

Effects of Age and Size in the Ears of Gekkonomorph Lizards: Middle-Ear Morphology with Evolutionary Implications

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ABSTRACT

The function of the ear depends in part on its absolute size and internal proportions. Thus, in both young individuals and small species, the middle ear is expected to be allometrically enlarged despite its smaller absolute size. Here we aim to compare the ontogenetic allometry of relevant middle-ear structures as observed within gecko (gekonomorph lizards) species, with the evolutionary allometry observed interspecifically. These observations also provide middle-ear data for future evaluation of variation in auditory sensitivity. The material comprised 84 museum specimens of geckos, representing nine species of three gekonomorph subfamilies. The results of dissections and measurements show that different reports notwithstanding, the middle-ear ossicular chain is indeed structured as described for geckos by Werner and Wever (*J Exp Zool* 1972;179:1–16) and Wever (*The reptile ear*, 1978). Some sexual dimorphism is indicated, but this requires further study. During postnatal ontogeny, the allometric growth in the ratio of the columellar footplate area to body length differed between the intraspecific and interspecific levels, hence species differences in the middle ear do not merely result from animal size. The ratio of the tympanic membrane area to the columellar footplate area increased during ontogeny. In this, geckos resemble birds and probably also mammals. Similarly, when the comparison was among adults representing different species, the ratio of the tympanic membrane area to the columellar footplate area increased with body size. In this, however, the geckos differed from birds and mammals, in which this ratio varied taxonomically, irrespective of body size. It would thus seem that middle-ear proportions have evolved among geckos to produce small interspecific differences, but among amniote tetrapods they have evolved according to different principles in the classes reptiles, birds, and mammals. © 2005 Wiley-Liss, Inc.

Key words: lizards; geckos; middle ear; directional asymmetry; sexual difference; ontogenetic allometry; interspecific allometry; evolution

The function of sensory organs such as the eye and ear depends in part on the organ's absolute size and internal proportions. As a consequence, in young individuals within a species, as well as in small species (compared with their larger relatives), the organ is expected to be allometrically enlarged despite its smaller absolute size (Walls, 1942; Schwartzkopff, 1957). Werner et al. (2002) reviewed the available evidence in reptiles, specifically in gecko lizards, and noted that young small individuals possess less sensitive hearing (as assessed electrophysiologically) than large adult individuals. This could conceivably have resulted from the smaller absolute size of

the ear, especially the tympanic membrane (Fig. 1), in those juveniles, even if relative to body size the ear was

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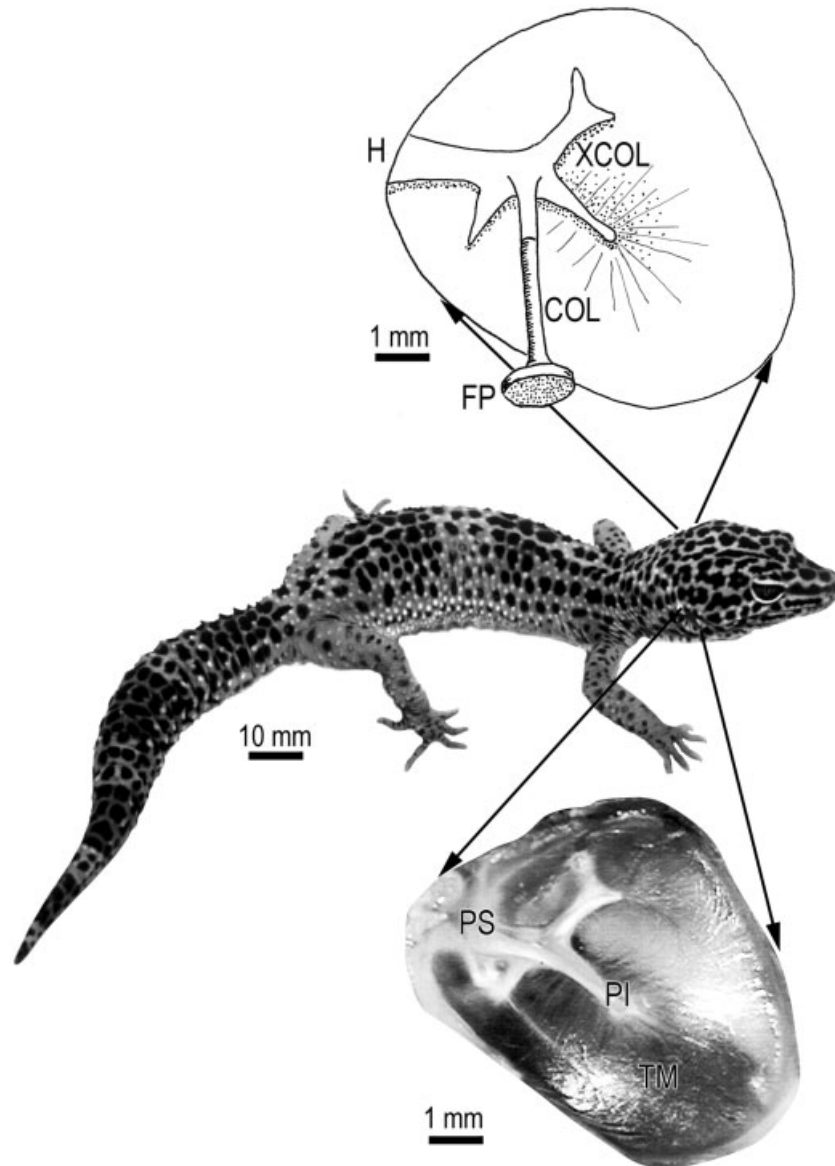


Fig. 1. The middle ear of an adult gecko, *Eublepharis macularius*. On its ipsilateral side (bottom), viewed from the lateral aspect (after widening the external ear canal), the tympanic membrane, slightly convex outward; on its contralateral side (top), seen from the dorsomedial aspect,

the columellar system and slightly concave tympanic membrane. H, hinge of the mechanical lever in the extracolumella; TM, tympanic membrane. See also "Abbreviations" and "Materials and Methods" (Morphology) sections.

larger than in adults. Werner and Igić (2002) presented evidence that the same holds true when comparing adults of smaller and larger gecko species. The studies supporting this idea, unfortunately, failed to distinguish between the effects of size and of age.

