

I have observed young bullfrogs on the banks attempting to capture calling *A. crepitans*. Since snakes and bullfrogs use vision to aid their search for prey, the advantage goes to the satellites. A calling frog, with its vocal sac actively forced in and out, is much more conspicuous and catchable than a satellite that maintains a characteristic low posture around the calling male. While the two advantages are seemingly obvious, they are difficult to document.

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LITERATURE CITED

- BUCHER, T. L., M. J. RYAN AND G. A. BARTHOLOMEW. 1982. Oxygen consumption during resting, calling and nest building in the frog *Physalaemus pustulosus*. *Physiol. Zool.* 55:10–22.
- BURKETT, R. D. 1984. An ecological study of the cricket frog, *Acris crepitans*, p. 89–103. *In: Vertebrate ecology and systematics*. R. A. Siegel, L. E. Hunt, J. L. Knight, L. Malaret and N. L. Zuschlag (eds.). The University of Kansas, Lawrence, Kansas.
- CAPRANICA, R. R., L. S. FRISHKOFF AND E. NEVO. 1973. Encoding of geographic dialects in the auditory system of the cricket frog. *Science* 187:1272–1275.
- FORESTER, D. C., AND D. V. LYKENS. 1986. Significance of satellite males in a population of spring peepers (*Hyla crucifer*). *Copeia* 1986(3):719–724.
- GERHARDT, H. C. 1975. Sound pressure levels and radiation patterns of the vocalizations of some North American frogs and toads. *J. Com. Physiol.* 102:1–12.
- . 1982. Sound pattern recognition in some North American treefrogs (Anura: Hylidae): implications for mate choice. *Amer. Zool.* 22:581–595.
- HOWARD, R. D. 1978. The evolution of mating strategies in Bull frogs, *Rana catesbeiana*. *Evolution* 32:850–871.
- MIYAMOTO, M. M., AND J. H. CANE. 1980. Behavioral observations of noncalling males Costa Rican *Hyla ebraccata*. *Biotropica* 12:225–227.
- NEVO, E., AND R. R. CAPRANICA. 1985. Evolutionary origin of ethological reproductive isolation in cricket frogs, *Acris*, p. 147–214. *In: Evolutionary biology*, Vol. 19. M. K. Hecht, B. Wallace and G. T. Prance (eds.). Plenum Press, New York, New York.
- PERRILL, S. A. 1984. Male mating behavior in *Hyla regilla*. *Copeia* 1984:727–732.
- , H. C. GERHARDT, AND R. DANIEL. 1978. Sexual parasitism in the green tree frog (*Hyla cinerea*). *Science* 200:1179–1180.
- , ———, AND R. E. DANIEL. 1982. Mating strategy shifts in male green treefrogs (*Hyla cinerea*): an experimental study. *Anim. Behav.* 30:43–48.
- PYBURN, W. F. 1958. Size and movements of a local population of cricket frogs (*Acris crepitans*). *Texas J. Sci.* 10:325–342.
- ROBLE, S. M. 1985. Observations on satellite males in *Hyla chrysocelis*, *Hyla picta*, and *Pseudacris triseriata*. *J. Herpetol.* 19:432–436.
- RYAN, M. J. 1980. Female choice in a neotropical frog. *Science* 204:523–525.
- TAIGEN, T. L., AND K. D. WELLS. 1985. Energetics of vocalization by an anuran amphibian (*Hyla versicolor*). *J. Comp. Physiol.* 155:163–170.
- WELLS, K. D. 1977. Territoriality and male mating success in the green frog (*Rana clamitans*). *Ecology* 58:750–762.

