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The operculum of the genus *Nerita*

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Abstract: Characteristics of opercula of *Nerita*-species are specified and examined. The operculum was described using 13 characteristics. Only external characteristics were observed. The characteristics and correlations between them are analysed. Results of a previous study of the characteristics of the shell itself are combined with the characteristics of the operculum in order to find significant relations between both sets of characteristics.

At the end six significant, non-spurious, correlations are found between characteristics of the operculum and five significant, non-spurious, correlations are found between characteristics of the operculum and characteristics of the shell. The most important correlations viz 1) ribbed nerites tend to have granulated opercula and 2) the curvature of the columellar area is opposite to the curvature of the operculum, are significant at a 0.05-level.

A functional explanation of the latter correlation is that the operculum needs less room under the columellar area while the snail is hatched on a rocky surface. Also during retraction of the operculum the snail does not have to lift itself much from the rocky

surface in order to close the aperture with the operculum. No functional explanation can be given for the first correlation.

Introduction: Krijnen (1997b) published a statistical study of the characteristics of shells in the genus *Nerita*. In that study significant relations between these characteristics were found. Krijnen also mentioned an ongoing study about the relations between characteristics of the operculum mutually and between characteristics of the shell and of the operculum.

In some papers (e.g. Rust, 1997 and Kano, 2006) specific relations between characteristics of a nerite and its operculum are discussed. Vermeij (pers. comm., Oct. 2006) wondered why ribbed nerites more often have a granulated operculum. These examples encouraged the present study of relations between the characteristics of the nerites and their opercula and, whenever possible give a functional explanation of the relations found. In this general context, two supposed relations draw our attention in particular:
- the conjecture of Vermeij that ribbed nerites have granulated opercula;
- the fact that the curvature of the operculum's exterior is opposite to the curvature of the columellar area (= septum, parietal shield) of the nerite.

Beforehand the restriction is made to explain the significant correlations from a purely functional point of view. It is known that phylogeny allows for establishing correlations, too, (e.g. Frey & Vermeij, 2008) but this is beyond the scope of the present study.

First a short compilation of facts about the operculum of a nerite is given. These turned out to be essential to get a better understanding of the relevant characteristics of the operculum. At the end of the introduction some thoughts and observations are given to explain our particular interest in the hypothesis of the oppositely curved operculum and septum.

Although extant characteristics of the operculum are analysed, the overview starts with some fossil studies in which opercula were involved. Such studies are rather limited (see Checa & Jiménez-Jiménez, 1998). Bandel (2007) showed that species of the genus *Neritaria* from the Late Triassic (210-245 Ma) already had a structure to adjust the operculum in the aperture. A small tooth at the basal part of the columella (*Neritaria* sp. and *Ruganeritaria* sp.) or centred on the columella (*Dentineritaria* sp.) secured the retracted thin operculum. The nucleus of the operculum lies close to the basal part of the columella, similar to the nucleus of opercula of modern *Neritina*/ *Nerita*. The possible presence of an apophysis remains unclear.

Jagt & Kiel (2008) showed that the genus *Otostoma*, which is closely related to *Nerita*, already had the typical asymmetric *Nerita*-operculum. They were able to mould the

operculum of *Otostoma retzii* (Nilsson, 1827), a species that lived during the Late Cretaceous (65-70 Ma). They concluded that it has a well developed apophysis and the nucleus was located in the lower third of the operculum, closer to the columellar margin than to the outer margin.

Rust (1997) discussed the operculum of fossil *Theodoxus trilophosensis* Rust, 1997 found in neogene deposits in the Northern-Aegean area. He discussed in detail the function of the operculum and its retracting process into the aperture, and showed the interaction between the apophysis, in his terminology, and a basal ridge in the aperture during retraction. He also showed that the development of the apophysis depended on the presence of a predator (i.e. a crab *Liocarcinus* sp.). Note that in his technical terminology he interchanged the terms apophysis and pseudo-apophysis (Krijnen, 1997a) respectively called 'Rippe' and 'Apophyse' in German.

Checa & Jiménez-Jiménez (1998) made an inventory of studies about opercula. They concluded that the number of studies is rather limited and in many different scientific fields. Most studies dealt with research about the secretion process or with the evolutionary development of opercula, while some studies dealt with the use of opercula in systematics.

Opercula of the genus *Nerita* are paucispiral and rigiclaudent. In paucispiral opercula growth and secretion only occur at the columellar edge and the operculum has to rotate, allowing more space for the growth of the new part. Rigiclaudent opercula grow when the operculum is retracted to assure an exact match with the shape of the aperture during growth (Checa & Jiménez-Jiménez, 1998).

From the nucleus onwards, the operculum grows gnomonically, i.e. it grows in size but does not change shape (Thompson, 1917). While growing the operculum rotates around its nucleus. This process is represented by the black curved lines in Figure 1.

On the outer surface of the operculum numerous striae are sometimes visible. These demarcate growth stages which are nicely accented, for example, by the transversal folds on the opercula of nerites of the subgenus *Linnerita* Vermeij, 1984. Granulated opercula show these growth stages by the curved radiating arrangement of their pustules.

Vermeij (1984) divided the genus *Nerita* into several subgenera based on the characteristics of the operculum. He described the different opercula in the genus *Nerita* which led him to distinguish 10 subgenera and to introduce the new subgenus *Linnerita*.

These facts are operationalised in characteristics 3, 4, 5, 6 and 11 (see Appendix 1).

Because the operculum has a fixed position with respect to the shell, the apophysis has to twist during growth in order to maintain its function of securing the aperture with the operculum. The apophysis grows 'out of the plane of the operculum' and has to twist continuously to 'keep in touch' with the same spot on the backside of the columella where it can act like a kind of hinge to adjust the operculum by sudden retraction. The rotation of the apophysis is operationalised in characteristic 1 (see Appendix 1).

In figure 4 the inner side of the operculum of *N. peloronta* Linnaeus, 1758 is shown clearly indicating how the (pseudo-)apophysis and the medial and lateral teeth are positioned behind the columella. The pseudo-apophysis and lateral tooth in combination with two calloused folds in the aperture also serve to adjust the operculum (operationalised in characteristics 8, 9 and 10, see Appendix 1). The arrows point at the places inside the aperture of the shell where two calloused folds are present. Note the development of the orange spot inside the shell along the columella.

Another function of the apophysis is to expand the surface of muscle attachment (Suzuki *et al.*, 1991). The size of the apophysis is operationalised in characteristic 2 (see Appendix 1).

It is known that many gastropods bear their operculum outside the shell at the end of the foot while crawling. Contrary to other gastropods the operculum of a *Nerita*-species is hidden on the foot under the shell while the snail crawls. From figure 5 in Gould, 1852 which pictures a crawling snail from below, it is clear that Gould already knew this phenomenon.

