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Author(s): Hobart M. Smith and Louis F. James

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The Taxonomic Significance of Cloacal Bursae in Turtles¹

HOBART M. SMITH and LOUIS F. JAMES

University of Illinois, Urbana

The presence of cloacal bursae in some species of turtles was recorded 225 years ago by Perrault (1733:183), who stated in connection with his thorough anatomical description of *Testudo elegans* that a number of freshwater turtles possess these bursae although *T. elegans* does not. Bojanus figured them 85 years later in his marvelously illustrated anatomy of the European *Emys orbicularis* (1819–1821: figs. 157, 158), but called no special attention to their uniqueness. Geoffroy St. Hilaire (1827: pl. 2, figs. 2–4) illustrates a pair of cloacal depressions closely resembling openings into cloacal bursae in what he calls the “tortuë à boîte” (box turtle, no scientific name given), but describes the depressions as attachments for a pair of pelvic ligaments. Le Sueur (1839) was the first to emphasize the peculiar nature of these structures, but even he did not list the 12 species in which he had found them. He did state that they do not occur in *Gopherus polyphemus* and North American *Amyda* (species not cited). Not until 1876 (Anderson) was the occurrence of cloacal bursae in the order Testudines surveyed with any degree of thoroughness; 12 genera and at least 17 species (as now recognized) were sampled. Since then two other surveys (Hoffman, 1890:293–296, and Pickel, 1899) have appeared. In none of these has a sufficient number of forms been sampled to permit any conclusions concerning the occurrence of these bursae except in limited groups such as the trionychids, emyids, and testudinids. To our knowledge, only Loveridge and Williams (1956) have made use of these structures as a taxonomic character.

The cloacal bursae have been described in numerous anatomy textbooks since the second edition of Cuvier's *Leçons d'anatomie comparée* by Duvernoy in 1835 (not seen by us); all such accounts we have seen are based upon species in which the bursae or lack of them are recorded elsewhere. References to the earlier works are given in Hoffman and Pickel.

Our purpose herewith is: to summarize the occurrence of cloacal bursae in turtles, based upon published reports and our own investigations which include numerous species and genera and several families not pre-

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viously sampled; to evaluate the taxonomic significance of the structures; and to review their functional possibilities.

Terminology

Bojanus was the first to utilize a specific name, anal bursae ("bursae anales"). Le Sueur called the same structures auxiliary vesicles, also lumbar vesicles ("vessies auxiliares;" "vessies lombaries"). Cuvier called them accessory vesicles, Anderson cloacal bladders, Pickel accessory bladders, and in various other works they have been termed cloacal sacculi, anal bladders, cloacal bladders, and anal pouches.

We regard all names involving "anus" ruled out, since the structures are not anal in position but open into the anterior part of the cloaca. Furthermore non-homologous anal pouches of scent function do occur in many vertebrates. All names involving "bladder" are also ruled out, since usage of that term courts confusion with the unpaired, non-homologous urinary bladder. We regard the term "cloacal bursae" as the most distinctive and appropriate name applicable to these structures.

Taxonomic Distribution

We have utilized Mertens and Wermuth's checklist (1955), with a few minor alterations, as our standard for chelonian taxonomy. Sources of information for the species listed below are symbolized as follows: A, Anderson; B, Bojanus; H, Hoffman; L, Le Sueur; Pe, Perrault; P, Pickel; X, the present authors. Sexes and number (if more than 1) of the individuals we dissected are recorded after the X.

CHELYDRIDAE. Two monotypic genera, both with bursae: *Chelydra serpentina* (PX3 ♀); *Macrolemys temmincki* (X ♂).

KINOSTERNIDAE. Four genera, all lacking bursae: *Claudius angustatus* (X ♀); *Kinosternon abaxillare* (X ♀), *K. flavescens* (X2 ♀); *Staurotypus salvini* (X ♂); *Sternotherus carinatus* (X ♂), *S. odoratus* (PX ♂ ♀).

DERMATEMYIDAE. One monotypic genus, *Dermatemys mawii* (X ♂), apparently lacking bursae. The single specimen dissected was a somewhat desiccated juvenile.

PLATYSTERNIDAE. One monotypic genus, *Platysternon mega-locephalum* (A), with bursae.