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SEX DETERMINATION IS INDEPENDENT OF INCUBATION TEMPERATURE IN ANOTHER CHELID TURTLE, *CHELODINA LONGICOLLIS*.—It is now well established that sex determination in many turtle species is strongly influenced by environmental conditions prevailing during incubation, particularly temperature but also the water potential of the incubation medium (see Bull and Vogt, 1979; Bull, 1980, 1983). Environmental sex determination (ESD) has been demonstrated for species in the families Carettochelydidae (Webb et al., 1986), Cheloniidae (Yntema and Mrosovsky, 1980; Miller and Limpus, 1981; McCoy et al., 1983), Chelydridae (Yntema, 1976), Dermochelidae (Mrosovsky in pers. comm. with Standora and Spotila, 1985), Emydidae (Pieau, 1975; Bull and Vogt, 1979, 1981), Kinosternidae (Vogt et al., 1982), Pelomedusidae (Alho et al., 1984, 1985) and Testudinidae (Pieau, 1971). The mechanisms by which temperature influences sex determination in reptiles are unknown. Its influence may be direct via one of

the mechanisms proposed by Standora and Spotila (1985) or indirect if embryonic developmental and metabolic rates are implicated (Webb and Smith, 1984). Heritable factors are also involved (Bull et al., 1982), but whether the sex ratio itself is heritable is not certain because many factors under maternal influence (egg size, shell porosity) may confound experiments to demonstrate heritability of sex ratios (Webb and Smith, 1984).

Although widespread, not all species of turtle exhibit ESD. Three species that possess heteromorphic sex chromosomes (Bull et al., 1974; Sites et al., 1979; Carr and Bickham, 1981) are assumed to have genotypic sex determination and four species without heteromorphic sex chromosomes lack ESD (Vogt and Bull, 1982; Bull et al., 1985; Thompson, 1988). The latter four species include the Australian chelid turtles *Emydura macquarii* and *E. signata*. With the possible exception of *Platemys radiolata* (McBee et al., 1985), all turtles in the family Chelidae lack heteromorphic chromosomes (Bull and Legler, 1980). The present study was designed to investigate the effects of incubation temperature on sex determination of *C. longicollis*, a species belonging to a second major monophyletic group within the Australian Chelidae (Burbidge et al., 1974).

Materials and methods.—Eggs of *C. longicollis* were obtained from nests laid adjacent to a pond at Gungahlin in the Australian Capital Territory. The site was searched thoroughly for signs of nesting following rain, and at least twice a week, in the final quarter of 1984. Thirteen nests were opened in Nov. and Dec. yielding 123 eggs, and a further two clutches, each of eight eggs, were obtained by hormonal induction (Ewert and Legler, 1978). All eggs were measured (+/-0.1 mm) and weighed (+/-0.1 g) immediately after collection. The length of the opaque patch that develops early in incubation (Thompson, 1985) was also measured parallel to the long axis of the egg. Twenty-two eggs of known age were incubated at 30 C to establish a developmental series and to establish a relationship between length of the opaque patch and duration of incubation. One egg from each nest was opened, fixed in 20% formalin, and its embryo later compared to the 30 C developmental series for an age determination. A second estimate of age was obtained for each clutch using the relationship between length of the opaque patch and age at 30 C. Most clutches were con-

sidered to have a 30 C age of 0–3 d and all were less than 1 wk old when collected.

One hundred eggs were systematically allocated to incubators set at 24, 26, 28, 30, 32 C so that an equal number of eggs from each clutch was incubated at each temperature. Any eggs remaining were spread evenly between the more extreme temperatures, with the sole remaining egg (if present) excluded from the experiment. Five eggs failed to begin development, as indicated by the lack of an opaque patch, and were discarded. The eggs were incubated on a fixed quantity of moist vermiculite in plastic bags. The moisture content of the vermiculite (4 g water per 3 g vermiculite) was monitored at weekly intervals and kept constant but humidity in the bags was not measured. Temperatures (+/-0.1 C) in close proximity to the eggs were recorded twice per day.

Hatchlings were weighed (+/-0.1 g) after yolk internalization and killed by intracranial injection of absolute alcohol. The hatchlings were dissected and the urinogenital system examined. In particular, the condition of the paramesonephric duct (Mullerian duct) was scored as absent (0), very fine and visible at the anterior of the kidney only (1), fine but visible for the entire length of the kidney (2), or prominent (3). The right gonad, kidney, and associated ducts were removed, embedded in wax, sectioned, and dyed with haematoxylin and eosin. The sex of each gonad was determined by examination under a light microscope.

