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A Revised Morphometric Formula for the Characterization of Cowries (Gastropoda: Cypraeidae)

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Text-Figs 1-20, 2 Tables

Keywords

Cypraeidae, morphometric formula, *Macrocypraea, Monetaria, Umbilia,* mass ratio.

Abstract

A variety of formulae have been proposed throughout the history of morphometric analysis of cowry shells based on shell dimension and tooth count data. A brief historical overview and comparison of various formulae notations for the presentation of cowry morphometric data is provided. Analyzing shells of the genera *Macrocypraea*, *Monetaria* and *Umbilia* revealed that the ratio between height and width, which is not used in current formulae, complements conchological criteria. For comparative purposes, normalized tooth counts work better than absolute counts. A shell mass ratio of measured versus theoretical mass allows objective comparison of shell volume and shell wall thickness. A revised cowry formula is proposed that includes the addition of the height to width ratio, and the mass ratio.

Zusammenfassung

Zu morphometrischen Analysen an Kauri-Gehäusen wurde eine Reihe von Formeln eingeführt, die auf Gehäuseabmessungen und Zahnzahl basieren. Eine kurze historische Übersicht vergleicht die verschiedenen Ansätze, solche morphometrischen Daten formelmäßig darzustellen. Analysen an Gehäusen der Gattungen *Macrocypraea, Monetaria* und *Umbilia* zeigen, dass das Verhältnis zwischen Gehäusehöhe und -breite hohe Aussagekraft besitzt, aber in bestehenden Formeln keine Berücksichtigung findet. Für vergleichende Analysen ist die Normalisierung der Zahnzahl besser geeignet als die bloße Anzahl. Das relative Gehäusegewicht dient zur Charakterisierung von Gehäusevolumen und Wanddicke und wird als relativer Massewert einer revidierten Kauri-Formel hinzugefügt, die auch das Verhältnis aus Höhe zu Breite berücksichtigt.

Abbreviations

av = average
ct = counted
CT = columellar teeth
ctd = columellar tooth density
H = height (mm)
H/L = height/length ratio in %
H/W = height/width ratio in %
L = length (mm)
LSS = labral spot size
LT = labral teeth
ltd = labral tooth density
mD = mass (actual, weighed in grams)
mR = mass ratio (see below)
nl = normalized
SD = spire diameter (mm)
W = width (mm)
W/L = width/length ratio in %

Introduction

Morphometrics as defined by OXNARD (1978) is, “the characterization of biologically relevant forms and patterns in ways that allow their quantitative handling: a considerably wider definition than usual” (p. 219). For a more constrained or a "stricter definition,” as well as a brief history of morphometric analysis, see REYMENT (2010). Nevertheless, OXNARD's rather encompassing view of morphometrics is especially appropriate when applied to the study of cowries (Cypraeidae). Using so called “traditional” or multivariate morphometric techniques, (see ROHLF & MARCUS 1993), comparisons between, as well as within, genera and species of cowries are possible. This is accomplished by using data sets of physical characteristics such as size and weight measurements and various ratios of these elements. Crucial to the validity and reliability of the statistical results obtained from using such quantitative data is the repeatable and objective nature of the measurements. Historically, the cowry literature has provided this type of data in addition to descriptions of more subjective features such as color, pattern, and spotting. Rarely can these subjective (or qualitative) features be reliably quantified, and they therefore have limited use in traditional multivariate statistical analysis. The qualitative features, though not necessarily useful in mathematical statistics, can however, provide useful and important taxonomical information.

Determinate growth is a characteristic that the cowry shares with only a few other families of gastropods (VERMEIJ & SIGNOR 1992; VERMEIJ 1993). Once the labrum has formed a fold that narrows the aperture, the shell growth becomes limited to the formation of callus on the extremities and along the sides. Eventually, ridges of differing thickness and number, the so-called teeth, are formed along the borders of the aperture. Hence, the mature cowry shell offers a number of specific physical features such as size (length, width, and height), tooth count, and weight (mass × gravity), which can be accurately and reliably measured and compared since these features become relatively static in mature adult specimens. Morphometric analysis of this quantitative data is integral to the study of cowries. It provides information beyond ecological, geographical, geological, molecular, and descriptive conchological data.

Most published work on cowries presents morphological data in an easily interpreted manner such as tabular, graphical, or formulaic presentation, (SCHILDER & SCHILDER 1938-1939, 1952; LORENZ & HUBERT 2000; LORENZ 2001, 2002). The term "formula" refers to the presentation of the data using characters such as parentheses or brackets to distinguish and separate the individual values, as typically used in mathematical equations. For the purpose of this report we have limited our review and analysis to only those studies and publications which utilize a formula style of notation to present the morphometric data.
In the following work we will present a brief historical overview of the development and evolution of the "cowry formula." To determine the effectiveness of these various formulae in the characterization of cowries we collected sample data from a variety of genera, species, and subspecies of cowries. We describe the methods used in obtaining our data and present the results from a number of comparisons. The usefulness of a height-width ratio and a mass ratio metric is shown in our comparisons and is ultimately included in a suggested formula revision.

Historical Overview of Cowry Formulae for Morphometric Data

The various formulae are reproduced in the same way as in the original reference.

VAYSSIÉRE (1910): L / W, LTct + CTct

VAYSSIÉRE presented the earliest use of a formula that we have determined, noting that if height is measured it would be added to the denominator with a + sign: **[L / (W + H), LTct + CTct]**.

SCHILDER, F. A. & SCHILDER, M. (1927 to 1963)

The husband and wife team, FRANZ A. SCHILDER (1896-1970) and MARIA H. SCHILDER (1898-1975), are widely recognized as being among the most important and prolific contributors to the scientific study of the cowries. Combined, they published more than 400 articles, primarily concerning malacology (WALLASCHEK 2006, ZEISSLER 1972, ZILCH 1971). The wealth of data in their publications was presented in forms of shorthand notation, abbreviations, and stylized formulas for size measurements and tooth counts. The development of their formula to abbreviate measurements and tooth counts can be followed chronologically:

SCHILDER, F. A. (1927): L (W/L – H/W)

SCHILDER's first approach to a formula for cowries did not give tooth count data, but did give width and height ratios.

SCHILDER, F. A. (1928): L : (W/L) / (H/L) – LTct : CTct

This formula had tooth counts added and the ratio for height was changed from (H/W) to (H/L). SCHILDER stated that the ratio (H/L) was better than (H/W), but, no reason was given.

SCHILDER, F. A. (1937): L (W/L . H/L) LTct : CTct (LTnl : CTnl)

Where: $LTnl = 7 + (LTct - 7)\sqrt{(25 / L)}$; $CTnl = 7 + (CTct - 7)\sqrt{(25 / L)}$;

During the period 1928-37 the SCHILDERs conducted several studies on cowries, (F. A. SCHILDER 1932, 1933a, 1933b; M. SCHILDER & F. A. SCHILDER 1936). Of particular importance was the analysis of the relationship between shell length and the number of teeth (F. A. SCHILDER 1930, 1931). This version was the first to include "normalized" tooth counts, which is a complex formula that changes the actual number of counted teeth to the normalized number of teeth on a theoretical shell of 25 mm length. The origins of the normalized tooth count formula are discussed in our chapter "Dentition (LT, CT)" in the Observations section.

