

Courtship Behavior and Systematics in the Subtribe Nectemydina

2. A Comparison above the Species Level and Remarks on the Evolution of Behavior Elements^{1, 2}

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Abstract

Based on a literature review and unpublished data of the author, the male courtship behavior of turtles of the genera *Chrysemys*, *Graptemys*, *Malaclemys*, *Pseudemys*, *Trachemys* (= subtribe Nectemydina), and *Deirochelys* is analyzed and its significant elements are applied to systematics above the species level. The results are discussed in a zoogeographic-evolutionary context. Head-nodding in a vertical plane is widely distributed in chelonian courtship and is a plesiomorphic character. Claw vibration is a synapomorphy of the subtribe Nectemydina, and claw vibration from a position above the female is a shared derived character of *Pseudemys* species. The different courtship modes represented by the species of the subtribe Nectemydina evolved from a common ancestral behavior pattern consisting of head-nodding plus claw vibration. Manifold variations of this basic pattern developed as character displacements. Today the highest diversity of courtship patterns occurs in the area with the highest species diversity, the southeastern United States. Differences in courtship which probably function as isolating mechanisms are listed.

Introduction

Behavioral characters have long been used to distinguish between closely related, morphologically similar, or otherwise indistinguishable species. However, only a few cases are known where strictly inherited behavior patterns are characteristic for higher taxa (Mayr, 1975). As a herpetological example, Zimmermann and Zimmermann (1988) recently presented a remarkable study which has encouraged intense, constructive discussions and highlighted the often impressive value of behavioral characters in taxonomic studies above the species level.

In the first part of this study (Fritz, 1990; also the English translation in Bull. Chicago Herp. Soc. 33(1):225-236, 1998), the utility of courtship behavior in the taxonomy of the turtle genus *Trachemys* was examined at the species level. Herein, in the second part of the study, it will be demonstrated that the complex courtship of turtles in the subtribe Nectemydina [the New World terrapins, in a broader sense than usually applied], also yields interesting conclusions pertaining to the higher taxonomy of these chelonians. [Editors' note: in this translation, "terrapin" is used for the German "Schmuckschildkröte," the vernacular term for a turtle of the genus *Trachemys*, *Pseudemys*, *Deirochelys*, or, less frequently, *Chrysemys*].

Claw vibration as a characteristic behavioral trait of the subtribe Nectemydina

Several authors have demonstrated over the years that the long-known characteristic claw vibration behavior of the red-eared slider (*Trachemys scripta elegans*) is a common behavior in the courtship display of aquatic turtles of the subfamily Emydinae (see Appendix). Moreover, until now, this behavior has been described only for species of the subtribe Nectemydina *sensu* Smith and Smith (1980), with the possible exception of the chicken turtle (*Deirochelys reticularia*; see Krefft, 1951).

It is highly improbable that the most complicated motion patterns displayed during claw vibration behavior would have developed independently several times through evolutionary convergence at the subfamily level or a lower taxonomic level.

Taking this into account, the claw vibration behavior clearly proves to be a shared derived character, a synapomorphy of the subtribe Nectemydina (possibly including *Deirochelys*). This character, in addition to many morphological criteria, serves to unite this subtribe as a natural group (Figure 1).

Krefft (1951) published anecdotal observations on the courtship of a single captive *Deirochelys*. However, the claw vibra-