Data from 27 hatchlings from a preliminary experiment, that was terminated because of excessive mortalities, were included in the analysis where indicated. They were not included in the statistical tests of the effects of temperature on sex determination because of the possibility of differential mortality between the sexes.

Results.—There was a clear association between hatchling sex, as determined histologically, and condition of the paramesonephric duct ($\chi^2 = 89.1$, $df = 3$, $P \ll 0.001$; Table 1). The duct was generally absent in males or if present it tended to be very fine. In females the paramesonephric duct was usually very prominent. A probability analysis revealed that if Class 0 and 1 hatchlings of Table 1 were classified as males, Class 2 hatchlings as of unknown sex, and Class 3 hatchlings as females, then the probability of making a correct assessment of the sex of *C. longicollis* based on the condition of the paramesonephric duct alone would range be-

TABLE 1. A CROSSTABULATION OF SEX VS CONDITION OF THE PARAMESONEPHRIC DUCT. Data from the preliminary study are included.

Class	Description	Male	Female	Indeterminate
0	No duct visible	31	0	0
1	Very fine duct, readily visible at anterior of kidney only	8	0	0
2	Fine duct for full length of kidney	6	3	1
3	Prominent duct	2	55	0
—	Sexed by duct alone	4	1	0

tween 83.0% and 94.7%, depending on the actual sex ratio of hatchlings examined. If in addition, the sexes of Class 2 hatchlings were determined histologically, then the procedure would have been between 95.7% and 100% reliable. Thus in future studies of sex determination of chelid turtles, it will not be necessary to section all gonads.

There was no significant association between hatchling sex ratio and the temperature prevailing during incubation ($\chi^2 = 3.52$, $df = 4$, $P > 0.05$; Table 2). Pooling the data across temperatures yielded a sex ratio of male : female = 35:51 which, although suggestive of a bias towards females, was not statistically significant ($\chi^2 = 1.31$, $df = 1$, $P > 0.05$). Including the data from the 27 hatchlings in the preliminary study only served to strengthen these conclusions.

Discussion.—Hatchling sex ratios of *C. longicollis*, like those of *E. macquarii* and *E. signata*, are independent of incubation temperature. This conclusion should be viewed in the context of studies in which temperature-dependent sex determination has been demonstrated. Such studies have generally revealed that most incubation temperatures produce only males or only females, with a narrow range of temperatures producing both sexes (Bull, 1983). It is therefore highly unlikely that failure to demonstrate an effect of incubation temperature on sex in the present study and those of Bull et al. (1985) and Thompson (1988), is the result of inadequate sample sizes.

Many populations of cryptodiran turtles are reported to have unequal adult sex ratios, especially ratios in favor of females (Bury, 1979; Table 5). This bias has been traditionally explained in terms of selective sampling (Gibbons, 1970), but in some species the preponderance of females may result from biased hatchling sex ratios under the influence of incubation temperature (Vogt, 1980). Many populations of Australian freshwater turtle have skewed adult sex ratios (Table 3), not only *Carettochelys insculpta* which has ESD (Webb et al., 1986). Of the three chelid species shown to be without ESD, *Chelodina longicollis* and *E. macquarii* have skewed adult sex ratios whereas *E. signata* (Macleay River) does not. Examination of hatchling sex ratios from field nests would seem warranted, to confirm the results of the laboratory experiments, but this has been done only for one nest of *E. victoriae* (McKinlay River, N.T.). The sex ratio was six females to four males, not sig-

TABLE 2. A SUMMARY OF THE RESULTS OF THE INCUBATION TRIALS. The five eggs that failed to begin development are not included.

