EVOLUTIONARY IMPLICATIONS OF THE KARYOTYPES OF THE STENODERMINE GENERA *ARDOPS*, *ARITEUS*, *PHYLLOPS*, AND *ECTOPHYLLA*

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EVOLUTIONARY IMPLICATIONS OF THE KARYOTYPES OF THE STENODERMINE GENERA *ARDOPS, ARITEUS, PHYLLOPS,* AND *ECTOPHYLLA*

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ABSTRACT: Karyotypes of representatives of four genera of the subfamily Stenoderminae (Phyllostomatidae), *Ardops, Ariteus, Phyllops,* and *Ectophylla* are presented. Karyotypic characteristics of *Ardops, Ariteus,* and *Phyllops* support a close relationship between these genera and the genera *Stenoderma* and *Ametrida.* The karyotype of *Ectophylla alba* does not support the conclusion that it is congeneric with the morphologically similar *Mesophylla.* Chromosomally, *Mesophylla* and *Vampyressa pusilla* are more closely related to each other than either is to *Ectophylla* or the other species of *Vampyressa* that have been karyotyped. Evolutionary, early distributional, and taxonomic aspects of the genera involved are discussed.

In 1973 when Baker constructed a phylogeny of the subfamily Stenoderminae (Phyllostomatidae) based on karyotypic characteristics, data were available from representatives of all genera except *Ardops, Phyllops, Pygoderma, Ariteus,* and *Ectophylla.* We report chromosomal data for all of these except *Pygoderma.*

METHODS

Specimens were collected from natural populations and standard bone marrow preparations (Patton, 1967; Baker, 1970) were made for *Ardops nichollsi, Ariteus flavescens,* and *Phyllops haitiensis.* Ear biopsies of a specimen of *Ectophylla alba* were collected and primary cultures were grown and karyotyped at Texas Tech University. Metacentric, submetacentric, subtelocentric, acrocentric, and fundamental number are defined by Patton (1967).

RESULTS

Ardops nichollsi, Ariteus flavescens, and *Phyllops haitiensis* have diploid values of $2N = 30$ ♀♀, 31 ♂♂, and a fundamental number of $FN = 56$ (Figs. 1, 2, and 3). The autosomal complement of the representatives of each genus is comprised entirely of biarmed elements with 10 pairs of metacentric or submetacentric chromosomes and four pairs of subtelocentric chromosomes. The sex-determining system in these species appears to be similar to that described for the stenodermine genus *Artibeus* where an autosome has been translocated to the X but its homologue has not been translocated to the Y (Hsu *et al.,* 1968; Becak *et al.,* 1969). In *Ariteus* and *Phyllops* (Figs. 2 and 3) the X appears to be a subtelocentric chromosome, whereas in *Ardops* (Fig. 1) the X appears to be a submetacentric chromosome. Male specimens of these three genera have two small Y chromosomes, one which shows a small second arm and one which is a small acrocentric.

The karyotype of *Ectophylla alba* has a diploid value of 30 and a fundamental value of 56 (Fig. 4). The autosomal complement is essentially identical to that described for the three genera discussed above. The sex-determining system of *Ectophylla* appears to be the classical XX/XY. The X chromosome is a medium size submetacentric chromosome and the Y is a medium acrocentric chromosome with a secondary constriction near the distal end.

DISCUSSION

Based on a shortened rostrum, a white spot on the shoulder, and geographic distribution, the genera *Ardops, Ariteus,* and *Phyllops* were believed to be closely related to each other and to the genera *Stenoderma* and *Ametrida* (Baker, 1973). Chromosomal data support this proposal. All five genera have $2N = 30$ ♀♀, 31 ♂♂, and a fundamental number of 56. Some minor variation in the morphology of the Y elements between the species has been observed (Figs. 1, 2, and 3) and the X chromosome in *Ardops* is apparently submetacen-