SCHILDER & SCHILDER (1938-1939): (L . W/L . LTnl . CTnl)

Published in their "Prodrome," this simplified version provided the basis for virtually all subsequent formulae.

SCHILDER, F. A. & SUMMERS (1963): L (W/L) LT : CT ltd ctd

This article is one of the first uses of SCHILDER's alphabetical notation for tooth density (F. A. SCHILDER 1958). Tooth counts were given as averages, and not normalized. In some papers after 1958, normalized tooth counts were still used instead of averaged tooth counts (F. A. SCHILDER & SCASE1964).

WALLES (1980): L, W, H, (W/L ; H/L)

The presentation of morphometric data in this paper was not strictly a formula, but it did once again give an H/L ratio. The author briefly discussed new metrics involving the angle of inclination of the teeth, the angle of the terminal ridge versus the shell axis, and the angle of the anterior canal versus the shell axis. WALLES was developing a comprehensive morphometric numerical formula, but to the best of our knowledge, this was never published (see Anonymous 1976; WALLES 1978, 1979, personal communication with the second author in 1983).

LORENZ (2001): L (W/L – H/L) LTnl : CTnl

The taxonomic publications by LORENZ on the Cypraeidae make use of formulae to present morphometric data (LORENZ 1985, 1997, 2002, 2009). In this formula, LORENZ added the H/L ratio to the SCHILDER & SCHILDER 1938-1939 version.

MORETZSOHN (2003): L / (W/L) / CTnl / SD / LSS

In this formula, proposed in his doctoral thesis on a study of the genus *Cribrarula*, MORETZSOHN eliminated the labral tooth count data and added average spire diameter and average labral (marginal) spot size to SCHILDERS' 1938-1939 version. The author refers to this as a “New cowrie formula” (p. 116).

LORENZ & BEALS (2012, in this issue)

These authors used the formula proposed by LORENZ (2001). In addition, they also introduced a new metric, the mass ratio (mR), the ratio of the actual measured mass of the shell (mD) to the theoretical mass of a block of aragonite of the same linear dimensions.

Material and Methods

Taxa representing three contrasting groups of cowries were used in this study, *Monetaria* (n = 90), *Macrocypraea* (n = 134), and *Umbilia* (n = 172). A variety of other taxa were also examined, primarily to visually illustrate particular morphometric features. Only fully adult specimens were measured, weighed and had their teeth counted. The adulthood of a cowry shell was determined by examination of various morphological features: the labrum and teeth are fully formed on both sides of the aperture, the marginal callosities obscure the fine transverse ridges of the juvenile bulla-shell dorsally above the labrum, and the spire is at least partly covered by callus. For illustration, the growth cycle of *Monetaria caputserpentis* (LINNAEUS 1758) from a young juvenile bulla-shell to an adult is shown in Figure 1.

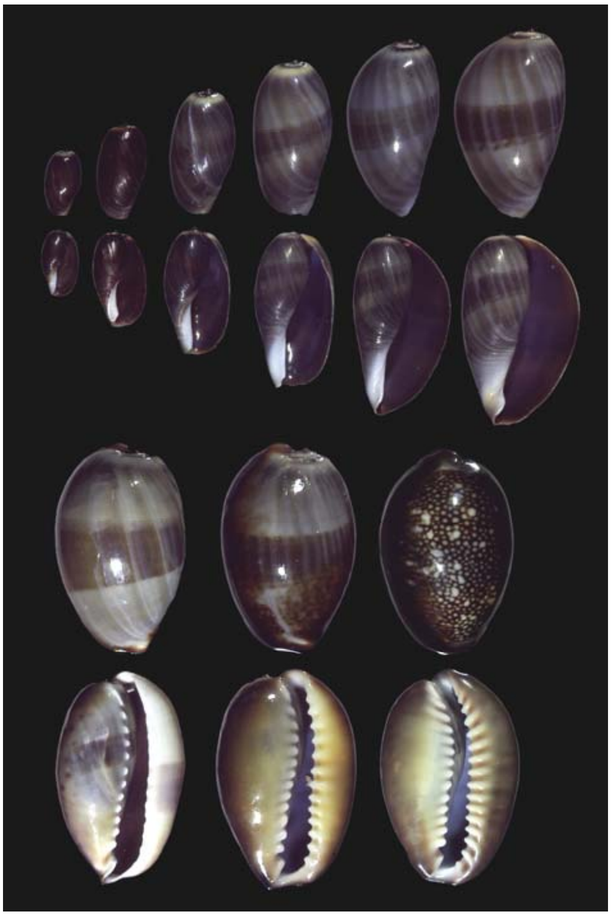

Figure 1: Sequence of growth stages in *Monetaria caputserpentis* (LINNAEUS 1758) from juvenile bulla-shell (top left) to mature adult (bottom right).

The small-shelled widespread Indo-Pacific members of the *Monetaria annulus* species-complex are planktonic developers (hatch as a free swimming veliger). We compared three sibling species: *M. annulus* (LINNAEUS 1758) from India (n = 30), *M. obvelata* (LAMARCK 1810) from Tahiti (n = 30), and *M. sublitorea* LORENZ 1997 from Western Samoa (n = 30).

Medium to quite large-shelled members of the *Macrocypraea* are also planktonic developers. We compared the three sibling species from a variety of locales: *M. cervus* (LINNAEUS 1771) from the Florida Panhandle area (n = 6), Florida Keys (n = 30), and Cuba (n = 20); *M. zebra* (LINNAEUS 1758) from the Florida Keys (n = 40) and Brazil (n = 8); and *M. cervinetta* (KIENER 1843) from Panama (n = 30).

In contrast, the genus *Umbilia* consists of large-shelled intracapsular developers (hatch as a crawling veliger). *U. armeniaca* is distributed along the southern half of Australia, with four morphologically and geographically distinct subspecies: *U. a. armeniaca* (VERCO 1912) along the Great Australian Bight (GAB) (n = 100), *U. a. clarksoni* LORENZ & BEALS 2012, off Esperance (n = 15), *U. a. andreyi* LORENZ & BEALS 2012, from the Cape Leeuwin to Rottnest Shelf area in the West (n = 15), and *U. a. diprotodon* LORENZ & BEALS 2012, from the Port Lincoln area in the East (n = 42).

Measurements of length, width, and height were taken with digital calipers and recorded to the nearest 0.1 millimeter (mm). It is a common misunderstanding that the length of a cowry must be measured parallel to the shell's axis or an imaginary line between the anterior and posterior canals. However, the shell's axis is not easily determinable in cowries since the larval shell often does not curl around a straight line. Therefore the length of a cowry shell should be defined as the maximum dimension of the shell found by measuring from extremity to extremity. In very few cowries, e.g. *Zoila friendii* (GRAY 1831), the spire may extend beyond the end of the canal. In this case the maximum length is measured from the tip of the spire. By positioning the shell until the maximum length is reached, the value for length is reliable and less subject to distortion. Likewise, width and height were measured as the maximum dimension along a plane approximately perpendicular to the maximum length and base, respectively. Mass was recorded to the nearest 0.01 gram by weighing the samples using an electronic digital scale. Before weighing, all specimens were examined to make sure that they were dry, and did not contain any detritus that could cause inaccuracies in the mass calculation. A graphical representation of the measurement axes and tooth count parameters is shown in Figure 2.

