

Chromosomes of Some Species of Vespertilionid Bats. II. Evolutionary Relationships of Plecotine Bats

Stanisław FEDYK & Andrzej L. RUPRECHT

Fedyk S. & Ruprecht A. L., 1983: Chromosomes of some species of vespertilionid bats. II. Evolutionary relationships of plecotine bats. Acta theriol, 28, 10: 171—182 [With 2 Tables, 1 Fig. & Plates VIII—IX]

Differential staining revealed a total accordance of banding pattern for all the chromosomes of *Plecotus auritus* (Linnaeus, 1758) and *Barbastella barbastellus* (Schreber, 1774). The karyotypes of these two species are identical and consist of 32 chromosomes, including 10 pairs of metacentric autosomes, 5 pairs of telocentric autosomes, a submetacentric X-chromosome, and a small acrocentric Y-chromosome. In the description of banded karyotypes of *P. auritus* and *B. barbastellus*, chromosome arms of Nearctic species are numbered from 1 to 25, as proposed by Bickham. The mechanism of karyotype formation in different *Plecotini* forms is discussed, as compared with the *Myotini* karyotype and the ancestral karyotype of the earliest *Vespertilionidae* ($2N=50$; $NFa=48$).

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1. INTRODUCTION

The term "*Plecotini* group" as an equivalent to a subfamily was introduced by Dobson (1863, in Handley, 1959). Dobson used it for a few genera of *Vespertilionidae* characterized by unusually long ears (*Plecotus*, together with American forms such as *Corynorhinus* and *Idionycteris*, *Euderma*, *Histiotus*, *Laephotis*, *Otonycteris*, *Nyctophilus*, *Pharotis*, *Antrozous*). Miller (1897, in Handley, 1959) used the term *Plecotinae* (as a subfamily) for American forms of *Plecotus* and *Euderma*. Later, however, Miller (1907) discarded the term *Plecotinae* and included big-eared bats in the family *Vespertilionidae*. The classification developed by Dobson (*l.c.*) and the original classification used by Miller (1897) were based on the structure of the auditory apparatus only and, as Handley (1959) noticed, these characters do not necessarily reflect relationships between genera. Tate (1942) used other characters, which can better reflect phylogenetic associations. He proposed that the forms of *Plecotus*, *Corynorhinus*, *Idionycteris*, and *Euderma* be included in *Myotini*, as descendants of the *Myotis* stock with a differentiated degree of evolution. H. Allen (1864, in Handley, 1959) recorded some similarities between *Plecotus* and *Barbastella*, introducing a common name *Synotus* for these two forms.

Handley (1959) basically accepted the classification developed by Tate (1942) and grouped the genus *Plecotus* in three subgenera: group *Myotini* — genera *Euderma*, *Plecotus* — subgenera *Idionycteris*, *Plecotus*, *Corynorhinus*.

Handley (1959) in his comprehensive morphological analysis concluded that *Idionycteris* is the basal or relict form, while *Plecotus* and *Corynorhinus* represent later stages of evolution. Williams *et al.* (1970), who studied the chromosomes of American forms (*Euderma* and *Plecotus*), suggested removing big-eared bats from *Myotini* and forming a group *Plecotini*, consisting of such genera as *Barbastella*, *Euderma*, *Idionycteris*, and *Plecotus* with subgenera *Plecotus* and *Corynorhinus*. These authors presented their views on the phyletic relationships between these forms. Very similar conclusions concerning *Plecotus*, *Corynorhinus*, and *Idionycteris* were reached by Fedyk & Fedyk (1971), who studied European forms of *Plecotus*.

