Journal of Herpetology, Vol. 35, No. 3, pp. 361–368, 2001

Validity of Taxonomic Changes for Turtles Proposed by Wells and Wellington

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ABSTRACT.—**The taxonomic changes proposed by Wells and Wellington (1985a, Australian J. Herpetol., Suppl. Ser. 1:1–61) are evaluated in light of the application of the fourth edition (1999) of the International Code of Zoological Nomenclature (ICZN). Of their proposed names, only the genus *Macrochelodina* (for which we fix a new type species), and the species *Elseya purvisi* and *Emydura worrelli* (a synonym of *Emydura subglobosa*) represent available names. Their lectotype designation for *Emydura victoriae* is complicated by their choice of a specimen of *Emydura macquarii* and will require action by the ICZN to prevent a destabilization of these names. To prevent a similar problem, we herein designate a lectotype for *Chelodina expansa*.**

In an apparent effort to expedite the developing taxonomy of Australian and New Zealand reptiles and amphibians, Wells and Wellington self-published three nonpeer-reviewed papers (1984, 1985a,b) in their own journal, and therein made approximately 739 taxonomic changes. These changes provoked an unprecedented firestorm of sentiment (King and Miller, 1985; Tyler, 1985; Grigg and Shine, 1985; Thulborn, 1986). Most Australian taxonomists were so angered that the International Commission of Zoological Nomenclature (ICZN) was petitioned to suppress all three works of Wells and Wellington (Case 2531; The President, Australian Society of Herpetologists, 1987). However, despite a majority of comments supporting this suppression [at least 91 authors: Shea, 1987; Hutchison, 1988; Ingram and Covacevich, 1988; King, 1988; Stone, 1988; Tyler, 1988; and others listed in the 1988 Bull. Zool. Nomenclat. 45(1): 54 and 45(2):153; but see contrary arguments by Birrel et al., 1988; Dubois et al., 1988; Greer, 1988; Holthuis, 1988; Meyer-Rochow, 1988], the ICZN (1991) declined to rule on the application and closed the case because the problems arising from the three publications were primarily taxonomic rather than nomenclatural. The ICZN stated "that the aim of the application would be best achieved by leaving the issues to specialists to be settled through usage" and that future "submissions to the Commission [should be] confined to names rather than works."

It is not our purpose here to engage in discussions of the motivations, intentions, ethics, or appropriateness of the publications of Wells and Wellington (e.g., Aplin, 1999). Rather, our intent is to evaluate objectively each of their proposed taxonomic changes for Australian turtles, in light of the specific rules set down in the fourth edition of the code (ICZN, 1999); Wells and Wellington (1999:110) noted that their papers were originally written to comply with the second edition of the code (ICZN, 1964).

The most critical section of the code pertinent to our discussion is Article 13.1, which states that to be available, a name published after 1930 must either (13.1.1) "be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon"; or (13.1.2) "be accompanied by a bibliographic reference to such a published statement." Wells and Wellington (1999:110) explicitly interpreted this section of the code (although referring to the second edition) by stating that the "rules of Zoological Nomenclature clearly state that in the description of a new species the description need only to purport to show difference" and (erroneously) that this "can be by way of reference to features, photographs or other published information which provides information of interpolative value."

We interpret Article 13.1.2 to mean a precise bibliographic reference to a specific written statement that purports to differentiate the taxon. To us, this means the explicit reference (i.e., by reference to a specific page or taxonomic account in a work), and not just by citing the complete text of a general work. The inclusion of the word "definite" in the equivalent Article 13a(ii) in the second edition (ICZN, 1964) also argues that this was the original intent of the commission. Furthermore, Article 13.1.2 clearly implies that simply referring to plates, figures, or pho-

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tographs (i.e., not "statements") in another work, without elaboration, is not sufficient by itself to constitute a valid diagnosis. We have used this interpretation in the evaluations that follow.

Museum abbreviations in the following text include AM (the Australian Museum in Sydney) and BMNH (the British Museum of Natural History in London). Although Wells and Wellington (1985a) referred to type specimens in the Australian Zoological Museum (AZM) in Katoomba, New South Wales, that collection apparently represents the personal collection of Richard Wells and not a public institution. Wells has responded to our inquiries about the existence of the specimens cited in their paper (1985a), but the specimens are still not available for public examination. Thus, their actual existence has not been confirmed.