EMYIDAE. Twenty-seven genera, of which seven (*Annamemys*, *Batagur*, *Callagur*, *Geoclemys*, *Hardella*, *Hieremys*, *Malayemys*) have never been examined. All species examined, except three, possess well-developed bursae. Those with bursae are as follows: *Chinemys reevesi* (X ♂); *Chrysemys picta* (PX ♂); *Clemmys guttata* (P), *C. insculpta*

(P), *C. japonica* (P); *Cuora amboinensis* (AP); *Cyclemys dentata* (APX ♂ ♀); *Deirochelys reticularia* (X ♂); *Emydoidea blandingi* (P); *Emys orbicularis* (B); *Geoemyda areolata* (X ♀), *G. depressa* (A), *G. grandis* (A), *G. trijuga* (A); *Graptemys geographica* (X ♀), *G. pseudo-geographica* (X ♂); *Kachuga dhongoka* (A), *K. kachuga* (A), *K. smithi* (A), *K. sylhetensis* (A), *K. tecta* (A); *Malaclemys terrapin* (PX ♀); *Morenia ocellata* (A), *Notochelys platynota* (X ♀); *Ocadia sinensis* (X ♀); *Orliitia borneensis* (X ♂); *Pseudemys rubriventris* (P), *P. scripta* (X ♀); *Siebenrockiella crassicollis* (A); *Terrapene carolina* (PX2 ♂ 2 ♀).

Those emyids lacking cloacal bursae are *Pyxidea mouhoti* (AX ♀), *Terrapene ornata* (X ♂ 2 ♀), and *T. mexicana* (X ♀).

TESTUDINIDAE. Seven genera, of which four have not been examined (*Goniocbersus*, *Homopus*, *Malacochersus*, *Pyxis*). None of the species examined of the other three genera possesses bursae: *Gopherus polyphemus* (L), *G. agassizi* (X ♂); *Kinixys erora* (X ♀); *Testudo denticulata* (X ♀), *T. elegans* (Pe), *T. graeca* (H).

CHELONIIDAE. Four monotypic genera, none with bursae: *Caretta caretta* (X ♂); *Chelonia mydas* (H); *Lepidochelys olivacea* (X ♀); *Eretmochelys imbricata* (H).

DERMOCHELYDIDAE. One monotypic genus, lacking bursae: *Dermochelys coriacea* (X ♀?).

CARETTOCHELYDIDAE. One monotypic genus, lacking bursae: *Carettochelys insculpta* (X ♀?).

TRIONYCHIDAE. Seven genera, two of which have not been examined (*Cyclanorbis*, *Cycloderma*). All species examined lack bursae: *Amyda cartilaginea* (X ♀), *A. spinifera* (X ♀ 3 ♂), *A. sinensis* (H ♀), *A. triunguis* (X ♂); *Cbitra indica* (A); *Pogania subplana* (X ♂); *Pelochelys bibroni* (A); *Trionyx punctatus* (A).

PELOMEDUSIDAE. Four genera, of which two possess bursae: *Erymnochelys madagascariensis* (X ♀); *Podocnemis expansa* (X ♂), *P. lewyana* (X ♂), *P. unifilis* (X2 ♀). The other two genera lack bursae: *Pelomedusa subrufa* (X ♂); *Pelusios subniger* (X ♀).

CHELIDAE. Ten genera, four of which have not been examined (*Batrachemys*, *Elseya*, *Mesoclemmys*, *Pseudemydura*). All species examined have large bursae: *Chelodina longicollis* (HP); *Chelus fimbriatus* (H); *Emydura krefftii* (P), *E. latisternum* (P), *E. macquarri* (H); *Hyromedusa maximiliani* (X ♀); *Phrynops geoffroyana hilari* (X ♀); *Platemys platycephala* (X ♀).

Discussion

The data now available indicate that the bursae are absent in all Kinosternidae, Dermatemyidae, Testudinidae, Cheloniidae, Dermochely-

dididae, Carettochelydidae and Trionychidae. They are present only in the families Chelydridae, Platysternidae, Emydidae, Pelomedusidae and Chelidae.

There are no exceptions known among the families in which the bursae are absent. All genera have been examined except a few in the Testudinidae and Trionychidae, and in none of these is there any reason to suspect a deviation from the known pattern. Only these two families are represented in both hemispheres and examples from both have been examined without discovery of differences. Pickel (1899:293) notes that an early textbook of anatomy credits the Testudinidae with bursae, but this is clearly in error. Hoffman (1890:296) reports another exception in a male *Amyda triunguis* with thin-walled bursae. He assumed it to be sexually dimorphic in *Amyda* since a female of another species lacked the bursae. Pickel (1899:297) expressed doubt on Hoffman's report for *A. triunguis*, and we deny its validity on the basis of a single male of this species we have dissected, and the universal absence of this structure in other trionychids examined by ourselves and others. Furthermore we have not detected any sexual dimorphism in the bursae of any species of turtle.