Nominal incubation temperature C	Mean incubation temperature (\pm SD)	Initial no. of eggs	Incubation period in days (\pm SE)	Unsexed mortalities	Sexed mortalities	Males	Females
24	23.89 (\pm 0.39)	25	108.3 (\pm 1.60)	5	1	7	13
26	25.86 (\pm 0.52)	13	81.6 (\pm 0.72)	2	1	4	7
28	28.12 (\pm 0.16)	13	77.8 (\pm 0.72)	0	0	4	9
30	29.97 (\pm 0.29)	18	70.8 (\pm 0.96)	1	0	6	11
32	31.86 (\pm 0.44)	27	67.6 (\pm 1.04)	1	5	14	11

TABLE 3. SEX RATIOS IN NATURAL POPULATIONS OF AUSTRALIAN FRESHWATER TURTLES. Abbreviations: T, trapped; H, hand capture with a dip net or by muddling; D, hand capture with the aid of mask and fins; S, seine netting; ns, not significant; M, males; F, females; ACT, Australian Capital Territory; NSW, New South Wales; NT, Northern Territory; Qld, Queensland; SA, South Australia.

Species	Location	Capture method	M	F	Sig. level	Source
Family Chelidae						
<i>Chelodina longicollis</i>	Laurendale, New England Tableland, NSW	H, T, D, S	86	60	$P < 0.05$	Parmenter, 1976
	Lake McKenzie, Jervis Bay Territory, ACT	T	43	82	$P < 0.001$	Rod Kennett, unpubl. data
	Lake Windermere, Jervis Bay Territory, ACT	D	73	87	n.s.	Rod Kennett, unpubl. data
	Ryan's Swamp, Jervis Bay Territory, ACT	T	49	51	n.s.	Rod Kennett, unpubl. data
<i>Elseya dentata</i>	Edith Falls, Daly Drainage, NT	D	6	5	n.s.	Present study
<i>Elseya latisternum</i>	Tweed River, NSW	D	13	7	n.s.	Present study
<i>Elseya</i> sp.	Barnard River, NSW	D	10	9	n.s.	Present study
	Bellingen River, NSW	D	17	8	n.s.	Present study
<i>Emydura krefftii</i>	Coomboo Lake, Fraser Island, Qld.	T	153	142	n.s.	Georges, 1982
	Gray's Waterhole, Burnett River, Qld.	T	74	42	$P < 0.005$	Georges & Hamley, unpubl. data
	Jones' Weir, Burnett River, Qld.	T	15	30	$P < 0.05$	Georges & Hamley, unpubl. data
<i>Emydura macquarii</i>	Lake Bonney, SA	H, T, S	69	125	$P < 0.001$	Thompson, 1978
<i>Emydura signata</i>	Brisbane region, Qld.	T	63	48	n.s.	Georges & Hamley, unpubl. data
	Tweed River, NSW	D	25	7	$P < 0.005$	Present study
	Richmond River, NSW	D	6	5	n.s.	Present study
	Clarence River, NSW	D	11	6	n.s.	Present study
	Macleay River, NSW	D	17	17	n.s.	Present study
	Hastings River, NSW	D	13	11	n.s.	Present study
	Jasper Gorge, Victoria Drainage, NT	T	4	4	n.s.	Present study
<i>Emydura</i> sp.	Waterhouse Creek, Roper Drainage, NT	T	8	9	n.s.	Present study
<i>Emydura</i> sp.	Cooper Creek, SA	T	46	137	$P < 0.001$	Thompson, 1983
<i>Pseudemydura umbrina</i>	SW. Western Australia	H	35	28	n.s.	Burbidge, 1981
Family Carettochelydidae						
<i>Carettochelys insculpta</i>	Ooloo Crossing, Daly River, NT	D, H	35	57	$P < 0.05$	Linda Heaphy, unpubl. data

nificantly different from 1:1 (Smith and Wood, 1985).

