

allowing the flies free rein for mating, other things being equal, would eventually result in pure cactus breeding 626 flies.

Positive assortative mating, on the other hand, by definition, occurs when the frequency of homogamic matings (matings between similar individuals) is significantly greater than that of heterogamic matings (matings between dissimilar individuals). If sexually mature individuals can meet, positive assortative mating must exist in order for ecological types to diverge. At a moderate level, assortative mating may tend to preserve intrapopulation diversity. If increased to its extreme level, it isolates sympatric populations. No evidence for this was found in our tests.

To summarize, *D. pegasa* males were capable of distinguishing between females that were reared on two different media. However, their subsequent behavior was such as to lead to the elimination of variability rather than to the fragmentation of the population.

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A PRELIMINARY TEST OF THE ADAPTIVE SIGNIFICANCE OF ENVIRONMENTAL SEX DETERMINATION IN REPTILES

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The processes of sex determination in reptiles fall into two broad categories: genotypic and environmental (Bull, 1980, 1983). Genotypic sex determination (GSD) includes familiar heterogametic mechanisms (XX:XY and ZZ:ZW) and less common arrangements (XXX:XXY, ZZZ:ZZW, ZZZ:ZWW, pseudo XO, homogamety, and perhaps others) (Olmo, 1986). Known environmental sex determination (ESD) mechanisms include hydric (Gutzke and Paukstis, 1983; Paukstis et al., 1984) and thermal (Bull, 1980, 1983; Pieau, 1985) effects on gonadal differentiation of developing embryos. Males generally are produced at intermediate temperatures (e.g., 25°C) in turtles and at

high temperatures (e.g., 31°C) in lizards and crocodilians. However, several turtles (Yntema, 1976; Vogt et al., 1982; Schwarzkopf and Brooks, 1985), one lizard (Tokunaga, 1985), and several crocodiles of the genus *Crocodylus* (Deeming and Ferguson, 1988) produce female hatchlings at both high and low (e.g., 21°C) incubation temperatures. These three general patterns of temperature effects on gonadal differentiation have been described by Bull (1980) as: Type A—females produced at intermediate temperatures, males produced at high temperatures; Type B—females produced at high temperatures, males at intermediate temperatures; and Type C—females produced at low and high

TABLE 1. Relationship between sexual dimorphism in adult body size and sex-determining mechanisms in turtles and lizards after potential phylogenetic constraints have been removed (see text). Information on sexual dimorphism and sex determination was collected from numerous sources in the literature and is presented in Figures 1 and 2. The data in this table were generated by subjecting Figures 1 and 2 to Ridley's method of phylogenetic analysis (Ridley, 1983). Where information on a given species indicated intraspecific variation in patterns of sexual dimorphism (four chelonians and ten saurians), the species was counted in the dimorphism category favorable to the hypothesis (e.g., if a lizard with GSD showed no dimorphism in some populations and large-female sexual dimorphism in others, the species was counted in support of the hypothesis). This methodology promotes a conservative test. Also, four lizard species were excluded from this analysis because they are strictly viviparous, a condition which apparently necessitates GSD (Bull, 1980) and which, therefore, would confound the analysis. Data for turtles and for lizards were analyzed with separate *G*-tests, (Sokal and Rohlf, 1981). Despite favorable changes, the null hypothesis (i.e., values do not differ from random) cannot be rejected for either turtles or lizards.

Pattern of sexual dimorphism	ESD	Pattern of sexual dimorphism	GSD	<i>G</i>	P <i>df</i> = 1
		Chelonians			
$\delta > \varnothing$; $\delta = \varnothing$	5	$\delta > \varnothing$	2	0.80	0.37
$\delta < \varnothing$	5	$\delta < \varnothing$; $\delta = \varnothing$	5		
		Saurians			
$\delta > \varnothing$	2	$\delta > \varnothing$; $\delta = \varnothing$	10	1.41	0.24
$\delta < \varnothing$; $\delta = \varnothing$	4	$\delta < \varnothing$	7		

temperatures, males at intermediate temperatures. These various mechanisms and patterns of ESD occur across broad taxonomical levels within the class Reptilia (Bull, 1980, 1983; Olmo, 1986; Deeming and Ferguson, 1988) and may occur even within the same family or genus (e.g., Ewert and Nelson, 1987).