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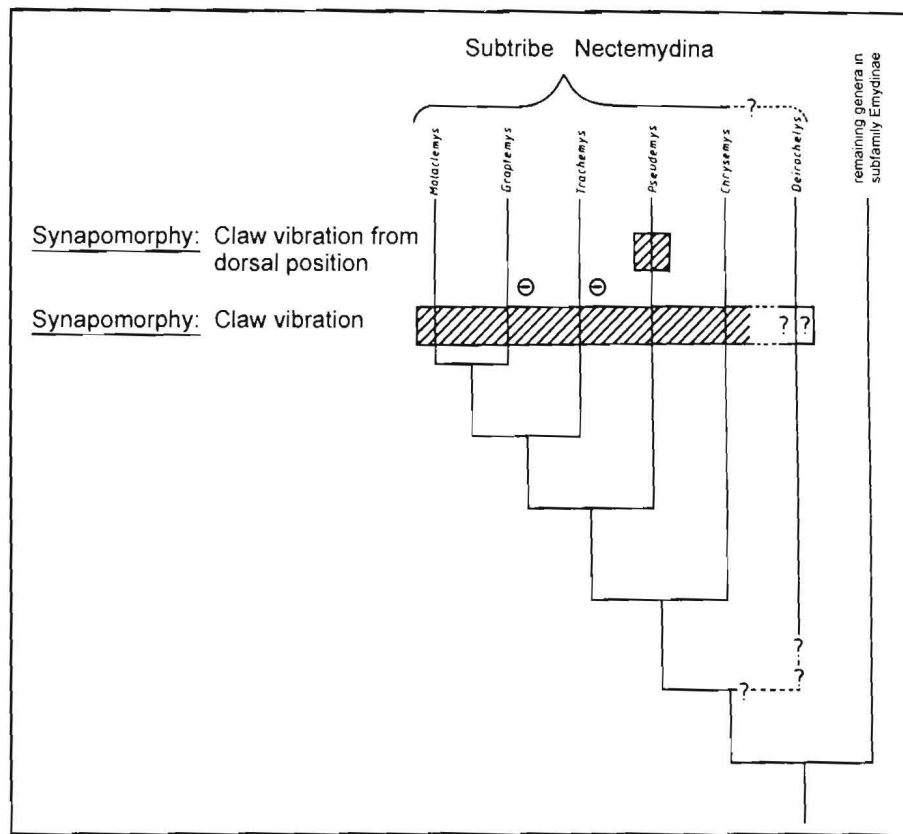


Figure 1. Cladogram of the subtribe Nectemydina showing courtship elements of taxonomic significance. For *Deirochelys* see discussion in text. Branches of cladogram were modified from Bramble (1974), Obst (1985), and Seidel and Smith (1986). The symbol \ominus indicates reduction (lack) of claw vibration behavior in certain species.

tion behavior exhibited by this specimen was directed towards individuals of other turtle species. Moreover, the observed male was not an adult.

The foreclaws of male *Deirochelys* are not elongated. If the observations by Krefft of claw vibration behavior are eventually verified, this would be, with the possible exception of *Malaclemys* (Sachsse, 1984), the only known case where the behavior element "claw vibration" is present in a species without this obvious sexual dimorphism [elongated foreclaws in males]. However, according to Sachsse, the claw vibration behavior in *Malaclemys* is "only rudimentary compared with [that of] *Graptemys* and *Chrysemys*," and is not always displayed during courtship. Hence, claw vibration without the obvious sexual dimorphism is surely an exception to the rule. Therefore the observations by Krefft should be treated with caution and a more detailed study of the courtship of *Deirochelys* is most important.

The relationship of *Deirochelys* to other emydids is still open to debate. Loveridge and Williams (1957) and some other authors (e.g., McDowell, 1964) favored a close relationship with *Emydoidea blandingii* because of a certain similarity in general habitus and in morphology, whereas recent osteological, paleontological and biochemical results clearly refute this arrangement (Bramble, 1974; Jackson, 1978; Frair, 1982; Gaffney and Meylan, 1988; Seidel and Adkins, 1989). According to these recent studies, *Deirochelys* is more closely related to turtles of the subtribe Nectemydina, as was assumed

prior to the study by Loveridge and Williams (1957); this fact is reflected by the color pattern of the soft parts and shell which is characteristic of terrapins. Therefore, Gaffney and Meylan (1988) placed *Deirochelys*, along with the subtribe Nectemydina (*sensu* Smith and Smith, 1980), in its own subfamily, the Deirochelyinae.

If claw vibration does indeed occur as part of the courtship of male *Deirochelys*, this would also provide evidence for a close relationship to the subtribe Nectemydina.

The genus *Pseudemys* has developed a unique variant of this behavior

A modified courtship position occurs exclusively in males of the genus *Pseudemys* (Figure 2). The male *Pseudemys* swims in the same direction above the female whereas in all other species the male faces the female during claw vibration. This courtship position is therefore a synapomorphy of the genus *Pseudemys* and distinguishes it from all other related genera (see Figure 1).