Personal observations learned that the operculum is stored on the foot under the parietal shield (Fig. 6; see also Quoy & Gaimard (1834), Eydoux & Souleyet (1852), and Martens (1889)).

The slanting parietal shield provides room for the operculum while the snail crawls or rests on its surface. It can also be favourable during retraction of the operculum in case a predator attacks. During the retraction the shell does not or hardly has to be lifted from the surface. More room can also be made when the operculum 'fits better' under the columellar area (characteristic 7, see Appendix 1).

This can be simulated with some *Nerita*-species (e.g. *N. grossa* Linnaeus, 1758) by gently pushing the operculum resting on the parietal shield, from the parietal shield towards the aperture. When the operculum turns over the columella, it will immediately be positioned in the aperture. Note the function of the fold(s) and teeth inside the aperture as well as the function of the apophysis, the medial and lateral teeth during retraction.
Summarising, the following characteristics of the operculum have been discussed with the exception of the pustulous callosity (= F) and the calloused outer ridge (= G) (also

see Figure 2). (Note that most of the characteristics were already discussed by Krijnen (1997a), partly based on Hill (1980) and Vermeij (1984)).

Inner side of operculum:
A: apophysis
B: pseudo-apophysis
C: medial tooth
D: lateral tooth
E: columellar side of operculum
F: pustulous callosity
G: calloused outer ridge

Outer side of operculum:
A: apophysis
B: pseudo-apophysis
C: medial tooth
D: lateral tooth
E: columellar side of operculum
H: nucleus
I: distal strip
J: outer edge
K: central area

At this point two characteristics on the inside of the operculum are highlighted.
A remarkable characteristic (characteristic 12, see Appendix 1) is the pustulous callosity at the base of the apophysis inside the operculum (Fig. 3). Krijnen (1997a) noticed that for example the opercula of *N. undata* Linnaeus, 1758 and *N. flammulata* Récluz, 1841 are lacking this callosity while the opercula of the closely related species *N. quadricolor* Gmelin, 1791 and *N. spengleriana* Récluz, 1843 do possess this callosity. Sometimes this callosity even forms a small ridge.

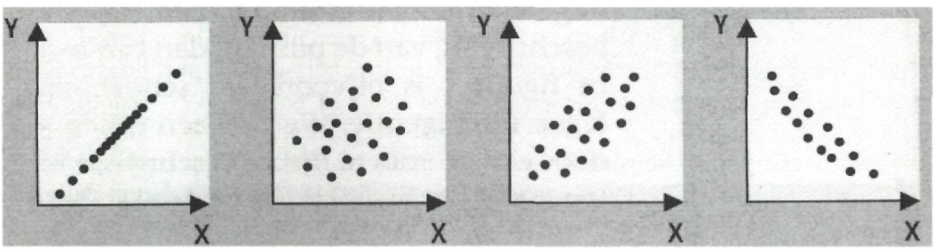
The second remarkable characteristic is the presence of ridges inside the operculum (characteristic 13, see Appendix 1). The variable is added because this characteristic is very conspicuous for some species (e.g. *N. longii* Récluz, 1841).

Materials and methods: Before the methodological approach is clarified, a brief explanation of the statistical techniques used is given.

The variables of the characteristics of the operculum and shell were related to each other. To find possible relationships one has to take into account the measurement levels of the variables. These levels determine the statistical techniques that can be used. The characteristics of the operculum were scored on a so-called nominal level: the use of categories with (hardly) no order. To examine relationships between nominal variables cross tables can be used. But because we had to reckon with the influence of a third variable we transformed the nominal categories to dichotomies (see below). Dichotomized variables have a so-called pseudo-metric level, so more advanced statistical techniques can be used. Relationships between nominal variables are called associations; relationships between metric variables are called correlations.
When two variables (e.g. A and B) are statistically related, this relationship can still be spurious. This means that the observed relationship between A and B was caused

by the influence of a third variable C on A and B separately. A well-known classic example is: Given: A = number of births; B = number of storks and C = degree of urbanization. Numerically it is easy to obtain a significant relationship between A and B without taken the influence of C into account. It is clear that in this example the relationship between A and B is spurious and was caused by the influence of C upon A and B respectively. The statistical approach to tackle spuriousness is explained in Appendix 4.

The correlation (indicated by 'r') is a number expressing the relation between two (pseudo-)metric variables X and Y. Range r lies between –1 and 1; r = 0 means no correlation at all. A negative sign denotes that when variable X increases, variable Y decreases. A positive sign denotes that when variable X increases, variable Y decreases. When r = -1 or 1 X and Y have a perfect linear relationship respectively a descending or ascending straight line. Plotting X against Y can result in the following examples:



(From: Slotboom, 1996)
From left to right: r = +1, r ≈ +0,3, r ≈ +0,7 and r ≈ -0,9 ('≈' means approximately).

For the tests a standard significance-level of 5% was used. When a test results in a significance less than 5% it means that we can accept that the correlation really exists. A significance more than 5% means that the test result can be ascribed to chance. It can be doubted that the found correlation exists. When a higher significance-level is used it becomes more difficult to discriminate real correlations and correlations by chance.

The opercula were studied without magnification. In Appendix 1 the characteristics describing the operculum that will be used as variables in our statistical study are listed. Their meaning can be derived from figure 2 and Appendix 1. Some explanations may be useful here, however:
- characteristics 3, 4 and 7 deal with the outer side of the operculum as a whole;
- with the angle of the apophysis (see characteristic 1) we mean the angle the apophysis makes with the inner part of the columellar side (towards medial tooth);
- with the ridges on the inside of the operculum (see characteristic 13) we mean a crescent-shaped ridge parallel to the outer edge and starting between the medial and lateral tooth (see for example the operculum of *N. articulata*).
-The colour of the operculum was not registered since we assume it is not a functional morphological aspect.

The characteristics of the shell had already been analysed by Krijnen (1997b). For the research described here all data were double-checked and were dichotomized to simplify statistical calculations.

For example variable **characteristic11** (*'undulation columellar side operculum'*) was originally measured with the categories strongly undulated, moderately undulated and hardly/not undulated; with undulating meaning the operculum has a wave-like columellar rim. In dichotomizing only two categories can be kept. This variable was therefore transformed to hardly/not undulated and undulated.

The transformation to dichotomized variables is always based on the frequencies of the original categories (see Appendix 2) resulting into two categories with the largest possible frequencies. These categories are coded to the values '0' and '1' deliberately (see below).

