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- vironments of Kansas. W. C. Johnson (ed.). Kansas Geol. Surv. Guidebook Ser. 5.
- . 1988a. Systematics of the *Notropis zonatus* species group, with description of a new species from the Interior Highlands of North America. *Copeia* 1988:153–173.
- . 1988b. Vicariance biogeography, parsimony, and evolution in North American freshwater fishes. *Syst. Zool.* 37:329–355.
- . 1989. Phylogenetic studies of North American minnows, with emphasis on the genus *Cyprinella* (Teleostei: Cypriniformes). Misc. Publ. 80:1–189, Publ. Mus., Univ. Kansas Mus. Nat. History, Lawrence.
- , AND C. R. GILBERT. 1989. *Notropis ludibundus* (Girard) and *Notropis tristis* (Girard), replacement names for *N. stramineus* (Cope) and *N. topeka* (Gilbert) (Teleostei: Cypriniformes). *Copeia* 1989:1084–1089.
- RITOSSA, F. M., AND S. SPIEGELMAN. 1965. Localization of DNA complementary to ribosomal RNA in the nucleolus organizer region of *Drosophila melanogaster*. *Proc. Natl. Acad. Sci. U.S.A.* 53:737–745.
- STOCK, A. D., AND T. D. BUNCH. 1982. The evolutionary implications of chromosome banding pattern homologies in the bird order Galliformes. *Cytogenet. Cell Genet.* 34:136–148.
- SUMNER, A. T. 1977. Banding as a level of chromosome organization, p. 17–22. *In*: Current chromosome research. K. Jones and P. E. Brandham (eds.). Elsevier/North-Holland Biomedical Press, Amsterdam, The Netherlands.
- WATROUS, L. E., AND Q. D. WHEELER. 1981. The out-group comparison method of character analysis. *Syst. Zool.* 30:1–11.
- DEPARTMENT OF WILDLIFE AND FISHERIES SCIENCES, TEXAS A&M UNIVERSITY, COLLEGE STATION, TEXAS 77843. PRESENT ADDRESS (PKP): SOUTHWEST FOUNDATION FOR BIOMEDICAL RESEARCH, 7620 NW LOOP 410, SAN ANTONIO, TEXAS 78227–5301. Accepted 6 March 1991.

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## Effects of Body Mass and Temperature on Standard Metabolic Rates for Two Australian Varanid Lizards (*Varanus gouldii* and *V. panoptes*)

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Standard metabolic rates (SMR) for two varanid lizards (*Varanus gouldii* and *V. panoptes*) were measured from 2400 and 0800 h, after the lizards had rested for at least 8 h. The relationship between SMR ( $\dot{V}O_2$ ; ml/h) and body mass for varanids at 20 C is  $0.04 \text{ g}^{0.95}$ ; at 30 C,  $0.030 \text{ g}^{1.15}$ ; at 35 C,  $0.089 \text{ g}^{1.05}$  and at 40 C,  $0.144 \text{ g}^{1.04}$ . The relationship between SMR ( $\dot{V}CO_2$ ; ml/h) and body mass at 20 C is  $0.017 \text{ g}^{1.04}$ ; at 30 C,  $0.028 \text{ g}^{1.12}$ ; at 35 C,  $0.045 \text{ g}^{1.10}$  and at 40 C,  $0.107 \text{ g}^{1.04}$ . There were no significant differences in the mass exponent between species at any temperature (20–40 C), with the pooled slope for *V. gouldii* of 1.12, for *V. panoptes* 1.10, and an overall pooled slope of 1.11. No plateau in  $\dot{V}O_2$  was found between the  $T_b$  of 30–40 C as previously reported for *V. gouldii* and *V. rosenbergi*.

LARGER lizards consume more oxygen than smaller lizards but less oxygen per gram body mass (see reviews of Bennett and Dawson 1976, and Bennett 1982). The allometric relationship between standard metabolic rate (SMR, ml  $O_2$ /h) and body mass (M; g) is  $SMR = aM^b$ , where  $a$  is the mass coefficient (SMR of a 1 g lizard) and  $b$  is the mass exponent (slope of a double logarithmic plot of SMR and M).

The relationship for mass-specific metabolic rate (e.g., ml  $O_2 \text{ g}^{-1} \text{ h}^{-1}$ ) is  $SMR/M = aM^{b-1}$ .

Andrews and Pough (1985) report the mean mass exponent ( $b$ ) of the multiple regression equation for 107 species of squamates as 0.80 ( $\pm SE \text{ } b = 0.012$ ). They also report no difference in the mass exponent ( $P < 0.05$ ) between Varanidae (the family with the highest mean SMR) and Boidae (the family with the lowest SMR).

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The mean intraspecific mass exponent for 17 species was 0.67.

Bennett (1972) reported that the SMR ( $\dot{V}O_2$ ) was independent of body temperature ( $T_b$ ) from 30–40 C for *V. gouldii* and *V. rosenbergi*, whereas Earll (1982) reported a linear semilogarithmic relationship between  $\dot{V}O_2$  and  $T_b$  for *V. bengalensis* from 20–40 C.