TAXONOMIC EVALUATIONS

Genera

Chelymys.—Wells and Wellington (1983:74, 1985a:12) resurrected *Chelymys* Gray 1844:42 from the synonymy of *Emydura* Bonaparte (1836:7) asserting that *Emydura* was a nomen nudum. This assertion is presumably based on the belief that *Emydura macquaria* (Cuvier, 1829: 11), the supposed type species, was a nomen nudum. The availability of the genus *Emydura* (and its type species) has been clarified by Stimson (1986), who also rejected the removal of the genus name *Chelymys* from the synonymy of *Emydura*.

Hesperochelodina.—Type species: *Chelodina steindachneri* Siebenrock, 1914. In naming this genus, Wells and Wellington (1985a:13) stated that "*Hesperochelodina* is readily identified by the excellent diagnostic data for '*Chelodina steindachneri*' in Cogger (1983:143, Plates 404, 405), Goode (1967:33–35) and Cann (1978:50–51, Plate 21)." However, they referred to no statements (in words) by these authors purporting to distinguish the new taxon, and in any case, none of the latter authors alluded to a new genus for this species. The text of Wells and Wellington, therefore, does not constitute a statement that purports to give characters differentiating the taxon (under Article 13.1.1 of the code) nor do they refer to such a diagnosis (13.1.2). The name *Hesperochelodina* is, thus, a nomen nudum under Article 13.1.1 and 13.1.2 of the International Code of Zoological Nomenclature and is, therefore, unavailable.

Macrochelodina.—Type species: *Chelodina oblonga* Gray 1841 (= *Chelodina rugosa* Ogilby 1890: 56; see below). In naming this genus, Wells and Wellington (1985a:13) provided the following diagnosis for *Macrochelodina*: "A genus of large freshwater chelids readily identified by the following combination of characters: Carapace extremely broad somewhat oval; plastron narrow about twice as long as broad lacking dark patterning of *Chelodina*; second and third vertebrals longer than wide; broad depressed head; gulars meet in front of intergular; four claws on forelimbs. . ." This is sufficient to differentiate the taxon and clearly purports to do so. We, therefore, regard this name to be available under Article 13.1.1 of the code.

This action by Wells and Wellington presents particular difficulties because of their choice of the type species. Thomson (2000) demonstrated that the holotype of *Chelodina oblonga* (BMNH 1947.3.5.89) is a representative of the form currently assigned to *Chelodina rugosa*, as suspected by Cann (1998:75). To minimize disruption of taxonomic stability by this discovery, Thomson is petitioning the ICZN to suppress the older name *oblonga* (Gray, 1841) and to conserve the younger name *rugosa* (Ogilby, 1890), which has been in common usage for the form in northern Australia.

Because the type species of *Macrochelodina* has been found to be misidentified (Thomson, 2000), we hereby fix *Chelodina rugosa* Ogilby 1890:56 as the type species of the genus *Macrochelodina*, in accordance with Articles 67.9 and 70.3 of the code. This recommendation reflects the clear original intent of Wells and Wellington (1985a) to describe as different the "broad-headed" clade of *Chelodina* (explicitly *C. rugosa, C. expansa,* and *C. siebenrocki*; see also Burbidge et al., 1974; Georges et al., 1998). Their first diagnostic character (1985a:13), "Carapace broad somewhat oval," applies to this broad-headed group but not to the taxon in southwestern Australia (formerly *C. oblonga* but now *C. colliei* Gray 1856: 200; Thomson, 2000). We believe that our action will minimize the confusion caused by the misidentification of the holotype of *C. oblonga*, as intended by Article 70 of the code, and will retain the proper relationship between the new genus and the holotype of its originally assigned species. Until further work on the taxonomy and phylogenetic relationships of this group is complete, the genus *Macrochelodina* should include *M. rugosa, M. expansa, M. siebenrocki, M.* sp. aff. *rugosa* (Mann; sensu Georges and Adams, 1992; Thomson et al., 2000; A. Georges, M. Adams, and W. P. McCord, 2000, unpubl. data), *M. parkeri* Rhodin and Mittermeier, 1976, and *C. kuchlingii* Cann, 1998. However, A. Georges, M. Adams, and W. P. McCord (2000, unpubl. data) include *Macrochelodina* as a junior synonym of *Chelodina*.