Only one variable (a shell-characteristic with label *'curvature columella'*) was dichotomized into two variables. One variable with the value-labels *not flat/flat*; one variable with the value-labels *not concave/concave*. Both categories, flat and concave of the original variable had approximately equal frequencies. Consequently, relevant correlations may disappear. If necessary the original variable will be used in further analysis.

Dichotomized variables (with value '0' and '1') can be analysed as metric variables regarding their bivariate correlation, so-called 'fourfold point correlation' (Hays, 1988). This also simplifies the analysis of spurious correlations by examination of the partial correlations.

For analysis of the correlation between metric variables three questions are important. First the correlation (= 'r') has to be significant. Under the zero hypothesis that no correlation exists ($r = 0$), the correlation significantly exists ($r \neq 0$) below a 0.05-level. Second, it is important to explain the direction and strength of the significant correlation. All questions can immediately be answered with the so-called correlation-matrix (see Appendix 3). For example the correlation between the size and the angle of the apophysis does not exist (denoted by 'Sig (2-tailed)': 0.648) while the structure of the operculum and the strips outside the operculum significantly correlate (0.000). Only in the latter case it is important to analyse the direction and strength of the correlation: $r = -0.691$. In this case the structure of the operculum and the strips outside the operculum correlate relatively strong and opposite.

When important correlations occur, sometimes the not dichotomized, original variables were analysed to get a better understanding of the correlation/association. In that case other statistical analysis were used (chi-square test of association).

An overview of the used variables for operculum characteristics can be found in Appendix 1. For an explanation of the variables of the characteristics of the shell, see Krijnen (1997b).

All analysis were done by SPSS (Statistical Package for the Social Sciences) version 12.

Results: The results of the analysis will now be discussed in four paragraphs (I - IV). First the analysis of the data of the characteristics of the opercula are discussed followed by an analysis of the correlations of these characteristics. Third, the relevant correlations (to the operculum) of the characteristics of the shell are discussed. For more results, see Krijnen, 1997b. Finally the joint data of shell and operculum characteristics are examined.

I. Discussion frequencies of operculum characteristics

Most opercula are flat (≈68%) and have a totally granulated outer surface (≈66%). Opercula mostly have a conspicuous apophysis (≈95%), appearing rectangular (≈80%) from under the columellar side of the operculum and a conspicuous pseudo-apophysis (≈82%),. They have a well developed medial tooth (≈77%) and a less developed lateral tooth (≈89%). On the inner side of the operculum the pustulous callosity and ridges are lacking (resp. ≈77% and ≈88%). See Appendix 2.

II. Correlation-analysis of the operculum characteristics

With the correlation-matrix (see Appendix 3) the correlation between the characteristics is examined. Note that the characteristics *structure distal strip* and *structure central area* are kept out of the analysis (n = 21, which is too few).
The following characteristics correlate significantly (significance level below 5%):

- *Size apophysis* and *presence medial tooth* (r = .356): opercula with a small apophysis tend to have hardly visible or no medial tooth; e.g. all species of the subgenus *Ritena*. Opercula with a well developed medial tooth tend to have a large apophysis; e.g. *N.* (*Theliostyla*) *textilis*, *N.* (*Theliostyla*) *albicilla*, *N.* (*Theliostyla*) *exuvia* or *N.* (*Cymostyla*) *grossa*, *N.* (*Cymostyla*) *spengleriana*, *N.* (*Cymostyla*) *quadricolor*.

- *Presence medial tooth* and *undulation columellar side operculum* (r = .337): opercula with no or a hardly developed medial tooth do not show a conspicuous undulation of the columellar side of the operculum; e.g. all species of the subgenus *Ritena*. A large medial tooth corresponds with more undulation. Many species through many subgenera like *N.* (*Nerita*) *peloronta*, *N.* (*Cymostyla*) *scabricosta*, *N.* (*Linnerita*) *antiquata*, *N.* (*Adenerita*) *adenensis*, *N.* (*Ilynerita*) *planospira*, *N.* (*Theliostyla*) *albicilla*, etc.

- *Size apophysis* and *undulation columellar side operculum* (r = .273): this correlation is spurious and will not be discussed anymore (see Appendix 4)!

- *Strips outside operculum* and *structure operculum* (r = -.691): the surface of an operculum with strips has different types of structure, like species of the subgenus *Linnerita*. On the other hand if the *surface has no strips it is totally granulated*. Many species follow this relationship with the exception of the totally smooth opercula of *N. adenensis*, *N. lirellata* and *N. planospira*.

- *Structure operculum* and *presence lateral tooth* (r = -.361): granulated opercula more often have a less developed lateral tooth. Many species, mainly of the subgenera *Amphinerita*, *Cymostyla* and *Theliostyla* like *N.* (*Amphinerita*) *incerta*, *N.* (*Cymostyla*) *undata*, *N.* (*Theliostyla*) *albicilla*, etc. comply with this.

- *Undulation columellar side operculum* and *presence ridges inside operculum* (r = .304): opercula with no or hardly undulated columellar side tend to have no or hardly developed ridges on the surface of the inner side of the operculum, like many species of the subgenera *Linnerita* and *Ritena* and some species of *Cymostyla* like *N. grossa*, *N. quadricolor*, *N. helicinoides*.

Only seven species have an undulated columellar side of the operculum and ridges on the inside of the operculum; e.g. *N.* (*Cymostyla*) *articulata*, *N.* (*Cymostyla*) *aterrima*, and *N.* (*Cymostyla*) *balteata*.

- *Presence pustulous callosity at base apophysis* and *presence ridges inside operculum* (r = .304): opercula without a pustulous callosity on the base of the apophysis tend to have no or hardly developed ridges on the surface of the inner side of the operculum. Many species follow this relationship. Only a few species have a pustulous callosity at the base of the apophysis and ridges on the inside of the operculum like *N.* (*Cymostyla*) *aterrima* and *N.* (*Cymostyla*) *balteata*.

Unfortunately a biological explanation of the significant correlations cannot be given.

III. Correlation-analysis of relevant shell characteristics

Before discussing the correlations of the shell and operculum characteristics, it is necessary to evaluate the relevant correlations between two shell characteristics. With relevant correlations we mean significant correlations between two shell characteristics which are also significantly related to an operculum characteristic (see Appendix 7). For a discussion of all correlations between two shell characteristics, we refer to Krijnen, 1997b. For convenience the correlation-matrix of shell characteristics is added in Appendix 5. The spuriousness of the relevant correlations between two shell characteristics controlled for a third shell characteristic are done in the analysis described here (for an example of the analysis on spuriousness, see Appendix 4). This

analysis was not done by Krijnen (1997b). The following relevant correlations between shell characteristics are found to be autonomous (i.e. real):

- *rib structure and surface columellar area* (r = -.314; see Appendix 5): a tendency that smooth nerites have a smooth columellar area;
- *surface columellar area* and *development ruff* (r = -.459): a tendency that nerites with a smooth columellar surface do not have a developed ruff;
- *surface columellar area* and *presence grooves in outer lip* (r = -.677): a tendency that nerites with a smooth columellar surface do not have conspicuous crenulations in the outer lip;
- *visibility columellar teeth* and *position columellar teeth* (r = -.697): a tendency that centered columellar teeth are (very) small;
- *position columellar teeth* and *visibility teeth in outer lip* (r = -.460): a tendency that nerites with centered columellar teeth have obscure teeth in the upper part of the outer lip.