The German terrarium fancier Gerhard Krefft (1950) may be credited as the first to point out the value of using courtship characters in taxonomy above the species level in the turtles now classified in the genera *Chrysemys*, *Pseudemys* and *Trachemys*. Also to his credit, Krefft correctly proposed that the courtship position of *Pseudemys* is derived from the ancestral courtship in *Chrysemys picta* and *Trachemys scripta*. As he

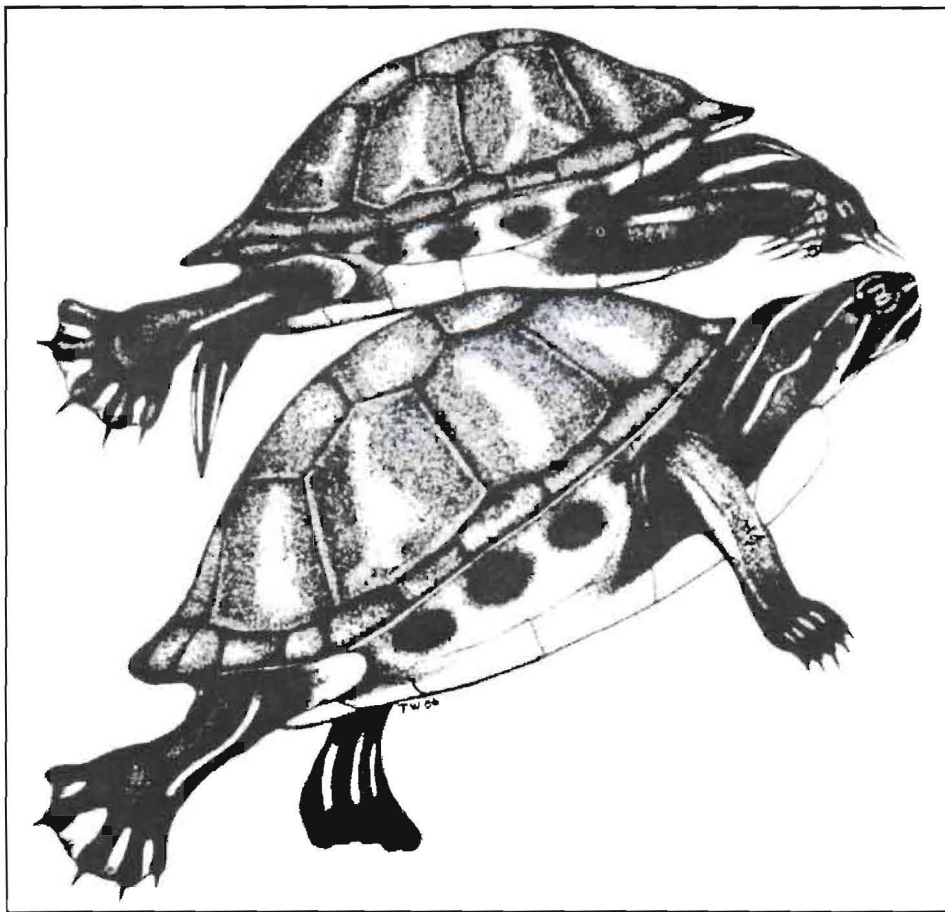


Figure 2. *Pseudemys nelsoni* in the courtship position characteristic of the genus *Pseudemys*. —From Kramer and Fritz (1989).

noted, this derived courtship “is characteristic of the *floridana* *Rassenkreis* [complex]” (now *Pseudemys concinna*, *P. floridana* and *P. texana*, thus a part of the genus *Pseudemys* as now defined).

Is head-nodding in the courtship display of many chelonian species of taxonomic relevance above the species level?

When considering the value of behavioral characters in systematics, one encounters the same problems that are present in the use of morphological criteria: that is, the danger that one will misidentify convergent characters as homologies, and thereby draw the wrong conclusions regarding relatedness, increases with increasing kinship distances of the taxa studied.

Accordingly, at lower taxonomic levels it is highly probable that inherited behavior patterns with complex, identical motion patterns will indeed represent homologies [characters of common origin]. However, this sort of generalization is quite risky at higher taxonomic levels.