Tropicochelymys.—Type species: *Hydrapsis victoriae* Gray, 1842. Wells and Wellington (1985a: 13) described this genus under the mistaken as-

sumption that the genus name *Emydura* was a nomen nudum (see above). Nevertheless, they did provide a valid diagnosis for this new genus, but ironically, by selecting BMNH 1947.3.5.95 as the lectotype for the type species, they have made *Emydura victoriae* a junior synonym of *Emydura macquarii* (see Lectotype Designations below). *Tropicochelymys*, thus, becomes a junior synonym of *Emydura*.

Species Names

Species names discussed below are corrected for the above generic evaluations.

Chelodina billabong.—Holotype: AM R72933 from "Bullo River Crossing, along the Katherine to Kunnunurra Rd., Northern Territory." Wells and Wellington (1985a:13) stated in their diagnosis that this new species was "most closely related to *Macrochelodina rugosa*" and could be "readily distinguished [from *Chelodina rugosa*] by consulting existing published data and illustrations." The illustrations to which they referred are provided by Cann (1978:plate 23) and Cogger (1983:plates 68, and 402–403). They also referred to morphological data in Cann (1978), Cogger and Lindner (1974), and Cogger (1983) and to reproductive data in Cann (1978), each of which referred only to *Chelodina rugosa* and included no statements purporting to distinguish this form. The text of Wells and Wellington (1985a) clearly does not constitute a statement that purports to give characters differentiating the taxon (under Article 13.1.1 of the code) nor did they specifically refer to such a statement (13.1.2). The name *billabong* is, thus, a nomen nudum under Article 13.1.1 and 13.1.2 of the International Code of Zoological Nomenclature and is, therefore, an unavailable name. In addition, the population to which this name referred is considered the same as *Chelodina rugosa* by Shea and Sadlier (1999:54).

Chelodina rankini.—Holotype: BMNH 1908.2.25.1 from "the lower Burdekin River, north east Queensland." In their diagnosis of this species, Wells and Wellington (1985a:11) referred to descriptions of *Chelodina novaeguineae* (Cogger, 1983: 142; Cann, 1978:49–50; Goode, 1967:31–32), and to various photographic plates published elsewhere (Cann, 1978:plates 16, 18–19; Cogger, 1983:plates 69, 399–400; Whitaker et al., 1982:10; Goode, 1967:plate 22). They did not provide any description in words to distinguish *Chelodina rankini* from other taxa nor did they include a specific bibliographic reference to such a diagnosis; none of the sources to which they referred provided any distinguishing statement in words. The name *rankini* is, thus, a nomen nudum under Article 13.1.1 and 13.1.2 of the International Code of Zoological Nomenclature and is, therefore, an unavailable name.

Elseya purvisi.—Holotype: AM R44654 from "a river [Manning River Basin] 15 km S, 32.3 km E of Nowendoc, New South Wales (Lat. 31°39'S, 152°04'E)." However, the holotype, although registered in the AM, was placed in the collection at the Utah Museum of Natural History by J. Legler at the University of Utah in Salt Lake City (Shea and Sadlier, 1999:54; J. Legler, pers. comm.).

In their diagnosis, Wells and Wellington (1985a:12) stated that this form was a member of the *Elseya latisternum* complex and that it was "readily separated from all other *Elseya*, by the excellent illustrations and descriptions of Cann (1978:plates 65–67)." Furthermore, they referred to "diagnostic illustrations of its nearest relative *Elseya latisternum*" provided by Cogger (1983: plates 408–410). These remarks do not constitute a statement that purports to give characters differentiating the taxon (under Article 13.1.1 of the code). Cann (1978:70) did note the "bright yellow band along the head and neck" of this form and stated that a large adult had "none of the serrations at the rear of the carapace typical of some *Elseya latisternum*." Thus, although this could be construed as a description, Wells and Wellington (1985a) did not refer specifically to these statements but rather cited only the plates in Cann's (1978) book. Therefore, their diagnosis does not constitute a specific bibliographic reference to a published diagnostic statement as required under Article 13.1.2. However, Wells and Wellington did state that "The presence of a bright yellow facial streak readily separates this species [*Elseya purvisi*] from *Elseya latisternum*." This clearly constitutes a statement that purports to give characters differentiating this taxon (under Article 13.1.1). We, therefore, regard the name *Elseya purvisi* as a valid and available name. Furthermore, it has been appropriately used by Allanson and Georges (1999), Cann (1997, 1998), Georges and Adams (1996), and Cogger (2000).