The latter correlation is partly autonomous. In such a case the correlation between both shell characteristics will be maintained.

The correlation between rib structure and the presence of grooves in the outer lip (r = .269) turned out to be spurious. Thus the second right 'triangle' (see second row of Appendix 7), in which this correlation was used, disappears. From the other two correlations of this 'triangle', it also turned out that the correlation between the structure of the operculum and the presence of the grooves in the outer lip is spurious. The third correlation in this 'triangle' between the structure of the operculum and the rib structure will be autonomous i.e. real (see below *Correlation-analysis* **Case 1**).

IV. Correlation-analysis of the operculum and shell characteristics (general)

Appendix 6 shows the correlations between the characteristics of the operculum and of the shell. It can be seen that the following characteristics of the operculum do not correlate with any shell characteristic: the size of the apophysis, the presence of the apophysis, the presence of the lateral tooth and the presence of the ridges on the inner side of the operculum.

When the significant correlations between variables of the operculum and shell characteristics are analysed on spuriousness, we theoretically have two possibilities ('triangles'), where x_i being an operculum characteristic (indicated by numbers in Appendix 7) and y_i representing a shell characteristic (indicated by alphabetical characteristics in Appendix 7).

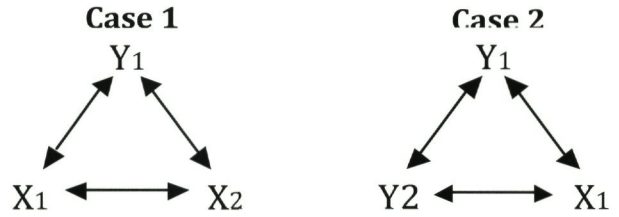


Fig. 7a-b: Two possible 'triangles' with variables of the operculum (= x_i) and shell characteristics (= y_i).

In the first case the correlation is controlled by an operculum characteristic in two different ways, x_1 for $x_2 \leftrightarrow y_1$ and x_2 for $x_1 \leftrightarrow y_1$; in the second case the correlation is controlled by a shell characteristic, also in two different ways: y_1 for $x_1 \leftrightarrow y_2$ and y_2 for $x_1 \leftrightarrow y_1$. Interaction effects are beyond this study. No analysis was done to see whether the controlling variable refines, distorts or suppresses the correlation (Pelsmacker & Kenhove, 2006: 235-237). One example of the analysis of spuriousness is given below to illustrate the approach.

Correlation-analysis of the operculum and shell characteristics (Case 1)
First '**Case 1**-triangles' (see Appendix 7) will be discussed.
From Appendix 6 it can be seen that the rib structure of the shell (= y_1) significantly correlates with the strips on the outside of the operculum [= x_1; (r = -.314)] and with the structure of the operculum [= x_2; (r = .458)]. The two characteristics of the operculum (x_1 and x_2) also correlate (r = -.691) (see Appendix 3).
Using partial correlations analysis (see Appendix 4 for an explanation) shows that the correlation between the rib structure of the shell (= y_1) and the structure of the operculum (= x_2) is autonomous (i.e. 'genuine'). The other correlation (between y_1 and x_1) turned out to be spurious.
Partial correlations analysis showed that the two possible correlations between shell and operculum characteristics in the other 'triangle' of **Case 1** (see Appendix 7) are also spurious.

Correlation-analysis of the operculum and shell characteristics (Case 2)
Analysis of spuriousness showed that only two correlations between operculum and shell characteristics are true correlations (in 'triangles' of **Case 2).** These autonomous correlations are:
- *rib structure* and *structure of the operculum* (r = .458; see Appendix 6): a tendency that ribbed nerites have a granulated operculum (see also **Case 1**);
- *position columellar teeth* and *presence pustulous callosity on base apophysis* (r = -.487): a tendency that nerites with centered columellar teeth do not have an operculum with a pustulous callosity on the base of the apophysis.

In the correlation-matrix of Appendix 6 three other significant correlations were found. These correlations were not involved in any 'triangles' for analysis of spuriousness. These significant correlations are:
- *development of the apex* and *angle of the apophysis* (r = -.351): a tendency that nerites with a well developed apex have an operculum with which, by front view, the angle with the columellar side of the operculum, is obtuse;
- *curvature columellar area* and *curvature operculum* (r = .279): a tendency that nerites with a flat columellar area have a flat operculum;
- *development ruff* and *presence medial tooth* (r = .458): a tendency that nerites with a (well) developed ruff have an operculum with a conspicuous medial tooth.

Discussion: To get a better (biological) understanding of the abovementioned significant correlations between the characteristics of the shell and of the operculum, the involved variables are crossed. For this analysis the original non-dichotomized variables are used. The cross tables are found in Appendix 8. In Appendix 9 the species which satisfy the relationship are given.

- *curvature of the columellar area* and *curvature of the operculum*
It seems that concave opercula occur in nerites with a convex columellar area while flat opercula occur in nerites with a flat columellar area and, finally, convex opercula occur in nerites with a concave columellar area.

The importance of the slanting columellar area has already been discussed. In the same way the oppositely curved columellar area and operculum can be explained as an advantage that the operculum needs less room under the columellar area while the snail is hatched on a rocky surface. Also during retraction of the operculum the snail does not have to lift itself much from the rocky surface in order to close the aperture with the operculum.

Remarkably, the significant correlation between the curvature of the columellar area and the columella disappeared after dichotomizing the original variable (see Appendix 5). But this relationship was found significantly correlated (r = 0.430, Krijnen, 1997b).

During the retraction-process it is also functionally favourable that the columella and the operculum are oppositely curved. Examine for example *N. costata*, *N. plicata* and *N. versicolor* (all with convex columella & septum and concave operculum) of the subgenus *Ritena* or *N. litterata* (with concave columella & septum and convex operculum) and *N. antiquata* (with convex columella and ditto septum and concave operculum) of the subgenus *Linnerita*.