As explained in greater detail in Werner et al. (2002), we have endeavored recently to determine the effects of size and of age on the functioning of the tetrapod ear as exemplified in geckos. The hearing ability of geckos, liz-

Abbreviations: HUJ-R, Hebrew University of Jerusalem, Herpetology Collection; RA, rostrum-anus length (Werner, 1971); PERCRA, percents of RA (Werner, 1971); TM, tympanic membrane; ANC, Anchorage length of the extracolumella (from tip of pars inferior to rim of tympanum); CL, Columella (osseous) length; CW, Columella (osseous) width (diameter in the middle of

its length); EOA, Ear opening area; EOL, External opening of the ear, length (greatest diameter); EOW, Ear opening width, greatest short diameter at right angle to EOL; FPA, Footplate of the columella, area; FPL, Footplate of the columella, length (greatest diameter); FPW, Footplate of the columella, width (greatest short diameter at right angle to the preceding); HL, Head length from snout tip to posterior margin of the ear opening (as is conventional in herpetology); HW, Head width at the greatest width.

ards of the family cluster Gekkonomorpha (Rösler, 1995), is of special interest because of their ability to communicate vocally (Frankenberg and Werner, 1992; Werner et al., 2001). Our experimental design compared the ear's structure and function among samples organized in triads. These triads consisted of adults of a relatively large species, adults of a closely related but significantly smaller species, and juveniles of the former but with the size of the latter. Comparable triads composed of different species are then examined, and our expectation was that parallel results among the triads would verify differences between the effects of size and of age. We applied to the same ears four methodologies for assessing the function of the ear and its underlying morphology. One allowed us to derive comparative audiograms based on electrophysiological threshold responses (data not shown). Other methodologies quantified the morphology of the inner ear auditory papilla and the number of auditory hair cells (Gehr and Werner, 2005), as well as the structure (present report) and function (Werner et al., 2002) of the middle-ear conductive apparatus.

The crucial contribution of the middle ear in hearing has been discussed by Lombard and Hetherington (1993), and its role in conducting aerial sound to the reptilian inner ear was demonstrated by Wever and Bray (1931) and reviewed by Wever (1978) and Manley (1990). Werner et al. (2002) assessed middle-ear function by measuring the transfer function of tympanic membrane vibrations in response to constant intensity sounds at different frequencies. Our other methodology for examining the middle ear, which is reported here, quantifies the morphology of the middle-ear conductive apparatus, as detailed in Figures 1 and 2 and discussed elsewhere (Wever and Werner, 1970; Werner and Wever, 1972; Wever, 1978).

Our aims in this presentation were two. One, to describe quantitatively middle-ear structures in sufficient detail so that it might help explain size-related variations in auditory sensitivity. Of particular importance were the extents of the hydraulic and mechanical middle-ear levers. Two, to compare the allometry of the specific middle-ear structures (e.g., the tympanic membrane) as observed within a species (this we define as ontogenetic allometry) with that observed among adults of species of varying body size (which we refer to as interspecific or evolutionary allometry). This comparison would provide us with an indication of whether middle ears differing in size and proportions among species of different body size are on a uniform growth curve. Such an observation would offer insight as to whether middle-ear structures vary merely as a function of the interspecific variation of adult body size, or because they have evolved through modifications of their own growth curves (Cheverud, 1982; Reiss, 1989). The latter possibility would imply the existence of past natural selection forces driving this evolutionary outcome.

In the present study we examined the intra- and interspecific variation in absolute size and relative proportions of a number of structural components in the conductive apparatus of the gecko middle ear. In addition, we first test whether the data include the complications of sex differences and, where possible, interaural differences in the conductive morphology. Differences due to both these factors have been reported to occur in the physiology of the ear in man (Kannan and Lipscomb, 1974; Newmark et al., 1997; Ismail and Thornton, 2003) and less often in the structures of the external and middle ears of gekkono-

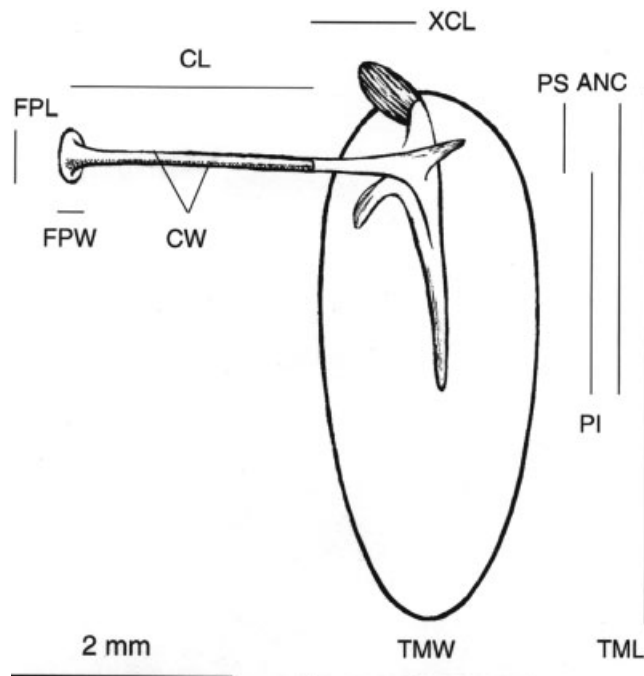


Fig. 2. Semidiagrammatic sketch of the right middle-ear mechanism of a gecko, *Ptyodactylus guttatus*, in ventral view, with the gecko's snout pointing down, showing measurements taken in this project. Scale bar = 2 mm. Reprinted from Werner and Igić (2002). ANC, Anchorage length of the extracolumella (from tip of pars inferior to rim of tympanum); CL, Columella (osseous) length; CW, Columella (osseous) width (diameter in the middle of its length); FPL, footplate of the columella, length (greatest diameter); FPW, Footplate of the columella, width (greatest short diameter at right angle to the preceding). See also "Abbreviations" and "Materials and Methods" (Morphology) sections.

morph lizards (Werner et al., 1991, 1997; Ruiz de la Concha et al., 1999).

MATERIALS AND METHODS

Materials

The material comprised 84 specimens belonging to nine nominal species representing three gekkonomorph subfamilies. The material, including species names, body sizes, sources, and sample sizes, is listed in Table 1. Basically, we used the same species and specimens that had served in physiological experiments (Werner et al., 1998, 2002). Collecting in Australia and exporting to the United States had occurred under permits SF001105 from the Department of Conservation and Land Management of Western Australia and PWS-P935483 from the Australian Nature Conservation Agency, Canberra. At the University of Pennsylvania, all geckos were maintained and tested under a protocol approved by the Institutional Animal Care and Use Committee.

Four of the samples are each subdivided into two subsamples: three according to age [as in Werner et al. (2002)] and one according to morphology because *Christinus marmoratus* is considered a composite species and the material included two provisional "races" (Teale, 1991; King and Horner, 1993). All carcasses are deposited as voucher specimens in the Herpetological Collection, The Hebrew University of Jerusalem (HUJ-R).