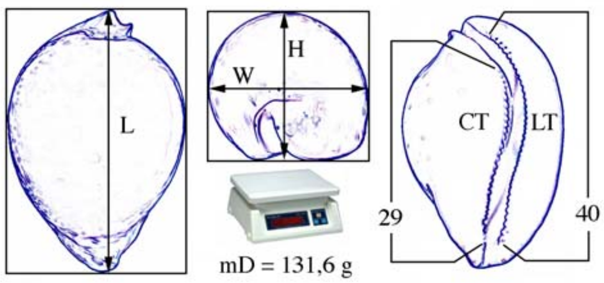

Figure 2: Shell measurement and tooth count parameters.

The dentition was counted while viewing the shell under 3.5 ×-magnification. In all cases the anterior terminal ridge was excluded from the counts as were any crenulations or ridges inside the posterior canal that did not become noticeable on the base. Occasionally, a small and weakly-developed tooth may exist between the anterior terminal ridge and the first columellar tooth, which is also not included in the tooth count. As illustrated in Figure 3, *Talparia talpa* (LINNAEUS 1758) (left) and *Mauritia eglantina* (DUCLOS 1833) (right) are examples for groups in which the posterior terminals are finely crenulated (blue circles). The determination between crenulations and the first tooth to be counted is difficult. Our method is to start in the area where the labrum meets the columella (green arrows). Usually, the first actual teeth that are a part of the basal aspect of the shell lie past this region (red arrows). In some species, as illustrated in Figure 4, the columellar teeth are replaced by ridges as in *Cypraeovula capensis* (GRAY 1828) (1), or are at least partly absent as in *Barycypraea teulerei* (CAZENAVETTE 1846) (2) and *Zoila venusta* (SOWERBY 1846) (3). In other species, there are finer intermittent ridges between solid teeth. Only those teeth that are reaching the apertural edge are counted, such as in *Nucleolaria granulata* (PEASE 1862) (4). In the formula, cases of incomplete sets of teeth or absent teeth are indicated by a dash (–).

Shell cross-sections were made by cutting through the peak height (perpendicular to the base and maximum width) with a diamond band saw. Thin sections of approximately 0.35 mm thickness for cross-sectional area analysis were also made by cutting out sections at the maximum width and height with a diamond band saw and grinding them on an electric diamond lapping machine. This was followed by hand polishing using 2500 grit wet or dry silicon carbide abrasive paper mounted on a glass plate. The thin sections were prepared for photography by mounting on 75 mm × 50 mm glass microscope slides using a cyanoacrylic adhesive. Area analysis on the thin sections was done using the "Analyze Particles" function in ImageJ (RASBAND, ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/, 1997-2012).

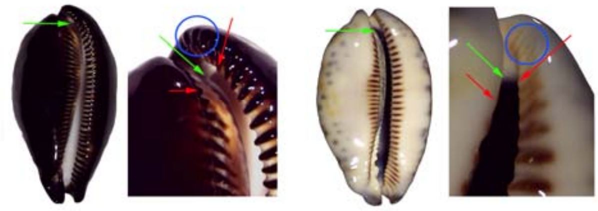

Figure 3: The difference between crenulations and countable teeth: *Talparia talpa* (LINNAEUS 1758) (left), and *Mauritia eglantina* (DUCLOS 1833) (right).

Figure 4: Problematic cases in the tooth count: 1-*Cypraeovula capensis* (GRAY 1828), 2-*Barycypraea teulerei* (CAZENAVETTE 1846), 3-*Zoila venusta* (SOWERBY 1846), and 4-*Nucleolaria granulata* (PEASE 1862).

It was not our intention for this paper to support or reject the status of any of the taxa that we studied or compared, nor did we attempt to produce any statistically significant results that would allow such statements. Instead, we simply examined and compared the various morphometric data that can be included in a formula used to characterize cowries. Table 1 summarizes the average measurement data from our sample groups. The complete raw datasets (in a tab delimited format) can be downloaded at the following URL: www.rbridges.com/formula/sampledata.txt.

Observations

The history of different cowry formula proposals reveals that most authors have adopted a modified version of an earlier approach of the SCHILDERs. The raw data derived from measurements of the shell consists of six components that can be acquired in the way described in Material and Methods:

- The shell's general dimensions: length, width, and height
- the number of labral and columellar teeth
- the shell's weight

Table 1: Summary data of the taxa compared herein.

Species	**Specimens (#), origin**	**Average measurements (millimeters) Lav x Wav x Hav (LTct : CTct) mD (grams)**
M. annulus	30, India	22.0×15.8×11.3 (12:10) 2.48
M. obvelata	30, Tahiti	19.6×14.5×9.4 (11:9) 2.43
M. sublitorea	30, W. Samoa	12.5×9.3×6.3 (9:8) 0.60
M. cervus	30, Florida Keys	92.7×54.2×42.3 (34:33) 45.36
M. cervus	20, Cuba	62.6×36.7×30.4 (29:28) 20.00
M. cervus	6, Panama City, Florida	118.8×67.4×54.4 (36:38) 50.77
M. zebra	40, Florida Keys	74.4×39.1×31.2 (31:32) 29.32
M. zebra	8, Brazil	84.8 × 44.0 × 34.0 (32:32) 37.62
M. cervinetta	30, Panama	55.5×27.2×21.0 (25:25) 15.16
U. armeniaca andreyi	15, W. Australia	72.2×45.5×41.2 (32:23) 55.0
U. armeniaca armeniaca	100, GAB	87.0×54.6×47.5 (40:30) 74.1
U. armeniaca clarksoni	15, Esperance	93.5×56.1×46.9 (39:30) 61.0
U. armeniaca diprotodon	42, Pt. Lincoln	106.7×67.3×58.0 (38:30) 142.5

MORETZSOHN (2003) added spire diameter and marginal spot size to his formula. Our attempts to objectively calculate spire diameter failed when applied to the *Monetaria* group in our study. In our study on the *Umbilia* groups we failed to reproduce the same data twice from the same shell. The thick callus deposit covering the spire area in the *Monetaria*s made it impossible to estimate the spire diameter, while different degrees of callus deposit and position of the spire above the posterior extremity in the *Umbilia* gave highly variable results. In our opinion, spire diameter may be of morphological value, but measuring it using non-destructive techniques is usually impossible.

Measuring the marginal spots raised similar issues. MORETZSOHN only proposed a ranking scale for the marginal spotting: "(0) none; (1) small; (2) medium; (3) large." (MORETZSOHN 2003: 248). Without direct correlation to a counted number of spots or a physical measurement of diameter, the values of 0 to 3 are merely subjective. Therefore, since they do not apply to the principles of reproducible morphometrics, these characteristics should only be part of a descriptive analysis of certain cowry taxa.