The position of the genus *Barbastella* is not so clear. Miller (1907) stated that despite great differences in the dental pattern, development of the auditory capsule, and zygomatic arch, *Barbastella* is more similar to *Plecotus* and *Euderma* than to any other genus. Tate (1942), however, suggested that the genera *Plecotus* and *Euderma* descended from the *Myotis* stock (*Myotini sensu lato*), while *Barbastella* is a representative of *Pipistrellini*. This view was questioned by Handley (1959), who argued that the similarity between *Barbastella* and *Pipistrellus* is of secondary character. He emphasizes, like Miller (1907), the similarity to *Plecotus* and *Euderma*, considering the genus *Barbastella* as a group *Plecotini* with non-specialized auditory apparatus. The analysis of chromosomes by conventional methods (Capanna *et al.*, 1968; Williams *et al.*, 1970) suggested that Handley (1959) was right.

The chromosomes of the Eurasian genera *Barbastella* and *Plecotus* were frequently described (Bovey, 1949; Capanna *et al.*, 1968; Fedyk & Fedyk, 1970, 1971; Uchida & Ando, 1972; Harada, 1973; Baker *et al.*, 1974; Ando, 1977; Zima, 1978; Tsuchiya, 1979). The chromosomes of Nearctic forms (*Euderma*, *Plecotus* and *Idionycteris*) were described by Baker & Patton (1967), Baker & Mascarello (1969), Williams *et al.* (1970), and Bickham (1979a). A detailed analysis of the American material based on the G-banding pattern is given by Bickham (1979a), together with conclusions on phylogenesis. The present study supplements this analysis with European species.

2. MATERIAL AND METHODS

The material for the analysis consisted of one male *P. auritus* captured at Kowal, Włocławek district, and two male *B. barbastellus* caught in Białowieża, Białystok district, in 1981 and 1982.

Chromosome preparation of the bone marrow and spleen were made. Colcemid was intraperitoneally injected in a dose of 0.002 mg per 1 g of body weight for 0.5 h. Hypotonization was carried out in 0.075 M solution of KCl at room temperature for 30 minutes. Air-dried preparations after a period of 4–6 days were digested with trypsin and stained with Giemsa solution using the Seabright (1971) method.

For the description of banded karyotypes of *P. auritus* and *B. barbastellus*, chromosome arms of Nearctic species were numbered from 1 to 25, according to Bickham (1979a, b). Banding patterns were compared with those of telocentric chromosomes of *Eptesicus serotinus*. It has been found (Fedyk & Ruprecht, 1983), that the banding pattern in *E. serotinus* is identical with that in *Eptesicus fuscus* (Bickham, 1979a).

3. RESULTS

The karyotypes of *P. auritus* and *B. barbastellus* were identical and consisted of 32 chromosomes: 10 pairs of metacentric autosomes, 5 pairs of telocentric autosomes, a submetacentric X-chromosome, and a small acrocentric Y-chromosome (Plate VIII).

The differential staining indicated that the banding patterns of all *P. auritus* and *B. barbastellus* chromosomes are exactly alike. According to the terminology used by Bickham (1979a, b), the arm combinations in metacentric autosomes of *P. auritus* and *B. barbastellus* were as follows: 1/2, 3/4, 5/6, 12/10, 13/9, 15/11, 22/8, 21/7, 19/14, and 16/17. The telocentric autosomes, because of their small size, had less clear-cut banding but were still comparable with the corresponding autosomes of *Eptesicus* and were numbered 18, 20, 23, 24, and 25. The X-chromosomes had a relatively weakly expressed banding pattern: on the short arm there occurred one conspicuous band located more or less in the medial part of this arm, while the long arm had one dark-stained block. The distal end of this arm remained unstained, while a very intense dark band was located at the centromere. On some metaphasal plates this last band was separated from a large block of dark bands by a narrow, light band. The Y-chromosome lacked clear-cut banding (Plate IX).