- *ribbed nerites* and *granulated opercula*
After analysis of the cross table we cannot refine the significant correlation between the rib structure of the shell and the structure of the operculum. It remains unclear why ribbed nerites more often have granulated opercula (personal communication with Geerat Vermeij (Eindhoven, Oct. 2006)). Further research may show whether this correlation is biologically functional or that the functionality has evolutionary been lost, but that the characteristics are still present. Some species obviously contradict this correlation, e.g. *N. plicata* (nearly smooth operculum and heavily ribbed) or nerites such as *N. senegalensis* and *N. atramentosa* (granulated operculum and not ribbed). It is also important to examine species that 'do not follow the rule'. Why are these species the exceptions?

- *development apex* and *angle apophysis*
A (biological) explanation for this relationship cannot be given. Maybe the relationship has some connections with the conclusions of Kano (2006), viz. the angle of the apophysis can be influenced by the mutual position of the spot on the back side of the columella and the nucleus of the operculum. Further research about this is necessary.

- *development ruff* and *presence medial tooth*

- *position columellar teeth* and *presence pustulous callosity base apophysis*
Again (biological) explanations for these relationships cannot be given. Further research may show whether the correlations are biologically functional or that the functionality has evolutionary been lost but that the characteristics are still present.

Conclusions: Six significant, non-spurious, correlations are found between characteristics of the operculum and five significant, non-spurious, correlations are found between characteristics of the operculum and characteristics of the shell. The most important correlations viz 1) the curvature of the columellar area is opposite to the curvature of the operculum and 2) ribbed nerites tend to have granulated opercula, are significant at a 0.05-level.

A functional explanation of the first correlation is that the operculum needs less room under the columellar area while the snail is hatched on a rocky surface. Also during retraction of the operculum the snail does not have to lift itself much from the rocky surface in order to close the aperture with the operculum. No functional explanation can be given for the second correlation.

Possible research: A restriction is made to analyse only the correlations between characteristics of the shell and the operculum. However, it could be interesting to intermediate the set of variables with e.g. the littoral occurrence of the nerite. In

combination with the occurrence of predators like crabs (e.g. Rust, 1997), it could be interesting too to take into account the thickness of the operculum. The thickness of the operculum is a known antipredator trait (Vermeij, pers. comm., 2008).

The significant correlations are purely functionally explained. To what extent phylogeny contributes to explain the significant correlations will be studied elsewhere.

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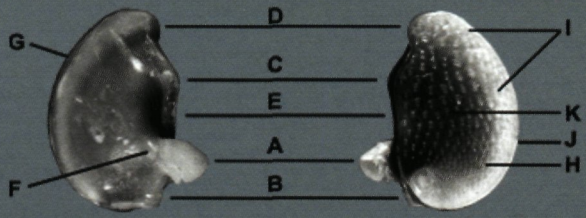
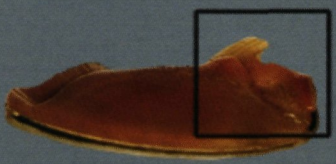
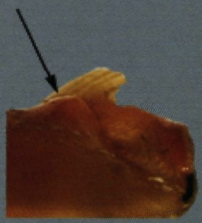
1



2



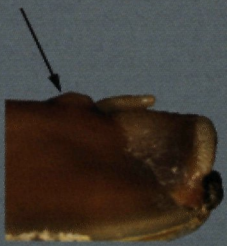
3a



3b

3c

3d



3e

4

5a

5b

6

PLATE 1:

Fig. 1: Gnomonic growth of operculum of *Nerita antiquata* Récluz, 1841. Photograph by Jeroen Goud.

Fig. 2: The characteristics of a *Nerita*-operculum. Photograph by Rob Vink (From Krijnen et al, 2006).
Legend:

Inner side of operculum:
A: apophysis
B: pseudo-apophysis
C: medial tooth
D: lateral tooth
E: columellar side of operculum
F: pustulous callosity
G: calloused outer ridge

Outer side of operculum:
A: apophysis
B: pseudo-apophysis
C: medial tooth
D: lateral tooth
E: columellar side of operculum
H: nucleus
I: distal strip
J: outer edge
K: central area

Fig 3a: The absence and presence of the pustulous callosity at the base of the apophysis (overview).
Fig. 3b: *Nerita undata* Linnaeus, 1758.
Fig. 3c: *Nerita flammulata* Récluz, 1841.
Fig. 3d: *Nerita quadricolor* Gmelin, 1791.
Fig. 3e: *Nerita spengleriana* Récluz, 1843.
Photographs by Rob Vink.

Fig. 4: The position of the operculum viewed from inner side of *Nerita peloronta* Linnaeus, 1758. Photograph by Rob Vink.

Fig. 5: A crawling *Nerita undata* Linnaeus, 1758 viewed sideways and from below (From Gould, 1852).

Fig. 6: Position of the operculum by retraction of the animal. *Nerita albicilla* Linneaus 1758. Sanur, Bali. Photograph by Charles Krijnen.

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Websites

www.nansaidh.us/operc

Appendix 1: Codebook with the variables for the operculum

For convenience the capitals of Fig. 2 have been added between brackets.

Characteristic 1 *Angle apophysis*

Value	Label
0	conspicuously obtuse
1	(nearly) rectangular

Characteristic 2 *Size apophysis* (= **A**)

Value	Label
1	conspicuously small
2	normal
3	conspicuously large

Characteristic 3 *Strips outside operculum*

Value	Label
0	no
1	yes

Characteristic 4 *Structure operculum*

Value	Label
1	totally smooth
2	different
3	totally finely granulated
4	totally coarsely granulated

Characteristic 5 *Structure distal strip* (= **I**)

Value	Label
1	smooth
2	folded
3	granulated

Characteristic 6 *Structure central area* (= **K**)

Value	Label
1	smooth
2	smooth + granulated
3	granulated

Characteristic 7 *Curvature operculum*

Value	Label
1	convex
2	flat
3	concave

Characteristic 8 *Presence pseudo-apophysis* (= **B**)

Value	Label
0	hardly or not
1	conspicuously

Characteristic 9 *Presence medial tooth* (= **C**)

Value	Label
0	hardly or not
1	conspicuously

Characteristic 10 *Presence lateral tooth* (= **D**)

Value	Label
0	hardly or not
1	conspicuously

Characteristic 11 *Undulation columellar side operculum* (= **E**)

Value	Label
1	strongly undulated
2	moderately undulated
3	hardly/not undulated

Characteristic 12 *Presence pustulous callosity base apophysis* (= **F**)

Value	Label
0	hardly or not
1	conspicuously

Characteristic 13 *Presence ridges inside operculum*

Value	Label
0	hardly or not
1	conspicuously

Appendix 2: Frequency tables of the characteristics of the operculum
For the associated SPSS data file, please email to the corresponding author.

