PRELIMINARY MORPHOMETRIC ANALYSIS FOR HIPPURITIDS TAXONOMY

This study is an attempt to establish biocharacters of Hippuritids (Hippuritoida) that could be easily recognized by means of biometric methods. For this purpose, for a given species a proportionality between the inner area and shell parts involved in the biological functions is supposed. With this assumption I tried to compare the area within the inner perimeter (Ia) with the area of the pillars (P1-P2a) and with that comprised between the inner and external perimeter (Sa) respectively in the right valve. Measures have been taken on several transverse sections of *Hippurites colliciatus* (Woodward), using the Optomax System of computerized image elaboration. To verify this proportionality, the following ratios have been considered: Ia/P1-P2a and Ia/Sa. The resulting histograms evidentiate, in both cases, a range of values that occur frequently. Moreover, both the Ia/P1-P2a and Ia/Sa trends have been plotted on diagrams where linear relationships are shown. The results obtained with this method suggest a clear biological proportionality among the considered characters and this could be used as an integrated method in the identification of species belonging to this family.

Introduction

Near S. Polo Matese (Matese Range, Molise) a rich Rudist bearing outcrop has been examined, forming a thicket with very well preserved specimens, (Fig. 1). The paleontological analysis enabled the recognition of the species *Hippurites colliciatus* (Woodward). A certain variability has also been observed within the population, sometimes quite accentuated. Owing to the great number of specimens, this variability can be quantified with statistical methods. In this respect, the same characters usually employed in taxonomic classification have been used: the S and E pillars, shell thickness and visceral cavity. In order to avoid error in data interpretation, the studied specimens have been compared to the original holotype described by Woodward (1855). The holotype is that specimen chosen within a population as representative of a series of morphological characters typical of the species, and is the main

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Fig. 1 — Location of the outcrop with *Hippurites colliciatus*. (modified from Accordi et alii, 1982).
— Ubicazione dell'affioramento a *Hippurites colliciatus* (modificato da Accordi et alii, 1982).

GEOLOGICA ROM., 28, 91-103, 8 figs, 3 tab., 1 pl., Roma (1992).
Fig. 2 — Diagrammatic radial sections through the valve margins, and their associated soft parts, in the ventral region of Hippuriella toucasi (A) and Vaccinistes dentatus (B). Left valve is on top, and right valve beneath: Thin arrows represent water currents generated by the cilia of the mantle linings to the radial canals, and the thick arrows the direction of ciliary transport of the particles trapped from these on the right mantle lobe margin (here represented as a broad flat middle marginal mantle fold zone). Explanation: AR, aragonitic shell layers; CP, ctenidial and/or palp mass; CT, calcitic fibrillar prismatic shell layer, showing the orientation of the fibrils with respect to the growth lines (dashed lines); FB, false boundary within the outer layer due to convergence of fibrils along the growth locus of the commarginal through; IF, inner mantle-marginal fold; ML, mantle lobe; OF, outer mantle-marginal fold, here represented as a small flap over a peripheral periostracal groove network.

Upper part of the right valve (C), showing most of the general cavity. The pseudofaecal rejection tract and exit are represented by a broad arrow with thick cross-bars. The faecal rejection is shown as a broad arrow with longitudinal stripes. Explanation: PS, “S” pillar; PE, “E” pillar. (modif. from Skelton, 1976).

— Sezioni diagrammatiche radiali attraverso i margini della valva e delle relative parti molli nelle regioni ventrali di Hippuriella toucasi (A) e Vaccinistes dentatus (B). La valva sinistra è in alto e quella destra al di sotto. Le frecce sottili rappresentano le correnti di acqua gener-ate dalle cilia delle foderature del mantello verso i canali radiali; le frecce più marcate indicano la direzione del trasporto ciliare delle particelle intrappolate lungo il margine destro del lobo del mantello (qui rappresentato come una ampia e piatta zona del margine medio della pie-ga del mantello). Spiegazione: AR, strato del guscio aragonitico; CP, massa dei ctenidi e/o dei palp; CT, strato del guscio calcitico prismatico fibrillare che mostra l'orientamento dei «fibrilli» rispetto alle linee di crescita (linee a tratteggio); FB, falso limite all'interno dello strato esterno del guscio dovuto alla convergenza dei «fibrilli» lungo il luogo di crescita del solco commarginale; IF, piega interna del margine del mantello; ML, lobo del mantello; OF, piega esterna del margine del mantello, qui rappresentata come un piccolo lembo sopra la struttura a solco del periostraco periferico (modif. da Skelton, 1976).