TABLE 1. Species and specimens (n = 84) comprising the material*

Subfamily and species	n	RA, mm, mean (range)	Source of the animals	Voucher specimens
Eublepharinae				
<i>Em</i> , <i>Eublepharis macularius</i> Blyth, 1854	8	112.5 (105–119)	Captive bred (Werner et al., 2002)	HUJ-R 18,885–18,893
<i>Emj</i> , <i>E. macularius</i> juveniles	6	51.6 (50–54)	Captive bred (Werner et al., 2002)	HUJ-R 18,894–18,900
<i>Cm</i> , <i>Coleonyx mitratus</i> (Peters, 1863)	7	66.5 (58–71)	Nicaragua (Werner et al., 2002)	HUJ-R 18,876–18,882; 19,008.
Diplodactylinae				
<i>Om</i> , <i>Oedura marmorata</i> Gray, 1842	8	96.3 (85–105)	Western Australia (Werner et al., 2002)	HUJ-R 18,934–18,940.
<i>Omj</i> , <i>O. marmorata</i> juveniles	5	67.4 (59–74)	Western Australia (Werner et al., 2002)	HUJ-R 18,941–18,944.
<i>Or</i> , <i>Oedura reticulata</i> Bustard, 1969	5	60.8 (51–68)	Western Australia (Werner et al., 2002)	HUJ-R 18,949–18,953.
Gekkoninae				
<i>Chm</i> (L), <i>Christinus marmoratus</i> (Gray, 1845) (“large race”)	9	49 (44–53)	SW western Australia, September–October 1993	HUJ-R 18,954–18,959; 18,961–19,963
<i>Chm</i> (S), <i>Christinus marmoratus</i> (Gray, 1845) (“small race”)	2	48.5 (47–50)	SW western Australia, September–October 1993	HUJ-R 18,969; 18,964; 18,965
<i>Cp</i> , <i>Cosymbotus platyurus</i> (Schneider, 1792)	12	53.1 (47–60)	Commercial	HUJ-R 18,976–18,987
<i>Gp</i> , <i>Gehyra punctata</i> (Fray, 1914)	9	57.2 (55–61)	Western Australia (Werner et al., 2002)	HUJ-R 18,910–18,916
<i>Gpj</i> , <i>G. punctata</i> juvenile	1	38	Western Australia (Werner et al., 2002)	HUJ-R 18,917
<i>Gv</i> , <i>Gehyra variegata</i> (Duméril and Bibron, 1836)	9	43.2 (38–47)	Western Australia (Werner et al., 2002)	HUJ-R 18,923–18,927; 18,929–18,930
<i>Hf</i> , <i>Hemidactylus frenatus</i> (Duméril and Bibron, 1836)	3	51.3 (48–56)	Commercial	HUJ-R 18,969–18,971

*Each species name is preceded by a code used hereafter. Not all specimens yielded data for all parameters (see Table 3).

Methods

The morphologic measurement methods have been described in detail by Werner et al. (1998). Briefly, after the physiological tests on the right ear (Werner et al., 1998, 2002), the animals were killed with an overdose of the anaesthetic; the specimens were fixed in 10% formalin (for a few days, at room temperature) and stored in 70% ethanol. A morphological examination of middle-ear structures was undertaken in the left ear because it was undamaged (the right ear had been used for physiological experiments). However, when both ears were available, both were used. The ear was dissected in stages, and the various middle-ear components were kept moist. The morphometry of each structure was measured with a video-equipped Nikon Multiphot macrophotography system that permitted computerized image analysis (JAVA, Jandel). The image analysis enabled us to trace the perimeter and thus calculate the area of structures such as the external ear opening, the tympanic membrane, and the columellar footplate.

Morphology

The following morphological characters (shown in Figs. 1 and 2) were measured as indicated. Character definitions are preceded by abbreviations used hereafter: ANC, anchorage length of the extracolumella (from tip of pars inferior to rim of tympanum); CL, columella (osseous) length; CW, columella (osseous) width (diameter in the middle of its length); EOA, ear opening area; EOL, external opening of the ear, length (greatest diameter); EOW, ear opening width, great-

est short diameter at right angle to EOL; FPA, footplate of the columella, area; FPL, footplate of the columella, length (greatest diameter); FPW, footplate of the columella, width (greatest short diameter at right angle to the preceding); HL, head length from snout tip to posterior margin of the ear opening (as is conventional in herpetology); HW, head width at the greatest width [the preceding two were measured under the dissecting microscope with callipers, to the nearest 0.1 mm; HL was taken parallel to the long axis of the body using the modified callipers of Goren and Werner (1993)]; PI, pars inferior of the extracolumella, length; PS, pars superior of the extracolumella, length; RA, animal length from rostrum to anus (Werner, 1971), to nearest 0.5 mm (measured by pressing the midline of the abdomen against a transparent mm ruler of verified accuracy); TMA, tympanic membrane area; TML, tympanic membrane (exposed in situ) length (greatest diameter); TMW, tympanic membrane width (greatest short diameter at right angle to TML); XCL, extracolumellar shaft (cartilaginous), length.

From the preceding measurements, we computed the following characters: ARa, area ratio of piston (hydraulic lever), as TMA/FPA. LRa, lever ratio (mechanical lever), as ANC/PS; %CART, percentage of cartilage in the ossicular chain, as 100 XCL/(XCL + CL).

Statistics

Since all the comparisons in this research were based on allometric measures similar in nature to ratios, all data were log-transformed before analysis. This transforma-

TABLE 2. Middle-ear measurements of geckos separate by sex*

Species	Sex	n		RA	HL	HW	TMA	FPA	ARa	LRa
<i>Chm</i> (L)	Males	5	Mean	48.60	11.09	9.62	3.41	0.15	22.46	5.00
			SE	1.86	0.49	0.33	0.35	0.01	1.28	0.37
	Females	3	Mean	49.67	10.35	10.73	3.73	0.14	26.78	4.53
			SE	4.18	0.45	1.14	0.60	0.01	4.12	0.11
<i>Cp</i>	Males	4	<i>P</i> of difference	NS	NS	NS	NS	NS	NS	NS
			Mean	55.00	14.21	9.71	4.16	0.16	27.09	5.55
	Females	5	SE	1.96	0.46	0.45	0.14	0.02	2.82	0.34
			Mean	52.00	13.19	9.71	4.10	0.15	29.14	5.09
<i>Gp</i>	Males	3	SE	1.73	0.30	0.27	0.27	0.01	2.14	0.97
			<i>P</i> of difference	NS	NS	NS	NS	NS	NS	NS
	Females	5	Mean	54.33	13.23	12.17	6.04	0.15	39.30	5.34
			SE	3.33	0.65	0.62	0.44	0.01	0.61	0.33
<i>Om</i>	Males	4	Mean	55.80	13.71	12.25	6.32	0.18	36.04	4.74
			SE	0.66	0.22	0.13	0.12	0.02	3.37	0.19
	Females	4	<i>P</i> of difference	NS	NS	NS	NS	NS	NS	NS
			Mean	86.00	21.70	18.04	12.97	0.40	34.97	4.87
			SE	4.42	1.23	1.04	0.81	0.06	5.12	0.38
			Mean	99.75	23.79	19.73	16.02	0.42	38.38	5.10
			SE	1.89	0.47	0.15	1.15	0.01	3.72	0.14
			<i>P</i> of difference	0.03	NS	NS	NS	NS	NS	NS

*Only the four relevant species and selected key characters are shown. See significance of allometric regressions in the text. Values in mm, mm², or proportions.

tion was chosen in order to create linear functions between the measures (Hills, 1978) and creates a data set that does not deviate significantly from normality, thus justifying the use of parametric statistics. All cases of inter- and intraspecific variation in the allometry of the various body and ear measurements were analyzed using simple linear regression models.