Size apophysis

					Cumulative
Valid	conspicuously small	3	5,4	5,4	5,4
	normal	31	55,4	55,4	60,7
	conspicuously large	22	39,3	39,3	100,0
	Total	56	100,0	100,0	

Strips outside operculum

					Cumulative
Valid	no	35	62,5	62,5	62,5
	yes	21	37,5	37,5	100,0
	Total	56	100,0	100,0	

Structure operculum

					Cumulative
Valid	totally smooth	3	5,4	5,4	5,4
	different	16	28,6	28,6	33,9
	totally finely granulated	27	48,2	48,2	82,1
	totally coarsely granulated	10	17,9	17,9	100,0
	Total	56	100,0	100,0	

Structure distal strip

					Cumulative
Valid	smooth	1	1,8	4,8	4,8
	folded	5	8,9	23,8	28,6
	granulated	15	26,8	71,4	100,0
	Total	21	37,5	100,0	
Missing	0	35	62,5		
Total		56	100,0		

Structure central area

					Cumulative
Valid	smooth	7	12,5	33,3	33,3
	smooth + granulated	8	14,3	38,1	71,4
	granulated	6	10,7	28,6	100,0
	Total	21	37,5	100,0	
Missing	0	35	62,5		
Total		56	100,0		

Curvature operculum

					Cumulative
Valid	convex	9	16,1	16,1	16,1
	flat	38	67,9	67,9	83,9
	concave	9	16,1	16,1	100,0
	Total	56	100,0	100,0	

Presence pseudo-apophysis

					Cumulative
Valid	hardly or not	10	17,9	17,9	17,9
	conspicuously	46	82,1	82,1	100,0
	Total	56	100,0	100,0	

Presence medial tooth

					Cumulative
Valid	hardly or not	13	23,2	23,2	23,2
	conspicuously	43	76,8	76,8	100,0
	Total	56	100,0	100,0	

Presence lateral tooth

					Cumulative
Valid	hardly or not	50	89,3	89,3	89,3
	conspicuously	6	10,7	10,7	100,0
	Total	56	100,0	100,0	

Undulation columellar side operculum

					Cumulative
Valid	strongly undulated	15	26,8	26,8	26,8
	moderately undulated	19	33,9	33,9	60,7
	hardly/not undulated	22	39,3	39,3	100,0
	Total	56	100,0	100,0	

Presence pustulous callosity base apophysis

					Cumulative
Valid	hardly or not	43	76,8	76,8	76,8
	conspicuously	13	23,2	23,2	100,0
	Total	56	100,0	100,0	

Presence ridges inside operculum

					Cumulative
Valid	hardly or not	49	87,5	87,5	87,5
	conspicuously	7	12,5	12,5	100,0
	Total	56	100,0	100,0	

Appendix 3: Correlation-matrix for the characteristics of the operculum

Correlations

		Angle apophysis	*Size apophysis*	*Strips outside operculum*	*Structure operculum*	Curvature operculum	Presence pseudo-apophysis	*Presence medial tooth*	Presence lateral tooth	*Undulation columellar side operculum*	*Presence pustulous callosity base apophysis*
Size apophysis	Pearson Correlation	-,062									
	Sig. (2-tailed)	,648									
	N	56									
Strips outside operculum	Pearson Correlation	,197	-,170								
	Sig. (2-tailed)	,145	,211								
	N	56	56								
Structure operculum	Pearson Correlation	-,164	,113	**-,691****							
	Sig. (2-tailed)	,226	,407	**,000**							
	N	56	56	**56**							
Curvature operculum	Pearson Correlation	,045	,084	-,020	,072						
	Sig. (2-tailed)	,744	,539	,885	,597						
	N	56	56	56	56						
Presence pseudo-apophysis	Pearson Correlation	,004	-,007	,072	,158	-,021					
	Sig. (2-tailed)	,976	,960	,597	,244	,876					
	N	56	56	56	56	56					
Presence medial tooth	Pearson Correlation	-,059	**,356****	-,011	,053	,165	,185				
	Sig. (2-tailed)	,666	**,007**	,936	,700	,224	,171				
	N	56	**56**	56	56	56	56				
Presence lateral tooth	Pearson Correlation	-,119	,194	,209	**-,361****	-,009	-,140	,190			
	Sig. (2-tailed)	,381	,151	,123	**,006**	,949	,303	,160			
	N	56	56	56	**56**	56	56	56			
Undulation columellar side operculum	Pearson Correlation	,154	**,273***	-,132	,041	,229	-,184	**,337***	,042		
	Sig. (2-tailed)	,256	**,042**	,332	,762	,089	,174	**,011**	,757		
	N	56	**56**	56	56	56	56	**56**	56		
Presence pustulous callosity base apophysis	Pearson Correlation	-,260	,077	-,164	,126	-,074	,256	,002	,083	-,077	
	Sig. (2-tailed)	,053	,571	,228	,355	,586	,056	,990	,543	,571	
	N	56	56	56	56	56	56	56	56	56	
Presence ridges inside operculum	Pearson Correlation	,051	,138	-,181	,157	,260	,176	,208	,044	**,304***	**,304***
	Sig. (2-tailed)	,709	,310	,181	,248	,053	,194	,124	,749	**,023**	**,023**
	N	56	56	56	56	56	56	56	56	**56**	**56**

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

Note that only a limited number of significant correlations are found. Compare with the correlation-matrix of the characteristics of the shell (see Appendix 5).Sig. (2-tailed) = significance level. N = sample size.

Appendix 4: Analysis of spuriousness between different variables (example)

When three variables are correlated with each other, one correlation can be spurious! This means that a correlation between two variables is caused by the third one which is also correlated with the first two variables. Partial correlations can solve this problem. E.g. Hays (1988) stated that the partial correlation between two variables is an index of the linear relationship that would still exist between these variables if all linear influences of one or more other variables were removed. The still significant correlation is called autonomous (van Dalen & de Leede, 2002).