Among the 5 families in which bursae do occur a number of interesting variations are noteworthy. Two families are small and occur in but one hemisphere (Chelydridae, Platysternidae); no noteworthy variation of bursae occurs in them. The other three families occur in both hemispheres, and certain variants occur in each.

The representatives of the Pelomedusidae in the western hemisphere (*Podocnemis* of South America, 3 of 7 species sampled) possess well-developed bursae as does the single Old World species (*madagascariensis*) sometimes referred to the same genus but here (following Williams) regarded as constituting a distinct monotypic genus *Erymnochelys*. Neither of the two African genera (the monotypic *Pelomedusa*, and *Pelusios*, 1 species of 5 sampled)² have any vestige of them. On the basis of this character and others described by Williams (1950:536, 552), Baur (1888:421), and Boulenger (1889:191–200) it is evident not only that monotypic generic allocation of *madagascariensis* to *Erymnochelys* (rather than to *Podocnemis* as in Boulenger and in Mertens and Wermuth) is justified, but also that a subfamily separation of that species is probably valid on grounds not only of morphology but also of probably zoo-

² One species each of *Pelomedusa* and *Pelusios* occurs on Madagascar as well as in Africa. No species of these genera are limited to Madagascar. Since the island populations of the two species found in both areas are not distinguishable from the continental populations, it seems probable that, as already suggested (Darlington, 1957:211), man was responsible for establishment of the Madagascar populations.

geographic history (Williams, 1954; Darlington, 1957:211). The ancient Pelomedusidae may be envisioned as formerly possessing a Holarctic distribution and the primitive characteristics of cloacal bursae, large mesoplastra, a solid temporal region and the vertebral features unique to the family. With isolation of one group in Madagascar, one in Africa and one in South America, independent deviations from the primitive structure evolved. The South American *Podocnemis* retained the primitive skull and bursae but evolved small mesoplastra and curious saddle joints of the cervical vertebrae. The African genera lost the bursae and developed a strongly emarginate skull, but both retained the primitive vertebrae and one retained the primitive mesoplastra. The Madagascar genus retained all the primitive characteristics except the large mesoplastra. It is believed unlikely that *Erymnochelys* actually is any more closely related to *Podocnemis* than are *Pelusios* and *Pelomedusa*; the important similarities of a solid skull and cloacal bursae are most reasonably regarded as parallel retention of primitive characteristics, and reduction of the mesoplastra as a widespread trend. The two genera differ importantly in the cervical vertebrae, and Baur (*loc. cit.*) has pointed out that in *Erymnochelys*, in contrast to *Podocnemis*, a distinct centrale is present in the tarsus, the jugal is very large, and the ilium closely approximates the postneural.

In our opinion the distinctions evident between these groups of pelomedusids, coupled with their probable course of phylogeny, are reasonably expressed at a subfamily level. We hereby erect the subfamily ERYMNOCHELYDINAE for *Erymnochelys*, and the PODOCNEMINAE for *Podocnemis*. Williams (1950:554, 557) has already recognized the subfamily *Pelomedusinae* for *Pelomedusa* and *Pelusios* in conjunction with the erection of the subfamily *Bothremydinae* for certain extinct types. Unfortunately we are not at present in a position to attempt allocation to subfamily of the numerous fossil genera of the Pelomedusidae (see Romer, 1956:515).

Of the Chelidae, 6 genera are South American, 4 Australian. Data are available on two Australian and four South American genera, all with well developed bursae. Thus no continental distinction such as occurs in the Pelomedusidae is evident. However, all Pleurodira with bursae differ from other families in possession of a single large middorsal opening for the two bursae (see Pickel, 1899:298, fig. 4). In all other turtles the bursae open separately and with rather small apertures in the dorsolateral cloacal wall (see Pickel, 1899:295, 296, figs. 1, 2).

In the Emydidae, by far the largest family, two exceptions to the universal presence of bursae are known. Neither involves continental

distinctions; only two genera (*Clemmys*, *Geoemyda*) occur in both hemispheres, and species in each were examined without discovery of a distinction. One exception involves *Terrapene*, distinctive not only because two species (*T. ornata*, *T. mexicana*) completely lack bursae whereas another (*T. carolina*) has them, but also because the bursae where they do occur are extremely small (see Pickel, 1899:295, fig. 1). Examination of all members of the genus would be of great interest. It may be noted that *T. mexicana*, often regarded as a race of *T. carolina*, resembles *T. ornata* more than *T. carolina* in the character of the bursae, adding another distinctive character for the species. In our opinion the degeneration of the bursae in *Terrapene* can be explained on a functional basis (see following discussion).