Parte superiore della valva destra mostrante gran parte della cavità generale (C). Il tratto della eiezione delle pseudofeci e la loro uscita sono rappresentate da una ampia freccia a tratteggio spesso. L'eiezione delle feci viene mostrata come una ampia freccia con strisce longitudinali. Spiegazione: PE, pilastro «E»; PS pilastro «S».

Subject to which refer in classification. Morphologic-al characters can widely vary when comparing two or more populations living in different ecological conditions. Therefore the holotype only represents one of the many morphological expressions of the species (maybe the most frequent), and hence gives no indication of the characters variability of the species itself. The result which is intended with this study is to have, together with the holotype, objective and statistically significant parameters for a better definition of the species. The reference to numeric values has already been used by Toucas in the first years of the centuary (1903-4), to point out the inclination of the cardinal apparatus and the angle between the
ligament ridge and the second pillar. Recently other Authors have referred to linear and angular measures of certain biocharacters to define a species (Skelton & Wriet, 1987; Sirna, 1990) or to discuss affinity among different species (Laviano & Guarnieri, 1989).

In a single species, the same biocharacter, measured in two distinct populations, can show different mean sizes, due to greater development of specimens of one population rather than the other. In these cases, the measured value will not be considered indicative for taxonomic purposes, and for this reason attention has been focalized on pure numbers, deriving from numeric ratios between biocharacters supposed in biological relationship.

Methodology

In a biometric study, a fairly large number of well preserved specimens is required, in order to be representative of the species and to enable exact measurements. In the attempt to define taxonomic parameters, the use of the pure numbers has been preferred for the following reasons:

a) in the ratio between two values expressed in the same unit of measurement, the eventual errors made during the measurement, are automatically eliminated;

b) a pure number is not conditioned by the different sizes of the measured specimens. In order to give taxonomic significance to the detected parameters, ratios have been made between areas corresponding to characters supposed biologically interdependant. The function of pillars as means of fecal expulsion and the importance of shell thickness as useful surface for the mantle expansion to introduce nutritive particles in the visceral cavity have been dealt in Skelton (1976), from which figure 2 is derived. Pillars function and indirectly shell thickness have been thought in close biological relationship with the internal cavity, site of the organic tissues, in order to justify the ratios Ia/P1-P2a and Ia/Sa as possible taxonomic parameters, in which Ia represents the inner area, P1-P2a the pillars area and Sa the shell area.

The hypothetical biological relationship between the functional parts of the shell and the visceral cavity can be expressed with a block scheme:

\[ \rightarrow \text{A} \rightarrow \rightarrow \rightarrow \text{B} \rightarrow \rightarrow \rightarrow \text{C} \rightarrow \]

in which the blocks represent respectively: A) mantle surface responsible for the incoming flux of nutritive particles in the inner cavity; B) the inner cavity with the organic tissues; C) the pillars. They represent various stages of the nutrition cycle of the organism; the nutritive particles are at first provided by that part of the mantle that rests upon the commissure (A), assimilated in the inner cavity (B), and the metabolic residues are expelled by the pillars (C). To make this three elements objective, their areas in transverse section have been considered (Fig. 3).

Their measurement has been ensured by the image analyser Optomax V, whose most important features are the certainty of a standardized error in the measurement, so to be considered irrelevant, and its realiability. The Ia/Sa ratios have been examined in: 1) serial transverse sections of every available specimen; 2) transverse sections of a same specimens; 3) transverse sections of specimens belonging
to different palaeogeographical areas. Such checks result necessary in order to: a) analyze the considered ratios relating to ontogenetic development; b) study their frequency in a population; c) verify which relationships occur between the reference population and specimens belonging to other geographical domains (Tab. 1-3).

