*: eurygamous, non-diapausing in winter, exophilic, zoophilic but not reluctant to bite man ("indifferent zoophily")."

None of the specimens originally investigated by Roubaud has been traced in my recent searches of the collections in Paris at the Institute Pasteur, Muséum National d'Histoire Naturelle and at the Office de la Recherche Scientifique et Technique Outre-Mer, Bondy. However, in the British Museum (Natural History) there are 5♀♀ labelled "Morocco/G.Sicault/B.M.1931-593" evidently belonging to this taxon. The letter submitted with these specimens is dated 8. xii.1931 and has been filed with the correspondence of F. W. Edwards; it bears a note that Edwards identified them simply as *maculipennis*. Because this material is topotypic, Rabat being in the Gharb region - i. e. the coastal plain of Morocco, and was supplied by the same person who sent the type-strain to Roubaud, I have designated as the neotype of *sicaulti* the best preserved female of the series sent to the BM(NH) by Dr. Sicault himself.

Sergent (1935) looked for *sicaulti* among supposed *labranchiae* populations at Algiers. He found that, while 90% of females laid typical *labranchiae*-type eggs, the other 10% laid eggs of a form that appeared to be intermediate between the *sicaulti* and *labranchiae* types. His report included photographs of both the normal and the abnormal kinds of eggs, with a footnote added by Roubaud to the effect that he agreed with the interpretation, which highlighted the need for further work on the characteristics of *sicaulti*. The recent observations by Coluzzi (Anon., 1974) and by Ramsdale (*vide supra*) tend to confirm the concept that *sicaulti* is taxonomically distinct and warrants more detailed investigation.

Discussion

Intensive morphometrical work on members of the *Anopheles maculipennis* complex might yet reveal methods to separate adults of the Eurasian sibling species. Such studies are not an attractive prospect, however, since so many past workers have failed to identify the adults of most species. Even the diagnostic characters advocated for the largely allopatric Nearctic members of the complex (Vargas, 1963) are difficult to assess and we would benefit from their better evaluation. While specific egg characters and hybridization tests have been the keys to interpretation of the Palaearctic complex, the species of which are so often sympatric, polytene chromosome banding patterns are the most exact features for identifying individual larvae or adult females of the different taxa.

Recent research by Stegnii, Kabanova and their Russian colleagues has explained some outstanding mysteries concerning Eurasian populations known as *maculipennis*, *messeae* and *sacharovi*. As the Russian work on anopheline cytogenetics has such serious nomenclatural implications, this paper explains the taxonomic background enough to conclude with some specific nomenclatural recommendations.

The most contentious case concerns the species generally known for over forty years as *messeae*. This is the most widespread member of the *maculipennis* complex, being endemic to Britain, Scandinavia, across Europe, Asia and far into China (Stegnii et al., 1976). As an essentially zoophilic species it has only moderate medical importance, and its veterinary significance is inadequately

understood. Because of its affinity to several more important vectors, however, it has been documented in many books and hundreds of scientific papers dealing with malariology, ecology and evolution. In this sense, all the members of the *maculipennis* complex are of equal scientific interest, and their nomenclature must be manipulated with extreme care. There seem to be no secondary publications whatsoever in which the name *messeae* has been properly and unconditionally applied to the species for which it was primarily proposed*. It becomes an academic point, therefore, that the type-locality of *messeae* in Italy is extralimital to the distribution of the species universally known by this name. Whereas the name *melanoon* is strictly a junior synonym of *messeae*, it would create nomenclatural havoc to return the name *messeae* to take precedence over *melanoon* (with its variety *subalpinus*). Article 23 of the Code, as amended in 1972, now aims to promote stability by encouraging the International Commission on Zoological Nomenclature to wield its plenary powers to uphold the usage of an established junior synonym, such as *melanoon*, whenever this is preferable, especially in the applied zoological literature. It should be no trouble to have this case approved, so that the name *messeae* is formally fixed for the northern species, while the junior name *melanoon* is maintained for the southern species.

Yet before the name *messeae* can be confirmed in its traditional usage for the most widespread Palaearctic member of the *maculipennis* complex, there is an obligation to settle the interpretation and the nomenclatural status of the two available names - *lewisi* and *selengensis* - that were published before *messeae* and may be synonymous with it. Gutsevich et al. (1974) and Stegnii et al. (1976) have recently endorsed the view that so-called *messeae* is endemic through the regions embracing the type-localities of both these names and *alexandraeschingarevi* so that, as Aitken (1945) suggested in connection with *lewisi* (= *selengensis*), the Code would require the sacrifice of *messeae* as a junior synonym.

As the Commission will have to be asked eventually to sanction the redefinition of *messeae* in accordance with its accustomed usage, it may be asked, at the same time, to suppress the nomina dubia *alexandraeschingarevi*, *lewisi* and *selengensis* for purposes of priority. Unless any characters for separation of *messeae* from *beklemishevi* adults can soon be found, all three nomina dubia require rejection, so to be rendered formally unavailable for application to either of the two sibling species that appear to be sympatrically endemic to the relevant type-localities in Siberia. It would gain nothing and would cause considerable confusion to drop either of the well understood names *messeae* or *beklemishevi* in favour of any of the three previously unused names that are technically available for resurrection. Rather than continuing to wait indefinitely in case some new method might be found to facilitate re-interpretation of the types of *alexandraeschingarevi*, *lewisi* and *selengensis*, these three unused names should formally be suppressed forthwith.

*Frizzi's (1951) paper on *messeae* and *maculipennis* at Pavia, in the Po valley of northern Italy, which included drawings of a wide range of egg patterns identified as *messeae*, was subsequently corrected by Frizzi (1952) when he found that local populations consisted of *subalpinus* (= *melanoon*), *messeae* and *maculipennis* in sympatric association, as determined cytogenetically.