The objectives of this study were to (1) compare the inter- and intraspecies relationship of SMR to body mass for two species of varanids (*Varanus gouldii* and *V. panoptes*) over a wide range in mass; (2) compare the interspecies allometry of SMR for *Varanus* with that of other lizards; and (3) examine the effect of  $T_b$  on SMR and determine whether SMR was "essentially independent of  $T_b$  between 30 and 40 C" as reported by Bennett (1972) for *V. gouldii* and *V. rosenbergi*.

#### MATERIALS AND METHODS

Seven *V. gouldii* (20–555 g) and 12 *V. panoptes rubridus* (227–3480 g) were collected under license from various locations in Western Australia and maintained at the University of Western Australia either in outdoor pens under natural photoperiod or indoors in cages with incandescent lighting for 12 h/day. The varanids were fed raw meat, live mice, or freshly killed mice. Water was provided at all times. Animals were fasted for at least 48 h prior to the measurement of metabolic rates. The SMR ( $\dot{V}O_2$ ) and carbon dioxide production ( $\dot{V}CO_2$ ) were determined only once for each lizard at each temperature, although not all individuals were measured at all temperatures.

Oxygen consumption rate ( $\dot{V}O_2$ ; ml  $O_2$ /h) and carbon dioxide production rate ( $\dot{V}CO_2$ ; ml  $CO_2$ /h) were measured using a flow-through respirometry system. The lizards were placed in opaque plastic cylinders that restricted but did not prevent voluntary activity. These cylinders were placed in a controlled temperature chamber at 20 C, 30 C, 35 C, and 40 C. Compressed air (<4 mg water/l) was passed through the chamber at a flow rate (25–400 ml/min) that was adjusted according to the size of the lizard so that the excurrent  $O_2$  content was about 20.1%. The temperature of the air in the chamber ( $T_a$ , C) was constantly measured with a chromel-alumel thermocouple. Cloacal temperatures ( $T_b$ , C) of the varanids were taken at the end of the measurement period to ensure that  $T_a$  and  $T_b$  were essentially the same. Excurrent

air was dried with a silica gel column before passing through one channel of a paramagnetic oxygen analyzer (Servomex 184A) and a  $CO_2$  analyzer (Hereus-Leybold Binos). The differential output of the oxygen analyzer (ambient air-excurrent air) and the analog outputs of the  $CO_2$  analyzer and thermocouple were connected via a multiplexer to a digital microvolt multimeter (Keithley 177). The BCD output of the multimeter was interfaced to a microcomputer (Commodore 128 and Schneider 641F22 VIA board) that monitored ambient temperature and excurrent  $O_2$  and  $CO_2$  content. The microcomputer calculated STPD  $\dot{V}O_2$  and  $\dot{V}CO_2$  every 60 sec for 16–20 h periods, commencing between 0800 and 1400 h. The lizards were at their lowest  $\dot{V}O_2$  level for the period from 2400–0800 h. The analog outputs of the  $O_2$  and  $CO_2$  analyzers were averaged for 25 consecutive values over about 40 sec to calculate a  $\dot{V}O_2$  and  $\dot{V}CO_2$  each 60 sec; the 60 sec values were stored on disk for subsequent analysis. The  $\dot{V}O_2$  and  $\dot{V}CO_2$  were calculated after Withers (1977). The minimum (i.e., standard)  $\dot{V}O_2$  and  $\dot{V}CO_2$  were calculated as the average for the longest continuous period of low  $\dot{V}O_2$  (normally 20–100 min). This ensured that the calculated value was SMR, and not affected by brief periods of activity, or transiently low  $\dot{V}O_2$  or  $\dot{V}CO_2$  values that were occasionally observed, presumably due to short apneic periods.

The difference in SMR between species and temperatures was tested by two-factor ANOVA (unequal sample sizes; Statview Software). The difference between the regression equations for the two species was tested by ANCOVA and Tukey Q test (Zar, 1984).

#### RESULTS

*Minimum metabolic rates.*—Most lizards needed at least 8 h to reach minimal levels of  $\dot{V}O_2$  and  $\dot{V}CO_2$ , and some required up to 16 h before minimal  $\dot{V}O_2$  and  $\dot{V}CO_2$  were attained. In many instances, there was a spontaneous increase in  $\dot{V}O_2$  and  $\dot{V}CO_2$  at about dawn, presumably reflecting a circadian rhythm in activity, hence metabolic rate. The mean minimal SMR values for each species at each  $T_a$  investigated are summarized in Table 1.

There was no significant difference in SMR between the two species at any  $T_a$ 's (two-factor ANOVA;  $P = 0.24$  for species), but there was a highly significant temperature effect ( $P < 0.0001$ ); there was no significant interaction ef-

**TABLE 1.** MASS-SPECIFIC STANDARD METABOLIC RATE ( $\dot{V}O_2$  AND  $\dot{V}CO_2$ ; ml g<sup>-1</sup> h<sup>-1</sup>) AT VARIOUS AMBIENT TEMPERATURES FOR TWO SPECIES OF VARANIDS. Values are mean,  $\pm$ SE with the sample size (n).