Elseya sterlingi.—Holotype: AM R68848 from "the Cairns district, Queensland." However, the specimen has been reregistered as R93048 (Shea and Sadlier, 1999:54).

In their diagnosis, Wells and Wellington (1985a:12) referred to this taxon as a member of the *Elseya dentata* complex and cited specific "diagnostic photographs," "diagnostic illustrations of the cranial osteology," and plates provided by Cann (1978:72, plates 49–50); "good diagnostic illustrations of *Elseya dentata*" provided by Cogger (1983:plates 406–407) and "morphological data, showing comparative features between the two species" provided by Goode (1967:54–57). Neither Cann (1978) nor Cogger (1983) provided any written description or diagnosis of this form. In addition, although Goo-

de (1967:54) mentioned that "a specimen [of *Elseya dentata*] with certain similarities but possibly subspecifically different, has been collected from . . . near Cairns," and provided some measurements of that specimen (1967:55), no description or diagnosis was included. Wells and Wellington (1985a) also cited "morphological, ecological and taxonomic references in Coventry and Tanner (1973), Cogger et al. (1983), Cogger (1983), and Goode (1967)," but none of these contains statements of description or diagnosis. The text of Wells and Wellington (1985a) clearly does not constitute a statement that purports to give characters differentiating the taxon (under Article 13.1.1 of the code) nor did they specifically refer to such a statement (13.1.2). The name *sterlingi* is, thus, a nomen nudum under Article 13.1.1 and 13.1.2 of the International Code of Zoological Nomenclature and is, therefore, an unavailable name. In addition, the population to which this name referred is considered the same as *Elseya dentata* by Shea and Sadlier (1999:54).

We also note that the plates referred to by Wells and Wellington as examples of *Elseya sterlingi* (i.e., Cann, 1978:plates 49–50) are of a different species from that represented by their stated holotype (Georges and Adams, 1992, 1996; Thomson et al., 1997).

Emydura cooki.—Holotype: AM R44816 from "the Macleay River, New South Wales (30°46'S, 152°18'E)." In their diagnosis, Wells and Wellington (1985a:12) provided no stated description or diagnosis of this taxon but instead referred to illustrations and plates provided by Cann (1978:56, plates 58–60). They claimed that *Emydura cooki* "can be easily distinguished from its nearest relatives" from these plates and others provided by Cann (1978:plates 32–34, 36–37, 62–63). This does not constitute a statement that purports to give characters differentiating the taxon, under Article 13.1.1 of the code. Wells and Wellington (1985a) also referred to comparative morphological data of Cann (1978), but Cann provided no morphological data nor did he include a statement purporting to provide a diagnosis. The name *cooki* is, thus, a nomen nudum under Article 13.1.1 and 13.1.2 of the International Code of Zoological Nomenclature (see also Shea, 1987) and is, therefore, an unavailable name. In addition, the population to which this name referred is considered the same as *Emydura macquarii dharra* Cann (1998) by Shea and Sadlier (1999:54).