4. DISCUSSION

There is a relatively large body of literature on the chromosomes of big-eared bats. The first information on the chromosomes of *P. auritus* and *B. barbastellus* was given by Bovey (1949), who found that each of

these two species collected in Switzerland had 32 chromosomes. A more detailed analysis, with the application of colchicine, confirmed Bovey's findings for *P. auritus* collected in Poland (Fedyk & Fedyk, 1970, 1971) and Czechoslovakia (Zima, 1978), and for an Asiatic subspecies, *P. auritus sacrimontis* (Harada, 1973; Ando *et al.*, 1977; Tsuchiya, 1979). Ten pairs of metacentric autosomes were recorded, *i.e.*, $NFa=50$. An identical chromosome pattern was described for *Plecotus austriacus* (Fedyk & Fedyk, 1970, 1971; Baker *et al.*, 1974; Zima, 1978). Zima (1978) recorded 52 autosome arms for the two European *Plecotus* species, because he included with the metacentric chromosomes also one of the smallest pairs of autosomes. An analysis of the measurements of the chromosomes of *P. auritus* and *P. austriacus* showed some differences in the position of the centromeres of three autosome pairs and the X-chromosome (Fedyk & Fedyk, 1971). In the light of these results, it is certainly interesting to compare the banding patterns in these two species.

More recent studies of the chromosomes of *B. barbastellus* captured in Italy (Capanna *et al.*, 1968) confirmed the findings of Bovey (1949): $2N=32$; $NFa=50$. The same karyotype was found in an Asiatic species, *Barbastella leucomelas* (Uchida & Ando, 1972; Ando *et al.*, 1977). Only Zima (1978) recorded 52 autosome arms at $2N=32$ for *B. barbastellus* as in *Plecotus* species caught in Czechoslovakia.

In all the cases described above, when NFa was greater than 50, an additional metacentric autosome of very small size was recorded, thus there is some doubt whether these are in fact metacentric chromosomes and, if so, whether they have been overlooked in the other cases. Ignoring these puzzling discrepancies, it should be stated that all Palaearctic species of *Plecotus* and *Barbastella* have uniform karyotypes (Table 1).

The chromosomes of three species of Nearctic *Plecotus* (subgenus *Corynorhinus*) were studied. These were *Plecotus townsendii* and *P. rafinesquii*, in which there were 32 chromosomes and 50 autosome arms (Baker & Patton, 1967; Baker & Mascarello, 1969; Williams *et al.*, 1970; Anthony & Kitchin, 1976; Bickham, 1979a), and also *Plecotus (Idionycteris) phyllotis* with 30 chromosomes and 50 autosome arms (Baker & Patton, 1967; Baker & Mascarello, 1969; Williams *et al.*, 1970; Bickham, 1979a).

The X-chromosomes are also differentiated in Nearctic *Plecotus (Idionycteris) phyllotis*. The X-chromosome is submetacentric, as in the Eurasian species of *Plecotus* and *Barbastella*, while in *Plecotus (Corynorhinus) townsendii* and *P. (C.) rafinesquii* it is acrocentric (Table 1).

In *Euderma maculatum*, 30 chromosomes were recorded and $NFa=52$

(Williams *et al.*, 1970). It was suggested that the karyotype of *Euderma* was closest to that of *P. (Idionycteris) phyllotis*, though also distinct morphological differences between these two species (Williams *et al.*,

Table 1

Chromosome patterns in big-eared bats. Morphology of sex-chromosomes: a — acrocentric, sm — submetacentric, m — metacentric.