The variety of sex-determining mechanisms in reptiles has resulted in considerable interest in this phenomenon, yet a sufficient explanation for the occurrence of these various mechanisms is lacking (Bull and Charnov, 1989). Charnov and Bull (1977) provided an important model to address this problem by delimiting circumstances under which selection should favor ESD over GSD: (1) the animals must inhabit a patchy environment wherein offspring in certain patches have different lifetime fitness than offspring in other patches, (2) the patchiness must influence male fitness differently than female fitness such that some patches are better for males than for females and vice versa, (3) the offspring cannot choose the patch type and the parents cannot preferentially put offspring of one genotype into other patches, and (4) mating takes place among individuals reared in different patches. Under these conditions, ESD theoretically is favored by selection over GSD because offspring whose sex is determined at conception often would be of low fitness in a given patch.

Researchers seeking to explain the adaptive significance of ESD in reptiles have concentrated on searching for fitness traits that correlate with incubation temperature (representing the "patch" in the Charnov-Bull model) and offspring sex. One possible interpretation of the Charnov-Bull model is that post-hatching growth may be a potential candidate for a fitness trait in reptiles with ESD, because it may correlate with both incubation temperature and offspring sex. According to this sexual dimorphism hypothesis, if the benefits of adult body size differ between the sexes, the sex that

benefits most from being large should be produced at the particular incubation temperature (cool, warm, or hot, as it may be) that will yield a larger adult. Thus, one possible test of the adaptive significance of sex-determining mechanisms in reptiles is to demonstrate that the pattern of sexual dimorphism in adult body size is correlated with the occurrence of either ESD or GSD in a given taxon. An additional test would be to demonstrate that the type of ESD is related to the pattern of sexual dimorphism in adult body size in a given taxon (Head et al., 1987).

Are the fitness effects of ESD manifested in sexual dimorphism in adult body size in reptiles? Snakes and the tuatara are not known to exhibit ESD (Bull, 1980, 1983; M. B. Thompson, pers. comm.) and amphisbaenids have yet to be studied, thus these taxa cannot be used to test the sexual dimorphism hypothesis. Crocodylians, of which all eight species examined to date possess ESD (Yamakoshi et al., 1987; Deeming and Ferguson, 1988), all have large-male sexual dimorphism (Lang, 1987). The evolutionarily conserved occurrence of ESD and pattern of sexual dimorphism in adult body size within the group imply potential phylogenetic constraints and thereby disallow application of the first of the two tests of the sexual dimorphism hypothesis described above. For the second test, five of the eight species show the Type A pattern of ESD, while the remaining three species show the Type C pattern of ESD. Thus, contrary to the sexual dimorphism hypothesis, the type of ESD (A, B, or C) in crocodylians is unrelated to the pattern of sexual dimorphism in adult body size.

Turtles and lizards, in contrast to the crocodylians, exhibit variation in sex-determining mechanisms (Bull, 1980, 1983; Olmo, 1986) and sexual dimorphism (Berry and Shine, 1980; Fitch, 1981), thus providing a better opportunity for tests of the sexual dimorphism hypothesis. For the first test of the sexual dimorphism