As the taxonomic cases for raising *martinius* from synonymy with *sacharovi* and for raising *sicaulti* from synonymy with *labbranchiae* involve no nomenclatural complications, it is now possible to give the following list of recommended names* for recognised members of the *Anopheles maculipennis* complex.

| Species | Distribution |
|--|--------------|
| 1. <i>A. atroparvus</i> Van Thiel, 1927 <i>fallax</i> Roubaud, 1934 <i>cambournaci</i> Roubaud & Treillard, 1936 | Fig. 3 |
| 2. <i>A. aztecus</i> Hoffmann, 1936 | Fig. 4 |
| 3. <i>A. beklemishevi</i> Stegnii & Kabanova, 1976 ? <i>lewisi</i> Ludlow, 1920 (for suppression by ICZN) ? <i>selengensis</i> Ludlow, 1920 (for suppression by ICZN) ? <i>alexandraeschingarevi</i> Shingarev, 1928 (for suppression by ICZN) | Fig. 1 |
| 4. <i>A. earlei</i> Vargas, 1943 | Fig. 4 |
| 5. <i>A. freeborni</i> Aitken, 1939 | Fig. 4 |
| 6. <i>A. labbranchiae</i> Falleroni, 1926 <i>pergusae</i> Missiroli, 1935 | Fig. 3 |
| 7. * <i>A. maculipennis</i> Meigen, 1818 <i>basilii</i> Falleroni, 1932 <i>typicus</i> Hackett, 1934 | Fig. 1 |
| 8. <i>A. martinius</i> Shingarev, 1926 <i>relictus</i> Shingarev, 1928 <i>elutior</i> Martini, 1931 | Fig. 2 |
| 9. <i>A. melanoon</i> Hackett, 1934 <i>messeae</i> Falleroni, 1926 (for redefinition by ICZN) <i>subalpinus</i> Hackett & Lewis, 1935 | Fig. 3 |
| 10. <i>A. messeae</i> authors, sensu Swellengrebel and DeBuck, 1933 ? <i>lewisi</i> Ludlow, 1920 (for suppression by ICZN) ? <i>selengensis</i> Ludlow, 1920 (for suppression by ICZN) ? <i>alexandraeschingarevi</i> Shingarev, 1928 (for suppression by ICZN) | Fig. 3 |
| 11. <i>A. occidentalis</i> Dyar & Knab, 1906 | Fig. 4 |
| 12. <i>A. sacharovi</i> Favr, 1903 <i>elutus</i> Edwards, 1921 | Fig. 2 |
| 13. <i>A. sicaulti</i> Roubaud, 1935 | Fig. 3 |

*An additional nomen nudum published as "*An. mac. maculipennis caucasicus* B. H." in a table (opposite p. 52) given by Shtakel'berg (1937) was evidently meant for typical *maculipennis* in the Caucasus and southwards, as distinct from more northerly populations now described as *beklemishevi*. Attribution of *caucasicus* to "B. H." is an inexplicable error; perhaps Shtakel'berg expected it to be adopted by Bates & Hackett (1939).

In conclusion, an attempt is made here to synthesize a phylogenetic picture from the mass of published information on systematics and chromosomal relationships of the *Anopheles maculipennis* complex. For the 9 Palaearctic species, as recognized above, Table 1 lists and codifies the various interspecific and intraspecific paracentric chromosomal inversions. These known inversions have been plotted in Figure 5 onto a standard idiogram of the *maculipennis* karyotype. The results and terminology of various investigators are sometimes hard to correlate, but the extent and relative positions of inversions as shown in Figure 5 are thought to be a satisfactory representation of the real cytogenetical situation. Finally, Figure 6 portrays putative chromosomal relationships between all members of the *maculipennis* complex, as traced (except for *sicaulti*) from inversion rearrangements seen in the polytene karyotype.

Figure 6 also embodies the reported chromosomal and taxonomic relationships between the *maculipennis* complex and the *pseudopunctipennis* complex via *atroparvus* and *punctipennis* (Kreutzer, 1977; Kreutzer & Kitzmiller, 1971; Smithson & McClelland, 1972) on the one hand, and between Nearctic members of the *maculipennis* complex and other dark-winged North American anophelines, possibly involving an *occidentalis-quadrifasciatus* link (Kitzmiller et al, 1967), on the other hand. It should be borne in mind, however, that Figure 6 is merely a tentative attempt to construct a framework which might support more definitive research on the phylogenetics of *Anopheles* sensu stricto. Perhaps the most interesting product of this presentation is the evidence indicating two possible Nearctic-Palaearctic movements of the *A. maculipennis* complex. These would be the *beklemishevi-earlei* link suggested by Stegnii & Kabanova (1976) as well as the *atroparvus-punctipennis* connection studied by Kreutzer (1977).

Identification key

Morphological information on Palaearctic members of the *A. maculipennis* complex remains so limited and, on the whole, so negative that identification of species is largely dependant upon characteristics of the eggs and of the chromosomes. Live broods are generally required, therefore, to facilitate satisfactory taxonomic examinations of series of specimens.

A. maculipennis complex, general characters: large *Anopheles*. Adults dark or medium brown; wings with scale clusters at junctions of forked veins (2 and 4) and more proximally on veins 2, 3 and 4; mesonotum laterally darkened and with conspicuous pale frontal scale-tuft (scales thinner and sparser than in other pale-tufted species). Male gonocoxite with 2 or 3 simple parabasal spines having raised basal tubercles. Pupa with seta 9 pinnately branched on abdominal segment VIII, simple on segments III-VII. Larva with frontal hairs plumose; outer clypeal hairs with numerous branches; palmate hair reduced on abdominal segments I and II.

- | | | |
|--------------|-----------|----|
| 1. Nearctic* | | .2 |
| Palaearctic | | .9 |

*Recognition of *aztecus*, *earlei*, *freeborni* and *occidentalis* is perhaps most soundly based their specific polytene chromosome banding patterns, for which standard chromosome maps originally published in a series of papers by Baker and Kitzmiller are all reproduced in the review by Kitzmiller et al., 1967.