Species	2N	NFa	No. of autosome pairs		Morphology of sex-chromosomes		References
			bi-armed	uni-armed	X	Y	
<i>Euderma maculatum</i>	30	52	12	2	sm	a	Williams <i>et al.</i> , 1970
<i>Plecotus (Idionycteris) phyllotis</i>	30	50	11	3	?	?	Baker & Patton, 1967
	30	50	11	3	sm	a	Baker & Mascarello, 1969
	30	50	11	3	sm	a	Williams <i>et al.</i> , 1970
	30	50	11	3	sm	a	Bickham, 1979a
<i>Plecotus (Corynorhinus) townsendii</i>	32	50	10	5	?	?	Baker & Patton, 1967
	32	50	10	5	a	a	Baker & Mascarello, 1969
	32	50	10	5	a	a	Williams <i>et al.</i> , 1970
	32	50	10	5	a	a	Anthony & Kitchin, 1976
	32	50	10	5	a	a	Bickham, 1979a
<i>Plecotus (Corynorhinus) rafinesquii</i>	32	50	10	5	a	a	Baker & Mascarello, 1969
<i>Plecotus (Plecotus) austriacus</i>	32	50	10	5	sm	a	Fedyk & Fedyk, 1970; 1971
	32	50	10	5	m	a	Baker <i>et al.</i> , 1974
	32	50	10	5	sm	a	Zima, 1978
<i>Plecotus (Plecotus) auritus</i>	32	50	10	5	m	a	Bovey, 1949
	32	50	10	5	sm	a	Fedyk & Fedyk, 1970; 1971
	32	54	12	3	sm	a	Ando <i>et al.</i> , 1977
	32	50	10	5	sm	a	Zima, 1978
	32	50	10	5	sm	a	This paper
<i>Plecotus auritus sacrimontis</i>	32	50	10	5	sm	a	Harada, 1973
	32	50	10	5	sm	a	Tsuchiya, 1979
<i>Barbastella barbastellus</i>	32	50	10	5	sm	a	Bovey, 1949
	32	50	10	5	sm	a	Capanna <i>et al.</i> , 1968
	32	52	11	4	sm	a	Zima, 1978
	32	50	10	5	sm	a	This paper
<i>Barbastella leucomelas</i>	32	50	10	5	sm	a	Ando <i>et al.</i> , 1977
<i>B. leucomelas darjelingensis</i>	32	50	10	5	sm	a	Uchida & Ando, 1972

1970) were recorded. The problem will not be solved until the banding pattern has been compared, but so far this has not been described for *Euderma*.

Anthony & Kitchin (1976) and Bickham (1979a) described G bands in

Plecotus (Corynorhinus) townsendii and Bickham (1979a) described them in *Plecotus (Indionycteris) phyllotis*. Together with the material used in the present work, we have data on banding patterns in four species of big-eared bats (Table 2). Bickham (1979a) stated that four pairs of metacentric autosomes (1/2, 3/4, 5/6, and 16/17) are totally homologous to the four pairs of metacentrics occurring in the karyotypes of various species of *Myotis* (Bickham, 1979b).

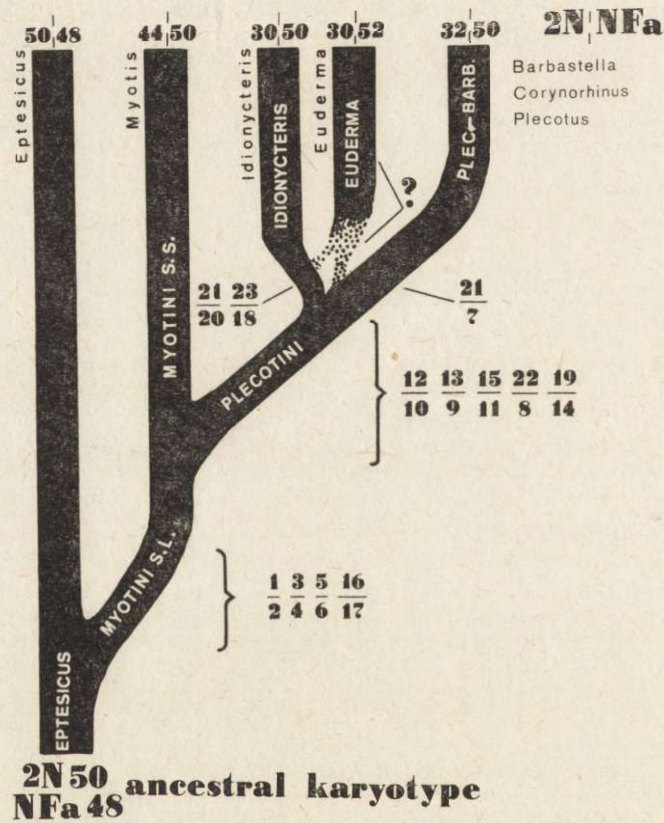


Fig. 1. Hypothetical differentiation of evolutionary lineages of *Plecotini* karyotypes. White letters denote 7 stages (evolutionary lines) of the karyotype; fractions represent arm combinations evolving in particular lineages.