With these factors in mind and using the data collected from our sample groups, we examined the ability of these six metrics to differentiate within and between the groups as described below:

General dimensions (L, W, H)

All authors agree that the shell's length and its width are important features to be listed. Most formulae give numerical data indicating both L and W/L ratios. The LORENZ formula adds data for H/L. None of them give H/W values. SCHILDER & SCHILDER and LORENZ provided data for both labral and columellar tooth counts (normalized).

Length and the ratios W/L, H/L and H/W allow for a numerical and statistical comparison of how shells expand laterally and dorsally. A shell analysis that considers the three-dimensional character of the object is impossible without height data. W/L ratios delineate whether a shell is wide or narrow, while H/L ratios indicate how inflated or depressed a specimen is. The H/W ratio is a numerical derivative of the transverse cross-section of a shell. At a minimum, it represents the ratio between the maximum lateral and dorsal expansion (e.g., wide and depressed, narrow and tall). Taken together, W/L, H/L and H/W ratios provide an objective measure of the shell in all its maximum dimensions. Various ratio percentages are graphically illustrated for comparison in Figure 5.

Comparing the group of *Macrocypraea* (Figure 6 and 7), in which the differences in ratios between the taxa is minor and gradual, it is clear that all three ratios confirm the subtle differences in shape visible in the illustration of the shells.
In certain groups, (e.g. *Monetaria*, Figure 8, middle column), the ratio between height and length (H/L) does not show distinct differences. In contrast, the height to width (H/W) ratio indicates that *M. annulus* is more inflated than the others (Figure 8, last column). A photograph of transverse cross-sections supports that the data derived from numerical measurements works (Figure 9). In other words, the subjective impression when holding the shells in hand can be supported by objective data.

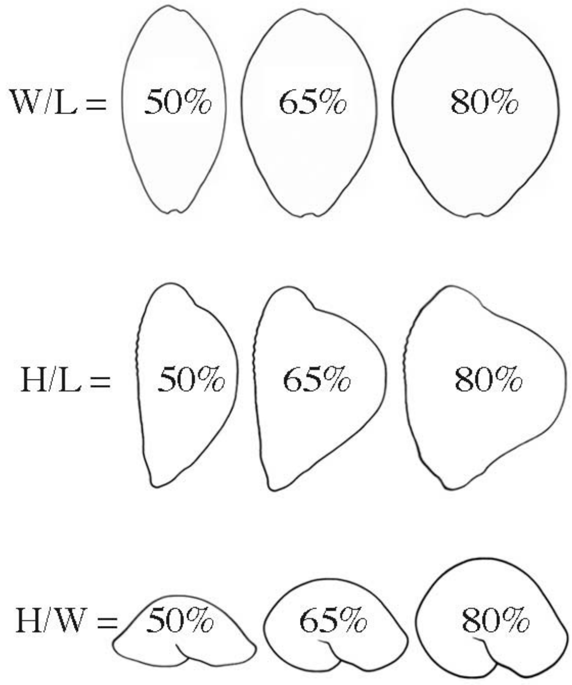

Figure 5: Examples for different length (L) width (W) and height (H) ratios for cowry shells.

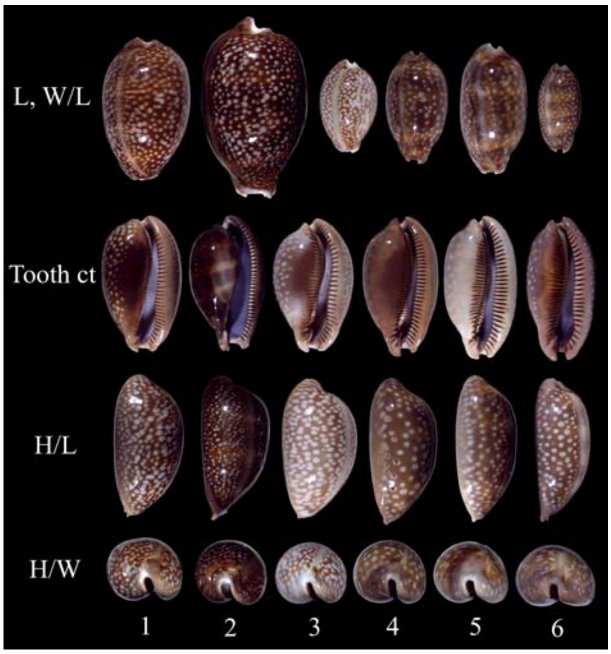

Figure 6: Visual depiction of size ratios in the *Macrocypraea*. 1- *M. cervus* (FL. Keys) , 2- *M. cervus* (P. City, FL.) , 3- *M. cervus* (Cuba) , 4- *M. zebra* (Florida), 5- *M. zebra* (Brazil), and 6- *M. cervinetta*.

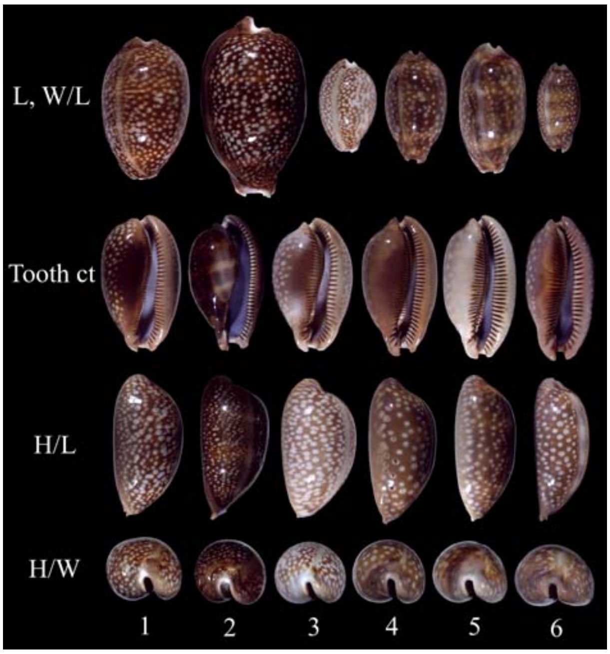

Figure 7: Size ratio comparisons of *Macrocypraea* taxa. The shell of *M. cervus* from Cuba shown here is the most inflated of the measured group, obvious in both the measurements and the shell itself.

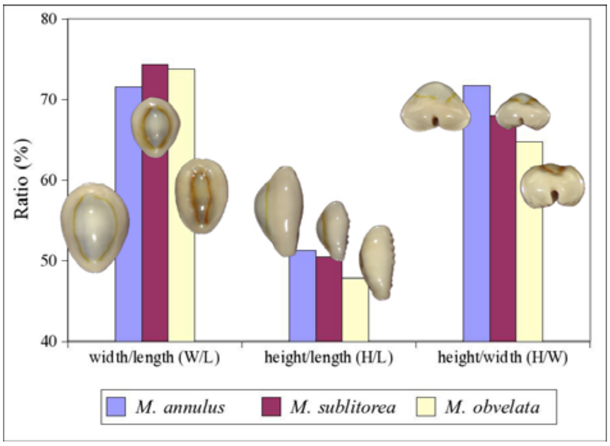

Figure 8: Size ratio comparisons of *Monetaria* groups.