The conflict between data on adult sex ratios and data from laboratory experiments on chelid sex determination may be artificial. Estimates of adult sex ratio might not adequately reflect hatchling sex ratios because of differential mortality of males and females, or because males and females differ in their susceptibility to cap-

ture, or because of difficulties in precisely identifying the range of ages included in each of the categories 'mature male' and 'mature female.' Hence, skewed adult sex ratios may be poor evidence of skewed hatchling sex ratios. However, in one intensive study (*E. krefftii*; Georges, 1982), a test for trapping bias was possible. The sex ratio of captures (mature males:mature females = 702:683) was not significantly different

from the sex ratio of individuals (153:142) ($\chi^2 = 0.1$, $df = 1$, $P > 0.05$), so trapping was not biased toward either sex. In this population the sex ratio was not significantly different from 1:1 ($\chi^2 = 0.41$, $df = 1$, $P > 0.05$).

The evolutionary history of sex determination for turtles is obscure, in part because the vast majority of studies have been of turtles within a single sub-order, the Cryptodira. Cryptodiran turtles exhibit the full ambit of sex determining mechanisms—species with heteromorphic sex chromosomes, species with genetic control of sex but without heteromorphic sex chromosomes and species with ESD. Most cryptodiran turtles fall into the last category, so it is possible that ESD is the ancestral state, and that genotypic sex determination evolved independently in a few lineages. Heteromorphic sex chromosomes are regarded as of recent and independent origin among the turtles that possess them (Bull, 1980; Carr and Bickham, 1981). Alternatively, genotypic sex determination may be the ancestral state for these turtles, having been retained in the distantly related *Trionyx spiniferus* and *Clemmys insculpta* (Vogt and Bull, 1982; Bull et al., 1985), developed further but independently with the advent of heteromorphic sex chromosomes in *Staurotypus* and *Siebenrockiella* (Bull et al., 1974; Sites et al., 1979; Carr and Bickham, 1981), but replaced in most lineages by ESD. If the Pleurodira are taken as an outgroup to the Cryptodira, the demonstration of genotypic sex determination in chelid turtles lends support to this latter alternative, but the support is considerably weakened by the discovery of ESD in *Podocnemis expansa* (Pleurodira: Pelomedusidae) (Alho et al., 1984, 1985).

The broader view, which takes crocodilians and lizards as an outgroup to turtles, is hampered by lack of knowledge of the mechanisms underlying ESD. Higher incubation temperatures produce males in most crocodilians and in lizards with ESD (Charnier, 1966; Ferguson and Joanen, 1983; Hutton, 1987) and females in turtles with ESD. One interpretation is that ESD may have independent origins in the three groups (Thompson, 1988) with the mechanisms operating in crocodilians and lizards fundamentally different from that operating in turtles. However, Webb and Smith (1984) demonstrated two thresholds for sex determination in *Crocodylus johnstoni*, with females produced at high and low temperatures as in some turtles (Yntema, 1976; Vogt et al., 1982; Wilhoft et al., 1983). They suggest that the potential to

produce females at high and low incubation temperatures is present in all reptiles with ESD, and governed by a single mechanism. Temperature related constraints on embryo survival may have eliminated low-temperature female turtles and high-temperature female crocodilians and lizards. A single mechanism operating in crocodilians, lizards, and turtles would lend strong support to the case for ESD as the ancestral state for turtles.

Evolution of genotypic sex determination from ESD and ESD from genotypic sex determination are both theoretically possible (Bull, 1981, 1983). However, the matter of the ancestry of sex determination in turtles is unlikely to be resolved until more species in the sub-order Pleurodira are examined for ESD, and until the mechanisms underlying ESD are identified and compared across major monophyletic lineages.