Correlation between **characteristic9** and **characteristic11** controlled by **characteristic2**:

Control Variables			Presence medial tooth	Undulation columellar side operculum
Size apophysis	Presence medial tooth	Correlation	1,000	,267
characteristic2	**characteristic9**	Significance (2-tailed)	.	,049
		df	0	53
	Undulation columellar side operculum	Correlation	,267	1,000
		Significance (2-tailed)	,049	.
	characteristic11	df	53	0

Correlation between **characteristic2** and **characteristic11** controlled by **characteristic9**:

Control Variables			Undulation columellar side operculum	Size apophysis
Presence medial tooth	Undulation columellar side operculum	Correlation	1,000	,174
		Significance (2-tailed)	.	,205
		df	0	53
	Size apophysis	Correlation	,174	1,000
		Significance (2-tailed)	,205	.
		df	53	0

Correlation between **characteristic 2** and **characteristic 9** controlled by **characteristic11**:

Control Variables			Size apophysis	Presence medial tooth
Undulation columellar side operculum	Size apophysis	Correlation	1,000	,291
		Significance (2-tailed)	.	,031
		df	0	53
	Presence medial tooth	Correlation	,291	1,000
		Significance (2-tailed)	,031	.
		df	53	0

Explanation:
When for example, **characteristic2** and **characteristic11** are controlled by **characteristic9** (see second table), the influence of **characteristic9** upon **characteristic2** and **characteristic11** is minimized to examine whether the correlation between **characteristic2** and **characteristic11** is (not) spurious. In this case the correlation between **characteristic2** and **characteristic11** disappears ($p = .205$). The correlation between **characteristic2** and **characteristic11** is spurious corresponding to the conclusion in *Correlation-analysis of the operculum characteristics* (see **Results**).
Note that in the other tables the significant correlation does not disappear. The significance remains below 0.05. Thus the correlation between these two characteristics is autonomous.

Appendix 5: Correlation-matrix for the characteristics of the shell

Correlations

		Development apex	Rib structure	Curvature columellar area	Surface columellar area	Development ruff	Visibility columellar teeth	Position columellar teeth	Visibility teeth in outer lip	Presence grooves in outer lip	Curvature columella 1
Rib structure	Pearson Correlation	**,351****									
	Sig. (2-tailed)	**,008**									
	N	**56**									
Curvature columellar area	Pearson Correlation	-,067	,092								
	Sig. (2-tailed)	,625	,498								
	N	56	56								
Surface columellar area	Pearson Correlation	-,221	**-,314***	,221							
	Sig. (2-tailed)	,102	**,018**	,102							
	N	56	**56**	56							
Development ruff	Pearson Correlation	,242	,030	-,008	**-,459****						
	Sig. (2-tailed)	,072	,826	,951	**,000**						
	N	56	56	56	**56**						
Visibility columellar teeth	Pearson Correlation	**,486****	,178	-,122	**-,315***	,156					
	Sig. (2-tailed)	**,000**	,189	,370	**,018**	,249					
	N	**56**	56	56	**56**	56					
Position columellar teeth	Pearson Correlation	**-,387****	-,122	,096	**,486****	-,159	**-,697****				
	Sig. (2-tailed)	**,003**	,371	,481	**,000**	,241	**,000**				
	N	**56**	56	56	**56**	56	**56**				
Visibility teeth in outer lip	Pearson Correlation	**,354****	**,425****	-,067	**-,508****	,242	**,413****	**-,460****			
	Sig. (2-tailed)	**,007**	**,001**	,625	**,000**	,072	**,002**	**,000**			
	N	**56**	**56**	56	**56**	56	**56**	**56**			
Presence grooves in outer lip	Pearson Correlation	**,404****	**,269***	-,116	**-,677****	**,359****	**,492****	**-,531****	**,548****		
	Sig. (2-tailed)	**,002**	**,045**	,396	**,000**	**,007**	**,000**	**,000**	**,000**		
	N	**56**	**56**	56	**56**	**56**	**56**	**56**	**56**		
Curvature columella 1	Pearson Correlation	,134	,149	,227	**-,300***	,056	**,283***	**-,377****	**,279***	**,270***	
	Sig. (2-tailed)	,323	,273	,092	**,025**	,682	**,035**	**,004**	**,037**	**,044**	
	N	56	56	56	**56**	56	**56**	**56**	**56**	**56**	
Curvature columella 2	Pearson Correlation	-,177	-,231	-,110	**,325***	,015	**-,370****	**,502****	**-,392****	**-,363****	**-,898****
	Sig. (2-tailed)	,193	,087	,419	**,015**	,911	**,005**	**,000**	**,003**	**,006**	**,000**
	N	56	56	56	**56**	56	**56**	**56**	**56**	**56**	**56**

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

Note that many significant correlations are found. Compare with the correlation-matrix of the characteristics of the operculum (see Appendix 3). The correlation-matrix above slightly differs from the correlation-matrix published by Krijnen (1997: 42), due to the addition of two new species and by dichotomising the variables. Both tables show the same significant correlations with only a few non-relevant exceptions.

Appendix 6: Correlation-matrix for the characteristics of the operculum and the shell

Correlations

		Angle apophysis	Size apophysis	*Strips outside operculum*	*Structure operculum*	*Curvature operculum*	Presence pseudo-apophysis	*Presence medial tooth*	Presence lateral tooth	*Undulation columellar side operculum*	*Presence pustulous callosity base apophysis*	Presence ridges inside operculum
Development apex	Pearson Correlation	**-,351****	-,016	-,129	,213	-,126	,247	-,082	,025	,016	,251	,189
	Sig. (2-tailed)	**,008**	,909	,342	,114	,355	,066	,549	,856	,909	,062	,162
	N	**56**	56	56	56	56	56	56	56	56	56	56
Rib structure	Pearson Correlation	-,104	-,057	**-,314***	**,458****	-,059	,217	-,164	-,089	-,019	,164	,070
	Sig. (2-tailed)	,444	,678	**,018**	**,000**	,665	,109	,228	,512	,890	,228	,610
	N	56	56	**56**	**56**	56	56	56	56	56	56	56
Curvature columellar area	Pearson Correlation	-,100	,016	-,018	,089	**,279***	,127	-,173	-,141	-,236	,173	,027
	Sig. (2-tailed)	,464	,909	,892	,514	**,037**	,351	,203	,301	,080	,203	,843
	N	56	56	56	56	**56**	56	56	56	56	56	56
Surface columellar area	Pearson Correlation	,100	-,016	**,314***	**-,316***	,027	-,033	-,167	,025	**-,278***	-,173	,081
	Sig. (2-tailed)	,464	,909	**,018**	**,018**	,841	,807	,220	,856	**,038**	,203	,552
	N	56	56	**56**	**56**	56	56	56	56	**56**	56	56
Development ruff	Pearson Correlation	-,260	,026	**-,271***	,227	,205	-,098	**,271***	-,103	,213	,097	,103
	Sig. (2-tailed)	,053	,852	**,044**	,092	,130	,473	**,043**	,449	,115	,477	,451
	N	56	56	**56**	56	56	56	**56**	56	56	56	56
Visibility columellar teeth	Pearson Correlation	-,230	,151	-,103	,092	-,108	,179	,143	,054	,146	**,373****	,206
	Sig. (2-tailed)	,088	,266	,450	,501	,427	,186	,294	,690	,283	**,005**	,128
	N	56	56	56	56	56	56	56	56	56	**56**	56
Position columellar teeth	Pearson Correlation	,227	,003	,047	-,062	**,280***	-,010	,057	-,063	-,003	**-,487****	-,014
	Sig. (2-tailed)	,093	,985	,732	,652	**,036**	,941	,678	,645	,985	**,000**	,920
	N	56	56	56	56	**56**	56	56	56	56	**56**	56
Visibility teeth in outer lip	Pearson Correlation	-,261	-,236	-,129	,213	**-,279***	,154	-,082	-,091	-,058	,167	-,244
	Sig. (2-tailed)	,052	,080	,342	,114	**,037**	,258	,549	,505	,673	,220	,070
	N	56	56	56	56	**56**	56	56	56	56	56	56
Presence grooves in outer lip	Pearson Correlation	,008	,208	-,195	**,267***	-,003	,144	,102	-,153	**,307***	,239	,014
	Sig. (2-tailed)	,953	,125	,150	**,047**	,984	,290	,455	,259	**,021**	,077	,921
	N	56	56	56	**56**	56	56	56	56	**56**	56	56
Curvature columella 1	Pearson Correlation	-,026	,116	,075	-,065	,055	-,067	,049	,167	,032	,208	-,109
	Sig. (2-tailed)	,849	,394	,585	,632	,686	,622	,721	,220	,817	,125	,423
	N	56	56	56	56	56	56	56	56	56	56	56
Curvature columella 2	Pearson Correlation	-,027	-,029	-,138	,139	,101	,017	,147	-,128	,102	-,147	,149
	Sig. (2-tailed)	,842	,833	,309	,308	,458	,903	,281	,347	,455	,281	,274
	N	56	56	56	56	56	56	56	56	56	56	56