T <sub>a</sub> C	Mass (g)	$\dot{V}O_2$	$\dot{V}CO_2$	n
<i>V. gouldii</i>				
19.7	76.9 $\pm$ 35.7	0.0382 $\pm$ 0.0061	0.0225 $\pm$ 0.004	4
30.7	169.0 $\pm$ 67.3	0.0678 $\pm$ 0.0156	0.0527 $\pm$ 0.010	5
35.5	154.6 $\pm$ 49.4	0.1232 $\pm$ 0.0147	0.0743 $\pm$ 0.006	7
40.0	179.1 $\pm$ 81.1	0.1677 $\pm$ 0.0173	0.1318 $\pm$ 0.017	6
<i>V. panoptes</i>				
20.5	2005 $\pm$ 338	0.0274 $\pm$ 0.0025	0.0232 $\pm$ 0.002	12
30.6	2003 $\pm$ 383	0.0889 $\pm$ 0.0060	0.0679 $\pm$ 0.005	10
35.3	1427 $\pm$ 375	0.1200 $\pm$ 0.0149	0.0930 $\pm$ 0.010	7
40.0	799 $\pm$ 308	0.2057 $\pm$ 0.0411	0.1588 $\pm$ 0.033	3

fect ( $P = 0.298$ ). There was a significant difference in  $\dot{V}CO_2$  between the two species of varanids (two-factor ANOVA;  $P = 0.037$ ), a highly significant effect of temperature on  $\dot{V}CO_2$  ( $P = 0.0001$ ), and no significant species-temperature interaction ( $P = 0.65$ ).

There was no significant difference in respiratory quotient (RQ) for the varanid species (two-factor ANOVA;  $P = 0.058$ ) or any difference at any of the temperatures ( $P = 0.378$ ). There was a significant interaction effect for RQ with species and temperature ( $P = 0.028$ ).

**Relationship between standard metabolic rate and body mass.**—There was a consistently high correlation between  $\log_{10} \dot{V}CO_2$  ( $r > 0.975$ ) and  $\log_{10} \dot{V}O_2$  ( $r > 0.980$ ) with  $\log_{10}$  body mass for the absolute SMR of the two species at all of the temperatures investigated (Table 2). There were not any significant differences in the slope of the allometric  $\dot{V}O_2$  relationships for either species at any temperature (ANCOVA; slope F-test is n.s.). The pooled slope was 1.12 for *V. gouldii* and 1.10 for *V. panoptes*; the overall pooled slope was 1.11. The slope ( $b$ ) of the regression equations for oxygen consumption rate (ml/h) at 20 C, 35 C, and 40 C are not significantly different from 1.0, but are significantly different from 0.75 and 0; the slope  $b$  at 30 C was significantly different from 1.0, 0.75, and 0 (Table 2).

Similarly, there was no significant difference in the slope of the allometric relationship for  $\dot{V}CO_2$  and the two species at varying  $T_a$  (ANCOVA slope F-test is n.s.). The common slope was 1.10. The slope values at 20 C, 30 C, and 40 C are not significantly different from 1.0, but were significantly different from 0.75 and

0; the slope ( $b$ ) at 35 C was significantly different from 1.0, 0.75, and 0 (Table 2).

**Relationship between mass-specific standard metabolic rate and body temperature.**—There was a significant positive semilogarithmic correlation ( $r = 0.98$ ) for mass-specific  $\dot{V}O_2$  (ml g<sup>-1</sup> h<sup>-1</sup>) with  $T_a$  for the two species examined (Fig. 1). In the range from 20–40 C, there was a significant difference between the slopes of the regression equations for SMR (ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) of *V. gouldii* and *V. panoptes* (Fig. 1, ANCOVA slope F-test  $P < 0.05$ ) but not between elevations ( $P > 0.05$ ).

There was a significant positive semilogarithmic correlation ( $r = 0.89$ ) for mass specific  $\dot{V}CO_2$  (ml CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) with  $T_a$  for the two species. In the  $T_a$ 's range of 20–40 C, there was no significant difference between the slope for the regression equations (ANCOVA slope test is n.s.; common slope 0.041); there was a significant difference in elevation (intercept test  $P < 0.05$ ).

The relationships between the mass-specific SMR ( $\dot{V}O_2$  and  $\dot{V}CO_2$ ) and  $T_a$  for the two species are best represented by the following equations: for *V. gouldii*,  $\log_{10} \dot{V}CO_2$  (ml g<sup>-1</sup> h<sup>-1</sup>) =  $-2.43 (\pm 0.139) + 0.037 (\pm 0.0042) T_b$ , ( $r = 0.89$ ;  $n = 22$ ), and  $\log_{10} \dot{V}O_2$  (ml g<sup>-1</sup> h<sup>-1</sup>) =  $-2.13 (\pm 0.17) + 0.033 (\pm 0.005) T_b$ , ( $r = 0.83$ ;  $n = 22$ ); for *V. panoptes*,  $\log_{10} \dot{V}CO_2$  (ml g<sup>-1</sup> h<sup>-1</sup>) =  $-2.53 (\pm 0.0972) + 0.043 (\pm 0.0033) T_b$ , ( $r = 0.92$ ;  $n = 32$ ), and  $\log_{10} \dot{V}O_2$  (ml g<sup>-1</sup> h<sup>-1</sup>) =  $-2.49 (\pm 0.096) + 0.045 (\pm 0.003) T_b$ , ( $r = 0.93$ ;  $n = 32$ ; intercept and slope values are mean  $\pm$ SE). The  $Q_{10}$  values determined from the average  $\dot{V}O_2$  values were for *V. gouldii*, 1.68 between 20 C and 30 C and 2.64 between 30 C and 40 C; for *V. panoptes*, 3.21 between 20 C and 30 C and 2.44 between 30 C and 40 C.  $Q_{10}$ 's for the