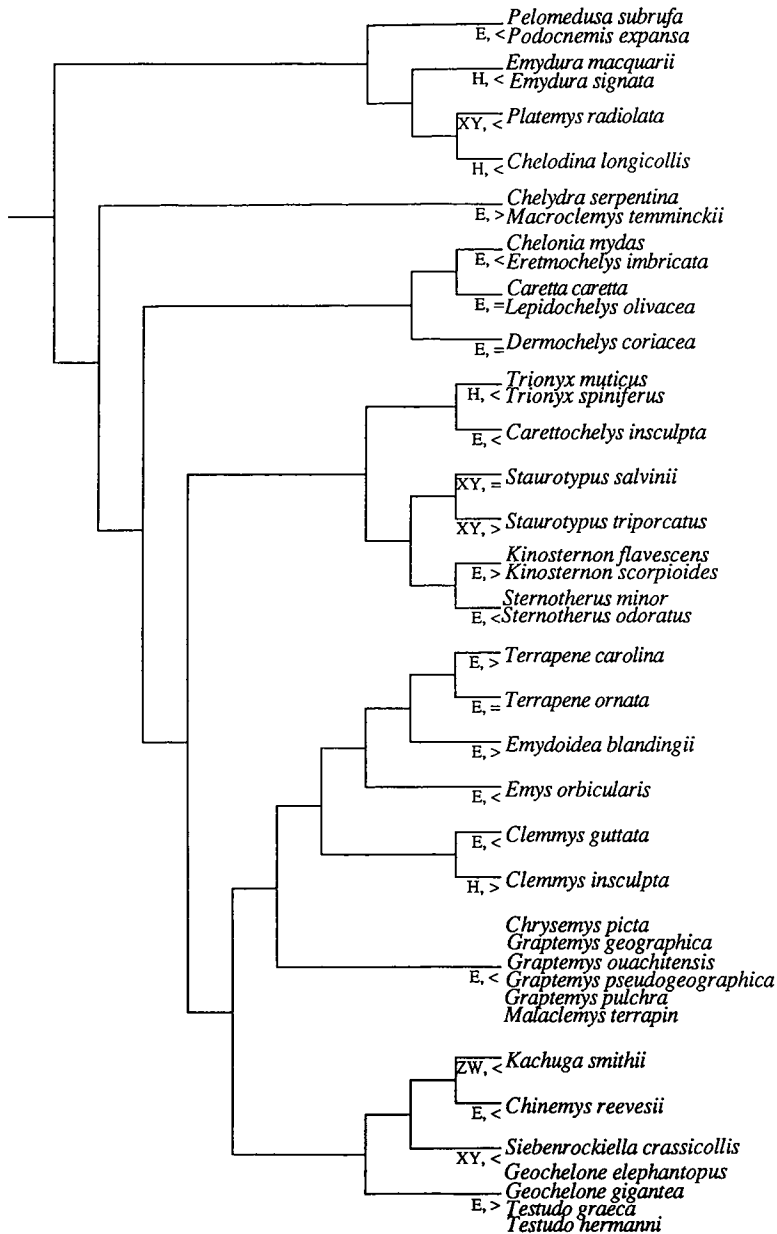


FIG. 1. Phylogenetic tree for turtles showing the sex-determining mechanisms and patterns of sexual dimorphism in adult body size. E = ESD, H = homomorphic sex chromosomes, XY = male heterogamety, ZW = female heterogamety. The equality and inequality signs indicate body size of adult males in relation to body size of adult females.

hypothesis, data for turtles and lizards (Figs. 1, 2, respectively) were analyzed with *G*-tests (Sokal and Rohlf, 1981) after taking into account possible phylogenetic constraints (Table 1). The approximate minimum number of phylogenetically independent combinations of sexual dimorphism and sex-determining mechanism was determined with Ridley's method (Ridley, 1983; see Swofford and Maddison [1987] and Coddington

[1988] for discussion of this technique). Phylogenetic relationships were determined from published phylogenies for turtles (Gaffney and Meylan, 1988) and lizards (Lutz and Mayer, 1985; Guyer and Savage, 1986; Kluge, 1987; Estes et al., 1988; Etheridge and de Queiroz, 1988). The relationships between sex-determining mechanisms and sexual dimorphism in adult body size for both turtles and lizards are inconsistent with pre-