Sexual dimorphism in the species' body-ear measures was analyzed using multiple regression models in which each of the various ear measurements was regressed over each of the three body measurements (RA, HL, HW). The two sex categories were included as dummy variables (Draper and Smith, 1998). The intraspecific variations were compared to the interspecific variation by comparing the values of each species' regression coefficients to the interspecific regression model using a Student's *t*-test with a calculated common standard errors of the means derived from the inter- and intraspecific coefficient values (Zar, 1999).

When testing for the presence of intraspecific directional asymmetry in ear measurements, in order to reduce the intraspecific variation caused by animal size, we calculated relative directional asymmetry: the difference between right and left ear size measures divided by the average of left and right ear size measurements (Werner et al., 1991). To test whether a species showed significant directional asymmetry, this new value was tested using a one-sample Student's *t*-test (Zar, 1999). All statistical test results were considered significant if the *P* value was 0.05 or less.

RESULTS

Intraindividual Variation: Asymmetry

Since most of the animals from which morphologic data were obtained had one of the ears compromised by physiological studies, few subjects were available for making left-right ear comparisons; five *Om* and six *Or* animals were available for the interear comparisons, and only for

EOA. No significant directional asymmetry was detected and for subsequent analyses the data from these individuals are represented by the average of the right and left ears.

Intraspecific Variation: Sexual Dimorphism

The available data yielded only a few instances of significant sexual dimorphism. The sample sizes, available for this purpose from four species, ranged from three to five per sex. None of the sexual differences in the measurements of middle-ear components was statistically significant in any of the four species (Table 2).

As to proportions, the regression of log TMA over log HL differed between the sexes in *Gehyra punctata* (three males, five females; *P* = 0.004 for both slope and intercept). Other than this, the regression equations of log TMA over log RA, log HL, and log HW did not differ between the sexes, in slope or intercept, in any species. This remained so when, by pooling congeners, we increased sample size from 6–9 animals per species to 10–14.

The regression of log FPA over log HL differed between the sexes in the pooled *Christinus marmoratus* (large and small races; seven males, three females; slope, *P* = 0.033; intercept, *P* = 0.036). In the remaining taxa, the regression equations of log FPA over log RA, log HL, or log HW did not significantly differ between the sexes in slope or intercept, and this remained true when pooling congeners or even all specimens.

However, the regression equations of log ARa over log RA, HL, or HW never differed significantly between the sexes, and this persisted after pooling congeners. Finally, the regression log LRa over log HW differed between the sexes in *Cosymbotus platyurus* (four males, five females; slope, *P* = 0.043; intercept, *P* = 0.045). But otherwise, in all species, the regression equations of log LRa over log RA, HL, or HW failed to differ significantly between the sexes. In view of this prevalent absence of significant

TABLE 3. Data reduction: taxon averages \pm SD of the morphological parameters*

Species	N	HL	HW	EOA	TMA	XCL	CL
Eublepharinae							
<i>Em</i>	7	25.12 \pm 1.37	20.11 \pm 1.45	7.16 \pm 1.52	28.49 \pm 2.94	0.64 \pm 0.08	3.09 \pm 0.26
<i>Emj</i>	6	13.16 \pm 0.60	10.23 \pm 0.64	2.45 \pm 0.31	8.23 \pm 0.34	0.33 \pm 0.07	1.07 \pm 0.11
<i>Cm</i>	6	15.58 \pm 1.49	11.80 \pm 1.21	1.80 \pm 0.42	8.83 \pm 1.08	0.37 \pm 0.06	1.32 \pm 0.23
Diplodactylinae							
<i>Om</i>	8	22.74 \pm 2.05	18.88 \pm 1.65	2.49 \pm 0.64	14.49 \pm 2.46	0.44 \pm 0.10	1.87 \pm 0.30
<i>Omj</i>	5	18.63 \pm 3.06	14.35 \pm 1.38	1.41 \pm 0.75	5.17 \pm 4.29	0.40 \pm 0.10	1.22 \pm 0.29
<i>Or</i>	5	13.85 \pm 0.35	11.29 \pm 0.60	1.19 \pm 0.02	5.64 \pm 0.50	0.29 \pm 0.03	1.02 \pm 0.07
Gekkoninae							
<i>Chm</i> (L)	8	10.88 \pm 0.99	10.04 \pm 1.32	0.59 \pm 0.19	3.53 \pm 0.83	0.33 \pm 0.07	0.86 \pm 0.16
<i>Chm</i> (S)	3	10.93 \pm 1.01	9.48 \pm 0.78	0.76 \pm 0.23	3.39 \pm 0.82	0.34 \pm 0.10	0.91 \pm 0.06
<i>Cp</i>	9	13.64 \pm 0.92	9.71 \pm 0.70	0.57 \pm 0.13	4.13 \pm 0.40	0.23 \pm 0.03	1.24 \pm 0.11
<i>Hf</i>	3	14.65 ^a	9.53 \pm 1.05	0.47 ^a	4.38 \pm 0.52	0.22 \pm 0.01	1.23 \pm 0.15
<i>Gp</i>	8	13.53 \pm 0.75	12.22 \pm 0.61	0.66 \pm 0.19	6.21 \pm 0.48	0.28 \pm 0.06	1.42 \pm 0.12
<i>Gpj</i>	1	8.95	8.00	0.50	3.22	0.31	0.93
<i>Gv</i>	6	10.19 \pm 0.44	9.68 \pm 1.28	0.43 \pm 0.06	3.69 \pm 0.47	0.26 \pm 0.04	0.87 \pm 0.10

*Species codes explained in Table 1. Character abbreviations explained in the text. Values in mm and mm².

^aData missing due to surgery.

sexual dimorphism, we pooled the sexes for the subsequent tests. This allowed us to include juveniles in the pooled data sets.

Intraspecific Variation: Ontogenetic Allometry

The morphological data for nine nominal species are summarized in Table 3. Two consistent patterns of results are shared by those three species, each of which is represented by both adults and juveniles (*Em* and *Emj*, *Om* and *Omj*, *Gp* and *Gpj*). First, in absolute terms, during ontogenetic development, the TMA grows by a greater factor than the FPA, leading to a considerable increase in the adult ARa (shown for *Em* as an example in Fig. 3). Second, the relative growth rates of the bony CL and the cartilaginous XCL result in a marked decrease of %CART in the adults, from about 24–25% to about 16–20%. In contrast, the effect of ontogeny on LRA is small, inconsistent, or negligible.

We also examined intraspecific developmental allometry of the principal conductive middle-ear structures and proportions (TMA, FPA, ARa, LRA) relative to measures of animal size (RA, HL, HW) through the regression equations made on their log₁₀ values. This analysis was undertaken in the eight species represented by samples of 4–12 individuals (sexes pooled). These included the three species that contained juveniles, *Em*, *Om*, and *Gp*. Table 4 presents the slopes (indicative of the rate of the organ's relative growth) and intersections (indicative of initial organ size) of only those 32 equations that relate to RA. Below we summarize the more general picture emerging from the analysis of all the equations, showing to what extent the data were significant, and to what extent species differed from each other in middle-ear morphology, beyond what follows directly from differences in body size.