2. Larvae/pupae 3
Adults 6
3. Larval inner clypeal hairs separated basally by width of 2 basal tubercles or more. Pupal apical spine (seta 9) of abdominal segment VII long and slender *aztecus*
Larval inner clypeal hairs separated by width of 1 basal tubercle or less. Pupal seta VII/9 short and thick 4
4. Larval inner clypeal hairs branched beyond middle. Pupal seta VII/9 stout, straight and blunt *earlei*
Larval inner clypeal hairs single. Pupal seta VII/9 curved and pointed 5
5. Larval abdominal segments with accessory tergal plates; antepalpmate hair (seta 2) branched on segment IV *freeborni*
Larval abdominal segments without accessory tergal plates; antepalpmate hair single on segment IV *occidentalis*
6. Wing scales (including clusters on veins 2-4) uniformly brown. 7
Wings with 4 spots formed by darker colour of scale clusters on veins 2-4 8
7. Head with anterior erect scales golden, not white; female with labella darker than proboscis. Central Mexico. *aztecus*
Head with anterior erect scales white; female with labella not darker than proboscis. Western North America. *freeborni*
8. Stem of wing vein 2 relatively evenly scaled. Pacific coastal belt of North America *occidentalis*
Stem of wing vein 2 with scaling forming a serrated outline. Alaska Central and Eastern North America, between lats 42-55°N *earlei*
9. Egg without floats (but rudimentary floats may develop at low temperature); deck uniformly pale from pole to pole 10
Egg with floats fully formed; deck dark, barred or mottled 11
10. Polytene chromosome karyotype conforming to the standard map by Stegnii, 1976: plate 2. Central & northeastern Mediterranean, Asia Minor, Middle East to Caspian Sea *sacharovi*
Polytene chromosomes with fixed paracentric inversions Xa (regions 2a-3b) and 3La (regions 37b-39b) as compared with the *sacharovi* standard map (see plate 1b in Stegnii, 1976). Middle Asia . *martinius*
11. Intercoastal membranes of floats smooth 12
Intercoastal membranes of floats rough (finely corrugated) 13
12. Upper surface of egg softly patterned with cuneiform (wedge-shaped) black marks on a pale background; ends of deck pale almost to the tips. Polytene chromosome karyotype conforming to the standard map by Frizzi, 1947 (reproduced as Fig. 4 in Kitzmiller et al., 1967; revised as Fig. 1 in Farci et al., 1973). Europe *atroparvus*

- Upper surface of egg entirely dark or with pattern of 2 transverse dark bars near the ends of the floats, poles dark and remainder of the deck irregularly mottled. Polytene karyotype with fixed paracentric inversion 3Rd (regions 28b-35b) as compared with the *atroparvus* standard map (see Fig. 3 in Frizzi, 1953). Northern Mediterranean, Asia Minor *melanoon*
13. Upper surface of egg marked with 2 transverse dark bars near the ends of the floats, with or without other pattern 14
Upper surface of egg with mottled pattern but without 2 dark transverse bars near ends of floats 16
14. Transverse dark bars on egg sharply contrasted with unmottled pale background colour of deck (see Fig. 4 in Stegnii & Kabanova, 1976) .15
Transverse dark bars on deck forming part of a diffuse mottled pattern. Polytene karyotype with fixed inversion 3Rd as in *melanoon*; general banding pattern conforming to the standard map by Kabanova et al (1972a). Northern Palaearctic *messeae*
15. Eggs with tips less acutely pointed; chorion of deck relatively rough; width of egg between floats about 17% of egg length. Polytene karyotype with fixed inversion 3Rd as in *melanoon** and *messeae**.
Europe, Asia Minor, Transcaucasia *maculipennis*
- Egg with tips more acutely pointed; chorion of deck relatively smooth; width of egg between floats about 12% of egg length. Polytene karyotype with fixed paracentric inversions Xf, 2Rb, 3Re and 3Lb as compared with the *atroparvus* standard map (see Figs 5 & 6; also Fig. 3 of Stegnii & Kabanova, 1976); general banding pattern conforming to the standard map by Stegnii et al. (1974, given as for *maculipennis*).
Siberia (? Eastern Europe, ? Scandinavia) *beklemishevi*
16. Larval abdominal segment II with seta 1 palmate. Upper surface of egg richly patterned with cuneiform dark marks on frosted pale background; poles narrowly dark. Polytene karyotype virtually homosequential with that of *atroparvus*. Mediterranean . . . *labbranchiae*
Larval seta II/1 filiform, not palmate. Upper surface of egg pale with little or no mottled pattern; poles broadly dark-capped. Chromosomes unknown. Morocco (? Algeria). *sicaulti*

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*See Figs. 5 and 6 for chromosomal inversion differences between *maculipennis* s.s., *melanoon*, *messeae* and other sibling species.

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Table 1

Coded list of chromosome inversions reported in Palaearctic members of the *Anopheles maculipennis* complex. (Figure 5 shows these inversions plotted on an idiogram of the karyotype; Figure 6 shows their evolutionary arrangement within and between species).