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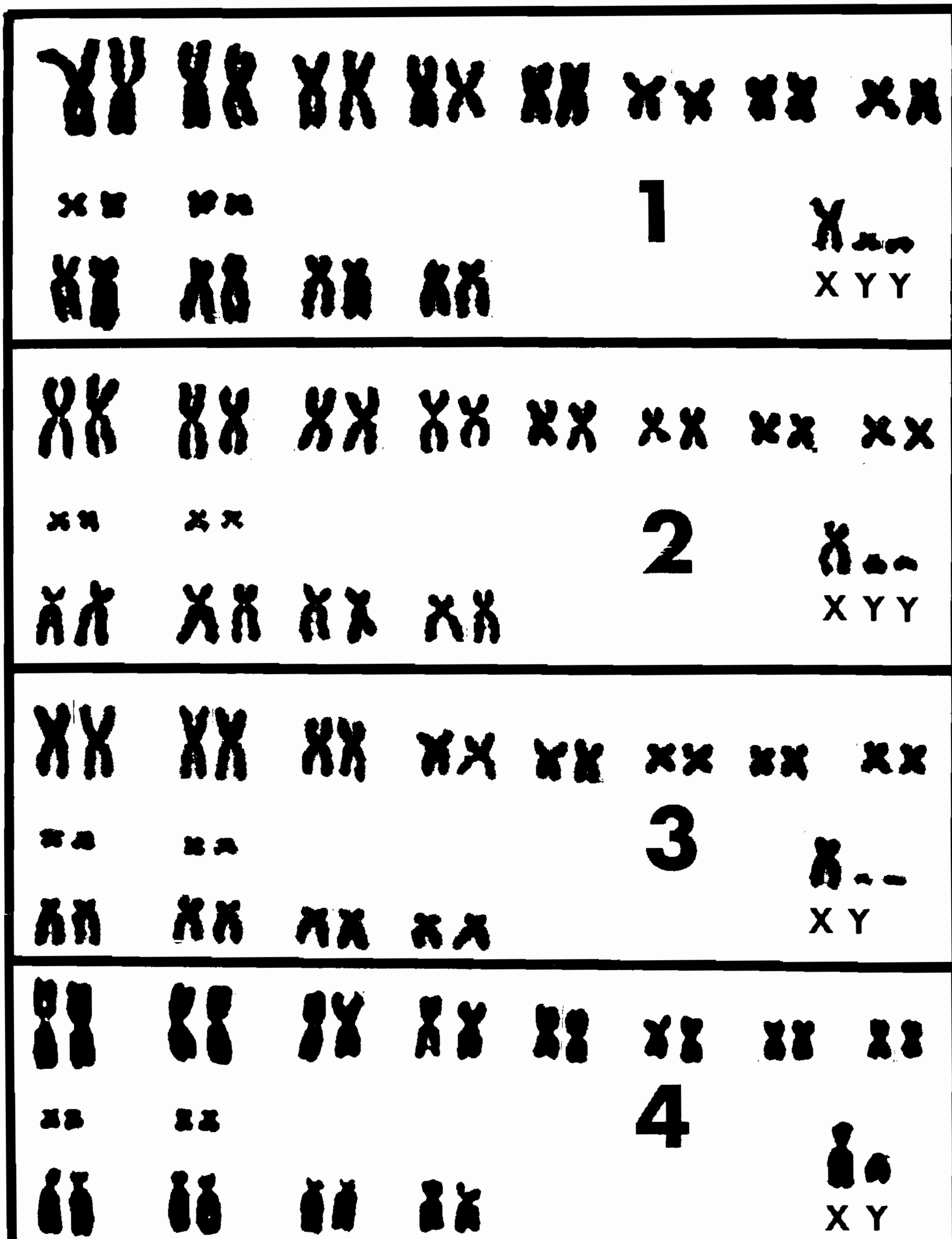

Figure 1. Karyotype of a male *Ardops nichollsi* from Guadeloupe: Basse-Terre; 1 km S, 4 km W Vernou. *Figure 2.* Karyotype of a male *Ariteus flavescens* from Jamaica: St. Ann Parrish; Queenhythe. *Figure 3.* Karyotype of a male *Phyllops haitiensis* from Haiti: Department du Sud: 1 km E Lebrun. *Figure 4.* Karyotype of a male *Ectophylla alba* from Costa Rica: Heredia; Finca "La Selva."