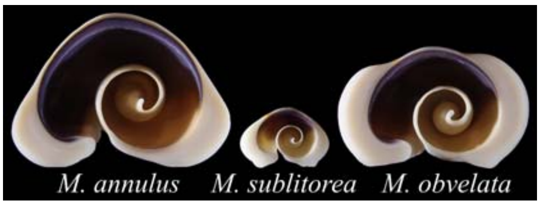

Figure 9: Transverse cross-section view: *M. annulus*, *M. sublitorea* and *M. obvelata* (left to right). The image depicts the intermediate status of *M. sublitorea* regarding H/W and mR.

A comparison of the four subspecies of *Umbilia armeniaca* is shown in Figure 10. *U. a. clarksoni* is less humped than its relatives. The H/W ratio further reveals that the shell is also the least inflated of the entire group. Likewise, the data indicate that *U. a. andreyi* is the highest and the most inflated. Again, this is also what is seen when the shells are examined visually.

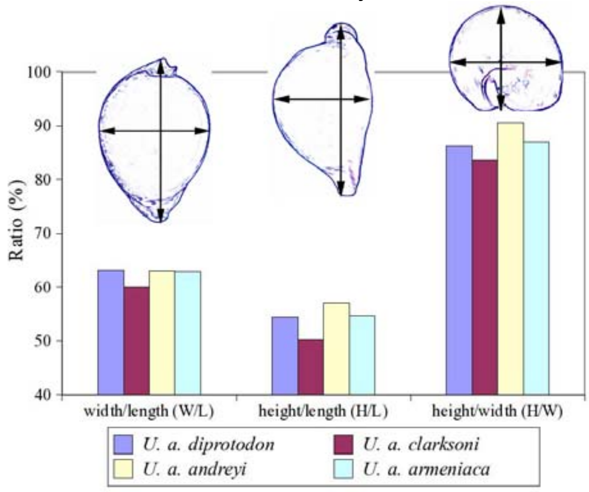

Figure 10: Size ratio comparisons of *Umbilia* groups.

Dentition (LT, CT)

Most authors provide numbers for both, the labral, and columellar teeth in their characterization of cowries. With large sample sizes, the figures are often reported as the arithmetic mean for the entire sample. A question that commonly arises is the reasoning behind the numeral 7 in the tooth count formula. During his initial studies on shell length versus tooth count, SCHILDER (F. A. SCHILDER 1930, 1931) determined two consistent relationships:

1: Tooth count increases as shell length increases within species, with tooth count in small-shelled species increasing faster than that in large-shelled species (see Figures 11 and 12).

2: When plotted on a graph, the data of approximately 10,000 specimens was modeled by a parabolic function, with its vertex at 7 on the tooth count axis (see Figure 12). The data actually displayed a square root function (the inverse of a parabola), which is acknowledged in later studies (F. A. SCHILDER 1937). The value of 7 in the equation simply indicates the length zero-point at which tooth count increases with length when modeled by a square root function. This was also the least number of teeth actually counted in non-pathological specimens of any species of the family. Therefore it is an experimental observation on the development of this morphological criterion.

The introduction of a normalization equation, allowed transformation of tooth count to a count relative to a standard length of 25 mm (F. A.

SCHILDER 1937). This permitted comparison of shells regardless of their size. After normalization, the tooth count data represents the density or closeness of the teeth, relative to the shell length. This has proven to be a reliable and repeatable measure of shell characterization (SCHILDER & SCHILDER 1938-1939, 1952; LORENZ 2001, 2002).

F. A. SCHILDER (1958) revised his method for tooth density calculations, citing two problems with the earlier method:

1: Confusing the relative number of teeth with the absolute number of teeth.

2: Differences in the actual length of the inner and outer lip of cowries. On average, the inner lip is 20% shorter than the outer lip.

The revised method used averaged instead of normalized tooth counts with the addition of alphabetical notation for tooth density. He published tables giving the new alphabetical values for tooth density (found by matching shell length and actual tooth count with those in the tables). The most ambitious use of this new method was made by his wife (M. SCHILDER 1967). However, we found discrepancies in her reported values versus those obtained by calculating from the new tables and question her methods. The same study reports statistical results showing "a general distinct correlation between the closeness of the labial and the columellar teeth, as coarse distant labial teeth generally are linked up to coarse columellar teeth, and numerous labial teeth to numerous columellar teeth (...) But there is no strict correspondence of the closeness of labial teeth to that of columellar teeth, as there are many species in which the columellar teeth are distinctly more numerous than the labial teeth, and *vice versa*" (p. 374-375). Additionally, "There is no correlation between the average length of the species and the number of teeth, a fact which justifies the method of calculating the relative closeness of dentition" (p. 375). Essentially, she concluded that labral and columellar tooth counts are generally correlated with one another, but that tooth counts are independent of shell size. Reducing the shells to a standard length therefore does not affect the validity of the metric, but instead it allows reliable comparison between two dissimilar-sized shells.

Especially within species with greater size variability, comparisons of tooth count benefits from using normalized tooth counts. This was demonstrated by LORENZ (2000) in his study on the *Cribrarula cumingii* complex. Differences in labral versus columellar tooth counts added morphological support to the separation of two taxa. Normalizing the tooth counts provided numerical values for dentition features; though visually obvious (much higher labral tooth density), these differences could not have been as accurately depicted using absolute counts due to the large size variation in the specimens studied. It is also important to note that in his study, the significant differences were in the labral tooth count, not the columellar count.

Recently, BERGONZONI (2012) discussed the importance of tooth count in his study of *Lyncina leucodon* (BRODERIP 1828). He stated: "I would say this is the only case in which I found, during my entire career as passionate cowrie collector, that teeth number is a useful character for a taxonomic distinction" (p. 44). As in LORENZ (2000), the difference between the labral and columellar tooth counts permitted separation of closely related taxa. He also described the methods used for counting the teeth, which is in concordance with what has been described in the present report (see Material and Methods).

The ability to compare labral to columellar dentition is an important function of tooth count data. When labral tooth count is excluded (as done by MORETZSOHN 2003), the ability to perform within-species comparisons is virtually eliminated. With only few exceptions, eg. *Barycypraea teulerei* (CAZENAVETTE 1846), cowries have two sets of teeth. In some genera, it is the columellar teeth that are not fully formed along the entire lip (e.g. in some *Zoila* and *Nesiocypraea*). Any valid comparison between or within species necessitates data from both tooth sets in order to make reasonable inferences.