| <u>Inversion</u> | <u>Regions</u> | <u>species/map (References)</u> |
|------------------|----------------|---|
| Xa | 2a-3b | <i>sacharovi</i> (Stegnii, 1976) |
| Xb | 2a-4a | <i>beklemishevi</i> (Stegnii et al, 1974; Stegnii & Kabanova, 1976) |
| Xc* | 2a-4c(IL1) | <i>messeae</i> (Kabanova et al, 1972a,b; Stegnii et al, 1976) |
| Xd* | ? (IL2) | <i>messeae</i> (Stegnii et al, 1976) |
| Xe | ? (small) | <i>sacharovi</i> (Frizzi 1947, 1952, 1953 etc.) |
| Xf | 3a-5a | <i>beklemishevi</i> (Stegnii et al, 1974; Stegnii & Kabanova, 1976) |
| Xg | 3b-5c | <i>beklemishevi</i> (Stegnii et al, 1974; Stegnii & Kabanova, 1976) |
| 2Ra | 6a-7d | <i>beklemishevi</i> (Stegnii et al, 1974; Stegnii & Kabanova, 1976) |
| 2Rb | 9b-12a | <i>beklemishevi</i> (Stegnii et al, 1974; Stegnii & Kabanova, 1976) |
| 2Rc | 9b-12c(IIIR1) | <i>messeae</i> (Kabanova et al, 1972a,b; Stegnii et al, 1976) |
| 2Rd | basal | <i>beklemishevi</i> (Stegnii & Kabanova, 1976) |
| 2La | 18 | <i>beklemishevi</i> Stegnii et al, 1974; Stegnii & Kabanova, 1976) |
| 3Ra | 23d-24b | <i>beklemishevi</i> (Stegnii et al, 1974; Stegnii & Kabanova, 1976) |
| 3Rb | 23d-26b(IIIR1) | <i>messeae</i> (Kabanova et al., 1972a,b; Stegnii et al, 1976) |
| 3Rc | 25c-27b | <i>beklemishevi</i> (Stegnii et al, 1974; Stegnii & Kabanova, 1976) |
| 3Rd | 28b-35b | <i>atroparvus</i> (Frizzi, 1947, 1953; Farci et al., 1973) |
| 3Re | 25-30 | <i>beklemishevi</i> (Stegnii et al, 1974; Stegnii & Kabanova, 1976) |
| 3La | 37b-39b | <i>sacharovi</i> (Stegnii, 1976) |
| 3Lb | 34a-39b | <i>beklemishevi</i> (Stegnii et al, 1974; Stegnii & Kabanova, 1976) |
| 3Lc | 37-38 | <i>beklemishevi</i> (Stegnii et al, 1974; Stegnii & Kabanova, 1976) |
| 3Ld | 35b-39b | <i>beklemishevi</i> (Stegnii et al, 1974; Stegnii & Kabanova, 1976) |
| 3Le | 35c-39b | <i>messeae</i> (Kabanova et al, 1972a,b; Stegnii et al, 1976) |
| 3Lf | 44a-48b | <i>atroparvus</i> (Frizzi, 1947, 1953; Farci et al, 1973) |

*A third possible polymorphism in the regions embraced by the overlapping inversions Xb and Xc may be inferred from the observations of Frizzi, 1951 (cf his Figs 3 and 4) on *messeae* in the Po valley of northern Italy.

Explanation of Figures

Figure 1.

Geographical distribution limits of *A. beklemishevi* and *A. maculipennis* in the Palaearctic Region; tentative reinterpretation of all available information, with suggested division between the two species (?----?) along a line NW-SE from the Baltic to the Ukraine. Relevant type-localities are marked by open circles. Black circles indicate *A. beklemishevi* localities reported by Stegnii & Kabanova (1976).

Figure 2.

Geographical distribution limits of *A. sacharovi* and *A. martinius* in the Palaearctic Region; tentative reinterpretation of all available information, with suggested division between the two species (?----?) along a line North-South through the Caspian Sea. Relevant type-localities are marked by open circles. Two black circles indicate *A. martinius* localities reported by Stegnii (1976) as "*A. sacharovi* chromosomal race from middle Asia".

Figure 3.

Geographical distribution limits of the Palaearctic species *A. atroparvus*, *A. labranchiae*, *A. melanoon* (dotted line), *A. messeae* and *A. sicaulti* (indicated within the range hitherto attributed to *labranchiae* in North Africa). Relevant type-localities are marked by open circles.

Figure 4..