TABLE 2. RELATIONSHIP BETWEEN  $\log_{10} \dot{V}\text{CO}_2$  AND  $\log_{10} \dot{V}\text{O}_2$  (ml/h) WITH  $\log_{10}$  BODY MASS (g) AT 20 C, 30 C, 35 C, AND 40 C FOR COMBINED DATA FOR *Varanus gouldii* AND *V. panoptes*; EQUATIONS ARE OF THE FORM  $\log_{10} \dot{V}\text{CO}_2 = a + b \log_{10} \text{Mass}$ . Values are  $a \pm \text{SE}$  and  $b \pm \text{SE}$  from the regression equation, with the correlation coefficient ( $r$ ) and sample size in parentheses. Body masses as in Table 1.

		$\dot{V}\text{CO}_2$	$\dot{V}\text{O}_2$
20 C	$a$	$-1.77 \pm 0.156$	$-1.40 \pm 0.15$
	$b$	$1.039 \pm 0.053^{a,b}$	$0.948 \pm 0.051^{a,b}$
	$r$	0.982 (16)	0.980 (16)
30 C	$a$	$-1.55 \pm 0.075$	$-1.52 \pm 0.15$
	$b$	$1.118 \pm 0.0472^{a,b}$	$1.146 \pm 0.052^{a,b,c}$
	$r$	0.988 (15)	0.987 (15)
35 C	$a$	$-1.35 \pm 0.10$	$-1.05 \pm 0.15$
	$b$	$1.102 \pm 0.039^{a,b,c}$	$1.05 \pm 0.059^{a,b}$
	$r$	0.992 (14)	0.982 (14)
40 C	$a$	$-0.97 \pm 0.21$	$-0.84 \pm 0.108$
	$b$	$1.042 \pm 0.088^{a,b}$	$1.037 \pm 0.075^{a,b}$
	$r$	0.976 (9)	0.982 (9)

<sup>a</sup> Slope is significantly different from 0.0 ( $P < 0.05$ ).  
<sup>b</sup> Slope is significantly different from 0.75 ( $P < 0.05$ ).  
<sup>c</sup> Slope is significantly different from 1.00 ( $P < 0.05$ ).

two species between 20 C and 30 C were 2.64 and between 30 C and 40 C, 2.32.

*Relationship between metabolism, body mass, and temperature.*—The multiple regression equations that predict SMR for the two species examined using the independent variables of body mass and  $T_a$  are given in Table 3.

# DISCUSSION

The diurnal pattern of  $\dot{V}\text{O}_2$  reported by Wood et al. (1978) for *V. exanthematicus* was apparent for many of the varanids examined in this study, with the lowest levels of  $\dot{V}\text{O}_2$  and  $\dot{V}\text{CO}_2$  most often recorded from 2400–0800 h. Only these minimal values of  $\dot{V}\text{O}_2$  and  $\dot{V}\text{CO}_2$  are considered here to be the SMR. Consequently, these values are expected perhaps to be lower than SMRs reported in other studies using less stringent methodology (e.g., closed respirometry) or selection of minimal values. Nevertheless the mass-specific SMR of *V. panoptes* and *V. gouldii* at 20 C (Table 1) are similar to or slightly higher than resting values reported by Bartholomew and Tucker (1964), Bennett (1972), and SMR values reported by Earll (1982) for other large varanids. At 35 C, the SMR for the species stud-