The second exception involves *Cyclemys* of Mertens and Wermuth, consisting as of their checklist of the two species *dentata* and *mouhoti*. All specimens dissected of *dentata* have very well-developed bursae; both Anderson and Pickel have so recorded and two we dissected agree. However, Anderson reported that *mouhoti* lacks the bursae, and to our surprise the single example we dissected verified his observation, for only the faintest vestiges of invaginations marked the position of the bursae. No other turtles exhibit comparable variation within a single genus. Since Gray (1863) has already pointed out the existence of unique external features in the nature of the hinge, we regard the generic distinction of *mouhoti* from *Cyclemys* (Bell, 1834:17, type *dentata*) as strongly supported by the distinction in cloacal bursae. Fortunately the name *Pyxidea* (Gray, 1863:175, monotype *mouhoti*) is available for the species. Both *Cyclemys* and *Pyxidea* are monotypic as of Mertens and Wermuth's list, but it is likely that the wide-ranging and varied *C. dentata* will eventually prove to embrace at least two distinct species.

The unexpectedly marked difference between *mouhoti* and *dentata*, even though the species are placed in separate genera, makes it plain that not until all species, at least of terrestrial or semi-terrestrial habits, are examined can the taxonomic distribution of bursae in the Emydidae be considered assured. All species of "box" or "semibox" turtles, in which the greatest possibility of deviation exists, have, however, now been checked except for *Terrapene coahuila* and *T. nelsoni*, in which genus the known extent of variation will probably not be exceeded, and certain species of *Geoemyda*.

Function

The function of the cloacal bursae has been a point of speculation for centuries, without proposal as yet of a satisfactory explanation. Three possibilities have been proposed: respiration, storage of fluid (for ground-

softening as an aid to nest-excavation, or for marking the site of nests), and control of specific gravity.

It is our opinion that the primary survival value channeling evolution of the bursae was *respiration during aquatic hibernation and estivation*, and that groups of turtles lacking bursae do not hibernate (or estivate), or do not do so under water, or that some other technique is used for respiration under these conditions. We do not hypothesize, as has commonly been done in the past, that these structures are useful for respiration in non-hibernating periods. The failure of numerous workers in the past convincingly to demonstrate a respiratory function for the bursae may be due at least in part to the fact that these structures, even aided by the buccopharyngeal epithelium, are incapable of maintaining a rate of oxygen exchange adequate for the *metabolically active*, non-hibernating state: all turtles drown when submerged completely during seasons of activity, in the same waters that are freely inhabited by unrestricted turtles. This is true even of species with the largest bursae. The same turtles readily survive much longer periods of submersion during the period of hibernation.

Certainly it may be accepted that no vertebrate is capable of survival under water for extended periods, even in hibernation, unless it possesses gills or a capacity for some other sort of aquatic respiration. Frogs and salamanders use buccopharyngeal and skin respiration, and cloacal bursae may at present reasonably be regarded as serving a respiratory purpose in the same manner. It should furthermore be emphasized that the ability these bursae may provide for minimal aquatic respiration to continue at a level sufficient to provide the needs during hypometabolic states is of survival value not only at temperatures at or near freezing but also at those inactivating temperatures, such as between 40° and 60°F., that occur commonly in winters even in subtropical regions. It is our opinion that the presence of bursae indicates a *capacity* to survive under water at *low temperatures* for long periods: a capacity that has evolved in various chelonian lines in accordance with the selective pressures to which they were long subjected. We do not hypothesize that all turtles now possessing bursae utilize them, for obviously some have become adapted to life where hibernation is unnecessary but have evolved from ancestors that did hibernate and did possess bursae. Furthermore, we do *not* hypothesize that all turtles that hibernate under water possess bursae, but we *do* hypothesize that if bursae are absent the turtles must utilize some alternative respiratory device, such as the skin, buccopharyngeal epithelium, and perhaps even the cloacal lining. It is held axiomatic that any hibernating turtle must possess some such accessory respiratory organs, or hibernate

on land; and very few do the latter. That the bursae have had much survival value for carrying water to soften or mark (by odor) the ground in nest-building seems to us highly unlikely; the urinary bladder can and does serve these purposes in terrestrial types such as *Terrapene* and *Gopherus*.

If this hypothesis is correct, the cloacal bursae should be absent only in those groups that characteristically hibernate or estivate on land (therefore *Terrapene*, *Pyxidea mouhoti*, Testudinidae) or do not hibernate at all (true of Carettochelyidae, African Pelomedusidae, Dermatemyidae), or that not only do not hibernate but would be faced with a salt-balance problem were the bursae present (true of all marine turtles: Cheloniidae, Dermochelydidae). The exceptions to these generalizations are the Trionychidae and Kinosternidae, some members of which hibernate for extended periods under water. We hypothesize that (1) these two exceptions are, as groups, primarily tropical and subtropical turtles in which, because of the absence of selective pressures favoring the retention or evolution of bursae, the bursae were either lost in early phylogeny or were never developed; and that (2) the few species of these groups existing in peripheral areas where underwater hibernation is necessary respire by some other device such as the skin or buccopharyngeal epithelium.