**Systematical description**

Classis Bivalvia  
Ordo Hippuritoida Gray, 1848  
Família Hippuritidae Gray, 1848  
Família Hippuritidae Gray, 1848  
Genus Hippurites Lamarck, 1801

**Hippurites colliciatus** (Woodward), 1855  
(Pl. 1, Figs. 1-13)

The right valve is initially conical, with apical angle of about 20°, and then becomes subcylindrical. The transverse dimensions are generally comprised between 1.5 and 3.0 cm., but specimens with 10-12 cm. in diameter are recorded, together with ones less than 1 cm. across. Ornamentation is constituted by about 18 pronounced ribs, sharp to slightly rounded, unevenly distributed along the external perimeter, that in transverse section shows an irregular profile. The internal perimeter, subcircular straightens between the two pillars, while in correspondence with the ligament crest a slight flexus occurs, that sometimes is exalted to become a strong fold. Pillars are always convergent and similar to each other, and their shape varies according to the greater or lesser shrinkage at the base, which confers, especially to the second pillars, a peduncle-like shape. Their apexes are rounded, and generally in both pillar the basal width is greater than the apical diameter. The cardinal apparatus makes an angle of about 85° with the ligament crest, while the posterior muscle print (mp) has an elliptical shape, with the greater axis nearly parallel to the first pillar. In longitudinal section the growth lines are inclined on the growth axis with an angle less than 45° and show a tight concave inflection with acute vertex, in correspondence with the internal perimeter.

**Palaeoecology**

This species is recorded in shelf-edge facies where it thrives on mobile sea-floors, protect from the areas of top-energy sea waves, in medium to sporadic high hydrodynamic conditions (Accordi G. et alii, 1982; Carbone F. & Sirna G., 1981; Cestari R. & Sirna G., 1987). In general the single cluster, with a density of 15-20 specimens per square dm, and single specimens mean size of 2 cm, form hardly relieved thickets. In *Hippurites colliciatus* (Woodward) clusters there is often the occurrence, in a very limited number, of specimens of different species, *Vaccinites gosaviensis*,
Table 2 — Transverse sections of the right valve of measured specimens with their number of sample.
— Sezioni trasversali della valva destra degli individui misurati e numerati.
Table 3 — Transverse sections of the right valve of measured specimens with their number of sample.
— Sezioni trasversali della valva destra degli individui misurati con i relativi numeri.
(Douville), *V. sulcatus*, (DeFrance) *Sauvagesia sp.*, of larger sizes of the dominant species. The high adaptability of *Hippurites colliciatus* (Woodward) also enables it to solitary life modality, as seen in the outcrops near Campitello Mateese (Piano della Corte).

**Results**

Considering the morphological features of the pillar and of the right valve ornamentation on serial transverse sections, the greater difference among these features are to be found comparing the first sections, which correspond to the juvenile stage of development, against the last sections, referred to the adult stage. Examining the S. Polo’ Mateese population, it has been observed that *Hippurites colliciatus* (Woodward) reaches the morphological stability of its taxonomic characters when the right valve starts to acquire a cylindrical shape (adult stage), in such conditions these characters do not undergo a substantial variation in shape and size during the following stages of growth. In this case, it has been verified that from this stage onwards, the ratios: 1a/Ps-P2a and 1a/Sa can be considered constant.

*Hippurites colliciatus* (Woodward) tends to acquire its typical features during the period of growth in which the shell gradually increases the diameter of the inner cavity. In this juvenile ontogenetic stage, characterized by cylindrical growth, the pillars initially equal in shape and size, tend to differentiate from each other, until they reach, in the adult stage,

![Diagram](image-url)

Fig. 4 — Seriate sections to check the 1a/Sa and 1a/P1-P2a ratios during the young growth stages. A, Maiella; B, S. Polo M.