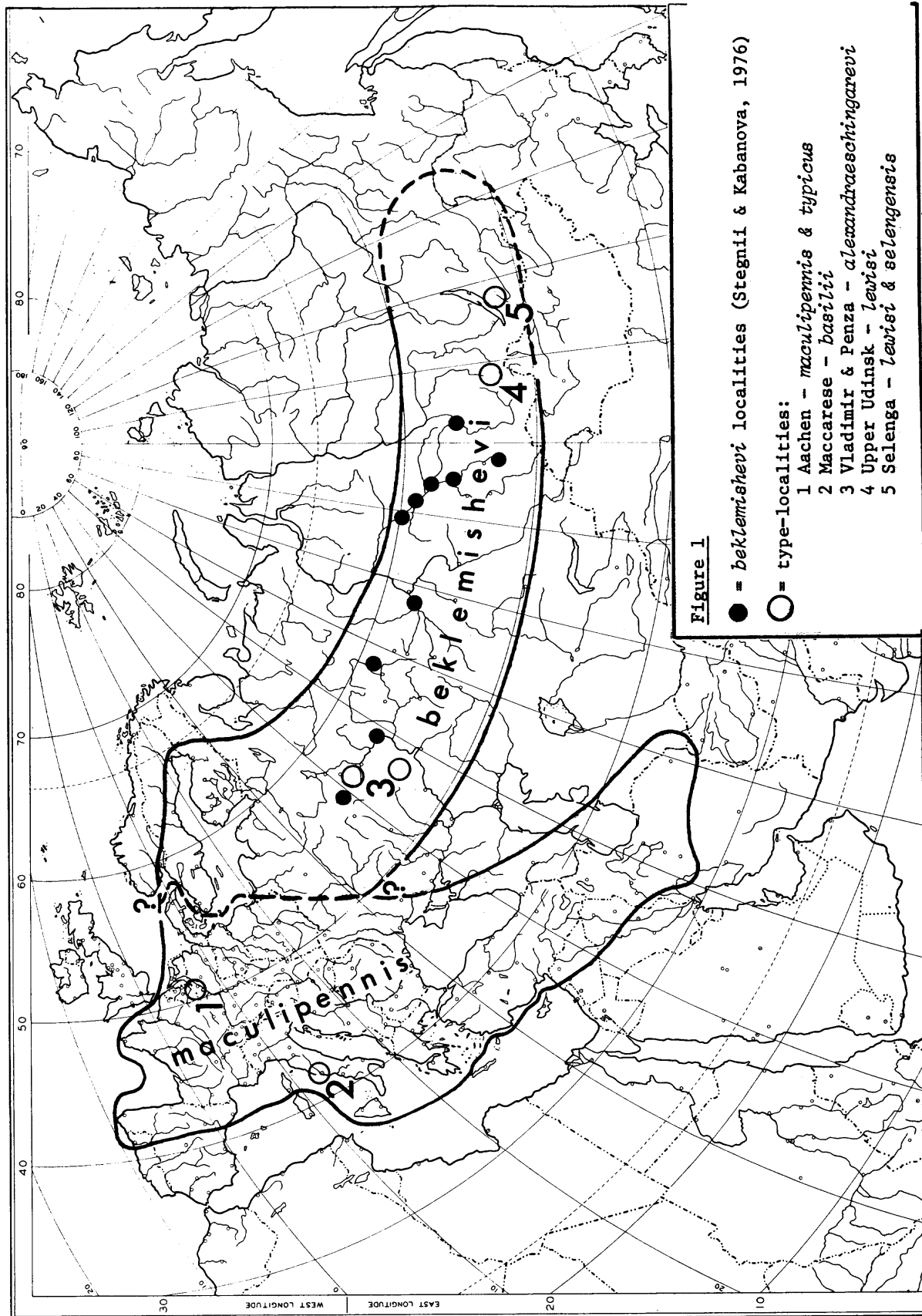
Geographical distribution of the Nearctic species *A. aztecus*, *A. earlei*, *A. freeborni* and *A. occidentalis* (from Pratt, 1952 and Gjullin *et al.* 1961). Relevant type-localities are marked by open circles.

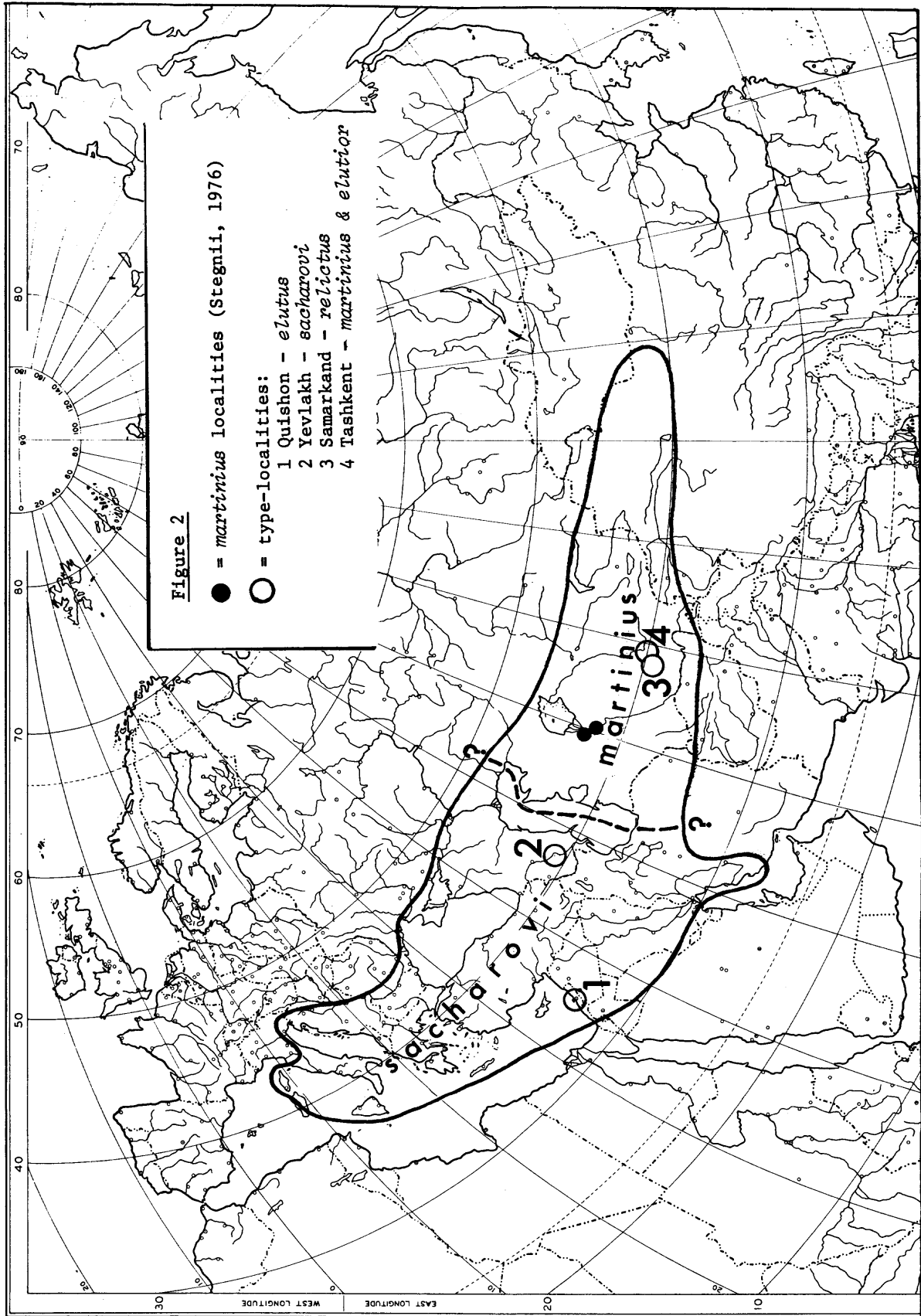
Figure 5.