Emydura goodei.—Holotype: Supposedly an adult in the Australian Museum (but see below). Wells and Wellington (1985a:13) named as the holotype "An adult in the Australian Museum. Collected along the Jardine River, Cape York Peninsula, Queensland." Prior to 1985, the Australian Museum had no specimens (of cf. *E. subglobosa*) from the Jardine River. However, they received four live specimens with the locality data "0.5 mi. N old Jardine River crossing" in 1985, and these are now cataloged as AM R37666–69 (Shea and Sadlier, 1999:54). However, in their diagnosis, Wells and Wellington (1985a:13) provided no description or diagnosis of this taxon but rather stated that this new species could be "readily identified by consulting the excellent diagnostic illustration and data in Cogger (1983:plates 72, 416 from the Jardine River, Queensland; see also p. 147)." Unfortunately, Cogger provided no statement purporting to distinguish this new taxon. Wells and Wellington (1985a) also referred to "diagnostic data" in Goode (1967), but Goode (1967:74) only provided measurements for New Guinea specimens of *E. subglobosa*. Furthermore they cited "comparative illustrations" of *Emydura subglobosa* provided by Cann (1978:plates 42–43), Goode (1967:plates 94–95), and Whitaker et al. (1982:7,9), but none of those authors made statements purporting to distinguish the new taxon. The text of Wells and Wellington (1985a) clearly does not constitute a statement that purports to give characters differentiating the taxon (under Article 13.1.1 of the code) nor did they specifically refer to such a statement (13.1.2). The name *goodei* is, thus, a nomen nudum under Article 13.1.1 and 13.1.2 of the International Code of Zoological Nomenclature and is, therefore, an unavailable name. In addition, the population to which this name referred is considered the same as *Emydura subglobosa* by Shea and Sadlier (1999:54).

Emydura insularis.—Holotype: supposedly AZM R102 from "Fraser Island, Queensland." In their diagnosis, Wells and Wellington (1985a:13–14) referred to unspecified "comparative morphological and distributional data on this species and other [*Emydura*] provided by Cann (1978)," "Plate 82 in Cann (1978)," and unspecified "reproductive data" in McNicol and Georges (1980). Cann (1978:74) referred to "a distinct race of small, short-necked tortoises," and stated that "the adult averages 17.5 cm in length, is slightly oblong in shape, and becomes very deep with old age." These statements could be interpreted as purporting to distinguish this form, but they were not specifically referred to by Wells and Wellington (1985a). Thus, Wells and Wellington made no statement that purported to give characters differentiating the taxon (under Article 13.1.1 of the code) nor did they specifically refer to such a statement (13.1.2). The name *insularis* is, thus, a nomen nudum under Article 13.1.1 and 13.1.2 of the International Code of Zoological Nomenclature and is, therefore, an unavailable name. Further-

more, we have been unable to verify that the holotype exists.

Emydura joncanni.—Holotype: AZM R101 from "Rouchel Brook, New South Wales." In naming this species, Wells and Wellington (1985a:12) referred to plates provided by Cann (1978:plates 62–63) and claimed that *Emydura joncanni* is "most readily identified by consulting the comparative data on the morphology and distribution of this and related species in Cann (1978)." This does not constitute a statement that purports to give characters differentiating the taxon (under Article 13.1.1 of the code). In addition, Cann (1978) provided no statement describing or diagnosing this taxon. Thus, Wells and Wellington (1985a) referred to no diagnosis in any other published literature (13.1.2). As a result, the name *joncanni* is a nomen nudum under Article 13.1.1 and 13.1.2 of the International Code of Zoological Nomenclature and is, therefore, an unavailable name. In addition, we have been unable to verify that the holotype exists.

Emydura leichhardti.—Holotype: supposedly AZM R103 from "the Leichardt River, Queensland." In their diagnosis, Wells and Wellington (1985a) referred to unspecified "comparative morphological and distributional data for this and other [*Emydura*]" and a specified plate (92) provided by Cann (1978). However, Cann (1978: 74) provided no description or diagnosis for the turtle figured in plate 92 (and which he called an "*Emydura* tortoise"). The text of Wells and Wellington, therefore, clearly does not constitute a statement that purports to give characters differentiating the taxon (under Article 13.1.1 of the code) nor did they specifically refer to such a statement (13.1.2). The name *leichhardti* is, thus, a nomen nudum under Article 13.1.1 and 13.1.2 of the International Code of Zoological Nomenclature and is, therefore, an unavailable name. Furthermore, we have been unable to verify that the holotype exists.