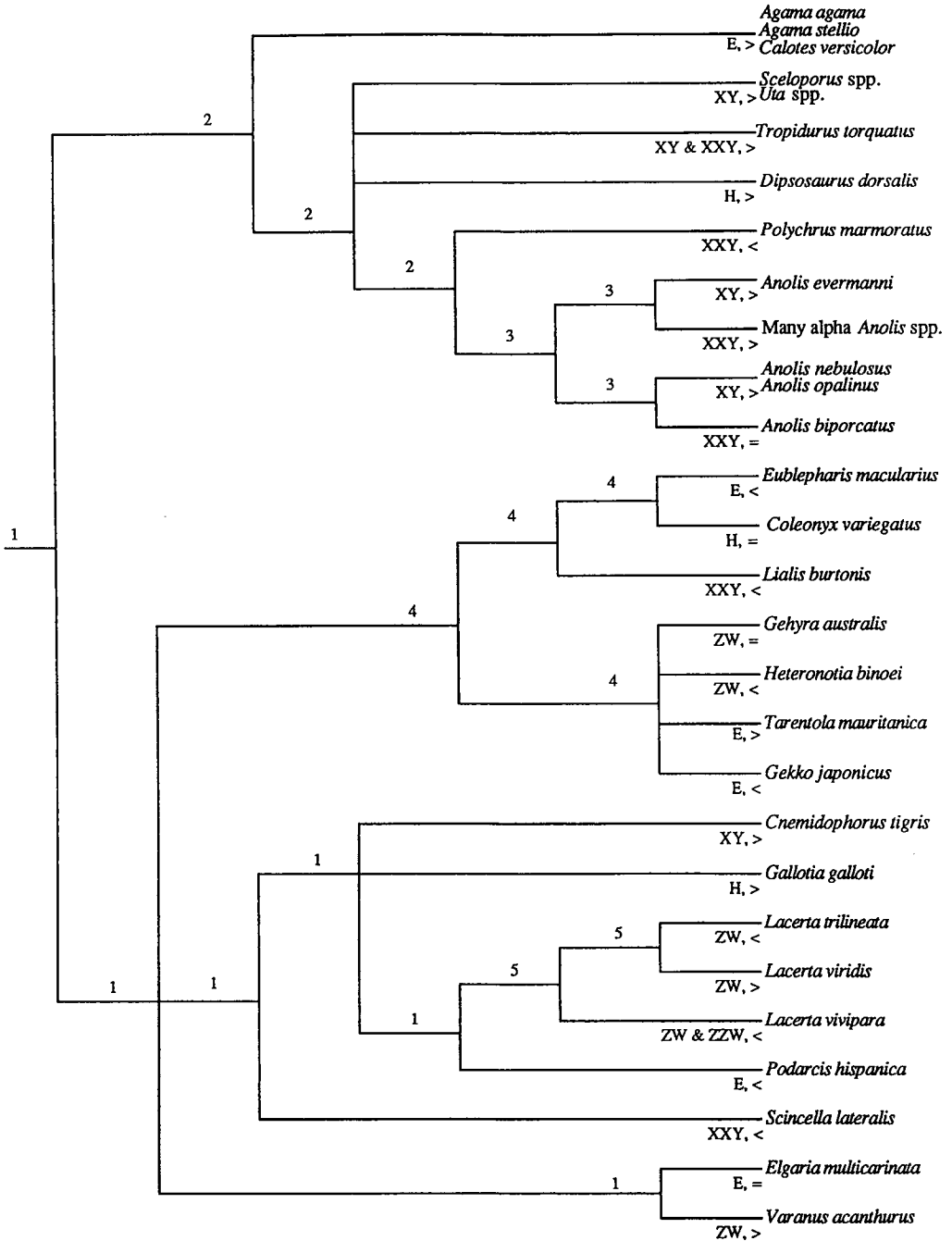


FIG. 2. Phylogenetic tree for lizards showing the sex-determining mechanisms and patterns of sexual dimorphism in adult body size. E = ESD, H = homomorphic sex chromosomes, XY and XXY = forms of male heterogamety, ZW and ZZW = forms of female heterogamety. The equality and inequality signs indicate body size of adult males in relation to body size of adult females. The taxonomic affinities of three lacertid lizards (*Meroles cuneirostris*, *Lacerta monticola*, and *Eremias arguta*) could not be determined precisely, although information on their sex-determining mechanisms (H, H and ZW, respectively) and patterns of sexual dimorphism in adult body size (>, <, and >, respectively) were used with the rest of the information for lizards in this figure to generate data for Table 1, using Ridley's method of phylogenetic analysis (Ridley, 1983). Although information for *Elgaria multicarinata* was used in this figure and in Table 1, the classification of this species as

dictions of the sexual dimorphism hypothesis. Only 6 of the 11 assemblages (i.e., phylogenetically independent combinations) of turtles with ESD exhibit a pattern of large-male sexual dimorphism. Only three of five assemblages of lizards with ESD also show large-female sexual dimorphism. Although there appears to be a correlation between pattern of sexual dimorphism and presence or absence of GSD, the relationship is not statistically significant (Table 1).