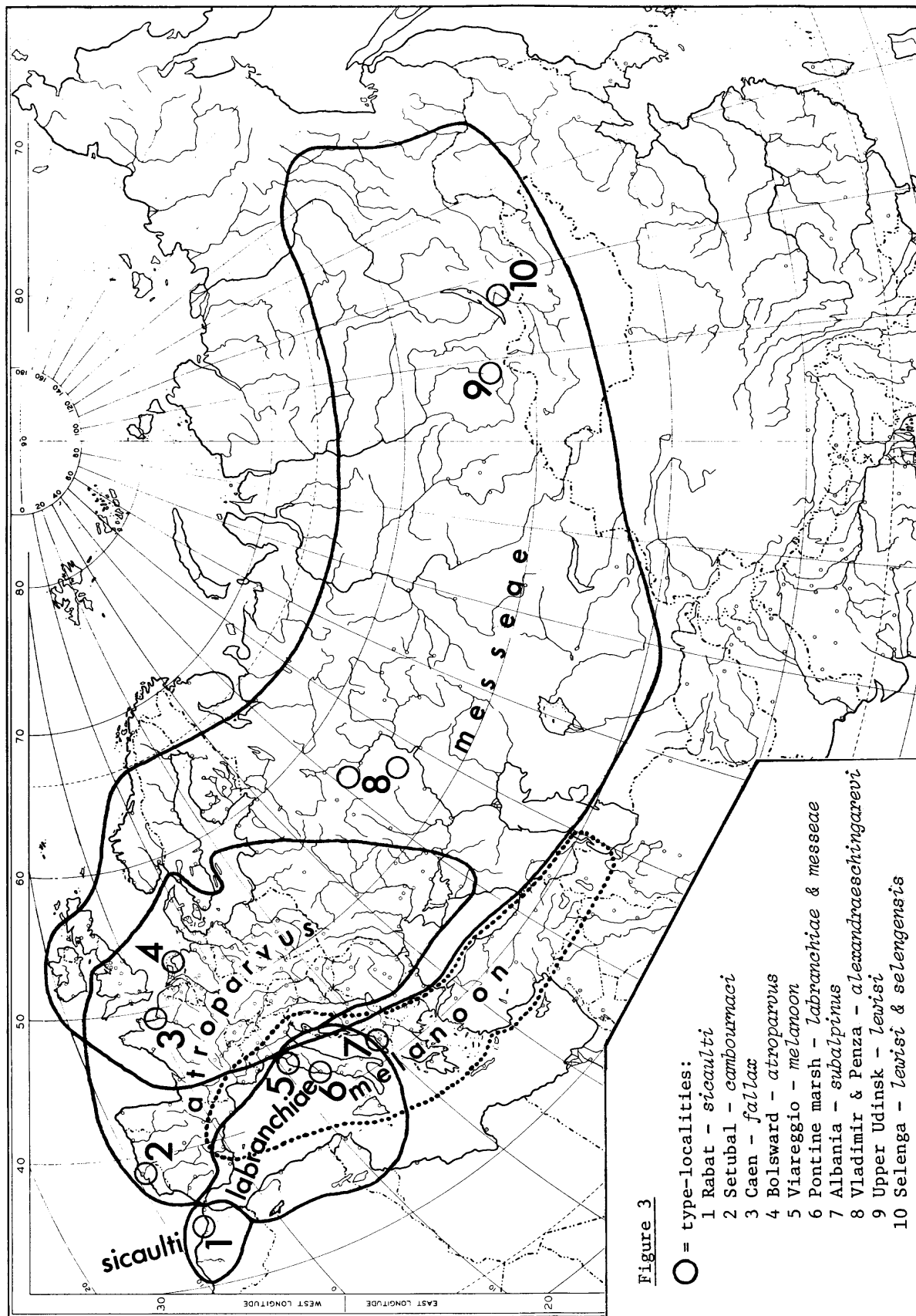
Chromosome inversions in the Palaearctic members of the *Anopheles maculipennis* complex; positions marked on an idealised ideogram (cf Table 1 for details and Figure 6 for specific chromosome inversion formulae).