Emydura windorah.—Holotype: supposedly AZM R104 from "the Windorah district of south-west Queensland." In their diagnosis, Wells and Wellington (1985a:12) referred to illustrations and plates provided by Cann (1978: plates 71, 73–74) and claimed that *Emydura windorah* is "readily identified by consulting the existing comparative morphological and distributional data in Cann (1978)." This does not constitute a statement that purports to give characters differentiating the taxon, under Article 13.1.1 of the code. However, Cann (1978:71) stated that in this turtle ("the Cooper Creek Tortoise") "young specimens have a yellow facial stripe and are somewhat similar to *Emydura macquaria*, but the difference between the two tortoises becomes more obvious with age. Mature Cooper Creek specimens lack facial markings." Both of these forms have yellow facial stripes (though their placement on the side of the head differs between the two), and old Cooper Creek specimens do tend to lose their head markings (e.g., Cann, 1998:147–148). Thus, although this could be construed as a description, Wells and Wellington did not refer specifically to these statements but rather cited the entire book (and its plates). Therefore, their diagnosis does not constitute a specific bibliographic reference to a published diagnostic statement as required under Article 13.1.2. The name *windorah* is, thus, a nomen nudum under Article 13.1.1 and 13.1.2 of the International Code of Zoological Nomenclature and, therefore, an unavailable name. In addition, we have been unable to verify that the holotype exists.

Emydura worrelli.—Holotype: AM R53689 from "Caranbirini Waterhole, ca. 21 km north of MacArthur River, Northern Territory (16°16′ S × 136°05′E)." However, the actual data with the specimen read "Caranbirini Water Hole, 21 km N McArthur River base camp" (Shea and Sadlier, 1999:54).

In their diagnosis, Wells and Wellington (1985a:14) stated that this new species is most closely related to *Emydura victoriae* but is "readily distinguished by consulting already published morphological data and illustrations." They also referred to unspecified "comparative morphological and distributional data for this and other [*Emydura*]" in Cann (1978) and explicitly cite plates (79–81, 88) provided by Cann (1978) as representative of this taxon. Wells and Wellington (1985a) also noted that "the distinctive carapace differences are readily observable in" plate 88 of Cann (1978). The latter illustration shows two forms regarded by Cann as *Emydura australis* and "*Emydura* species No. 2 from Batten Creek, Northern Territory" (= *E. worrelli*). The legend to that plate specifically distinguishes the former from the latter by its "characteristic hump" (i.e., more highly domed carapace). In addition, in the text Cann (1978: 74) stated that this "distinct but as yet undescribed tortoise" has "reddish-orange" facial stripes. Thus, although Wells and Wellington (1985a) did not refer to the specific diagnostic statements made by Cann (1978) on page 74 in the text of his book, they did cite a specific (though weak) diagnosis in the legend to plate 88.

In conclusion, although Wells and Wellington's (1985a) statement about "carapace differences" is brief, it does constitute a statement that purports to give characters differentiating the taxon (under Article 13.1.1 of the code). In addition, they also specifically refer to such a statement in another work (13.1.2) by citing

Plate 88 in Cann (1978), the legend of which contains a rudimentary diagnosis. Thus, under both Article 13.1.1 and 13.1.2 of the International Code of Zoological Nomenclature *worrelli* is a valid name. It has also been used correctly by Cann (1997, 1998) and Cogger (2000); however, based on molecular comparisons, Georges and Adams (1996) believe this form to be synonymous with *Emydura subglobosa*.

Lectotype Designations

Chelodina novaeguineae.—Lectotype: BMNH 1946.1.22.36. Both junior authors have examined this specimen, and we have no objection to its designation as the lectotype by Wells and Wellington (1985a:12).

Elseya dentata.—Lectotype: BMNH 1947.3.6.3. Both junior authors have examined this specimen, and we have no objection to its designation as the lectotype by Wells and Wellington (1985a: 12).

Emydura victoriae.—Lectotype: BMNH 1947.3. 5.95. *Emydura victoriae* (Gray, 1842:55) was represented by two syntypes (BMNH 1947.3.5.95 and 1947.3.5.96; see photographs in Cann, 1998:159). Unfortunately, Wells and Wellington apparently did not examine the syntypes, and the specimen designated as the lectotype by Wells and Wellington (1985a:14) is clearly an *Emydura macquarii* (SAT, unpubl.). The other syntype represents a distinctive, recognized taxon to which the name *victoriae* has been applied (e.g., Cann, 1998). If their lectotype designation were to stand, *Emydura victoriae* would have to be regarded as a junior synonym of *Emydura macquarii*. To reduce the confusion that this designation would create, we propose to petition the ICZN to suppress the lectotype designation of Wells and Wellington and to support the lectotype designation of the other syntype.