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LITERATURE CITED

- ALHO, C. J. R., T. M. S. DANNI AND L. F. M. PADUA. 1984. Influencia da temperatura de incubacao do sexo da tartaruga da Amazonia *Podocnemis expansa* (Testudinata: Pelomedusidae). *Rev. Brazil. Biol.* 44: 305–311.
- , ——— AND ———. 1985. Temperature-dependent sex determination in *Podocnemis expansa* (Testudinata: Pelomedusidae). *Biotropica* 17:75–78.
- BULL, J. J. 1980. Sex determination in reptiles. *Quart. Rev. Biol.* 55:3–21.
- . 1981. Evolution of environmental sex determination from genotypic sex determination. *Hereditas* 47:173–184.
- . 1983. Evolution of sex determining mechanisms. Benjamin-Cummings Publ. Co., Inc., United Kingdom.
- , R. H. MOON AND J. M. LEGLER. 1974. Male heterogamety in kinosternid turtles (genus *Staurotypus*). *Cytogenet. Cell Genet.* 13:419–425.
- , AND R. C. VOGT. 1979. Temperature-dependent sex determination in sea turtles. *Science* 206:1186–1188.

- , AND J. M. LEGLER. 1980. Karyotypes of side-necked turtles (Testudines: Pleurodira). *Can. J. Zool.* 58:828–841.
- , AND R. C. VOGT. 1981. Temperature-sensitive periods of sex determination in emydid turtles. *J. Exp. Zool.* 218:435–440.
- , AND M. G. BULMER. 1982. Heritability of sex ratio in turtles with environmental sex determination. *Evolution* 36:333–341.
- , J. M. LEGLER AND R. C. VOGT. 1985. Non-temperature dependent sex determination in two suborders of turtles. *Copeia* 1985:784–786.
- BURBIDGE, A. A. 1981. The ecology of the western swamp tortoise *Pseudemadura umbrina* (Testudines: Chelidae). *Aust. Wildl. Res.* 8:203–223.
- , J. A. W. KIRSCH AND A. R. MAIN. 1974. Relationships within the Chelidae (Testudines: Pleurodira) of Australia and New Guinea. *Copeia* 1974:392–409.
- BURY, R. B. 1979. Population ecology of freshwater turtles, p. 571–602. *In: Turtles: perspectives and research.* M. Harless and H. Morlock (eds.). John Wiley & Sons, New York, New York.
- CARR, J. L., AND J. W. BICKHAM. 1981. Sex chromosomes in the Asian black pond turtle, *Siebenrockiella crassicolis* (Testudines: Emydidae). *Cytogenet. Cell Genet.* 31:178–183.
- CHARNIER, M. 1966. Action de la temperature sur la sex-ratio chez l'embryon d'*Agama agama* (Agamidae, Lacertiliens). *Soc. Biolog. de L'ouest Africain* 160:620–622.
- EWERT, M. A. AND J. M. LEGLER. 1978. Hormonal induction of oviposition in turtles. *Herpetologica* 34:314–318.
- FERGUSON, M. J. W., AND T. JOANEN. 1983. Temperature-dependent sex determination in *Alligator mississippiensis*. *J. Zool., London* 200:143–177.
- GEORGES, A. 1982. Ecological studies of Krefft's river tortoise, *Emydura krefftii* (Gray), from Fraser Island, Queensland. Unpubl. Ph.D. dissert., University of Queensland, Brisbane, Queensland, Australia.
- GIBBONS, J. W. 1970. Sex ratio in turtles. *Res. Popul. Ecol.* 12:252–254.
- HUTTON, J. M. 1987. Incubation temperatures, sex ratios and sex determination in a population of Nile crocodiles (*Crocodylus niloticus*). *J. Zool. (Lond.)* 211:143–155.
- MCBEE, K., J. W. BICKHAM, A. G. J. RHODIN AND R. A. MITTERMEIER. 1985. Karyotypic variation in the Genus *Platymys* (Testudines: Pleurodira). *Copeia* 1985:445–449.
- MCCOY, C. J., R. C. VOGT AND E. J. CENSKY. 1983. Temperature-controlled sex determination in the sea turtle *Lepidochelys olivacea*. *J. Herpetol.* 17:404–406.