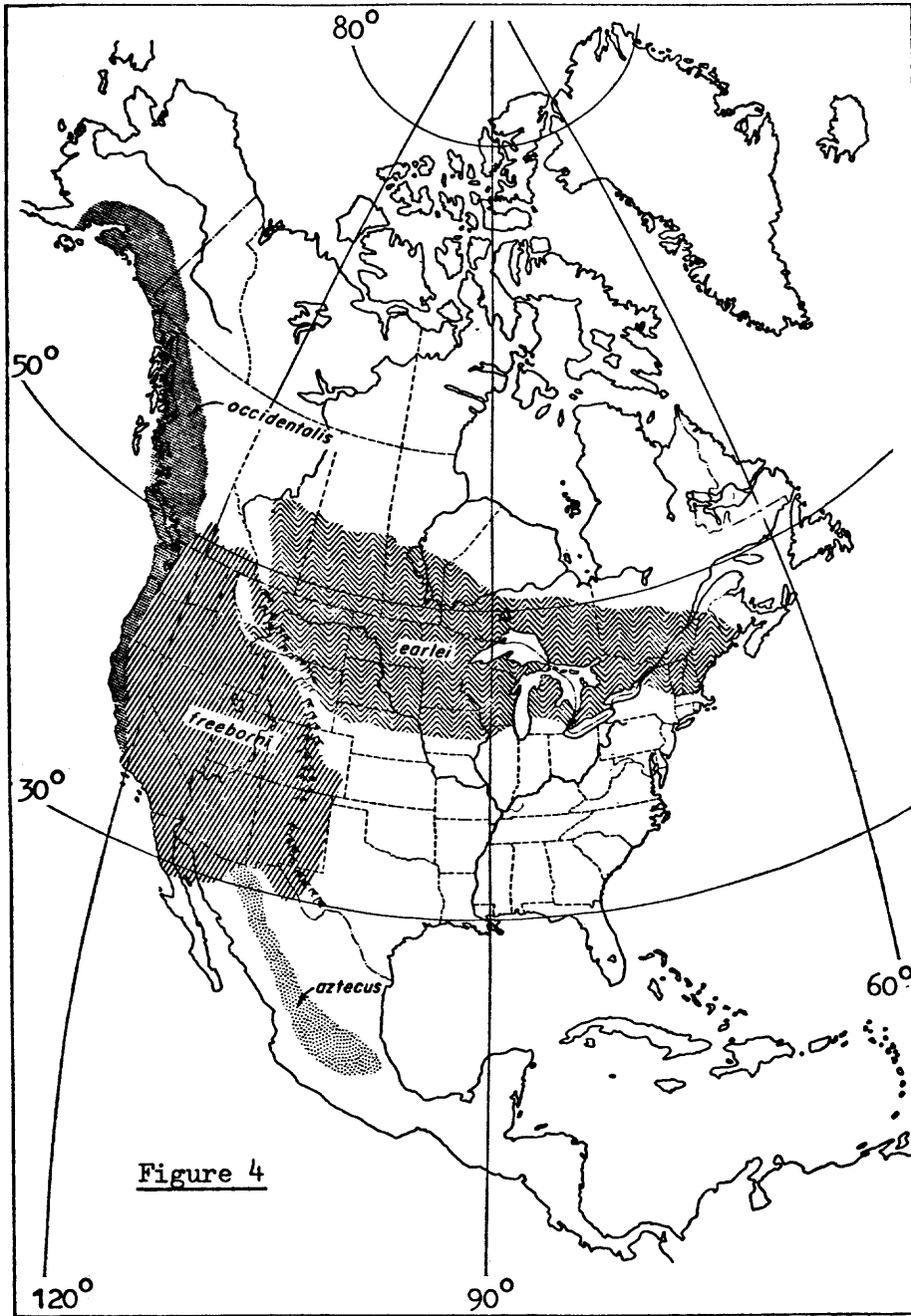
Figure 6.

Tentative chromosomal phylogeny of the *Anopheles maculipennis* complex and some related taxa; based on the works of Frizzi (1947 *et seq.*), Kabanova *et al.* (1972 *et seq.*), Kitzmiller *et al.* (1967 and references cited therein, particularly studies by Baker & Kitzmiller), Kreutzer (1977), Kreutzer & Kitzmiller (1971), Smithson & McClelland (1972) and Stegnii *et al.* (1974 *et seq.*). The Code for paracentric chromosome inversions is explained in Figure 5 and Table 1. Each inversion step is derived from the standard karyotype (X,2R,2L,3R,3L). Fixed homozygous inversions are coded a,b,c etc. for each chromosome arm; floating heterozygous inversions are coded a/+,b/+,c/+ etc. The number of inversion steps between species can be read cumulatively from box to box, e.g. *martinius* differs from *maculipennis* by 5 fixed inversions (Xa,Xe,3Rd,3La and 3Lf); it differs from *messeae* by the same fixed steps plus at least 5 floating inversions found in *messeae*.