Among the 24 specific regression equations of log TMA over log RA, log HL, or log HW, the slope was significant ($0.03 > P > 0.0001$) in 14, and in all of these the allometry was positive with slope values between 1.36 and 3.65. The intercepts were significant ($0.038 > P > 0.0001$) in 13 of the same cases, ranging from -3.42 to -0.84 . Testing the variation among the eight species, each represented by its logarithmic regression equations, none of the slopes of log

TMA over log RA, log HL, or log HW significantly differed, the pooled slopes being respectively 2.1, 2.07, and 2.14. The intercepts of the three regressions, however, varied significantly ($P = 0.0001$) among the eight species.

Among the 24 specific regression equations of log FPA over log RA, log HL, or log HW, the slope was significant ($0.038 > P > 0.0001$) in 13. The significant slopes ranged from 0.6 (negative allometry) to 2.70. The intercepts were significant ($0.05 > P > 0.0001$) in 20 of the 24 regressions, and 19 were in the range from -4.87 to -1.33 ; the 20th was 1.74 (FPA over HW in *Cm*). When the variation among the eight species was tested, the slopes of log FPA over log RA and over log HL did not significantly differ among the species, the pooled slopes being respectively 1.70 and 1.73. Only for the regression of log FPA over log HW did the slopes vary significantly ($P = 0.001$). However, the intercepts for each of the three equations were significantly different ($P = 0.0001$) among the eight species.

Only 6 of the 24 specific regression equations of log ARa over log RA, log HL, or log HW had a significant ($0.039 > P > 0.0001$) slope. In these, and also in almost all of those that were insignificant, the allometry was negative, with the slope normally between 0.65 and 0.81. However, in *Cp*, the slopes of log ARa over log RA and log HW were -1.85 and -2.15 . The intercepts were significant ($0.036 > P > 0.0001$) for 7 of the 24 regressions, and these ranged from 0.45 to 4.63. Testing the variation among the eight species, the slope of the regression log ARa over log HW varied significantly ($P = 0.021$), but the slopes of the regressions log ARa over log RA and over log HL did not. The pooled slopes were low, 0.37, 0.34, and 0.35, respectively. However, the intercepts of the three types of regression varied significantly ($P = 0.0001$) among the eight species.

Finally, among the 24 specific regressions of log LRA over log RA, log HL, and log HW, the slope was insignificant in all, its values ranging from -1.36 to 1.39 (plus exceptional values up to 4.01 in *Cp*). The intercept was significant in five cases; in all five, the (insignificant) slope had a negative value. Testing the variation among the eight species, only the slopes of log LRA over log RA varied significantly ($P = 0.008$); the pooled slope was 0.05. The

TABLE 3. Data reduction: taxon averages \pm SD of the morphological parameters* (continued)

CW	PS	PI	FPA	ARa	LRa	%CART
0.46 ± 0.10	0.63 ± 0.09	2.60 ± 0.18	0.79 ± 0.10	36.61 ± 4.38	5.18 ± 0.63	17.22 ± 1.51
0.24 ± 0.05	0.33 ± 0.03	1.48 ± 0.17	0.40 ± 0.05	22.10 ± 2.94	5.59 ± 0.70	23.55 ± 5.45
0.28 ± 0.03	0.44 ± 0.08	1.65 ± 0.18	0.25 ± 0.04	36.28 ± 3.19	4.90 ± 0.87	22.12 ± 3.95
0.40 ± 0.08	0.53 ± 0.07	2.09 ± 0.20	0.41 ± 0.08	36.68 ± 8.48	4.98 ± 0.54	18.82 ± 2.53
0.39 ± 0.08	0.47 ± 0.07	1.69 ± 0.16	0.35 ± 0.01	18.39 ± 11.5	4.65 ± 0.69	25.18 ± 8.17
0.22 ± 0.01	0.25 ± 0.02	1.34 ± 0.06	0.18 ± 0.02	33.46 ± 2.43	6.43 ± 0.42	22.17 ± 1.03
0.21 ± 0.02	0.27 ± 0.03	1.03 ± 0.13	0.15 ± 0.03	24.08 ± 4.92	4.83 ± 0.67	28.17 ± 6.56
0.17 ± 0.03	0.28 ± 0.05	1.10 ± 0.17	0.13 ± 0.03	28.56 ± 13.0	4.97 ± 0.68	26.68 ± 5.30
0.19 ± 0.02	0.33 ± 0.26	1.06 ± 0.29	0.15 ± 0.03	28.11 ± 4.76	5.29 ± 1.61	15.14 ± 1.83
0.18 ± 0.01	0.21 ± 0.04	1.00 ± 0.16	0.16 ± 0.04	27.68 ± 2.74	5.93 ± 1.55	15.28 ± 1.03
0.18 ± 0.03	0.28 ± 0.04	1.10 ± 0.08	0.17 ± 0.04	37.24 ± 5.96	4.96 ± 0.54	16.43 ± 3.22
0.18	0.23	0.78	0.14	23.00	4.49	25.00
0.16 ± 0.05	0.24 ± 0.03	1.00 ± 0.07	0.12 ± 0.01	30.29 ± 3.23	5.12 ± 0.36	22.85 ± 3.11

TABLE 4. Correlation coefficients and regression equations (log-log) of four key parameters of the middle ear over RA in each of eight species of geckos

Ear parameter (log)	Species	n	R ² _{adjusted}	Model ^a	Slope	Slope <i>P</i>	Intercept	Intercept <i>P</i>
TMA	<i>Em</i>	10	0.983	0.0001	1.60	0.0001	-1.83	0.0001
	<i>Cm</i>	6	0.563	NS	0.93	NS	-0.76	NS
	<i>Om</i>	13	0.891	0.0001	1.37	0.0001	-1.53	0.0001
	<i>Or</i>	5	0.970	0.002	1.42	0.002	-1.79	0.006
	<i>Chm</i> (L)	8	0.676	0.012	1.96	0.012	-2.78	0.025
	<i>Cp</i>	8	0.112	NS	0.42	NS	-0.10	NS
	<i>Gp</i>	9	0.914	0.0001	1.6	0.0001	-2.0	0.0001
	<i>Gv</i>	6	0.107	NS	0.80	NS	-0.77	NS
FPA	<i>Em</i>	12	0.891	0.0001	0.89	0.0001	-1.93	0.0001
	<i>Cm</i>	6	0.538	NS	1.17	NS	-2.75	0.05
	<i>Om</i>	12	0.358	0.040	0.60	0.040	-1.57	0.009
	<i>Or</i>	5	0.622	NS	1.17	NS	-2.84	NS
	<i>Chm</i> (L)	8	0.606	0.023	1.20	0.023	-2.86	0.005
	<i>Cp</i>	9	0.709	0.004	2.34	0.004	-4.87	0.002
	<i>Gp</i>	9	0.277	NS	0.725	NS	-2.03	0.032
	<i>Gv</i>	7	0.010	NS	0.19	NS	-1.24	NS
ARa	<i>Em</i>	10	0.830	0.0001	0.65	0.0001	0.22	NS
	<i>Cm</i>	6	0.069	NS	-0.24	NS	2.00	NS
	<i>Om</i>	12	0.360	0.039	0.81	0.039	-0.004	NS
	<i>Or</i>	5	0.057	NS	0.26	NS	1.04	NS
	<i>Chm</i> (L)	8	0.154	NS	0.76	NS	0.09	NS
	<i>Cp</i>	8	0.638	0.017	-1.85	0.017	4.63	0.003
	<i>Gp</i>	9	0.278	NS	0.88	NS	0.02	NS
	<i>Gv</i>	6	0.243	NS	0.72	NS	0.30	NS
LRa	<i>Em</i>	12	0.095	NS	-0.09	NS	0.91	0.0001
	<i>Cm</i>	6	0.567	NS	1.39	NS	-1.86	NS
	<i>Om</i>	13	0.095	NS	0.20	NS	0.30	NS
	<i>Or</i>	5	0.140	NS	0.35	NS	0.18	NS
	<i>Chm</i> (L)	8	0.218	NS	0.64	NS	-0.40	NS
	<i>Cp</i>	9	0.348	NS	4.01	NS	-6.23	NS
	<i>Gp</i>	9	0.185	NS	0.36	NS	0.07	NS
	<i>Gv</i>	7	0.011	NS	0.21	NS	0.39	NS