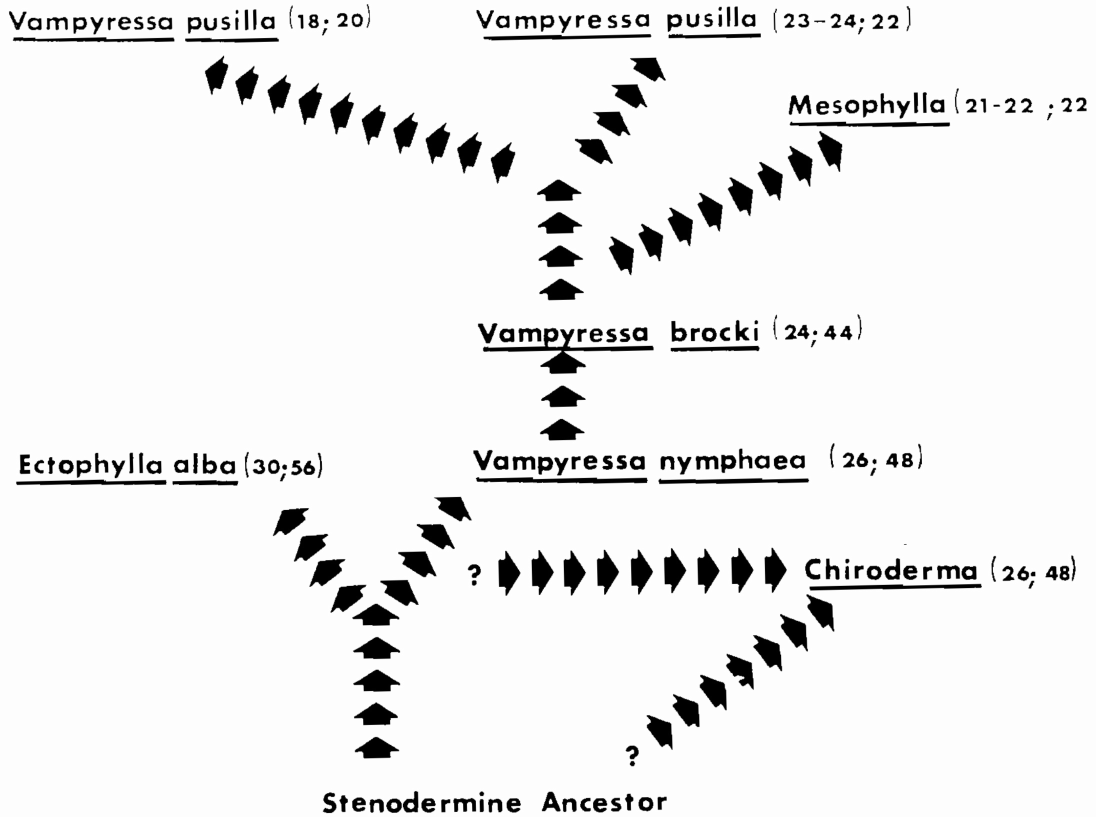

Figure 5. Proposed phylogenetic tree for the *Vampyressa*, *Mesophylla*, and *Ectophylla* line of evolution. Numbers in parentheses are diploid number followed by fundamental number.

tric, whereas in *Ariteus*, *Phyllops*, *Stenoderma*, and *Ametrida* the X is subtelocentric. We are under the impression that the genera *Ardops*, *Ariteus*, *Phyllops*, and *Stenoderma* represent a single invasion from the mainland of an ancestral stock which has found its way to most of the Lesser and Greater Antillian Islands with subsequent speciation. Minor changes such as extinctions and reinvasions may have occurred several times but the close morphological and karyotypic relationship of the four genera in question supports the idea of a single invasion. Varona (1974) has proposed that the genera *Ardops*, *Ariteus*, and *Phyllops* are congeneric with *Stenoderma*. Although Varona may be correct, we will follow the old arrangement until a proper revision accompanies the proposed change. How *Stenoderma* (as used by Varona) is distinguished from *Pygoderma* and *Ametrida* and what features serve as the basis for lumping the four Caribbean genera needs to be discussed. There are two other genera of "white-shouldered bats", *Sphaeronycteris* and *Centurio*, however these two genera are distinguished from the other "white-shouldered bats" by a diploid number of 28 and a classical XX/XY sex determining system. The white spot on the shoulder and the shortened rostrum of *Ametrida*, *Ardops*, *Ariteus*, *Phyllops*, *Centurio*, *Stenoderma*, *Sphaeronycteris*, and *Pygoderma* to us reflects a common evolutionary history that distinguishes these genera from the other stenodermines.

