A Statistical Study in Fossil Cowries

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HEILPRIN (1887, p. 86) established the monotypic genus *Siphocypraea* as the type species *Cypraea (Siphocypraea) problematica* HEILPRIN (*ibid.*, p. 87, pl. 4, fig. 12) differs from all fossil and living cowries by the curious posterior outlet which turns to the right so that its top opens towards the base (the name *Siphocypraea* is deplorable because its peculiarity consists in the posterior outlet and not in the quite normal anterior one, from which the animal's sipho protrudes). The species was said to be common in the Pliocene ("Floridian") beds at Fort Thompson, Caloosahatchee River, south western Florida.

Though the characters of the posterior outlet of *Siphocypraea problematica* are unique, HEILPRIN (*l. c.*, p. 87) compared it with *Cypraea carolinensis* CONRAD (1841, p. 346, pl. 2, fig. 6) and DALL (1890, p. 167) with the living *Cypraea mus* LINNAEUS, 1758. SCHILDER (1926, p. 367) recognized that *Siphocypraea problematica* is an "abnormal descendant" of *Cypraea carolinensis* and adopted the generic name *Siphocypraea* in all subsequent papers (1932, p. 119; 1941, p. 82) to designate the group of cowries which includes, besides the two species named above, also *S. henekeni* (SOWERBY, 1849) and its American allies including the only Recent survivor *S. mus* from the north coast of Colombia and Venezuela.

Nevertheless, GARDNER (1948, p. 213) established a "section" AKLEISTOSTOMA with *carolinensis* as type species on account of the weak columellar teeth and the absence of the "curious hook shaped opening" of *problematica;* GARDNER observed that the tendency of columellar teeth to become obsolete also occurs in the Recent *S. mus.* Moreover, WOODRING (1957, p. 88) established the subgeneric name *Muracypraea* with the just mentioned *mus* as type species, including also its Tertiary allies *henekeni,* etc.

In a recent paper, however, OLSSON & PETIT (1964, pp. 556 - 560, pl. 83) have demonstrated that there is a gradual evolution in development of the posterior outlet from the late Miocene *Siphocypraea carolinensis carolinensis* (CONRAD, 1841) (Duplin beds of North Carolina) over *S. carolinensis floridana* (MANSFIELD, 1931) and two new subspecies of *S. carolinensis,* viz. *S. c. hughesi* and *S. c. transitoria* (all three from Upper Miocene Pinecrest beds of Florida) to *S. problematica* (HEILPRIN) (overlying Pliocene Caloosahatchee marls of Florida).

In 1963 and 1964 I received as gift from Mrs. J. W. Donovan (Palm Beach, Florida) many Neogene cowries from Florida, true *Siphocypraea problematica* as well as specimens which evidently are intermediate between *S. problematica* and the less singular species of *Siphocypraea,* especially *S. carolinensis.* I prepared a statistical paper and intended to name the connecting link (see DONOVAN 1963), but I postponed to publish the paper when I learned that Dr. A. A. Olsson had a paper on this subject in press, naming the intermediates *hughesi* and *transitoria.* As this paper is now published (OLSSON & PETIT, 1964), I should like to integrate it with my statistical research. The examined specimens are not very numerous if compared with the several hundred *Siphocypraea* preserved in American collections. Nevertheless, they seem sufficient to demonstrate my methods of investigating such a problem of gradual evolution.

In this paper I have restricted the study to the geologically younger members of the non-tuberculate branch of *Siphocypraea,* viz. the species *S. carolinensis* and *S. problematica.* The total range of variation in each essential character has been divided into six equal classes, numbered from 1 to 6, so that the extreme development in *S. carolinensis* is called 1, the other extreme occurring in *S. problematica* is called 6. The five chief characters are:

a) the length of the shell (measured in tenths of a mm);
b) the relative breadth (expressed in percent of the length);
c) the average closeness of teeth on both lips (classified by letters according to SCHILDER, 1958; the formula of labial : columellar teeth *il* becomes *k,* as well as the formula *li, hm, mh,* etc., while the mean of *kl, im,* etc. becomes *k*.5);
d) the width of the aperture in its central part (varying from the very broad aperture in *S. carolinensis* to the narrow one in *S. problematica*);
e) the turning of the posterior outlet to right (characterized by the flattened terminal part of the canal which tends towards the dorsum in *S. carolinensis*

but almost towards the base in *S. problematica*, and by the upper part of its right wall which, when seen from behind, is about vertical or even bent to the left in *S. carolinensis* as it is in most cowries, but becomes about horizontal in *S. transitoria* and invertedly vertical in extreme *S. problematica*: therefore one can classify the outlet by the turning of the top of its right wall from 0° to almost 180°, i.e. through two right angles).