^aThe significance of the complete regression equation.

slopes of the regressions over log HL and over log HW did not vary significantly, the pooled slopes being respectively 0.01 and 0.004. The intercepts of all three regressions did not significantly vary among the species.

Interspecific Variation: Evolutionary Allometry

The species averages of morphological data for adults of nine nominal species are included in Table 3. The interspecific allometric relations among the species averages

TABLE 5. Regression equations (log-log) and correlation coefficients of four key parameters of the middle ear (FPA, TMA, ARa, LRa) over three measures of body size (RA, HL, HW) among eight species of geckos based on their mean values (adults only)

Equation	R ²	Slope <i>P</i>	Intercept <i>P</i>	Model <i>P</i>
log (TMA) = 2.26 × log (RA) - 3.23	0.95	< 0.001	< 0.001	< 0.001
log (TMA) = 2.22 × log (HL) - 1.76	0.93	< 0.001	< 0.001	< 0.001
log (TMA) = 2.46 × log (HW) - 1.84	0.93	< 0.001	< 0.001	< 0.001
log (FPA) = 1.92 × log (RA) - 4.12	0.97	< 0.001	< 0.001	< 0.001
log (FPA) = 1.86 × log (HL) - 2.84	0.93	< 0.001	< 0.001	< 0.001
log (FPA) = 2.06 × log (HW) - 2.90	0.91	< 0.001	< 0.001	< 0.001
log (ARa) = 0.33 × log (RA) + 0.91	0.44	0.053	0.009	0.053
log (ARa) = 0.35 × log (HL) + 1.09	0.50	0.032	< 0.001	0.032
log (ARa) = 0.39 × log (HW) + 1.07	0.51	0.030	< 0.001	0.030
log (LRa) = 0.03 × log (RA) + 0.65	0.01	NS	0.010	NS
log (LRa) = 0.02 × log (HL) + 0.69	0.004	NS	0.001	NS
log (LRa) = 0.03 × log (HW) + 0.68	0.01	NS	0.001	NS

based on adults of the presumably functional middle-ear structures (TMA, FPA, ARa, LRa) to measures of animal size (RA, HL, HW) are expressed by the appropriate regressions listed in Table 5. Conspicuously, relative to all three measures of animal size, TMA shows the strongest positive allometry, and FPA shows more moderate positive allometry; in contrast, ARa shows negative allometry (the interspecific regression lines are included in Fig. 3). Finally, LRa presented no significant interspecific relationship with animal size.

Comparing Ontogenetic and Evolutionary Allometry

Finally, we compared the intraspecific (Table 4, showing only the RA-based formulas) and interspecific (Table 5) allometric formulas. For each of eight species and for each combination of one middle-ear structure (TMA, FPA, ARa, LRa) and one measure of animal size (RA, HL, HW), we tested whether the intraspecific regression (slope and intercept, Table 4) significantly differed from the equivalent interspecific regression (Table 5). Differences between intraspecific regressions and the equivalent interspecific regression were statistically significant only for two species. The slope of log FPA over log RA differed ($P = 0.05$) in *Em* and *Om*. The intercepts of the same function differed ($P = 0.01$) in the same two species and for *Em* the intercepts also differed ($P = 0.05$) for log TMA over log RA, and log FPA over log HL and over log HW. The comparison of intraspecific, ontogenetic, and interspecific, evolutionary, allometric growth is illustrated in Figure 3, where the intraspecific situation is represented by one species, *Em*.

DISCUSSION

Morphology

Our examination of the middle ears of 84 specimens, representing 9 or 10 species of seven genera belonging to three gekkonomorph subfamilies (Table 1), reconfirms the basic structure of the gecko (and saurian) middle ear (Figs. 1 and 2). Despite detailed descriptions of the reptilian middle-ear structure (Wever, 1978), more recent studies have offered inaccurate depictions of its organization. As a consequence, a clear appreciation of middle-ear function has suffered. For example, one description of the columella reports that it reaches all the way from the footplate to the inside of the tympanic membrane, imply-

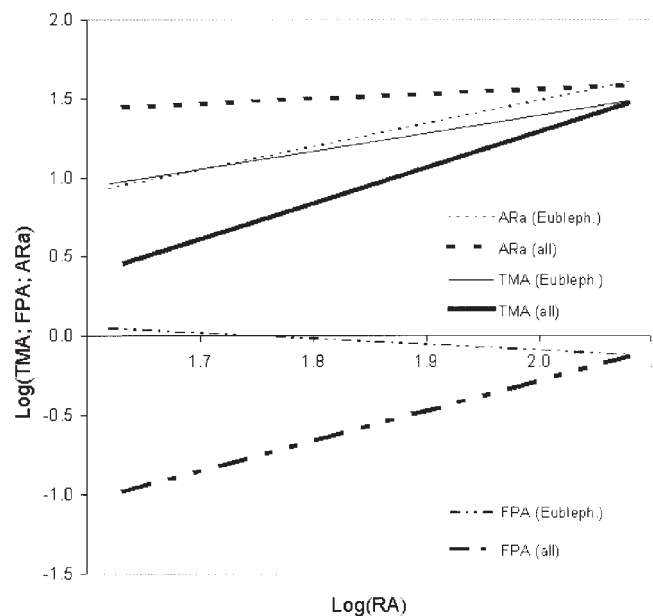


Fig. 3. Allometric growth curves (log-log regressions) of FPA, TMA, and ARa relative to RA, both within one species, *Eublepharis macularius* (light lines; data from Table 4), and, in comparison, among nine species (adults only), based on their species averages (heavy lines; from Table 5). Statistically significant are the slope and intercept of each of the six lines (excepting the intercept of ARa over RA, which is not) and also the differences between the two FPA-over-RA lines (slope and intercept) and the two TMA-over-RA lines (intercept only).