Among *Vespertilionidae*, the most primitive karyotype was recorded in species of the genus *Eptesicus*. This karyotype can be considered as ancestral for all the *Vespertilionidae*. With respect to morphological characters, however, the genus *Eptesicus* underwent deep transformation. On the other hand, in the traditional systematics, based on morphology (the dental pattern being, among other features, of great importance for bats), the genus *Myotis* is considered as very conservative, having

many ancestral characters of *Vespertilionidae*. As to the chromosomes, the modern *Myotis* are at a fairly early stage of evolution (three centric fusions giving rise to pairs 1/2, 3/4, 5/6, and an inversion giving rise to an autosome pair 16/17). The occurrence of the same four metacentric autosome pairs in the genera *Plecotus* and *Barbastella* suggests that the group *Myotini s. l.* (according to Tate, 1942) branched from common ancestors with chromosomes of the *Eptesicus* type, the ancestors of *Myotini s. s.* and *Plecotini* then forming a common group until the karyotype of the modern *Myotis* emerged. Only after the formation of the four pairs of metacentric autosomes mentioned above did *Plecotini* separate from *Myotini* (Fig. 1).

Table 2

Arm composition in big-eared bats. The arms are numbered according to the system used for American forms (Bickham, 1979a) and *E. serotinus* (Fedyk & Ruprecht, 1983)

Arm composition of autosomes		Morphology of X-chromosome; References
<i>Plecotus (Idionycteris) phyllotis</i>		sm;
1/2, 3/4, 5/6, 16/17	12/10, 13/9, 15/11, 22/8, 19/14 23/18, 21/20	Bickham, 1979a
<i>Barbastella barbastellus</i>		sm;
1/2, 3/4, 5/6, 16/17	12/10, 13/9, 15/11, 22/8, 19/14 21/7	This paper
<i>Plecotus (Corynorhinus) townsendii</i>		a;
1/2, 3/4, 5/6, 16/17	12/10, 13/9, 15/11, 22/8, 19/14 21/7	Anthony & Kitchin, 1976; Bickham, 1979a
<i>Plecotus auritus</i>		sm;
1/2, 3/4, 5/6, 16/17	12/10, 13/9, 15/11, 22/8, 19/14 21/7	This paper
<hr/>		
<i>Myotis</i> stage		
<hr/>		
Hypothetical form of ancestral <i>Plecotini</i>		
		<hr/>
		<i>Plecotini</i> differentiation
		<hr/>
Specific for <i>Plecotini</i> only		
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The next five pairs of metacentric autosomes (12/10, 13/9, 15/11, 22/8, and 19/14) are typical only for *Plecotini* (Bickham, 1979a). These nine pairs of metacentric autosomes are wholly homologous in *Plecotus*, *Corynorhinus*, *Idionycteris*, and *Barbastella* (Table 2) and therefore must have developed before the big-eared bats split up into Eurasian and Nearctic forms, as well as before the splitting up of Nearctic forms into *Idionycteris* and *Corynorhinus*. The occurrence of such a hypothetical karyotype, composed of nine metacentric autosomes, was theoretically suggested even before the first study on the banding pattern in *Plecotini* had been carried out (Fedyk & Fedyk, 1971). Further differentiation into two karyotypically different groups was due to various