The absence or great reduction of the bursae in *Terrapene* we interpret as an expected resultant of the presumably long-established habit of hibernating on land where the services of aquatic respiratory organs are not required. No other emyid turtles, to our knowledge, hibernate on land although the absence of bursae in *Pyxidea mouhoti* suggests that it either does not hibernate at all or must hibernate on land. If *P. mouhoti* simply does not hibernate at all (thus having no need for bursae), as seems likely in view of its range, it constitutes an unusual exception for many other emyids inhabit tropical and subtropical zones where neither hibernation nor estivation are practiced, yet in no other have the bursae become degenerate. Both *Pyxidea* and *Terrapene* are box turtles, having hinged plastra, but other box turtles do not exhibit degeneration of the bursae.

The presence of bursae in the non-hibernating Pleurodira, excepting only the African representatives, suggests that in these turtles the bursae may have evolved as a resultant of a somewhat different environmental stress, and we suggest that this may have been underwater estivation, which would exert much the same sort of selective pressure as underwater hibernation. The rather different structure of the bursae in the Pleurodira confirms that these organs either evolved independently in

this suborder or these turtles had a long ancestry independent from other turtles. The absence of the bursae in African representatives of the Pelomedusidae may be (1) a reversion to an ancestral condition with loss of the necessity for hibernation or estivation, or (2) a retention of a primitive condition, or (3) the substitution of another means of aquatic respiration as in the northern Kinosternidae and Trionychidae. Inasmuch as we regard possession of bursae as primitive in turtles, we favor the third possibility, but we have no suggestion of what selective pressures may have operated to bring about this change.

Unfortunately the habits and habitats of living pleurodires furnish no tangible clues to the selective pressures responsible for the peculiarities of the bursae of this group. The accounts of various pleurodires in Loveridge (1941) for African species, Waite (1929) for Australian species, and Gadow (1923) for South American species does not reveal any consistency in habits or habitat that correlates well with the presence or absence of bursae. The African *Pelomedusa* estivates for long periods on land, but *Pelusios* is primarily an inhabitant of permanent waters.

Summary. As a result of our dissections and survey of the literature, embracing every family and most genera of living turtles, we conclude that:

1. Paired cloacal bursae are present only in the Chelydridae, Platysternidae, Emyidae, South American and Madagascar Pelomedusidae, and the Chelidae. Absence is regarded as a secondary loss except perhaps in marine types.

2. In the Pleurodira the bursae possess a single large mid-dorsal opening; in all other turtles each bursa has a small dorsolateral cloacal opening.

3. The bursae are present in all members of the groups indicated, except in *Terrapene* and *Pyxidea mouhoti*.

4. Cloacal bursae are thought to have evolved under selective pressures favoring the perfection of an organ serving to provide the minimal respiration needs existing during extended periods of underwater hibernation (for most turtles) or estivation (for the Pleurodira); this is regarded as the function of the bursae in those species in which a function is retained.

5. Not all species with bursae are regarded as utilizing them (tropical emyids), and not all species that hibernate or estivate under water have them (temperate trionychids, kinosternids). In the latter, the skin or buccopharyngeal epithelium are thought to function as analogs of the bursae.

6. The absence or reduction of bursae in *Terrapene* is thought to

be correlated with its unique habit of terrestrial hibernation. Absence in *Pyxidea mouhoti* may possibly be explicable in the same manner; its habits are unknown to us.

7. On the basis of plastral characters and the absence of bursae in *mouhoti* the resurrection of *Pyxidea* for this species is warranted; the other, formerly congeneric species, *Cyclemys dentata*, possesses well-developed bursae. In no genus of turtles are the bursae well developed in one species, absent in another.

8. African pelomedusids lack bursae; South American and Madagascar representatives possess them. This distinction, coupled with the presence of saddle cervical joints in the South American group, a deep temporal notch in the African group, and their probable course of isolation, is regarded as significant at the subfamily level; the South American subfamily is designated the *PODOCNEMINAE* (new), the African subfamily the *PELOMEDUSINAE* of Williams, the Madagascar subfamily the *ERYMNOCHELYDINAE* (new).

9. An explanation of the absence of bursae in the African Pelomedusinae is not obvious.

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