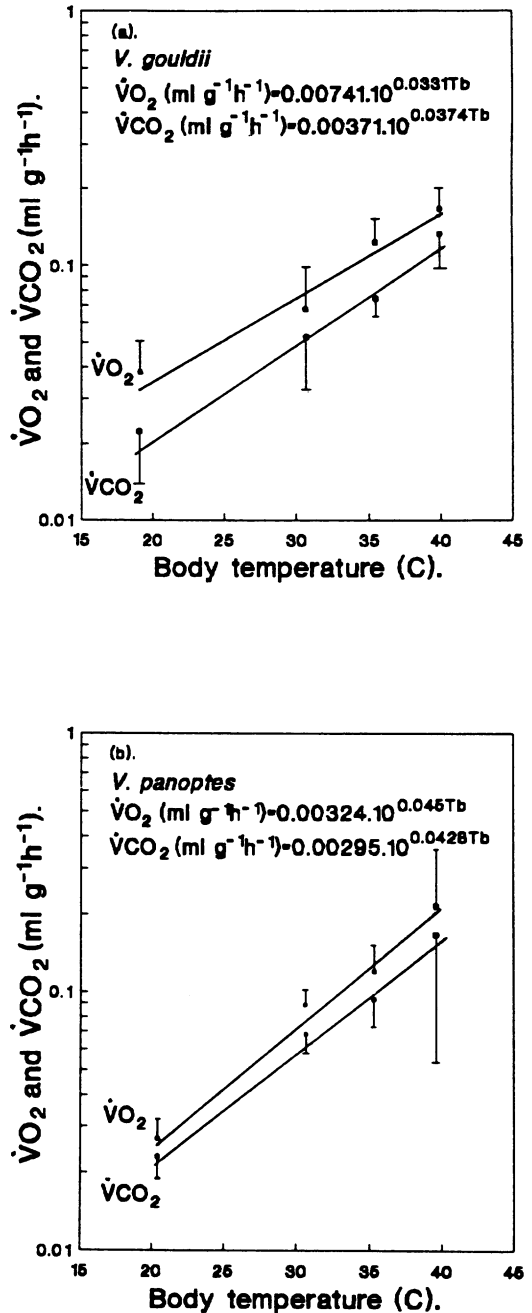


Fig. 1. Oxygen consumption and carbon dioxide production for *Varanus gouldii* (a) and *V. panoptes* (b). Means and two standard errors shown.

ied here are similar to resting values reported by Bennett (1972) for *V. gouldii* and *V. rosenbergi* and SMR values reported by Wood et al. (1977a, 1977b) for *V. exanthematicus* but are lower than

TABLE 3. RELATIONSHIP BETWEEN  $\dot{V}\text{CO}_2$  AND  $\dot{V}\text{O}_2$  (ml/h), BODY MASS (M) AND  $T_b$  FROM 20–40 C FOR *Varanus gouldii* AND *V. panoptes*. Equations are in the form of  $\log_{10} \text{SMR} = a + b \log_{10} \text{mass} + c T_b$ , with the correlation coefficient (r) and number of observations in parentheses.

	a	b	c	r (n)
<i>V. gouldii</i>				
$\dot{V}\text{O}_2$	$-2.30 \pm 0.2014$	$1.11 \pm 0.0777$	$0.0317 \pm 0.004947$	0.97 (7)
$\dot{V}\text{CO}_2$	$-2.62 \pm 0.1617$	$1.12 \pm 0.06239$	$0.0358 \pm 0.003972$	0.97 (7)
<i>V. panoptes</i>				
$\dot{V}\text{O}_2$	$-2.89 \pm 0.2267$	$1.11 \pm 0.05904$	$0.0466 \pm 0.003202$	0.97 (12)
$\dot{V}\text{CO}_2$	$-2.81 \pm 0.2381$	$1.08 \pm 0.06201$	$0.0439 \pm 0.003363$	0.96 (12)
Combined data				
$\dot{V}\text{O}_2$	$-2.47 \pm 0.1304$	$1.04 \pm 0.02931$	$0.0408 \pm 0.002807$	0.98 (19)
$\dot{V}\text{CO}_2$	$-2.70 \pm 0.1148$	$1.07 \pm 0.02581$	$0.0409 \pm 0.002471$	0.99 (19)

the resting values reported by Bartholomew and Tucker (1964) for four species of Australian varanids, by Louw et al. (1976) for *V. albigularius*, by Mitchell et al. (1981) for *V. exanthematicus*, and by Gleeson (1981) for *V. salvator*.

$\dot{V}\text{CO}_2$  has been less frequently reported than  $\dot{V}\text{O}_2$  for varanids. The results of this study concur closely with those reported by Wood et al. (1977a, 1977b) for *V. exanthematicus* but are lower than those reported by Gleeson (1981) for *V. salvator*, by Mitchell et al. (1981) for *V. exanthematicus*, and by Mitchell and Gleeson (1985) for *V. salvator* at 35 C.

The RQ varied between 0.63 and 0.83 for *V. gouldii* over the  $T_a$  range of 20–40 C; it was relatively more constant with the range of 0.76–0.84 for *V. panoptes*. These values are within the range reported for other lizards (Bennett and Dawson, 1976) and other varanids [0.68 at 35 C by Mitchell et al. (1981), 0.63 at 25 and 35 C by Mitchell and Gleeson (1985), and 0.73 at 35 C by Gleeson and Bennett (1982)].

**Intraspecific allometry.**—Wood et al. (1978) reported  $b$  values for *V. exanthematicus* of 0.57 at 25 C and 30 C and 0.51 at 35 C. The  $b$  values reported here for *V. gouldii* were consistently about 1.1 for each  $T_a$ ; the common  $b$  was 1.12. Similarly, the  $b$  values for *V. panoptes* were about 1.1 with a common  $b$  of 1.10. The  $b$  values for lizard species vary widely. Andrews and Pough (1985) calculated the mean intraspecific  $b$  value for 17 species examined as 0.67 but pointed out that the values ranged from 0.51–0.80. High  $b$  values are reported by Garland (1984) for *Ctenosaura similis* (0.858), Garland and Else (1987) for *Amphibolurus nuchalis* (0.83), and John-Al-

der (1984) for *Dipsosaurus dorsalis* (0.839), but the slope for both *V. gouldii* and *V. panoptes* at about 1, are unaccountably much higher than those reported for other lizards.

The intraspecific allometric analyses for  $\dot{V}\text{CO}_2$  of *V. gouldii* and *V. panoptes* yield similar conclusions. The scaling exponent  $b$  is about 1, rather than 0.67. Garland (1984) reports *Ctenosaura similis*  $\dot{V}\text{CO}_2$  scaling at 0.95.