combinations of fusions. One group is represented by forms in which a fusion occurred between chromosomes 7 and 21. This lineage then gave rise to the Eurasian species *Barbastella* and *Plecotus* and Nearctic species of the subgenus *Corynorhinus*. In the other group, two centric fusions occurred. Probably the fusion between chromosomes 21 and 20 (instead of chromosome 7) gave rise to the isolation of later *Idionycteris* from the preceding group. The second fusion occurred between chromosomes 23 and 18. Further differentiation of the chromosome pattern concerned the X-chromosome. As Bickham (1979a) has suggested, the acrocentric X-chromosome in *Corynorhinus* was formed as a result of a pericentric inversion. It is possible that this aberration effectively isolated the ancestors of the present *Corynorhinus* from the stock that gave rise to the modern Eurasian forms *Plecotus* and *Barbastella*. Thus it must have occurred before *Plecotini* spread over Asia. Great morphological differences, which resulted in the differentiation of the genera *Plecotus* and *Barbastella*, must have been developed relatively recently, after the ultimate termination of the evolution of the chromosome pattern. Karyological data support the suggestion made by Handley (1959) that the majority of cranial characters common to *Barbastella*, *Plecotus*, and *Corynorhinus*, had been evolved before the auditory specialization of the last two genera. Hence, the high degree of specialization of the auricle and auditory capsules in *Plecotini* is a relatively recent evolutionary acquisition.

As there are no data on banding patterns in *Euderma*, it is difficult to decide when this genus arose from the common *Plecotini* ancestors (Fig. 1). It should be emphasized that the term *Myotini s. l.* introduced by Tate (1942) on the basis of morphological analysis is very useful here, since it characterizes a certain degree of karyotype evolution, i.e., the development of the karyotype of modern species of the genus *Myotis*. It should be concluded that all *Vespertilionidae* species in which there are four pairs of autosomes with arm combinations 1/2, 3/4, 5/6, and 16/17 (cf. Bickham, 1979a, b), independent of fusion or other transformations of autosomes 7—15 and 18—25, must have passed through the chromosome stage of *Myotini s. l.* Thus they must have been a common evolutionary group. In the present study, the term *Plecotini* is considered as an evolutionary lineage branching from *Myotini s. l.* (the second group consisting of *Myotini s. s.*). For a long time *Plecotini* must have formed one Mendelian population until five successive fusions had occurred in it. Consequently, this term denotes here the next stage in the evolution of the chromosome pattern (*Plecotini* stage). Such an interpretation does not exclude the use of the term *Plecotini* in the sense of a taxonomic unit involving the modern forms of *Euderma*,

Barbastella, *Corynorhinus*, *Idionycteris*, and *Plecotus*. On the other hand, *Myotini s. s.* is to be considered a modern species of the genus *Myotis*. Karyologically these are forms with completed karyotype evolution after the pairs 1/2, 3/4, 5/6, and 16/17 had been formed (if we ignore some small transformations of the karyotype, cf. *e.g.* Harada, 1973).

Capanna & Civitelli (1970) discussed the direction of Robertsonian processes in *Vespertilionidae*. They stated that the genus *Myotis*, with the most primitive dental pattern, should be considered as the most primitive also with respect to karyotype. According to these authors (Capanna & Civitelli, 1970) this ancestral karyotype, made up of four pairs of metacentric autosomes, evolved in two directions: some species (*e.g.* of the genus *Eptesicus*) by fissions, while in the other group centric fusions occurred. This reasoning was based on the assumption that all characters evolve in a coordinated way, *i.e.*, if *Myotis* is conservative in its anatomical characters, then its chromosome pattern must be conservative too. This simplified view is also supported by Baker (1970) and Bickham (1979a), who assume that the modern *Myotis* have an ancestral karyotype, though Bickham (1979a) agrees that "In general, it would appear that the acrocentric condition is primitive due to the remarkably high frequency of situations in which centric fusions are indicated. Because of this, it is attractive to consider the karyotype of *Eptesicus* as ancestral...". However, he rejects this concept because of the advanced evolution of morphological characters in *Eptesicus*.

Certainly, it cannot be stated unequivocally that the ancestral form of *Vespertilionidae* did not possess the karyotype of the modern *Myotis*. However, in spite of speculations no evidence has so far been found for the occurrence of centric fissions in *Vespertilionidae*. It is much more probable that the chromosome pattern evolved owing to centric fusions and, in some rare cases, as a result of inversions and tandem fusions (a complete documentation of the present state of knowledge is given by Bickham, 1979a). It is postulated that the ancestral karyotype of *Vespertilionidae* consisted of 50 telocentric chromosomes ($2N=50$; $NFa=48$) and thus was identical with the karyotype of modern *Eptesicus*.