As an amendment incidental to this paper, we note that one of the two syntypes of *Chelodina expansa* Gray 1857:370 (BMNH 1947.3.5.88) is actually a *Chelodina longicollis* (SAT, unpubl.). To avoid a repetition of the unfortunate situation with *Emydura victoriae*, we hereby designate the other syntype (BMNH 1947.3.4.21) as lectotype for *Chelodina expansa*.

Discussion

It is our hope that this paper will stimulate similar objective assessments of the availability of other amphibian and reptile names proposed by Wells and Wellington. We also conclude with a plea that future authors of turtle names do their best to follow the letter and the spirit [e.g., the Code Ethics (Appendix A), and the individual Recommendations of the International Code (ICZN, 1999)].

Acknowledgments.—The comments of K. Adler, R. Bour, J. Hooper, P. Meylan, E. Moll, A. Rhodin, and H. Smith on early portions of this manuscript are greatly appreciated, as are the several discussions on the issues covered in this paper with H. Cogger, G. Shea, and R. Sadlier. S. Penhale and T. Kirk expedited the arrival of critical literature for the senior author.

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Accepted: 24 August 2000.

Journal of Herpetology, Vol. 35, No. 3, pp. 368–378, 2001

Maternal Effects on Life-History Traits in the Amazonian Giant River Turtle *Podocnemis expansa*

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ABSTRACT.—**Energy allocation to eggs and nest site selection by females can affect life-history variables such as offspring size, offspring number, developmental rate, survivorship, growth rate, and performance in oviparous reptiles. Nest site selection can affect offspring phenotype by altering incubation conditions. I present evidence of a positive effect of female size on clutch size, egg mass, and nest depth through the study of trackways left by female river turtles, *Podocnemis expansa*, on their nesting beaches. Larger females laid larger clutches composed of larger eggs, which were buried deeper than clutches laid by smaller females. The data suggest that *P. expansa* does not conform to optimal propagule size models. Neither egg size nor clutch size reached a plateau as female size increased. Females seem to allocate the extra energy (in absolute terms) gained allometrically with increasing size and age to both number and size of eggs. There was no evidence of a trade-off between egg size and number after removing the effect of female size. Larger eggs produced larger hatchlings that survived better but grew less than individuals of smaller initial size during the first two months of life, under unlimited food conditions. I suggest that fitness of female *P. expansa* increases by producing larger eggs because of the advantage that larger hatchlings have in survival. Deeper nests experience cooler temperatures and tend to produce a higher percentage of males than more superficial nests. Therefore, there is a potential for important effects of nest depth on sex ratios produced by different sized females within the population and possibly by single females throughout their lifetime. Constant temperature in artificial incubation experiments had an effect on the size of individuals at hatching, but differences vanished by the second month of age via the greater growth rate shown by individuals of smaller initial size.**

Life-history variables such as offspring size, offspring number, developmental rate, survivorship, growth rate, and performance may be influenced by maternal factors such as energy allocation and nest site selection in oviparous reptiles. Because those parameters affect offspring fitness, females could maximize their own fitness by optimizing that of their offspring (Brockelman, 1975). On one hand, species with larger clutches and no parental care are expected to show the patterns of energy allocation predicted by optimality models (Smith and Fretwell, 1974), which may involve compromises between longevity and fertility, and trade-offs between offspring size and offspring number (Roff, 1992; Stearns, 1992; Bulmer, 1994; Sikes, 1998 and references therein). On the other hand, nest site selection can alter incubation conditions experienced by the offspring that can affect their phenotype (Shine and Harlow, 1996). Incubation conditions such as temperature vary with nest substrate characteristics, sun and wind exposure, and nest depth (Souza and Vogt, 1994; Janzen, 1994; Shine and Harlow, 1996). Incubation temperature has profound effects on

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