**Interspecific allometry.**—There were some significant differences in  $\dot{V}\text{O}_2$  and  $\dot{V}\text{CO}_2$  values for *V. gouldii* and *V. panoptes* (e.g., mass-specific  $\dot{V}\text{CO}_2$  of *V. panoptes* was significantly different from that for *V. gouldii*), but there was no difference in the scaling exponent for  $\dot{V}\text{O}_2$  of the species ( $\bar{x} = 1.11$ ) or  $\dot{V}\text{CO}_2$  ( $\bar{x} = 1.10$ ). These  $b$  values are appreciably higher than those reported by Bartholomew and Tucker (1964) for four species of Australian varanids (0.82 at 30 C). They are also much higher than the mass exponent calculated for all lizards by Andrews and Pough (1985) of 0.80 (SE  $\pm$  0.012), values given by Bennett and Dawson (1976), and the value of 0.75 generally used to describe the relationship of SMR and body mass for different taxonomic groups (Blaxter, 1989).

The allometric equations at 35 C calculated by Wood et al. (1978) for *V. exanthematicus* (172–7500 g) and Andrews and Pough (1985) for all squamates are appreciably different from the data from this study (Fig. 2). The high  $b$  value for all varanids reported here (1.11) is due to the lower-than-expected SMR of the small *V. gouldii* and the higher-than-expected  $\dot{V}\text{O}_2$  of the large *V. panoptes* (Fig. 2). Such high  $b$  values are unusual but not without precedent. Galvao et



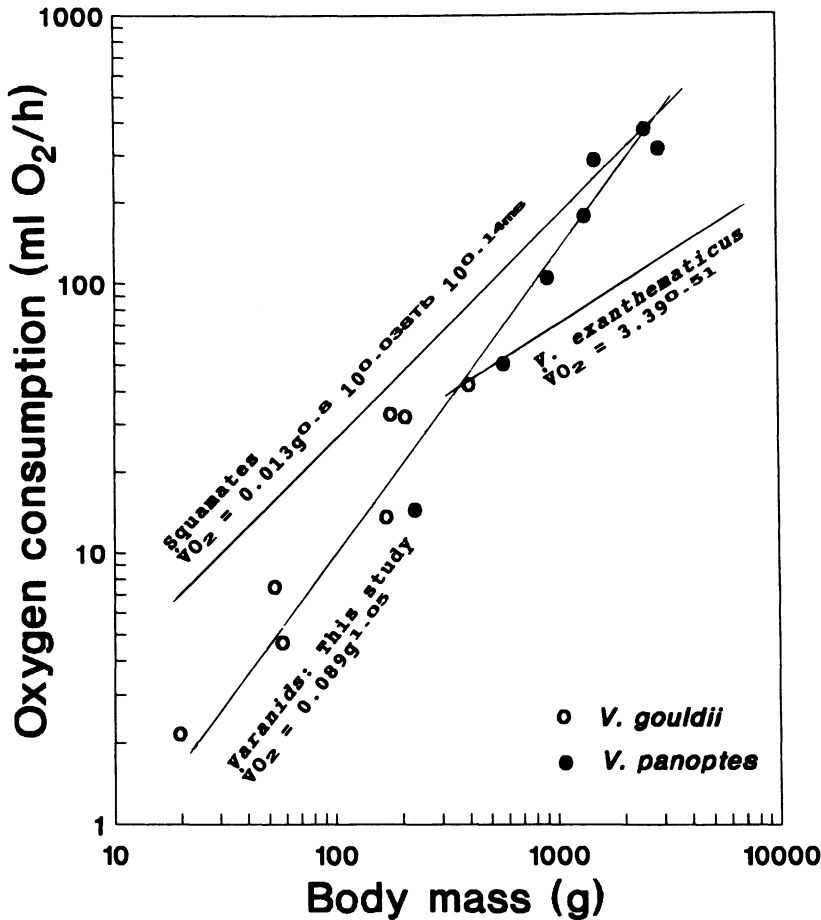


Fig. 2. The relationship of absolute oxygen consumption to body mass at 35 C for *Varanus exanthematicus* (Wood et al., 1978), all squamates (Andrews and Pough, 1985), and *V. gouldii* and *V. panoptes* in this study.

al. (1965) report a  $b$  value of 0.98 for Colubridae and 1.09 for Boidae at 21.5 C, and Huggins et al. (1971), a  $b$  value of 0.926 over a small mass range (191–382 g) for small caimans at a  $T_b$  of 24.5 C. It is interesting to note that Dryden et al. (1990) report a mass exponent of 1.10 for field metabolic rates of three species of varanids (*V. acanthurus*, *V. rosenbergi*, and *V. giganteus*; mass 60–7700 g) based on the compilation of data from four studies.