The six classes have been defined as follows (the quoted figures illustrating the aperture and the posterior outlet refer to Olsson & Petit, 1964, pl. 83):

class	1	2	3	4	5	6
length (mm)	27 - 35	35 - 45	45 - 55	55 - 65	65 - 75	75 - 81
breadth (%)	69 - 73	66 - 68	63 - 65	60 - 62	57 - 59	53 - 56
teeth	g.5 - h.5	i - k	k.5 - l.5	m - n	n.5 - o.5	p - q
aperture	very wide	wide	rather wide	rather narrow	narrow	very narrow
= fig.	1 a	2 a	3 a	5	-	4 a
post. outlet	0°	30°	60°	90°	120°	150°
= fig.	1 b	2 b	5 b	-	3 b	4 b

It seems useful to publish a complete list of the examined specimens (preserved in CS = coll. Schilder or BM = British Museum, Natural History) and good pictures published in various papers (marked with an asterisk *) so that students can plot other pairs of characters (or sums of characters) against each other if they think such an arrangement more apt to distinguish the species than the way I have published below. Each specimen is indicated first by a letter designating the species to which it seems to belong according to my investigations, viz.:

c = *carolinensis* *h* = *hughesi* *p* = *problematica* *t* = *transitoria*

the letter is followed by a formula composed of figures which indicate the observed class in the five characters enumerated above: the first figure indicates the length, the second figure indicates the class of breadth, etc. (for each character the low figures indicate tendency toward *carolinensis*, high figures characterize *problematica*; x = class unknown).

Florida

St. Petersburg, Pinellas Cty.:
* Olsson & Harbison, 1953, pl. 27, fig. 2 (*problematica*): *p* 35455

Acline, Charlotte Cty., "Pliocene":
CS (don. Helen Tucker, 1933): *p* 44556, *p* 55646, *p* 36556, *p* 56646

Fort Denaud, Caloosahatchee River, Hendry Cty.
CS (leg. Donovan, 1943; don. Donovan, 1964): *p* 45655, *p* 34646, *p* 45456, *p* 35556

Fort Thompson, Caloosahatchee River, Hendry Cty.:
* Heilprin, 1887, pl. 4, fig. 12 (holotype of *problematica*): *p* 56556
* Du Bar, 1958, pl. 11, fig. 1 (*problematica*): *p* 36x56

Caloosahatchee River, Hendry and Glades Counties:
* Heilprin, 1887, pl. 16 a, fig. 73 (*problematica*): *p* 35xx6
* Cossmann, 1903, pl. 7, figs. 3, 7 (*problematica*): *p* 45655
CS (from an old collection): *p* 45556
BM (No. 11809, from W. F. Webb, Albion, N. Y.): *p* 45556, *p* 45556, *p* 46456, *p* 56556, *p* 55656
BM (Nos. 4782 and 9523, no collector): *p* 45454, *p* 34455, *p* 46456

Harney Pond Canal, Glades Cty. (WNW of Lake Okeechobee):
* Olsson & Petit, 1964, pl. 83, fig. 4 (*problematica*, Caloosahatchee marl): *p* 65466
CS (leg. Raeihle, 1961; don. Old, 1963): *p* 35445, *p* 45455, *p* 44446
CS (leg. Emerson, 1960; don. Old, 1964): *p* 45445, *p* 45455, *p* 46556, *p* 46556

Clewiston, Hendry Cty. (SW of Lake Okeechobee):
CS (leg. Donovan, 1962; don. Donovan, 1964): *h* 21223, *t* 54345, *p* 46556
CS (leg. Donovan, 1963, don. Donovan, 1964): *h* 31123, *h* 33334, *t* 43444, *p* 35446, *p* 45556

Kissimee, Okeechobee Cty. (15 miles NNW of Lake Okeechobee):
CS (leg. Donovan, 1963; don. Summers, 1963): *h* 23232, *h* 22332, *h* 22223, *h* 32423, *h* 42423, *t* 46244, *t* 44454, *t* 43335, *t* 44445, *p* 33456, *p* 45456, *p* 35466
CS (leg. Donovan, 1963; don. Donovan, 1964): *h* 43323, *h* 53233, *t* 34554, *t* 55245, *t* 54355, *p* 35545, *p* 44455, *p* 44456, *p* 45456, *p* 46666