The relationship of *Ectophylla* to the rest of the stenodermine genera is not so clear. A close relationship between *Ectophylla alba* and *Mesophylla macconnelli* has been proposed by Laurie (1955) and Goodwin and Greenhall (1961) who suggested that the two genera were congeneric. Starrett and Casebeer (1968) concluded that *Ectophylla* and *Mesophylla* were distinct genera and that these two plus *Vampyressa* formed a distinct unit within the Stenoderminae. Further, Starrett and Casebeer (1968) concluded that *Ectophylla* was the most derived (dentally) of the species involved. From a chromosomal standpoint the genera *Vampyressa* (three species karyotyped) and *Mesophylla* formed the derived components of a proposed evolutionary line within the stenoderminae. This line was characterized by a reduced diploid and fundamental number. The genus *Chiroderma* was also included with this group (Baker, 1973). *Mesophylla* at the end of this line has the most derived karyotype, 2N = 21–22, FN = 22 with the autosomal complement having all acrocentric elements. A diploid number of 2N = 30 is assumed as primitive for the Stenoderminae (see Baker, 1973 for the theory behind this assumption). *Ectophylla alba* appears to have a karyotype that is less derived (based on Baker's hypothesis of a 2N = 30 being primitive for the subfamily) than any of the species of *Vampyressa* and *Mesophylla* thus far karyotyped. This is in contrast to the conclusion of Starrett and Casebeer (1968) that *Ectophylla* appears to be the most highly modified dentally and cranially of the three genera. Our interpretation of the evolutionary position of *Ectophylla* (Fig. 5) is that it probably evolved from the stock that gave rise to *Mesophylla* and *Vampyressa* before there was any reduction in the diploid number. The development of the "derived" cranial and dental features then could have taken place after the *Ectophylla* line separated from the *Mesophylla-Vampyressa* line. If the above relationships are valid then *Ectophylla* must remain a genus distinct from *Mesophylla* unless the species of *Vampyressa* are also considered as congeneric with *Ectophylla* and *Mesophylla*. A close relationship of *Vampyressa pusilla* to *Mesophylla* was pointed out by Starrett and Casebeer (1968) based on cranial and dental characteristics and this relationship is reinforced by our chromosomal data (Fig. 5). If a single event resulted in the reduction in diploid number that now characterizes the evolutionary line that gave rise to *Chiroderma* and the *Vampyressa-Mesophylla* stock then *Ectophylla* is even more distantly related to this group than is the genus *Chiroderma* which is cranially and dentally very unique from *Mesophylla* and *Vampyressa*.

Specimens examined.—Voucher specimens are deposited in The Museum, Texas Tech University (*Ardops*, *Ariteus*, and *Phyllops*) or in The United States National Museum (*Ectophylla*). All microscope slides with karyotypic preparations are on deposit at Texas Tech University.

Ardops nichollsi.—Guadeloupe: Basse-Terre; 1 km W Vernou, (N = 3). 2 km E St. Claude, (N = 1). 1 km S, 4 km W Vernou, (N = 6).

Ariteus flavescens.—Jamaica: Trelawny; Duanvale, (N = 1). St. Ann Parrish: Queenhythe, (N = 1). Orange Valley, (N = 9). St. Thomas Parrish: Yallahs, (N = 1).

Phyllops haitiensis.—Haiti: Dept. du Sud; 1 km E Lebrun (N = 4). 2 km N, 2 km E Lebrun, (N = 4).

Ectophylla alba.—Costa Rica: Heredia; Finca "La Selva", (N = 1).

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