**Effect of  $T_b$  on metabolic rate.**—Body temperature ( $T_b$ ) has a profound effect on SMR, of the general form  $SMR = j 10^{k(T_b)}$ . Bartholomew and Tucker (1964) found that, for four species of Australian varanids (16–4400 g), the relationship between mass-specific  $\dot{V}O_2$  and  $T_b$  (20–40 C) was best represented by the equation:  $\dot{V}O_2$  ( $ml\ g^{-1}\ h^{-1}$ ) =  $0.00253\ 10^{0.518(T_b)}$ . Bennett (1972) reported that the overall relationship between

SMR and mass for *V. gouldii* and *V. rosenbergi* (139–1280 g) [ $\dot{V}O_2$  ( $ml\ g^{-1}\ h^{-1}$ ) =  $0.000147\ 10^{0.15(T_b) - 0.00195(T_b)^2}$ ] was linear for the semilogarithmic relationship between SMR and  $T_b$  from 15–30 C but that SMR was independent of  $T_b$  from 30–40 C. No evidence of a plateau effect for  $\dot{V}O_2$  as reported by Bennett (1972), or  $\dot{V}CO_2$ , was apparent between 30 C and 40 C for either of the two species of varanid studied here (Fig. 1). The value of  $k$  is 0.033 for  $\dot{V}O_2$  of *V. gouldii*, and 0.045 for  $\dot{V}O_2$  of *V. panoptes*; these  $k$  values are significantly different. For  $\dot{V}CO_2$ ,  $k = 0.037$  for *V. gouldii* and 0.043 for *V. panoptes*; these are not significantly different. Earll (1982) found a simple nonlogarithmic relationship between  $\dot{V}O_2$  and  $T_b$  for *V. bengalensis* between 20 C and 40 C, represented by the equation  $\dot{V}O_2$  ( $ml\ g^{-1}\ h^{-1}$ ) =  $0.00304T_b - 0.03612$  ( $n = 3$ ,  $r = 0.96$ ).

The  $Q_{10}$  generally declines with increasing  $T_b$  (from 20–40 C), but there are many exceptions

to this pattern of thermal dependence (Bennett and Dawson, 1976).  $Q_{10}$  values are similar at 2.6 and 2.3 for all varanids in this study, for  $T_b$ 's of 20–30 C and 30–40 C. Wood et al. (1977b) report a  $Q_{10}$  of 2.15 for *V. exanthematicus* between 25 C and 35 C, Bennett (1972) a  $Q_{10}$  of 1.07 between 35 C and 40 C for *V. gouldii*, Bartholomew and Tucker (1964) a  $Q_{10}$  of 3.30 between 20 C and 40 C for *V. gouldii*, and Earll (1982), reported  $Q_{10}$  values of 1.91 from 20–30 C; for *V. bengalensis* the reported  $Q_{10}$  values were 1.74 from 30–40 C and 1.82 from 20–40 C.

*Species comparisons.*—After extensively reviewing the data for  $\dot{V}O_2$  of lizards, Andrews and Pough (1985) gave the following general equation to predict the oxygen consumption rate of lizards, taking into account body temperature, body mass, and the lizards' metabolic state:  $\dot{V}O_2$  (ml/h) =  $0.013 \text{ g}^{0.80} 10^{0.038(T_b)} 10^{0.14(ms)}$  (where ms = metabolic state; 0 = standard, 1 = resting). The corresponding regression equations that predict SMR for the two species of varanid examined in this study have a different mass coefficient but similar temperature coefficient:  $\dot{V}O_2$  (ml/h) =  $0.00646 \text{ g}^{0.98} 10^{0.036(T_b)}$ ; and  $\dot{V}CO_2$  (ml/h) =  $0.00363 \text{ g}^{1.02} 10^{0.038(T_b)}$ . However, it should be kept in mind that these equations are only a generalization for the highly significant effects of body mass (80.4% of total variance) and temperature (15.9% of total variance) on metabolic allometry of varanid lizards; there are minor, though statistically significant, differences in allometry of SMR for the two species studied here.