Brighton, Okeechobee Cty. (NW of Lake Okeechobee):
* Olsson & Petit, 1964, pl. 83, fig. 3 (holotype of *transitoria*, Pinecrest beds): *t* 64335
* Olsson & Petit, 1964, pl. 83, fig. 5 (holotype of *hughesi*, Pinecrest beds): *h* 51343

CS (leg. Donovan, 1962; don. Summers, 1963): *h* 33222 jun., *h* 33223, *h* 54233, *h* 31233, *h* 43333, *h* 52333, *h* 44314, *h* 53224, *h* 43424, *t* 43235 juv., *t* 33345, *p* 55456

CS (leg. Donovan, 1962; don. Donovan, 1964): *h* 32222, *h* 33123, *h* 64324, *t* 44354, *t* 62435

CS ("Brighton or Clewiston" don. Donovan, 1963): *h* 42334, *h* 23244, *t* 54335

Tarrytown, Indian Pierce Canal near Brighton, ibid.:

CS (leg. Donovan, 1963; don. Summers, 1963): *p* 54556

Tamiami Trail 42 miles W of Miami, Dade and Monroe Counties (13 miles E of Pinecrest):

* Mansfield, 1931, pl. 1, figs. 2, 7 (holotype of *floridana*): *f* 64221

* Mansfield, 1931, pl. 1, fig. 6 (paratype of *floridana*): *f* 52221

* Olsson & Petit, 1964, pl. 83, fig. 2 (*floridana*, Pinecrest): *f* 66321

Acline, Charlotte Cty. (see also above):

* Tucker & Wilson, 1932, pl 5, figs. 4, 5 (*floridana*): *f* 64211

Port Charlotte, Charlotte Cty.:

CS (don. Du Bar, 1964: "Tamiami beds"): *f* 32111, *f* 51221, *f* 43311, *f* 34411, *f* 45321, *f* 23112

North (and South) Carolina

Natural Well, Duplin Cty., North Carolina:

* Gardner, 1948, fig. 2 (*carolinensis*): *c* 44xx1

* Olsson & Petit, 1964, pl. 83, fig. 1 (*carolinensis*): *c* 63111

Duplin Cty., North Carolina:

* Conrad, 1841, pl. 2, fig. 6 (holotype of *carolinensis*): *c* 43211

BM (No. 7893): *c* 53112, *c* 54211

North Carolina:

* Emmons, 1858, fig. 131 (*carolinensis*): *c* 42111

* Cossmann, 1903, pl. 7, figs. 5, 9 (*carolinensis*): *c* 54111

Pee Dee, Horry District, South Carolina:

* Tuomey & Holmes, 1857, pl. 27, figs. 1, 2 (*carolinensis*): *c* 42311

Cape Fear River, North Carolina:

* Ingram, 1939, pl. 9, fig. 2 (holotype of *pilsbryi*): *c* 12211; ibid. p. 120 (paratype of *pilsbryi*): *c* 11xxx

There is a distinct correlation between the four last named characters, e. g. the classes of breadth and dentition, and the classes of aperture and posterior outlet:

dentition \ breadth	1	2	3	4	5	6
6	-	-	-	1	4	2
5	-	-	-	3	6	6
4	-	3	3	7	13	2
3	1	4	6	7	1	1
2	3	4	8	4	1	1
1	1	2	4	1	-	-

posterior outlet \ aperture	1	2	3	4	5	6
6	-	-	-	5	23	3
5	-	-	5	7	8	-
4	1	3	3	3	4	-
3	-	8	4	1	-	-
2	2	2	2	-	-	-
1	11	5	-	-	-	-

The length, however, varies rather independently from the other characters, e. g. from the posterior outlet:

posterior outlet \ length	1	2	3	4	5	6
6	-	-	8	16	7	1
5	-	-	5	9	4	2
4	-	1	2	8	1	1
3	-	2	5	3	4	-
2	-	2	2	-	1	-
1	1	1	2	6	4	4

Therefore we can add the figures indicating the breadth, dentition, aperture, and three times the figure indicating the posterior outlet, as it is evidently the most important character in the evolution of *Siphocypraea*; the length should be omitted altogether. If we plot these sums of characters against the various localities we obtain the following diagram:

	Sum	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
M	St. Petersburg																							1							
L	Acline																										1	1	2		
K	Fort Denaud																									1	2	1			
J	Fort Thompson																												①		
H	Caloosahatchee																				1		1			1		5	2		
G	Harney Pond										*hughesi*												2	2	1			1	2		
F	Clewiston							1	1							1		1			1					1		1	1		
E	Kissimmee								2	1		4							2	1	2	2	1	1	1	1	2	1			1
D	Brighton						1	1		2	1	②	2	2	2	2		1	2	③							2				
C	Tamiami			1		①			1																						
B	Acline, P. Char.	1	1		1	2	1	1			*floridana*								*transitoria*										*problematica*		
A	Carolina	1	2	③	1	1	*carolinensis*																								

valid taxa (with names) ◯ holotypes

In this table the localities have been arranged according to the presumable geological age of the strata in which the fossil shells have been collected. According to Olsson & Petit (1964, p 514) the Upper Miocene Duplin age of Carolina (A) is contemporary with the Pinecrest beds of Florida; but from the successive development of characters in *Siphocypraea* I suspect that they are slightly older, even older than the Pinecrest beds from which *S. floridana* came (B, C). In the (possibly upper) Pinecrest beds around Lake Okeechobee (D - F) the two intermediates named by Olsson & Petit in 1964 occur in different percentages, but these localities also supply the true *S. problematica,* probably coming from the uppermost cowrie-bearing beds, the Pliocene Caloosahatchee marls. The absence of these intermediates in the remaining localities (G - L) may be accidental, as the Pinecrest beds also occur there underlying the Caloosahatchee marls from which the collected *S. problematica* undoubtedly came.

The taxonomy of the six taxa *pilsbryi, carolinensis, floridana, hughesi, transitoria* and *problematica* is difficult to be decided, as there is a continuous development of characters; these characters do not change equally as in every specimen some characters may be rather primitive, while other characters are more advanced, so that the sum of characters only indicates the place of the shell within the trend of evolution. In my opinion three species can be distinguished:

Siphocypraea Heilprin

(differs from the other Cypraeorbini with smooth fossula by the flat, slightly umbilicate spire)

(Akleistostoma) Gardner

(posterior outlet vertical as in other Cypraeidae)

1. *S. (A.) carolinensis* (Conrad) from late Miocene beds of Carolina with the local dwarf variety *pilsbryi* (Ingram) and the often more callous geographical (and probably also stratigraphical) subspecies *floridana* (Mansfield) from the late Miocene Pinecrest beds of Florida.

(Siphocypraea) Heilprin

(posterior outlet dilated above to being recurved)

2. *S. (S.) hughesi* Olsson & Petit with its ecological (or also younger stratigraphical?) subspecies *transitoria* Olsson & Petit from Pinecrest beds of central Florida: *hughesi* approaches *floridana,* while *transitoria* gradually passes into *problematica.*
3. *S. (S.) problematica* (Heilprin) from the Pliocene Caloosahatchee marls of Florida with exaggerated characters of the posterior outlet which probably caused this extreme terminal offspring to become extinct since Pleistocene times.

The following key may be useful to identify the taxa of *Siphocypraea.*

1 Posterior outlet vertical, parallel-sided as in other cowries 2
- Posterior outlet dilated or recurved in its upper part 4
2 Base flattened 3
- Base mostly convex to swollen ..... *S. carolinensis floridana*
3 Shell less than 30 mm long .. *S. carolinensis pilsbryi*
- Shell more than 30 mm long ..... *S. carolinensis carolinensis*
4 Posterior outlet dilated above, but hardly recurved *S. hughesi hughesi*
- Posterior outlet distinctly recurved to the right .. 5
5 Posterior outlet rather recurved, aperture wide *S. hughesi transitoria*
- Posterior outlet extremely recurved, aperture narrow ..... *S. problematica*

Color. One *Siphocypraea carolinensis* (British Museum) seems to exhibit large brown blotches on the dorsum, while in *S. hughesi* and in *S. problematica* the dorsum is more finely punctate with fulvous; in *S. floridana, S. hughesi* and *S. problematica* several specimens show still the brown color of the teeth as it is in the recent *S. (Muracypraea) mus* (Linnaeus).

SUMMARY

There is a gradual evolution of several morphological characters in the Neogene *Siphocypraea,* by the sum of which three species and two subspecies can be distinguished; the excessive development of the posterior outlet in the Pliocene *S. problematica* seems to have caused the extinction of this group of cowries.

In future collecting these fossils the exact position of each specimen within the stratigraphical beds should be indicated carefully so that the chronological development of characters could be shown more accurately than in this paper.

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