— Sezioni seriate per verificare le variazioni dei rapporti 1a/Sa e 1a/P1-P2a nel corso degli stadi di crescita giovanili. A, Maiella; B, S. Polo M.
stability in shape and size. Similarly, the thickness and the external perimeter of the shell tend to become stable in the same interval of growth. Due to the development modalities of the right valve, it has been considered prioritarious for ontogenetic reasons to verify the la/P1-P2a and Ia/Sa ratios in the conical growth portion of the valve. In figure 4 serial sections of two specimens from Maiella (fig. 4A) and S. Polo Matese (Fig. 4B) are shown, in the first, the shell is not entirely preserved, but the presence of the apical portions allows the measurement of the Ia and P1-P2a areas in the very first stage of growth, the second allows the measurement of all the considered areas and to compare the Ia/P1-P2a and Ia/Sa ratios from the juvenile to the adult stage. From the examples shown in figure 4, it is clear how, in the portion of the shell with a conical development, the Ia/P1-P2a ratio varies noticeably from the calculated average; instead, the variations of the Ia/Sa ratio are less accentuated, as appears in the sequence of figure 4A.

![FREQUENCY HISTOGRAM of la/Sa](image1)

**Fig. 5** — Frequency histograms of the Ia/Sa ratio.
— Istogramma di frequenza del rapporto Ia/Sa.

**FREQUENCY HISTOGRAM of Ia/P1-P2a**

**Fig. 6** — Frequency histogram of the Ia/P1-P2a ratio.
— Istogramma di frequenza del rapporto Ia/P1-P2a.

Considering the morphological stability of the taxonomic features of the right valve in the adult stage, it appears that in the ontogenetic development the Ia/P1-P2a and Ia/Sa ratios have two different behaviours: the first one is characterized, in the first stage of growth, by large variations around an average value, that tend to decrease and to remain constant in the portion of the shell that corresponds to the adult stage; the second one is usually constant from the first stage of development. In order to define the range of variation of the Ia/Sa and Ia/P1-P2a ratios, data from every available specimen have been analyzed, and to identify the most frequently occurring values.

In this case, measurements have been taken at a casual stage of growth, and on a relatively high number of specimens, as to be representative of any transverse section of *Hippurites colliciatus* Woodward. The results of these areal measurements, expressed in square mm, and the related ratios are
shown in table 1; the use of the "quattro" professional software 2.1 version, allowed the elaboration of the data of table 1, to obtain the histograms in Figs. 5-6. In order to have a sufficient detailed graphic representation, the dispersion fields have been divided into 11 classes, with an increase of 0.13 for the Ia/Sa ratio (fig. 5) and 1.97 for the Ia/P1-P2a ratio (Fig. 6). One particular class appears to be the most representative, with values between 12.87 and 14.84 for the Ia/Sa ratio and values 1.04 and 1.18 for the Ia/P1-P2a ratio. The same features used for the ratios (Ia/P1-P2 a Sa) have been plotted on a cartesian diagram (Figs. 7-8) in which the pillars area and the shell area have been compared with the inner area.

The resulting correlation coefficient, close to the unit, suggest a linear proportionality between the area of the pillars and the shell and the inner areas. Considering this proportionality, the angular coefficients of the regression lines between Ia/P1-P2a and Ia-Sa could be considered as further parameters for Hippuritid taxonomy. As a final analysis it has been considered important to confront our specimens with others from different geographical areas, examining, besides the holotype, specimens of Hippurites colliciatus Woodward from Maiella (Italy), Tabernes (Spain), Leposavic (Yugoslavia). The examined biocharacters of these specimens are pointed out in the dispersion diagrams of figure 7-8, in which appears clearly the alignment of the points that correspond to the S. Polo Matese specimens. Moreover, the Ia/P1-P2 a and Ia/Sa ratios are comprised within the variation field of the species. These results suggest a good representativeness of the studied ratios not only for a single fossil population, but also for all the specimens belonging to the species.

Conclusions

The results emerging from this first morphometric analysis of the taxonomic features, point out a clear mathematical relationship between inner area, pillars

![Diagram](image-url)
Regression of P1-P2a on Ia

\[ \text{Correlation Coefficient} = 0.88 \]
\[ \text{Slope} = 0.07 \]

Area and shell area supposed in biological relationship. In particular between Ia and P1-P2a and between Ia and Sa exists a linear proportionality described by the angular coefficients of the respective lines of regression (Figs 7-8). A check of such relationship is shown by the histograms in Figs 5-6, in which the most frequent classes for the Ia/P1-P2a and Ia/Sa ratios correspond to the reciprocal of the angular coefficients of the respective lines of regression. In order to confirm their validity these results have been ontogenetically controlled, and compared with same specimens of the same species from other localities. At the end of this research these parameters can be given as representative of the species:

- Ia/P1-P2a = > 12.87 \leq 14.84
- Ia/Sa = > 1.04 \leq 1.18
- Slope Ia; P1-P2a = 0.07
- Slope Ia; Sa = 0.96

The intent of this work has been to verify the possibility of a morphometric approach to taxonomic problems of Hippuritids. The results confirm this possibility, and we believe that with the improvement of these methods better results can be obtained, for example describing more realistically the areas of the functional parts of the pillars (their terminal portion) or the inner area occupied by the organism, that is only really part of what has been actually measured. A greater number of specimens would improve reliability of results.

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RIASSUNTO

I risultati emersi da questo studio preliminare sulla morfometria di *Hippurites colliculata* Woodward, indicano l’esistenza di una chiara relazione matematica tra l’area interna, l’area dei pilastri e l’area del guscio (spettrose in relazione biologica tra loro). In modo particolare, esiste una proporzionalità lineare tra l’a e P1-P2a e tra l’a e Sa, messa in risalto dai coefficienti angolari delle rispettive rette di regressione (Figs 7-8). Un controllo di tale relazione è mostrato negli istogrammi in Figs 5-6 dove le classi maggiormente rappresentate per i rapporti l/a,P1-P2a e l/a,Sa corrispondono ai reciproci dei coefficienti angolari delle rispettive rette di regressione. Per confermare la loro validità, questi risultati sono stati controllati ontogeneticamente e comparati con valori di esemplari di altre località. Al termine di questo studio, i seguenti parametri possono essere considerati come rappresentativi della specie:

\[
\text{l/a} = 12.87 \leq 14.84; \\
\text{l/a,Sa} = 1.04 \leq 1.18; \\
\text{slope l/a} = 0.07; \\
\text{slope l/a,Sa} = 0.06.
\]

L’intento di questo lavoro è stato quello di verificare la possibilità di un approccio morfometrico alle problematiche tassonomiche delle Hippuritidi. I risultati confermano tale possibilità e crediamo che, con il perfezionamento di queste metodologie, i risultati possano essere ottenuti. Ad esempio, descrivendo più realisticamente le aree delle parti funzionali dei pilastri (corrispondenti alle loro porzioni terminali) o l’area interna occupata dall’organismo che è veramente parte di ciò che è stato misurato. Inoltre, un più alto numero di misure dovrebbe migliorare il grado di affidabilità dei risultati.

REFERENCES


PLATE I

Fig. 1 — Hippurites colliciatus (Woodward). Transverse section of right valve. Campanian, S. Polo Matese. × 1.5.

Fig. 2-10 — Hippurites colliciatus (Woodward). Transverse section of right valves, showing the variability of the: ornamentation, pillars and ligament ridge. Campanian, S. Polo Matese. × 1.5.

Fig. 11 — Hippurites colliciatus (Woodward). Transverse section of the right valve. Campanian, Maiella. × 1.5.

Fig. 12 — Hippurites colliciatus (Woodward). Transverse section of the right valve. Senonian, Spain. × 1.5.

Fig. 13 — Hippurites colliciatus (Woodward). Transverse section of right valve. Senonian, Jugoslavia. × 1.5.

TAVOLA I

Fig. 1 — Hippurites colliciatus (Woodward). Sezione trasversale della valva destra. Campaniano S. Polo Matese. × 1.5.

Fig. 2-10 — Hippurites colliciatus (Woodward). Sezioni trasversali di valve destre, mostranti la variabilità intraspecifica delle ornamentazioni, pilastri e cresta ligamentare. Campaniano, S. Polo Matese. × 1.5.

Fig. 11 — Hippurites colliciatus (Woodward). Sezione trasversale della valva destra. Campaniano, Maiella. × 1.5.

Fig. 12 — Hippurites colliciatus (Woodward). Sezione trasversale della valva destra. Senoniano, Spagna. × 1.5.

Fig. 13 — Hippurites colliciatus (Woodward). Sezione trasversale della valva destra. Senoniano, Jugoslavia. × 1.5.