- MILLER, J. D., AND C. J. LIMPUS. 1981. Incubation period and sexual differentiation in the Green Turtle *Chelonia midas* L., p. 66–73. *In: Proceedings of the Melbourne Herpetological Symposium.* C. B. Banks and A. A. Martin (eds.). 19–21 May 1980. Royal Melbourne Zoological Gardens, Melbourne, Victoria. Zoological Board of Victoria, Melbourne, Victoria, Australia.
- PARMENTER, C. J. 1976. The natural history of the Australian freshwater turtle *Chelodina longicollis* Shaw (Testudinata, Chelidae). Unpubl. Ph.D. dissert., University of New England, Armidale, New South Wales, Australia.
- PIEAU, C. 1971. Sur la proportion sexuelle chez les embryons de deux Cheloniens (*Testudo graeca* L. et *Emys orbicularis* L.) issus d'oeufs incubés artificiellement. *C.R. Acad. Sci., Paris* 271D:3071–3074.
- . 1975. Temperature and sex differentiation of two chelonians, *Emys orbicularis* L. and *Testudo graeca* L., p. 332–39. *In: Intersexuality in the animal kingdom.* C. Reinboth (ed.). Springer-Verlag, Berlin, West Germany.
- SITES, J. W. JR., J. W. BICKHAM AND M. W. HAIKUK. 1979. A derived X chromosome in the turtle genus *Staurotypus*. *Science* 206:1410–1412.
- SMITH, A. M. A., AND T. C. WOOD. 1985. A nest and hatchlings of *Emydura victoriae* (Gray 1842). *Northern Territory Nat.* 1985(8):3–4.
- STANDORA, E. A., AND J. R. SPOTILA. 1985. Temperature dependent sex determination in sea turtles. *Copeia* 1985:711–722.
- THOMPSON, M. B. 1983. Populations of the Murray River tortoise, *Emydura* (Chelodina): the effect of egg predation by the red fox *Vulpes vulpes*. *Aust. Wildl. Res.* 10:363–371.
- . 1985. Functional significance of the opaque white patch in eggs of *Emydura macquarii*, p. 387–395. *In: Biology of Australasian frogs and reptiles.* G. Grigg, R. Shine and H. Ehmann (eds.). Royal Society of New South Wales, Sydney, New South Wales, Australia.
- . 1988. Influence of incubation temperature and water potential on sex determination in *Emydura macquarii* (Testudines: Pleurodira). *Herpetologica* 44(1). In press.
- VOGT, R. C. 1980. Natural history of the map turtles *Graptemys pseudogeographica* and *G. ouachitensis* in Wisconsin. *Tulane Stud. Zool. Bot.* 22:17–48.
- , AND J. J. BULL. 1982. Genetic sex determination in the spiny softshell *Trionyx spiniferus* (Testudines: Trionychidae) (?). *Copeia* 1982:699–700.
- , AND C. J. MCCOY AND T. W. HOUSEAL. 1982. Incubation temperature influences sex-determination in kinosternid turtles. *Ibid.* 1982:480–482.
- WEBB, G. J. W., AND A. M. A. SMITH. 1984. Sex ratio and survivorship in the Australian freshwater crocodile *Crocodylus johnstoni*. *Symp. Zool. Soc. Lond.* 52:319–355.
- , D. CHOQUENOT AND P. J. WHITEHEAD. 1986. Nests, eggs and embryonic development of *Carettochelys insculpta* (Chelonia: Carettochelyidae) from northern Australia. *J. Zool. (Lond.)* 1B:521–550.
- WILHOFT, D. C., E. HOTALING AND P. FRANKS. 1983. Effects of temperature on sex determination in embryos of the snapping turtle, *Chelydra serpentina*. *J. Herpetol.* 17:38–42.

YNTEMA, C. L. 1976. Effects of incubation temperature on sexual differentiation in the turtle, *Chelydra serpentina*. J. Morphol. 150:453-462.

_____, AND N. MROSOVSKY. 1980. Sexual differentiation in hatchling loggerheads (*Caretta caretta*) incubated at different controlled temperatures. Herpetologica 36:33-36.