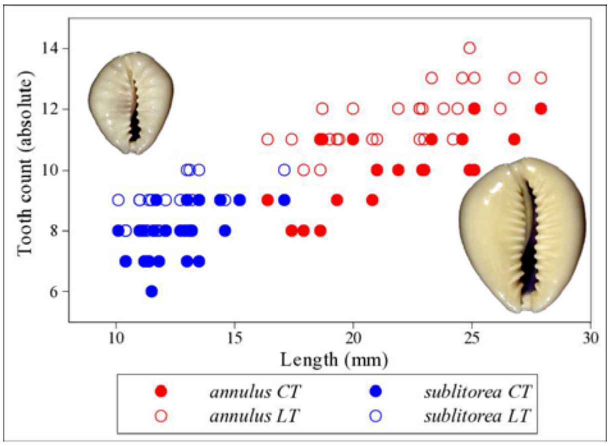

Figure 11: Tooth count versus length in *M. annulus* and *M. sublitorea,* displaying the general trend of more teeth in longer shells. A difference between labral and columellar tooth counts within species is also apparent.

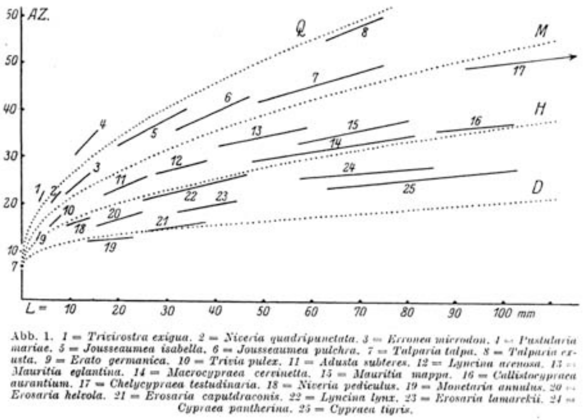

Figure 12: Tooth count versus length in 25 taxa from the Cypraeoidea and Trivioidea. The solid black lines represent the linear relationship of more teeth with increasing length within individual species. The dotted lines show the best fitting square-root relationship of tooth count to length among all species groups. Graph reproduced from F. A. SCHILDER 1930: 69, Figure 1.

Mass

None of the cowry formulae we are aware of provide shell mass data. This is not unusual, as mass statistics are virtually absent from the cowry literature with few exceptions, (VAYSSIÉRE 1905 and BRAND 1964). In his article on *Notocypraea comptonii "f. casta"* SCHILDER & SUMMERS 1963, BRAND (1964) gave weight data as the raw measured mass for individual specimens. In addition, he provided values for what he termed a “Mass Factor” (p. 85), which was defined as [(weighed mass * 1000) / L * W * H]. He did not discuss any reason for including this mass factor, and as far as we know it was never used in any later publications. Within this chapter we re-introduce a variation of BRAND's mass factor and demonstrate its usefulness for cowry characterization. For shells of the gastropod family *Conidae*, a relative weight factor (RW) was proposed as the relation between weight and length of the shell (RÖCKEL, KORN & KOHN, 1995). MELAUN (2008) demonstrated that this factor is not linear, but first exponential and then stationary. Consequently, RW does not serve as reliable tool for species characterization.

The mass of a cowry shell allows inferences to be made about the internal volume and average thickness of the shell walls when considered in relation to the overall size. In shells of different dimensions, the masses cannot be directly compared unless the measured weight (mD) of a shell and the mass of a solid object of the same dimensions are brought into relation, with the result being a dimensionless mass ratio (mR).

The volume (V) of a simple solid rectangular object is the product of length * width * height. The mass (m) is the product of the volume and the density (ρ), which depends on the material the object is made of: $m = V\rho$. In this case we are using the density of aragonite, the primary component of cowry shells: 0.00293 grams per cubic mm. Through extensive experimental observation on the *Umbilia* group (LORENZ and BRIDGES, unpublished data), we have found that the mass of a theoretical (solid) shell using the above formula is significantly correlated with the measured mass of the actual shell using the density of aragonite for ρ, $r(161)=.95$, $p<.0001$. In addition, using a water displacement procedure to accurately calculate the actual volume of a shell compared to the theoretical volume, in *M. annulus*, resulted in a correlation of $r(13)=.998$, $p<.0001$, graphically illustrated in Figure 13. Finally, we also performed analysis on thin sections from *M. annulus* to determine the percentage of the thin section area to the overall area bounded by its maximum height and width. Comparing this to the mR resulted in a correlation of $r(8)=.93$, $p<.0001$. Since the thin section area represents the average shell wall thickness at maximum width and height, the high correlation supports the mR as a valid indicator of shell wall thickness. See Figure 14 for visual representation of the area analysis.

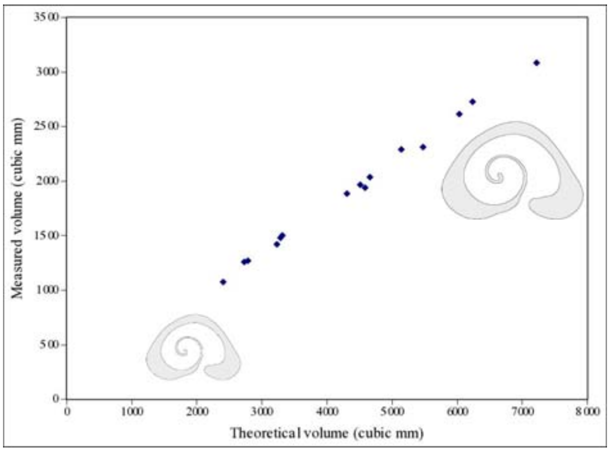

Figure 13: Calculated volume versus theoretical volume in *M. annulus*.

The mass of an object is always 100% correlated to its exact volume. Calculating the mass then only requires knowing the density of its material constituents and its volume. In the case of our calculation for the mR of a cowry shell, the choice of a value for the density is irrelevant to the results (as long as the density value used is the same among all comparisons). However, the confining shape of the hypothetical mass must be a rectangular box with the same maximum dimensions as the cowry shell. This is the only shape that will always contain within its boundaries the maximum dimensions of an irregularly (and typically asymmetrically) shaped object such as a cowry shell. Other shapes such as spheres, spheroids, and ovoids may often not be able to contain an irregularly shaped object within their boundaries when those boundaries are based upon the maximum dimensions of that object.

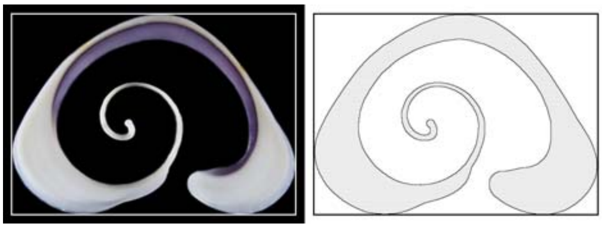

Figure 14: Thin section photograph and the transformed photograph used to calculate the surface area in *M. annulus*. The shaded area within the shell outline represents the average shell wall thickness at the shell's maximum width and height.

The mass ratio (mR) for cowries can be calculated using this formula:

mR = (mD / (L * W * H * 0.00293)) * 100

The mass ratios from our study are depicted graphically in Figure 15.