ing that it includes the cartilaginous extracolumellar shaft. This description restricts the term “extracolumella” to the inferior and superior processes anchoring the columella complex to the TM (Manley, 1990: Fig. 3.2a). Fortunately, this error did not mislead this author’s analysis of middle-ear function since he discovered bending of the inferior process at high stimulus frequencies (Manley, 1972, 1990). Nevertheless, the erroneous description of the extracolumella seems to have led others to conclude incorrectly that the extracolumellar shaft was bending (Werner, 2003). In addition, Lombard and Hetherington (1993: Fig. 6:18) depict the posterior process as continuing opposite the inferior process, but without reaching the rim

of the TM, and do not depict a superior process. This error resulted in a scheme for sound conduction that excluded the well-documented mechanical leverage of the conductive apparatus (Wever and Werner, 1970; Wever, 1978; Manley, 1990). The illustration of the middle-ear apparatus in Lombard and Hetherington (1993) helped generate the conclusion that "the precise lever arrangement and movements of the ossicular chain of nonmammalian tetrapods is therefore not totally understood." Incidentally, this conclusion also ignores the evidence of Lombard and Bolt (1979) that amphibians and sauropsidians have separately evolved different middle ears [supported in Werner (2003)].

Directional Asymmetry

The search for directional asymmetry, i.e., structural differences in the middle ear between the left and right sides, was motivated by three issues, additional to the functional asymmetry in man, mentioned above. These issues were that, one, minor but significant directional asymmetry in assorted body parts is quite frequent in geckos (Werner et al., 1991) and other lizards (Seligmann, 1997; Seligmann et al., 2003). Two, asymmetry of the external ears has evolved several times in owls and assists in three-dimensional sound localization (Norberg, 1977; Volman, 1994). Scansorial geckos also operate in a three-dimensional world, and especially the nocturnal species, such as all those used here, often communicate vocally (Werner et al., 1991; Frankenberg and Werner, 1992). Three, first reports already document directional asymmetry in the diameter of the external ear opening in *Ptyodactylus* (Werner et al., 1991) and in the area of the tympanic membrane in *Gekko* (Werner et al., 1997). Unfortunately, in our material in most specimens one ear had been damaged by the physiological examination and the scant data available revealed no significant directional asymmetry. Nevertheless, the results of Werner et al. (1991, 1997) suggest that this issue warrants further investigation.

Sexual Dimorphism

The question of sexual dimorphism in the middle ear arises from two considerations. One, the dependence of the ear's function on its absolute size (Schwartzkopff, 1957) raises questions for species with sexual size dimorphism. According to Fitch (1981), in 60% of the 43 gecko taxa examined, the female was larger than the male, average female length (without tail) being up to 115% of average male length, while in 31% of the taxa the female was smaller than the male, down to 84% of male length. The question these observations raise is whether or not the smaller sex has a proportionately smaller TM and perhaps poorer hearing ability? Alternatively, if the TM is of the same absolute size, is it accommodated in a relatively larger head, or do the ears take up more space in the head? Two, to the extent that geckos employ vocal communication (Frankenberg and Werner, 1992; Werner et al., 2001) as do frogs, one could expect a matching of the TM's size and resonant frequency to the dominant frequency of the voice of the other sex, as has been reported in frogs (Tandy and Keith, 1972).

The token evidence for sexual differences that we found (Table 2 and the few differences in allometric equations listed in the text) is supported by the sexual difference in

columellar length found by Werner et al. (1997) in *Gekko* and the sexual difference in the rate of ossification of the columellar footplate found by Ruiz de la Concha et al. (1999). Together, these observations indicate that the subject warrants further investigation. We do not know of similar data in birds, and Nummela (1995b) has commented that there are no proper data about sexual dimorphism in ossicle size in mammals.

Ontogenetic Allometry

Our present finding, beyond what could be shown by Werner and Igić (2002), that %CART greatly decreased during ontogeny in the eublepharine *Em* and the diplodactyline *Om*, and apparently in the gekkonine *Gp* (Table 3), has been qualitatively confirmed for the gekkonine *Tarentola mauritanica* by Ruiz de la Concha et al. (1999).

Some of the variation in ontogenetic allometric slopes that we encountered between species may well be due to the fact that the range of body sizes varied among species. Overall, our results confirm the recent discovery that in gekkonomorph lizards the middle-ear's hydraulic ratio ontogenetically increases with animal size (Werner et al., 1998), though the allometry is negative. This differs from the situation reported in the alligator lizard, in which ARA was independent of body size during growth (Rosowski et al., 1988). As to comparative data from other amniotes, the avian middle ear generally resembles the saurian middle ear (Manley, 1990), and its ontogenetic allometry resembles that in geckos. In small samples of chicks (*Gallus domesticus*), Schwartzkopff (1957) found that between hatching and adulthood the absolute sizes of TMA and FPA increased, their relative sizes decreased, and the ARA grew from 11 to 22. Schwartzkopff's observations on ducklings (*Anas platyrhynchos*) suggested the same trend. The more detailed work of Cohen et al. (1992b) confirmed that in the chick the ontogenetic growth rates of FPA and TMA lead to a doubling of ARA.

For mammals, whose middle-ear morphology differs greatly from that of the lizard, the evidence is uncertain. According to Schwartzkopff (1957), in white mice that grew from 6.5 to 33 g, the TMA and FPA increased moderately, their relative size decreased, and ARA remained stable at 24. In contrast, Huangfu and Saunders (1983) reported that the TMA (pars tensa) of C57BL/6J mice increased during development from 0.72 to 2.72 mm², while the oval window area grew from 0.036 to 0.083 mm², implying a moderate increase in the ARA from 20 to 32.8. Similarly, Cohen et al. (1992a) showed that the TMA (pars tensa) increased during development in Mongolian gerbils, from 6.35 to 16.9 mm², and FPA expanded from 0.51 to 0.80 mm², yielding a growth of ARA from 12.45 to 21.1. Finally, Zimmer et al. (1994) examined Long Evans rats at ages 1, 3, 6, 12, 16, 22, 34, 60, and 80 days after birth. During ontogeny, TMA (pars tensa) increased from 5.3 on day 1 to 8.9 mm² on day 80. At the same time, the area of the oval window expanded from 0.24 to 0.35 mm², indicating that the area ratio increased from 17 to 24. Interestingly, the area ratio attained 90% of the adult value already by postnatal day 8. This observation demonstrated the need for standardized temporal points of reference when comparing ontogenies among species.