Head-nodding is known to be an important element of courtship in nearly all taxonomic groups within the order Testudines (see Appendix; and Carpenter and Ferguson, 1977). In the first part of this study (Fritz, 1990), it was also described for the first time for a species of the genus *Trachemys*. Head-nodding is therefore a plesiomorphic [ancestral] character for the Nectemydina species and not useful for investigating their

systematics. Because head-nodding also occurs in squamates (Carpenter and Ferguson, 1977), it is even possible that this behavior is a common heritage of several reptile groups and therefore a plesiomorphic character for the chelonians as a whole.

The courtship within the subtribe Nectemydina exhibits manifold variations of the same primary types

Hence, the motion pattern of head-nodding in the courtship of certain terrapins does not allow one to draw any direct conclusions regarding their taxonomic relationships to other turtle species. However, despite this, it does allow for some interesting statements on the evolution of courtship in the different genera of the Nectemydina.

In the courtship of *Graptemys* and *Malaclemys* species, the characteristic claw vibration behavior occurs either alone or in combination with head-nodding motions, or head-nodding occurs alone (see Appendix). *Graptemys* and *Malaclemys* together probably comprise the sister group of *Trachemys* (Seidel and Smith, 1986; see also Figure 1). Therefore the head-nodding behaviors of *Graptemys*, *Malaclemys* and *Trachemys ornata* are most probably homologies.

The southeastern United States is regarded as the Pleistocene radiation center of *Trachemys* (Barbour and Carr, 1940; Auffenberg and Milstead, 1965; Seidel, 1988), and is probably

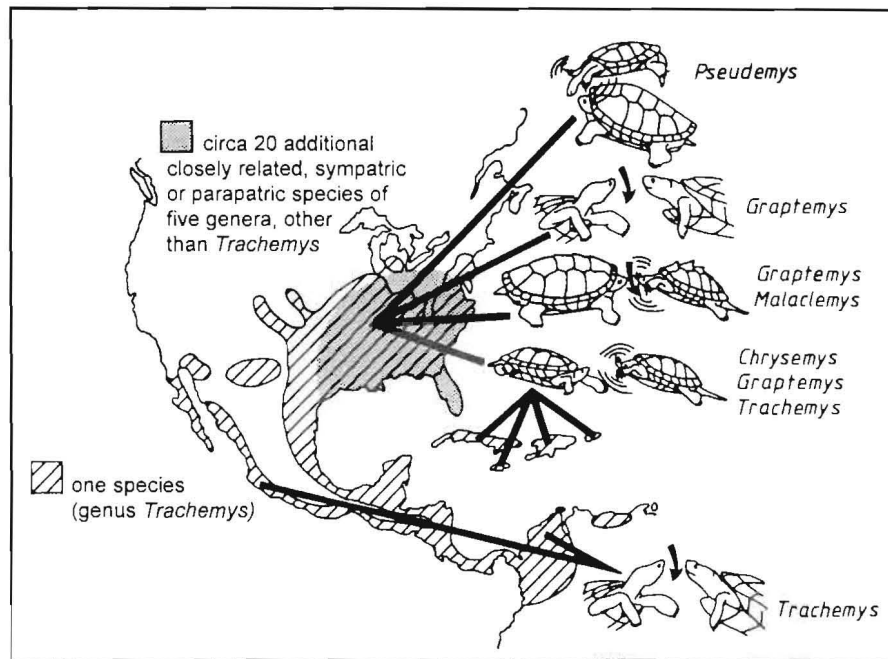


Figure 3. Diversity of courtship patterns of the subtribe Nectemydina corresponding to the number of sympatric species. The region with the highest species diversity is the southeastern United States. Several variants of the same primary courtship pattern developed in this area by character displacement. In a similar manner, at least two courtship modes of the parapatric *Trachemys* species may have evolved.

also the Pleistocene radiation center of the whole subtribe Nectemydina. The present, highly overlapping distribution patterns of the different nectemydine genera and of *Deirochelys* in this geographic area (see maps in Conant, 1975; and Figure 3) and the extensive similarities of the different behavior elements among these closely related taxa allow one to conclude that a common ancestral behavior pattern existed and that a species-specific differentiation (character displacement) occurred during speciation. It is exactly in the radiation center of *Trachemys*, which is presently the region with the highest species density (circa 20 sympatric and parapatric, closely related species in five genera, excluding *Deirochelys*), that one finds the greatest diversity of different courtship elements (Figure 3). This high number of species must require highly effective isolating mechanisms to maintain the genetic independence and the diversity of the different taxa. The motion patterns displayed during courtship surely have a great importance as isolating mechanism.