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LITHODYTES CINEREUS COPE, 1885, A NEGLECTED JUNIOR SYNONYM OF ELEUTHERODACTYLUS FENESTRATUS (STEINDACHNER), 1864 (AMPHIBIA: LEPIDODACTYLIDAE).—The discovery of an old and forgotten name potentially threatens existing stability. Cope (1885), and a footnote at the end of a paper reporting herpetological finds from Peru, reported on the contents of a small collection from western Brasil. Cope (1885:103) merely listed six species from the Rio Purus, but he named the seventh as *Lithodytes cinereus*. Cope made no comparisons of *L. cinereus* with other species and his description was typically brief for the era. Insofar as I have been able to determine, the name was mentioned only twice after its original publication. The obscurity of the name is probably a result of George Boulenger's failure to mention it in the 1886 Zoological Record (Boulenger, 1886).

Dunn (1949:20) reported a specimen (ANSP 14735) of the microhylid frog, *Ctenophryne geayi*, as bearing a paper label containing the notes of "Upper Purus R., Steer, type of *Lithodytes cinereus* Cope." Dunn denied that the specimen was the type of *L. cinereus* because "... the specimen does not in any way agree with the type description of the *Lithodytes* . . ." ANSP 14735 is a juvenile female 41.8 mm in snout-vent length (SVL). The third citation of the name was by Malnate (1971:350) who reported ANSP 14735 as the type of *Lithodytes cinereus* in spite of, and without mention of, Dunn's remarks. Neither mention was indexed in the Zoological Record and the name remained lost. Dunn (1949) argued that ANSP 14735 must have been mislabeled as the type of *Lithodytes cinereus*, a position with which I agree; Malnate's (1971) ci-

tation of this specimen as the holotype must be rejected.

However, Cope provided sufficient information (digits with truncate pads, toes free, skin of venter smooth, first finger longer than second, traces of dorsolateral folds) to permit assignment of the name to the *conspicillatus* group of *Eleutherodactylus* (for usage of the group name, see Lynch, 1986). Although the genus *Eleutherodactylus* is intimidating for its sheer number of species, the genus is not especially diverse in the Amazon Basin (Lynch, 1980). If Cope's *L. cinereus* is a known species, then it must be one of those Lynch (1980) included in the *fitzingeri* group: *E. conspicillatus* (Günther), 1859, *E. fenestratus* (Steindachner), 1864, *E. lanthanites* Lynch, 1975, *E. malkini* Lynch, 1980, *E. peruvianus* (Melin), 1941, *E. vilarsi* (Melin), 1941, or *E. zeuctotylus* Lynch and Hoogmoed, 1977. Each of these exhibits three of the potentially discriminating traits cited by Cope (truncate digital pads, smooth venter, long first finger). The presence of this combination of traits serves to distinguish *L. cinereus* from at least 90% of the species presently included in the genus (Frost, 1985), irrespective of geographic clues.

In the description, Cope recorded some features useful in discriminating among these seven Amazonian *Eleutherodactylus*. Cope reported that there are "slight traces of dorsolateral folds." Leg length was recorded as "heel of extended hind leg to end of muzzle." Two color pattern characteristics are of use, viz., "Lower surfaces dirty-white" and "concealed surfaces brown." The concealed surfaces to which Cope refers must be taken to be the anterior and posterior surfaces of the thighs as well as the ventral surfaces of the shanks. Body size was given as "Length of head and body M. .053." Sex was not reported. The other elements of the species description do not appear useful in identification of the species, at least at this stage.

The dermal fold trait would appear to exclude *E. conspicillatus* and *E. peruvianus*, both of which have obvious dermal folds, and *E. lanthanites*, *E. malkini*, and *E. vilarsi*, in which such folds are not found. However, some individuals have color pattern features which might be confused with folds (e.g., see Lynch, 1975:11, photo of *E. lanthanites*). The hind limbs of *E. lanthanites* and *E. vilarsi* are too short to fall within the range that might be described as heel reaching to end of muzzle; the other species have hind limbs that are sufficiently long to match such a description. The description of the color