For the second test, data for the type of ESD and the pattern of sexual dimorphism in adult body size for turtles and lizards were tabulated (Table 2). These data also do not support the sexual dimorphism hypothesis because there is no relationship between the type of ESD and pattern of sexual dimorphism in adult body size. For example, four assemblages of turtles with Type B ESD have large-female sexual dimorphism, three have large-male sexual dimorphism, and two show no sexual dimorphism at all. One could argue, however, that many species currently classified as showing a Type A or B pattern of ESD have not been tested specifically for the presence or absence of a lower threshold of sex determination that, if present, would cause the species to be reclassified as Type C. Even if the test is restricted to analysis of Type C species (i.e., species whose classification is unambiguous), the sexual dimorphism hypothesis remains unsupported (column C for Chelonians in Table 2).

Potential problems with tests of the sexual dimorphism hypothesis do exist. First, if conditions of the Charnov-Bull model are violated substantially (and there is no evidence that this is the case), then the first test of the sexual dimorphism hypothesis could be invalidated. However, these violations would leave the second test unaffected. Second, the phylogenetic relationships of the various reptilian species presented here (Figs. 1, 2) are working hypotheses based on the data that currently are available. These phylogenetic hypotheses may undergo future changes and, consequently, the numbers of assemblages present in the cells of Tables 1 and 2 may change. Although numbers in the cells may change, as would the statistical values, no cell currently containing at least one assemblage ever would be reduced to zero. Thus, any currently nonempty cell that is unfavorable to the sexual dimorphism hypothesis always would remain so. Third, any species that does not conform to the sexual dimorphism hypothesis may so deviate because strong selection favors a particular pattern of sexual dimorphism that is unrelated to the type of ESD in that species. In this scenario, evolution of a different sex-determining mechanism or type of ESD lags behind evolution of a different pattern of sexual dimorphism. This sort of ad hoc argument would undermine the generality of the sexual dimorphism hypothesis. Finally, because sexual dimorphism can vary intraspecifically among populations (see text of Table 1), certain species may be miscategorized in this analysis, although that seems unlikely.

Based on the limited number of reptile species examined to date, the sexual dimorphism hypothesis

TABLE 2. Relationship between sexual dimorphism in adult body size and type (A, B, or C of Bull [1980]) of environmental sex determination in turtles and lizards after potential phylogenetic constraints have been removed (see text). The number of assemblages for each taxon differ from those in Table 1 because additional assemblages were created when classifying species by type of ESD.

Pattern of sexual dimorphism	Chelonians			Saurians		
	A	B	C	A	B	C
$\delta > \varphi$	0	3	1	2	0	0
$\delta = \varphi$	0	2	0	1	0	0
$\delta < \varphi$	0	4	2	2	0	1

appears unable to explain the predictions of the Charnov-Bull model (Charnov and Bull, 1977). Our results suggest that if ESD is adaptive in reptiles, then an explanation for its occurrence might be found in organisms with GSD (Janzen and Paukstis, 1988) or in alternative traits that may correlate with offspring sex and incubation temperature (e.g., length of incubation period [Packard and Packard, 1988], post-hatching growth rates or size at various life stages [Joanen et al., 1987]). Gutzke and Crews (1988), for example, recently have provided evidence for the current adaptive significance of ESD in leopard geckos (*Eublepharis macularius*). They found that female leopard geckos produced at warm incubation temperatures apparently are functionally sterile, while females produced at cool incubation temperatures exhibit sexual receptivity when courted by males. Thus, although the sexual dimorphism hypothesis is unsupported at this time, the news is encouraging for researchers interested in this area.

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having ESD is questionable owing to small sample size. Numbers on branches indicate references in support of the tree as follows: (1) Estes et al., 1988; (2) Etheridge and de Queiroz; (3) Guyer and Savage, 1986; (4) Kluge, 1987; (5) Lutz and Mayer, 1985.

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