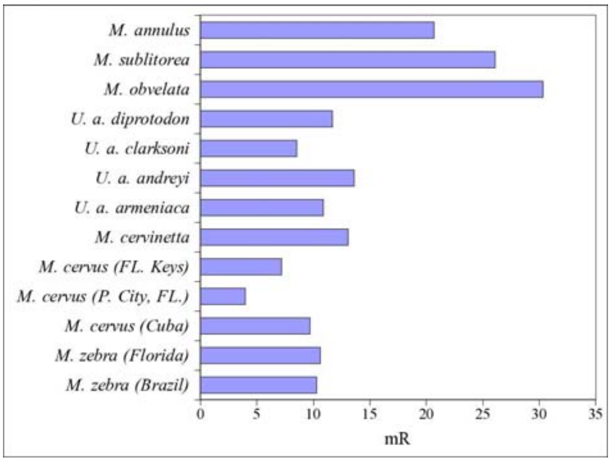

Figure 15: The mass ratios (mR) for the taxa examined.

This mass ratio metric allows quantification of the subjective sense of shell "heaviness." It is applicable to any fully adult and non-pathological cowry due to the trait of determinate growth. As shown in Figure 16, *M. obvelata* is significantly "heavier" (mR = 30.3) than *M. annulus* (mR = 20.7) even though the average size in the studied specimens is similar (20 vs. 22 mm). The much smaller *M. sublitorea* (13 mm) falls intermediate to these (mR = 26.8). Its mR appears as an indicator of shell thickness when compared with the cross-sections.

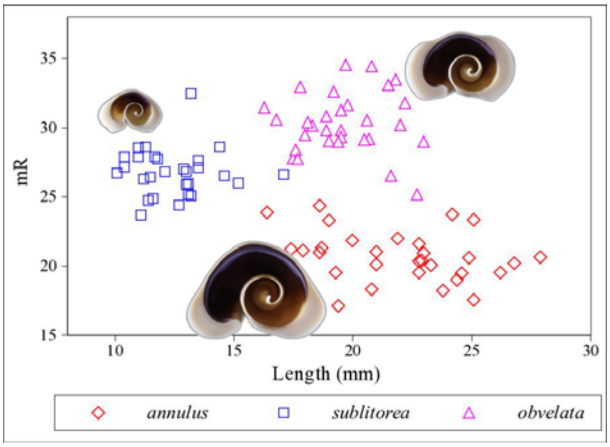

Figure 16: Mass ratios for the *Monetaria* species showing the intermediate status of *M. sublitorea*. The transverse cross-section view supports this data.

In Figure 17, the relative masses of the four *U. armeniaca* subspecies from our study are presented. The separation of the heavy-shelled *U. a. andreyi* from the others is obvious. On the other hand, *U. a. clarksoni*, even though intermediate in average size among the other groups (94 mm), is noticeably "lighter" in relative mass.

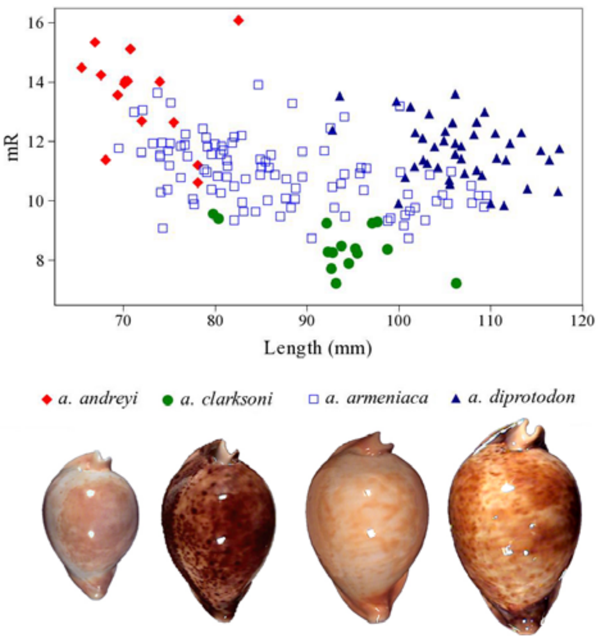

Figure 17: Mass ratios for the *U. armeniaca* subspecies.

The *Macrocypraea* group is interesting in that it shows the general trend of cowries toward an increase in mR as size decreases, as shown in Figure 18. This is not surprising and suggests that the cowry animal is programmed to produce a shell of a certain thickness, regardless of the ultimate size of the final shell.

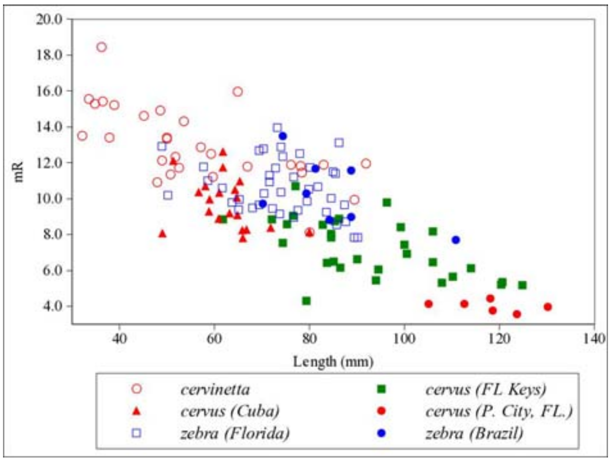

Figure 18: Mass ratios for the *Macrocypraea* group.

Discussion

A morphometric cowry-formula that allows a comparison of all members of the family should include only objectively measurable data. In cowry shells, the general dimensions, tooth count and weight were found appropriate, whereas, other features (spot-size and spire diameter) were not.

For size and shape comparisons, length, (W/L), (H/L), and (H/W), all the data necessary to interpret the measurements of general shell dimensions are provided. The normalized tooth counts provide data that allows objective comparison. The addition of the relative mass of a shell (mR) offers a new perspective on shell structure and has already become a factor that we use in morphological characterization.

An improved formula that includes the six reproducible measurements of a cowry shell based on SCHILDER & SCHILDER (1938-1939), LORENZ (2001), and LORENZ & BEALS (2012) should be:

L (W/L–H/L–H/W) LTnl : CTnl [mR]

For shells with incomplete or absent dentition we suggest the use of a (–) instead of a value for LTnl or CTnl, respectively. The accuracy of the mR should be 0.1, which displays reasonably the accuracy of the measurements reached by electronic scales.

In statistical analysis, the average shell formula is derived by first establishing the formulae for every specimen in a group, then calculating the averages of each formula parameter. In this manner, it is easier to eliminate or add specimens to an existing set of measurements and compare the individual formulae. To facilitate the calculation of the formula it is possible to use spreadsheet or database programs such as Microsoft Excel™ (Microsoft, Redmond, Washington, USA) or FileMaker™ (FileMaker, Inc., Santa Clara, California, USA). In addition, we have made an online calculation program available at the following URL: www.rbridges.com/formula/calculator.php .