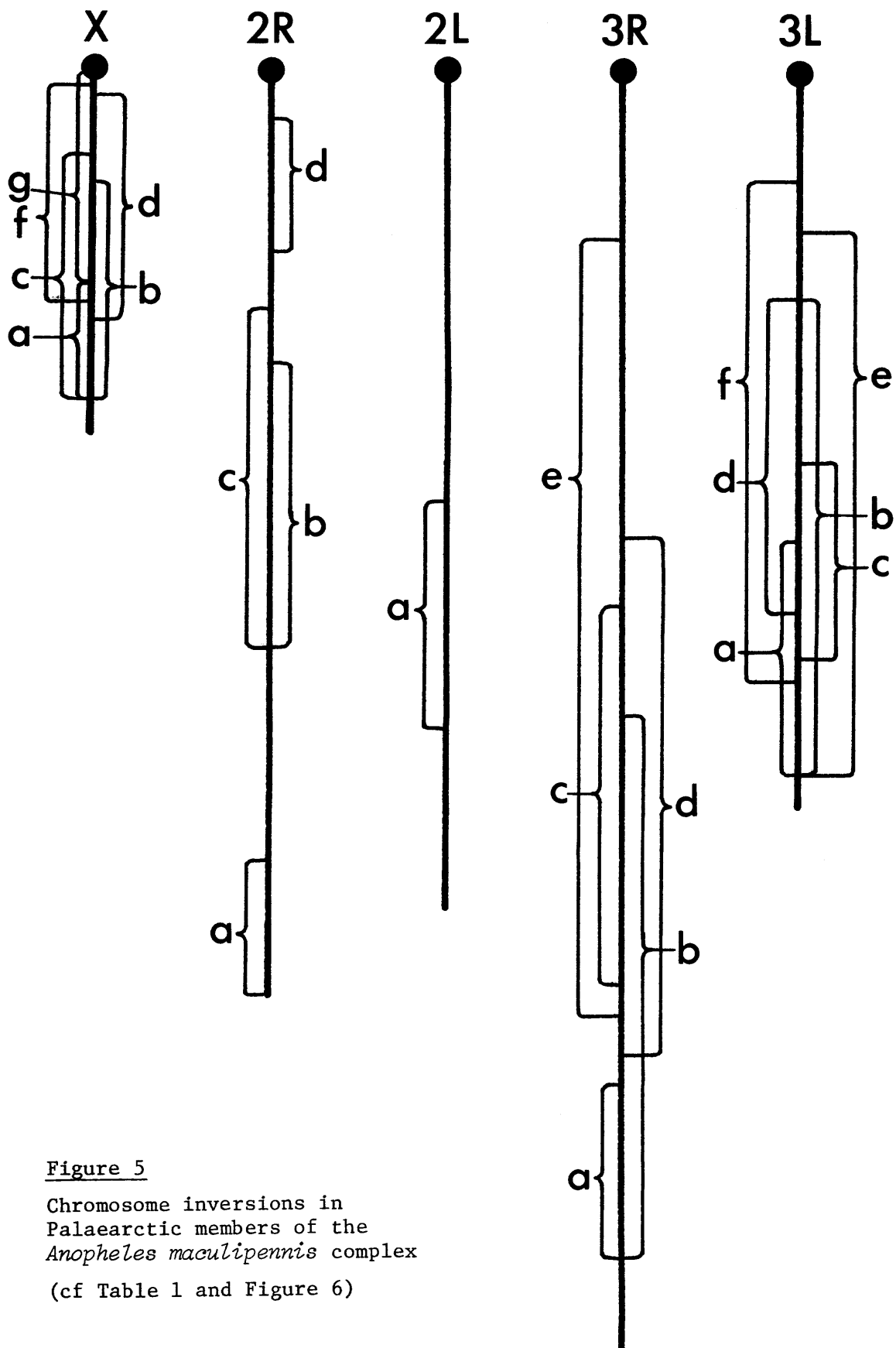


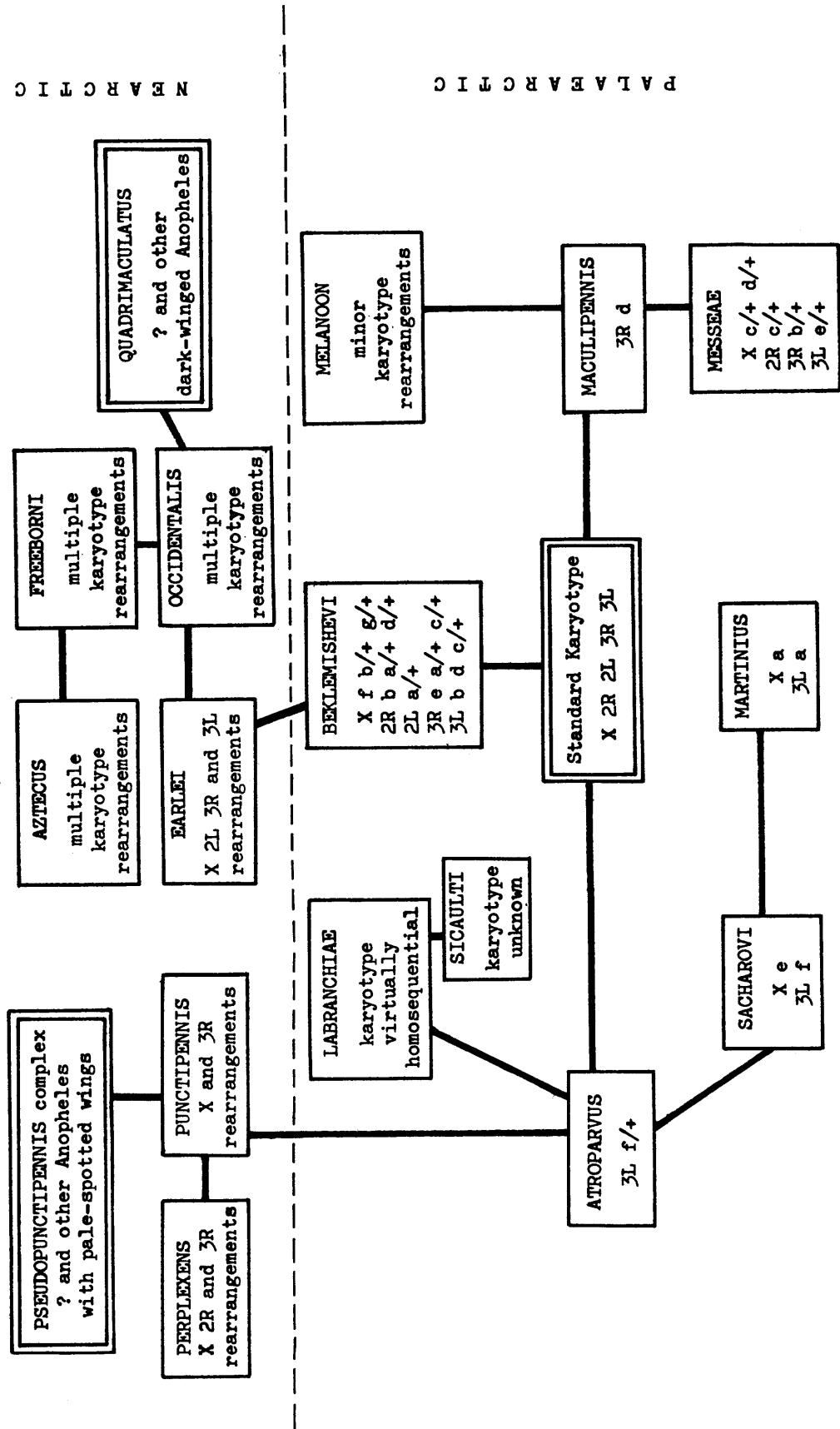
Figure 5

Chromosome inversions in Palaeartic members of the *Anopheles maculipennis* complex

(cf Table 1 and Figure 6)

Figure 6.

Tentative chromosomal phylogeny of the *A. maculipennis* complex and some related taxa (see Table 1, Figure 5 and p. 35 for further explanation).



CORRECTION

This illustration should be substituted for Figure 4 in the following reference: White, G. B. 1978. Systematic Reappraisal of the *Anopheles maculipennis* Complex. Mosq. Syst. 10(1): 13-44. It was provided as a substitute in the prepublication period but was subsequently overlooked. The Editor.