Obviously, the statement that the modern *Eptesicus* with highly specialized morphological characters are ancestors of *Vespertilionidae* would be a misunderstanding. Similarly, the modern *Myotis*, morphologically most conservative, cannot be considered their ancestors either. It should be emphasized that the chromosome pattern is a morphological character equivalent to other characters, *e.g.* dental characteristics. Moreover, it should not be expected that any animal group includes species with all morphological characters specialized in the same degree,

while all the characters of other species remained primitive. It should be remembered that an asynchronous evolving of particular characters is in the very nature of evolution.

It has frequently been argued that the chromosome pattern of *Eptesicus* cannot be ancestral because paleontologically this is a relatively young genus. This argument can easily be rejected in the light of what has been said above; namely, in order to consider the karyotype of *Eptesicus* as ancestral, it is not necessary to consider the other morphological characters of *Eptesicus* as ancestral. Simply, it should be stated that the most remote ancestors of *Vespertilionidae* had a chromosome pattern of $2N=50$, $NFa=48$, and cranial characters, mostly teeth, similar to those in modern *Myotis*. Thus, in this case the absence of *Eptesicus* fossils in earlier geological strata cannot be used as an argument against a hypothetical ancestral karyotype.

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Stanisław FEDYK i Andrzej L. RUPRECHT

CHROMOSOMY KILKU GATUNKÓW MROCZKOWATYCH. II. EWOLUCYJNE
ZALEŻNOŚCI W OBRĘBIE PLECOTINI

Streszczenie

Zbadano morfologię kariotypów samców gacka wielkoucha, *Plecotus auritus* (Linnaeus, 1758) i mopka, *Barbastella barbastellus* (Schreber, 1774) z terenu Polski, przy zastosowaniu barwienia różnicującego (wzór prążków). Wykazano, że kariotypy obu gatunków są identyczne i składają się z 32 chromosomów; 10 par dwuramiennych i 5 par jednoramiennych autosomów, X — submetacentryczny a Y — mały akrocentryk (Tablica VIII). Barwienia różnicujące pozwoliły stwierdzić całkowitą zgodność wzoru prążków wszystkich chromosomów *P. auritus* i *B. bar-*

bastellus. Wzory prążków porównywano ze wzorem prążków na jednoramiennych chromosomach mroczka późnego, *Eptesicus serotinus* (Schreber, 1774), stosując numerację od 1—25 ramion chromosomów wprowadzoną dla gatunków nearktycznych. Kombinacja ramion autosomów dwuramiennych *P. auritus* i *B. barbastellus* jest następująca: 1/2, 3/4, 5/6, 12/10, 13/9, 15/11, 22/8, 21/7, 19/14 i 16/17. Jednoramienne autosomy są porównywalne z odpowiednimi autosomami *Eptesicus* i mają następującą numerację: 18, 20, 23, 24 i 25. Chromosomy X i Y pozbawione są wyraźnych prążków (Tablica IX). W oparciu o dane własne i pochodzące z literatury, porównano kariotypy *P. auritus* i *B. barbastellus* na tle kariotypu wyjściowego dla *Vespertilionidae* (analogiczny z kariotypem *Eptesicus*) oraz przedstawicieli *Myotini* i *Plecotini*. Omówiono przypuszczalne mechanizmy powstawania kariotypów tych form (Ryc. 1) oraz zestawiono porównanie kariotypów omawianych gatunków (Tabela 1 i 2).

EXPLANATION OF PLATES VIII—IX

Plate VIII

Chromosomes of *P. auritus* and *B. barbastellus* conventionally stained.

Plate IX

Chromosomes of *P. auritus* and *B. barbastellus*.

In each pair there is a chromosome of *P. auritus* to the left (P) and *B. barbastellus* to the right (B).

P. auritus



B. barbastellus