To compare two specimens, such as any of the subspecies ~~of~~ of *armeniaca*, with an existing set of formulae, the procedure would be the following:

There are two shells (Figure 19), A (*a. clarksoni*) and B (*a. diprotodon*) that have been measured, teeth counted and weight taken. The data lines up as follows:

Length (L) x width (W) x height (H) (counted labral teeth (LT) : counted columellar teeth (CT), measured weight (mD):

A) 92.4×52.4×43.5 (37 : 29) 57.7 in the formula, the data translates to: 92(57–47–83)23:18[9.4]

B) 104.6×65.7×56.7(40 : 29) 131.6 which translates to: 105(63–54–86)23:18[11.6]

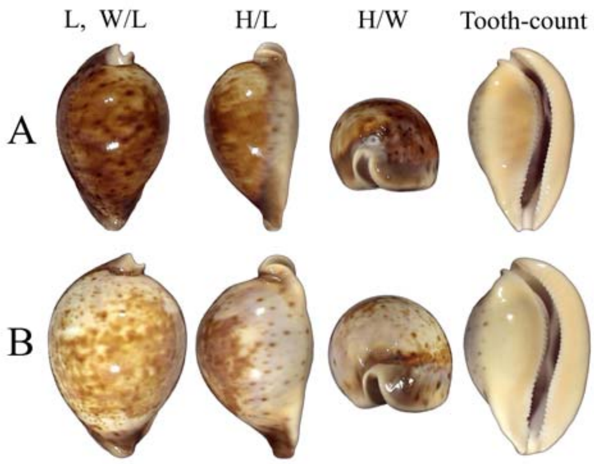

Figure 19: Comparison of shells A: *U. a. clarksoni* (top row) and B: *U. a. diprotodon*. The four views allow visual comparison of (L) and (W/L), (H/L), (H/W), and tooth count respectively.

In both cases, the parameters in the formula are quite different from the measured data. However, it is possible to compare the two shells in relation to each other. The width and height measurements are now given in percentages to each other, the tooth counts are normalized to a hypothetical shell of 25 mm, and the weight is given relative to the shell's dimensions.

For example, comparison of the raw data only allows the statement that A is a much smaller shell than B, has less labral teeth and weighs less than half. The formulae help interpret this data and give a clearer picture: Indeed, A is smaller than B, much narrower and less high in relation to the length, and also in the relation between its width and its height. Therefore, B is the wider and more inflated shell. The difference in the counted labral teeth becomes irrelevant when normalized. Also, the impression that A is lighter than B is supported. As shell A is smaller, the difference in the measured weight is easily explained. However, in the formula, the subjective feeling that shell A is relatively lighter in weight than shell B is supported by the data of the relative mass: the mR of A [9.4] is less than the mR of B [11.6].

In addition to comparisons based on single shells it is interesting to compare datasets derived from measuring large quantities of shells and observe where individual specimens fit in.

Average measurements from LORENZ & BEALS (2012) (modified to the revised formula):

a. armeniaca: 87(63–55–87)24:19 [10.9]

a. diprotodon: 107(63–54–86) 22:18 [11.7] - our shell B: 105(63–54–86)23:18[11.6]

a. clarksoni: 94(60–50–84) 24:19 [8.5] - our shell A: 92(57–47–83)23:18[9.4]

a. andreyi: 72(63–57–90)22:17[13.6]

Comparing the formulae of A and B with the formulae of the four subspecies of *armeniaca* confirms that the data of shell A corresponds closest to that of *a. clarksoni* - the most narrow, flat, and lightweight of the four subspecies, and B agrees with *a. diprotodon*, based on the relative mass and size of the shell.

The subjective visual comparison of shells versus the objective comparison of their formulae leads to results that allow for a critical evaluation on how useful the formula is and its limitations. Individual shells of six species of cowries have been measured (Table 2).

Table 2: The raw data for six cowry species and their corresponding formulae. Minimum values are indicated in green and maximum values in red.

Species	L	W	H	LTct	CTct	mD	Formula
Umbilia hesitata (IREDALE 1916)	23,7	15,7	12,1	16	15	2,75	**92**(58-48-83)21:19[8.7]
Erosaria eburnea (BARNES 1824)	38,9	23,1	18,9	16	15	6,22	39(59-49-82)**14**:**13**[12.5]
Cypraeovula cruickshanki KILBURN 1972	31,4	25,4	21,5	19	19	3,28	31(**81**-**68**-85)18:18[**6.5**]
Cribrarula melwardi (IREDALE 1930)	23,7	15,7	12,1	16	15	2,75	24(66-51-**77**)16:15[**20.9**]
Notocypraea pulicaria (REEVE 1846)	15,7	8,5	6,7	23	23	0,35	16(**54**-**43**-79)27:27[13.4]
Pustularia cicercula tuamotensis (LORENZ 1999)	10,5	5,7	5,3	26	23	0,14	**11**(**54**-50-**93**)**36**:**32**[15.1]

The specimens are shown in Figure 20.

Figure 20: Size measurement ratios illustrated for: 1-*Umbilia hesitata*, 2-*Erosaria eburnea*, 3-*Cypraeovula cruickshanki*, 4-*Cribrarula melwardi*, 5-*Notocypraea pulicaria*, and 6-*Pustularia cicercula tuamotensis*. Shells scaled differently to allow for a better comparison of their outlines.

Taking this set of shells, statements on size, shape, dentition and mass can be made, based on the extremes found within the dataset. In the table, the respective minimum is marked green and the maximum red. Reading the data for size, *U. hesitata* would be considered "large," *P. tuamotensis* "small," *N. pulicaria* "moderately small," and so on. *E. eburnea* would be "medium-sized, with average width, moderately humped, with coarse dentition, and would be a moderately heavy shell." Comparing all of the parameters of the formulae with the actual shells in Figure 20, leads to similar subjective visual impressions and objective measurements: *C. cruickshanki* is seen as a lightweight, quite inflated shell, and *C. melwardi* as a wide, depressed, and heavy shell. The formula adds interesting details that are not immediately visible when comparing the shells: *P. cicercula tuamotensis* is the most humped shell in relation to its width and it also has the finest dentition.

Our revised cowry-formula basically puts objectivity to the descriptive terms "larger," "wider," "coarser teeth," as well as to the subjective feeling that one shell is "heavier" than another.

However, the weak point of the formula against the visual comparison becomes obvious: the cylindrical shell of *N. pulicaria* and the rostrated shell of *P. cicercula tuamotensis* have the same W/L ratios. The H/L ratios reveal that *N. pulicaria* is more depressed than *P. cicercula tuamotensis*, whose H/W is the most extreme, both of which may be viewed as indications that the difference in the outlines of these shells is considerable. This is where the shell characterization needs to become descriptive. A further enhancement of the cowry formula could evaluate the relation between the length of the extremities and the dorsum of a shell, which would certainly aid in the differentiation. However, the techniques of how to retrieve such measurements objectively would go beyond the capabilities of a standard caliper.

There is no doubt that modern systems of three-dimensional scanning and computer calculating may offer additional morphological features such as an objective method to measure spire and spot diameters, angles of inclination, and so forth. Our current formula, based on six objectively measurable parameters, is working for all species of the family. Each of its parameters adds information that may serve in the comparison and characterization of specimens, populations, species or genera.

How the shell formulae of cowries correlate with other features, such as relationships based on mtDNA information may become a fascinating subject for future study.

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