The ancestral courtship of the subtribe Nectemydina must have been composed of both motion patterns, head-nodding and claw vibration

The widespread occurrence of head-nodding movements and of claw vibration in the courtship of these species (see Appendix) implies that the ancestral courtship consisted of both motion patterns. At present, a courtship behavior consisting of both of these distinct behaviors is found in *Malaclemys* and in some *Graptemys* species (see Appendix). Claw vibration alone presently occurs in some of the *Graptemys* species; in the sympatric *Chrysemys*, *Pseudemys*, and *Trachemys* species (of North America); and in the West Indian *Trachemys*. However,

in the parapatric or allopatric *T. ornata* and in *G. geographica*, *G. pulchra*, and *G. versa*, only head-nodding has survived.

How is the information about the species identity of the courting male encoded in the courtship?

The two ancestral nectemydine behavior patterns, head-nodding and claw vibration, may be exhibited separately or together; thus, alone they comprise three different behaviors which may encode the species identity of the courting male for the courted female.

In all species of the subtribe Nectemydina, one of these three variants occurs (see Appendix). In the parapatric or allopatric *Trachemys scripta* and *T. ornata*, two different behaviors occur as a form of character displacement. The same is true for some sympatric species pairs.

In addition to these primary behavior patterns, there seems to exist a diversity of species-specific variations of behaviors which are poorly understood and have been little studied. Moreover, these variations may occur in combination. Through this variation, the potential number of different behavior patterns is increased. These additional differences in male courtship pattern may function as isolating mechanisms, and are briefly listed as follows:

1) Different courtship positions: from above, and in the same direction as the female (genus *Pseudemys*: Jackson and Davis, 1972b; White and Curtsinger, 1986; Kramer and Fritz, 1989; Fritz, 1989) compared to a frontal position during claw vibration (all other genera of the subtribe Nectemydina: see Appendix for literature citations).

2) Species-specific differences in the duration of the claw vibrations (recorded for *Trachemys scripta elegans* and *Pseudemys concinna*: Jackson and Davis, 1972a, b).

3) Species-specific differences in the vibration frequency of the claws [within a motion pattern] (recorded for *Chrysemys picta*: Ernst, 1971; and *Pseudemys nelsoni*: Kramer and Fritz, 1989).

4) Species-specific differences in the repetition frequency of displayed claw vibrations [within a courtship behavior sequence] (recorded for *Graptemys pseudogeographica* and *G. ouachitensis*: Vogt, 1978).

Moreover, Ernst (1971) notes for *Chrysemys picta* that the receptive female will respond to the claw vibrations of the courting male with an identical behavior, but with a slower vibration frequency, which is followed by copulation. Perhaps this active participation of the female plays an important role in the selection of the sexual partner because such participation during courtship is probably unique within the subtribe Nectemydina. However, during two years of observations of the courtship of two males and one female of *C. picta bellii*, I never observed claw vibration by the female as a response to a courting male. On the other hand it is known that female terrapins sometimes display behaviors similar to the courtship of the males in other behavioral contexts (see for example, Kramer and Fritz, 1989; Fritz, 1990). Therefore, it appears that more evidence is needed to ensure that the observations by Ernst were not misinterpreted.

In summary, more investigations are urgently needed, especially to determine what "cues" function as isolating mech-

anisms in the courtship of chelonians.

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Appendix

Turtle taxa in which ritualized head-nodding and/or foreclaw vibration are present (+) or absent (-) as elements of courtship behavior. The symbol (*) indicates information from Carpenter and Ferguson (1977); see this reference for original citations.