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#### LITERATURE CITED

- ANDREWS, R. M., AND F. H. POUGH. 1985. Metabolism of squamate reptiles: allometric and ecological relationships. *Physiol. Zool.* 58:214–231.
- BARTHOLOMEW, G. A., AND V. A. TUCKER. 1964. Size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian varanid lizards. *Ibid.* 37:341–354.
- BENNETT, A. F. 1972. The effect of activity on oxygen consumption, oxygen debt, and heart rate in the lizards *Varanus gouldii* and *Sauromalus hispidus*. *J. Comp. Physiol.* 79:259–280.
- . 1982. The energetics of reptilian activity, p. 155–199. *In: Biology of the Reptilia.* C. Gans and F. H. Pough (eds.). Academic Press, London, England.
- , AND W. R. DAWSON. 1976. Metabolism, p. 127–223. *In: Biology of the Reptilia.* C. Gans and F. H. Pough (eds.). Academic Press, London, England.
- BLAXTER, K. 1989. Energy metabolism in animals and man. Cambridge Univ. Press, Cambridge, England.
- DRYDEN, G., B. GREEN, D. KING, AND J. LOSOS. 1990. Water and energy turnover in a small monitor lizard, *Varanus acanthurus*. *Aust. Wildl. Res.* 17:641–646.
- EARLL, C. R. 1982. Heating, cooling, and oxygen consumption rates in *Varanus bengalensis*. *Comp. Biochem. Physiol.* 72A:377–381.
- GALVAO, P. E., J. TARASANTCKI, AND P. GUERTZENSTEIN. 1965. Heat production of tropical snakes in relation to body weight and body surface. *Am. J. Physiol.* 209:501–506.
- GARLAND, T. 1984. Physiological correlates of locomotory performance in a lizard: an allometric approach. *Ibid.* 247:R806–R815.
- , AND P. E. ELSE. 1987. Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. *Ibid.* 252:R439–R449.
- GLEESON, T. T. 1981. Preferred body temperature, aerobic scope, and activity capacity in the monitor lizard, *Varanus saluator*. *Physiol. Zool.* 54:423–429.
- , AND A. F. BENNETT. 1982. Acid-base imbalance in lizards during activity and recovery. *J. Exp. Biol.* 98:439–453.
- HUGGINS, S. E., H. E. HOFF, AND M. E. VALENTINUZZI. 1971. Oxygen consumption of small caimans under basal conditions. *Physiol. Zool.* 44:40–47.
- JOHN-ALDER, H. B. 1984. Seasonal variations in activity, aerobic energetic capacities, and plasma thyroid hormones ( $T_3$  and  $T_4$ ) in an iguanid lizard. *J. Comp. Physiol. B* 154:409–419.
- LOUW, G. N., B. A. YOUNG, AND J. BLIGH. 1976. Effect of thyroxine and noradrenaline on thermoregulation, cardiac rate, and oxygen consumption in the monitor lizard, *Varanus albigularis albigularis*. *J. Therm. Biol.* 1:189–193.
- MITCHELL, G. S., AND T. T. GLEESON. 1985. Acid-base balance during lactic acid infusion in the lizard *Varanus saluator*. *Resp. Physiol.* 60:253–266.
- , ———, AND A. F. BENNETT. 1981. Ventilation and acid-base balance during graded activity in lizards. *Am. J. Physiol.* 240:R29–R37.
- WITHERS, P. C. 1977. Measurement of  $\dot{V}O_2$ ,  $\dot{V}CO_2$ , and evaporative water loss with a flow-through mask. *J. Appl. Physiol.* 42:120–123.
- WOOD, S. C., M. L. GLASS, AND K. JOHANSEN. 1977a.



- Effects of temperature on respiration and acid-base balance in a monitor lizard. *J. Comp. Physiol.* 116: 287–296.
- , K. JOHANSEN, AND R. N. GATZ. 1977b. Pulmonary blood flow, ventilation/perfusion ratio, and oxygen transport in a varanid lizard. *Am. J. Physiol.* 233:R89–R93.
- , ———, M. L. GLASS, AND G. M. O. MALOIY. 1978. Aerobic metabolism of the lizard *Varanus exanthematicus*: effects of activity, temperature, and size. *J. Comp. Physiol.* 127:331–336.
- ZAR, J. H. 1984. *Biostatistical analysis*, 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.
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## Monophyly and Relationships of the Argentinoid Fishes

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Evidence of monophyly and relationships of the Argentinoidei is provided, based on a phylogenetic analysis including aregentinoids, osmeroids, and other euteleosts. the Argentinoidei is monophyletic and is composed of two monophyletic clades, Argentinoidea and Alepocephaloidea. The evidence for monophyly of the Argentinoidei is largely drawn from anatomy of the branchial basket, and other potentially corroborating evidence is presented. The Argentinoidea is monophyletic. In this analysis, bathylagids are the sister taxon of opisthoproctids, argentinids the sister of these two. The Alepocephaloidea, usually composed of three to four families, is restricted here to a single family, Alepocephalidae. The highly derived Platytroctidae is more closely related to some alepocephalids than others, and is not recognized as a separate family. The monotypic Bathylaconidae, Bathypriionidae, and Leptochilichthyidae are not recognized, because doing so would both obscure the shared history of these taxa and render the Alepocephalidae paraphyletic.

The sister taxon of the Argentinoidei is the Osmeroidei. Together they comprise the Osmerae. Previous hypotheses have placed either the Salmonidae or the highly derived galaxioid *Lepidogalaxias* as the sister taxon of the Neoteleostei. It is hypothesized here that the Osmerae is the sister taxon of the Neoteleostei on the basis of two synapomorphies: presence of a postmaxillary process of the premaxilla and loss of laminar bone on the anterior margin of the hyomandibula. The relationships of other euteleostean clades to the Osmerae and Neoteleostei are as yet unresolved.

BEFORE 1971, the argentinoid and alepocephaloid fishes (sensu Greenwood et al., 1966) had not been grouped together. Both groups had instead been variously associated with clupeoid or even salmonid fishes. In 1971, Greenwood and Rosen first recognized what they believed to be evidence of common ancestry between argentinoids and alepocephaloids. This was drawn largely from a unique branchial structure, the crumenal organ. Located at the posterolateral portion of the branchial basket, the crumenal organ is an outpocketing of the posterior pharynx, supported by specialized branchial skeletal elements. Unlike other epi-

branchial organs (Nelson, 1967), the crumenal organ has a novel element: a so-called accessory cartilage that connects the fifth ceratobranchial to the fifth epibranchial (Nelson, 1967, fig. 1H; Greenwood and Rosen, 1971, figs. 1–6). Greenwood and Rosen (1971) also considered an “argentinoid” caudal skeleton to be diagnostic of the Argentinoidei, though only one alepocephaloid (*Searsia*) shares the condition. On the basis of this evidence, they erected the Argentinoidei to include the Argentinoidea and Alepocephaloidea.

Since that time, there has been no new evidence for the monophyly of the Argentinoidei