Evolutionary Allometry

At the interspecific level among adults of different size, our results (Fig. 3) confirm the earlier report that in rep-

tiles, or at least in gekkonomorph lizards, ARA increases moderately but consistently with animal size (Werner and Igić, 2002). This occurs despite the negative allometry of the middle ear relative to body or head size and is very different from the situation among birds and among mammals. In a series of 47 bird species represented by adults ranging in body mass from 8 to 8,730 g, an interspecific comparison found that while TMA and FPA increased with body mass, their relative sizes decreased with increasing body mass (Schwartzkopff, 1955, 1957). Thus, ARA was mass-independent. Although ARA ranged from 15 to 40 (with the majority of birds between 20 and 30), most of this variation was between taxonomic groups, with the minimum occurring in waterfowl and the maximum in owls. The same author summarized mammalian middle-ear data of eight species ranging in mass from mouse to elephant. As in birds, although TMA and FPA increased with body mass, their relative sizes decreased with increasing body mass and ARA was independent of body mass, ranging in adults from 19 to 34 (Schwartzkopff, 1957). In a larger series of 63 mammalian species, with a range of skull mass spanning six orders of magnitude, the proportions among middle-ear parts were isometric, producing similar amplification and impedance matching, even though middle-ear size was negatively allometric to animal size (Hemila et al., 1995; Nummela, 1995a, 1997). In 35 of 36 mammal species for which both TMA and FPA were available (Nummela, 1995b), ARA was between 15.2 (chimpanzee) and 43.2 (hedgehog) without any correlation to size. Only the shrew was exceptional with a ratio of 4.3; it must be mentioned, however, that Henson (1974) had stated that ARA ranged in different mammals from 14 to 60, but this was not linked to animal size.

From a functional and ecological point of view, it seems reasonable that larger species should possess somewhat greater area ratios, with an accompanying greater sensitivity of hearing (Werner et al., 1998). This assumption is based on the fact that in nature the individuals of larger species are more widely spaced (Wynne-Edwards, 1962) and thus communicate across longer distances. Good hearing would facilitate that communication. It seems surprising that, at least in terms of ARA, the principle that the ear of larger animals is adapted to receiving sound over greater distances is realized in geckos but not in birds and mammals. Further, the fact that this principle is realized in geckos, the most vocal of lizards, leaves the question open concerning what happens among less vocal reptiles, especially in view of the difference at the ontogenetic level between geckos and the alligator lizard noted above.

Comparing Intra- and Interspecific Allometry

Our general finding for geckos, that increases in body size are accompanied by increases in the ARA by negative allometry for both intraspecific and interspecific comparisons, was expected. The function of the ear depends on its absolute size and internal proportions (Schwartzkopff, 1957). Based on functional considerations, the gecko middle ear would appear similarly oversized in young individuals and in small species. Nevertheless, in our data, some few specific growth curves significantly differed between the intraspecific and interspecific levels. Because those two species in which this difference was significant (*Em* and *Om*) were the only ones with a wide range of body sizes (due to the planned inclusion of juvenile specimens),

morphological difference between intra- and interspecific size series may actually be the rule. While no similar comparative analysis of intra- and interspecific allometry of the middle ear seems to be available for birds or mammals, nevertheless from the data quoted above, the situation is clear. In those two groups, while intraspecifically ARA depends on size, interspecifically it does not. To what extent the situation in geckos is unique to them or, more probably, typical of lizards and perhaps reptiles in general remains to be seen.

The varying internal proportion of the columellar system (i.e., the phenomenon that %CART is greater in the smaller animals) occurs in parallel both intraspecifically (herein) and interspecifically (Werner and Igić, 2002), though the data were inadequate for mathematical comparison. The functional aspect of this was partly discussed by Werner and Igić (2002).

Evolution

Our findings have several evolutionary implications. First, at least for some middle-ear components, in at least some species, the intraspecific allometric growth curves significantly deviate from the comparable interspecific allometric growth curves derived from comparing adults of the different species. Hence, when middle-ear proportions vary among gecko species, not all of this variation can be explained as an allometric consequence of the variation in body size. Rather, part of this variation is due to specific selection pressures. These pressures could relate to auditory function, to other requirements of cranial anatomy, or both. In either case, this is evidence that in geckos some evolutionary radiation of middle-ear proportions has occurred at the species (or genus) level, below the family level.

Second, this last observation is of interest for the following reason. Thus far, the comparative study of middle-ear morphology in lizards has acknowledged variation at four levels. One, the well-known middle-ear differences among the classes of tetrapod vertebrates (Amphibia, Reptilia, Aves, Mammalia). Two, the less well-known but profound differences among the reptilian orders or suborders (Testudines, Crocodilia, Rhynchocephalia, Lacertilia, Serpentes, Amphisbaenia). Three, the almost esoteric structural differences among the families of the Lacertilia. For example, unlike in geckos, in iguanid lizards the middle of the columellar chain is anchored sideways to the quadrate bone by an internal process. Four, obvious structural-functional adaptations in genera within families, for example, the closure of the external ear aperture in burrowing scincid lizards (Wever, 1978). Now our evidence shows for the first time subtle changes in middle-ear proportions within a family, demonstrating the gradualness of the evolutionary process.

Third, we have seen that among gecko species (adults), the ratio of the tympanic membrane area to the columellar footplate area increases with body size. This is different from the situation in birds and mammals, in which this ratio varies taxonomically but not with body size.

The fact that the evolutionary strategy for middle ear functional adaptation differs between the gekkonomorphs (and perhaps all lizards) on the one hand, and mammals on the other hand, seems to agree with the notion that the middle ear has evolved separately and differently in the two groups (Lombard and Bolt, 1979; Maier, 1990). But the fact that in this respect the birds, which also have a

columella middle ear, resemble the mammals rather than the geckos means that the situation should be examined in other reptile groups in order to determine the generality of the phenomenon. This is necessary to avoid evolutionary speculation.

Fourth, in either case, on this background it is noteworthy that in both apparent lines of middle-ear evolution (the saurian and the mammalian), and also in the third independent line, the anuran (Werner, 2003), middle-ear gain is in part achieved by the combination of at least two types of levers, the hydraulic (increasing the pressure) and the mechanical (increasing the force). This parallelism probably means that this combination is efficient, relative to other solutions, and that it was similarly available in the evolution of these groups thanks to their similar genetic infrastructure.

CONCLUSIONS

Different reports notwithstanding, the middle-ear ossicular chain of geckos (gekkonomorph lizards) is indeed structured as described by E.G. Wever and associates. Although in this study no directional asymmetry of middle-ear structures could be shown, and sexual dimorphism was barely indicated, both questions warrant further examination.

In geckos, the ratio of the tympanic membrane area to the columellar footplate area increases during postnatal ontogeny, and in this they resemble the birds and very probably also the mammals.

Among gecko species (represented by adults), the ratio of the tympanic membrane area to the columellar footplate area increases moderately but significantly with body size; in this they differ from birds and mammals, within which groups this ratio varies taxonomically but not with body size.

In geckos, the allometric growth of the ratio of the columellar footplate area to body length differs between the intraspecific and interspecific levels. This shows that at least to some extent species differences in the middle ear do not merely result from animal size. Rather, middle-ear proportions have undergone some evolutionary radiation within the group.

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