Species	Behavior pattern		Source
	Foreclaw vibration	Head-nodding	
Suborder Cryptodira (Hidden-neck Turtles)			
Kinosternidae (Mud and Musk Turtles)			
<i>Kinosternon bauri</i>	-	+	(*)
Emydidae (Pond Turtles)			
Emydinae (New World and European Pond Turtles)			
<i>Chrysemys picta</i>	+	-	(*)
<i>Deirochelys reticularia</i>	+?	-	Kreff (1951)
<i>Emys orbicularis</i>	-	+	Fritz, unpubl. data
<i>Graptemys barbouri</i>	+	-	(*)
<i>G. flavimaculata</i>	+	-	Vogt (1978)
<i>G. nigrinoda</i>	+	+	Vogt (1978)
<i>G. geographica</i>	-	+	Vogt (1978, 1980)
<i>G. o. ouachitensis</i>	+	-	Vogt (1978, 1980)
<i>G. o. sabinensis</i>	+	-	Vogt (1978, 1980)
<i>G. p. pseudogeographica</i>	+	+	Vogt (1978, 1980)
<i>G. p. kohni</i>	+	+	Vogt (1978, 1980)
<i>G. pulchra</i>	-	+	Shealey (1976)
<i>G. versa</i>	-	+	Fritz, unpubl. data
<i>Malaclemys terrapin centrata</i>	+	+	Sachsse (1984)
<i>Pseudemys concinna</i>	+	-	(*)
<i>P. floridana</i>	+	-	White and Curtsinger (1986); Fritz, unpubl. data
<i>P. nelsoni</i>	+	-	Kramer and Fritz (1989)
<i>P. texana</i>	+	-	Fritz (1989)
<i>Trachemys s. scripta</i>	+	-	Fritz, unpubl. data
<i>T. s. troostii</i>	+	-	Fritz, unpubl. data
<i>T. s. elegans</i>	+	-	(*)
<i>T. ornata ornata</i>	-	+	Fritz (1990)
<i>T. o. callirostris</i>	-	+	Fritz (1990)
<i>T. decorata</i>	+	-	Seidel (1988)
<i>T. decussata</i>	+	-	Seidel (1988)
<i>T. stejnegeri</i>	+	-	Seidel (1988)
<i>T. terrapen</i>	+	-	Seidel (1988)

Appendix (cont'd)

Species	Behavior pattern		Source
	Foreclaw vibration	Head-nodding	
Batagurinae (Old World Pond Turtles)			
<i>Rhinoclemmys funerea</i>	-	+	(*)
<i>R. pulcherrima incisa</i>	-	+	Hidalgo (1982)
<i>R. rubida</i>	-	+	Ernst and Barbour (1989)
<i>Sacalia bealei</i>	-	+	Rödel (1985)
Testudinidae (Tortoises)			
<i>Agrionemys horsfieldii</i>	-	+	Kirsche (1971)
<i>Geochelone carbonaria</i>	-	+	(*)
<i>G. denticulata</i>	-	+	(*)
<i>G. elephantopus</i>	-	+	(*)
<i>Gopherus flavomarginatus</i>	-	+	(*)
<i>G. polyphemus</i>	-	+	(*)
<i>Indotestudo forstenii</i>	-	+	(*)
<i>Manouria emys</i>	-	+	McKeown et al. (1982)
<i>Testudo graeca</i>	-	+	(*)
<i>Xerobates agassizii</i>	-	+	(*)
<i>X. berlandieri</i>	-	+	(*)
Trionychidae (Softshells)			
<i>Lissemys punctata andersoni</i>	-	+	Duda and Gupta (1981)
Suborder Pleurodira (Sideneck Turtles)			
Pelomedusidae (Helmeted and Tropical River Turtles)			
<i>Pelomedusa subrufa</i>	-	+	Bels (1983)
Chelidae (Snakeneck Turtles)			
<i>Acanthochelys spixii</i>	-	+	Lehmann (1988)
<i>Chelodina expansa</i>	-	+	Fritz, unpubl. data
<i>C. parkeri</i>	-	+	Fritz and Jauch (1989)
<i>Emydura albertisii</i>	-	+	Fritz, unpubl. data
<i>E. macquarrii</i>	-	+	Murphy and Lamoreaux (1978)
<i>Elseya latisternum</i>	-	+	Murphy and Lamoreaux (1978)
<i>Phrynops hilarii</i>	-	+	Fritz, unpubl. data