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

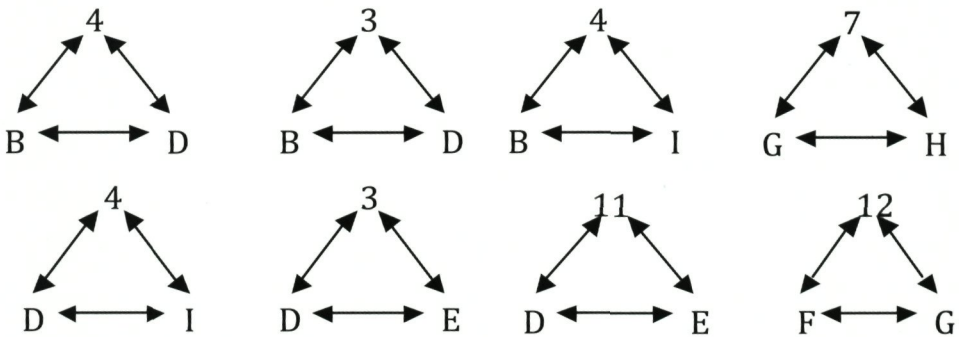
Appendix 7: Triangles between characteristics of the operculum and the shell

The following 'triangles' can be derived from Appendices 3, 6 and 7:

Characteristics of operculum	Characteristics of shell
1 = Angle apophysis	A = Development apex
2 = Size apophysis	B = Rib structure
3 = Strips outside operculum	C = Curvature columellar area
4 = Structure operculum	D = Surface columellar area
7 = Curvature operculum	E = Development ruff
8 = Presence pseudo-apophysis	F = Visibility columellar teeth
9 = Presence medial tooth	G = Position columellar teeth
10 = Presence lateral tooth	H = Visibility teeth in outer lip
11= Undulation columellar side operculum	I = Presence grooves in outer lip
12= Presence pustulous callosity base apophysis	J = Curvature columella 1
13 = Presence ridges inside operculum	K = Curvature columella 2

'Triangles' **case 1**:

'Triangles' **case 2**:



Appendix 8: Cross tables for correlated characteristics of the operculum and the shell

In the cross tables below the shell characteristics are represented in the columns; the operculum characteristics in the rows. When Count and Expected Count are equal no association exists (see note at the end of this appendix), otherwise (some) association occurs. It is sufficient to emphasize only scores where Count is relatively much larger than Expected Count (see bold figures in tables below). For example: in the second table we see that ribbed nerites more often have finely/coarsely granulated opercula.

In Appendix 9 the species are given which correspond with these bold figures..

Curvature operculum * Curvature columellar area Crosstabulation

Curvature operculum	convex	Count	0	3	**6**	9
		Expected Count	1,4	4,8	**2,7**	9,0
	flat	Count	3	**24**	11	38
		Expected Count	6,1	**20,4**	11,5	38,0
	concave	Count	**6**	3	0	9
		Expected Count	**1,4**	4,8	2,7	9,0
Total		Count	9	30	17	56
		Expected Count	9,0	30,0	17,0	56,0

The table above shows the most important association found, viz. the curvature of the columellar area is opposite to the curvature of the operculum.

Structure operculum * Rib structure Crosstabulation

			Rib structure			
			ribbed	incised ribs	smooth	Total
Structure operculum	totally smooth	Count	1	2	0	3
		Expected Count	1,9	,5	,6	3,0
	different	Count	5	2	**9**	16
		Expected Count	10,0	2,9	**3,1**	16,0
	totally finely granulated	Count	**21**	5	1	27
		Expected Count	**16,9**	4,8	5,3	27,0
	totally coarsely granulated	Count	**8**	1	1	10
		Expected Count	**6,3**	1,8	2,0	10,0
Total		Count	35	10	11	56
		Expected Count	35,0	10,0	11,0	56,0

The table above clarifies the conjecture of Geerat Vermeij. It shows that ribbed nerites tend to have granulated opercula.

Angle apophysis * Development apex Crosstabulation

			Development apex			
			well developed	moderately	hardly/not developed	Total
Angle apophysis	conspicuously obtuse	Count	**9**	0	2	11
		Expected Count	**5,1**	2,0	3,9	11,0
	(nearly) rectangular	Count	17	**10**	**18**	45
		Expected Count	20,9	**8,0**	**16,1**	45,0
Total		Count	26	10	20	56
		Expected Count	26,0	10,0	20,0	56,0

Presence medial tooth * Development ruff Crosstabulation

			Development ruff			
			conspicuously	moderately	hardly or not	Total
Presence medial tooth	hardly or not	Count	1	0	**12**	13
		Expected Count	2,3	1,6	**9,1**	13,0
	conspicuously	Count	**9**	**7**	27	43
		Expected Count	**7,7**	**5,4**	29,9	43,0
Total		Count	10	7	39	56
		Expected Count	10,0	7,0	39,0	56,0

Presence pustulous callosity base apophysis * Position columellar teeth Crosstabulation

Presence pustulous callosity base apophysis	hardly or not	Count	**31**	12	43
		Expected Count	**25,3**	17,7	43,0
	conspicuously	Count	2	**11**	13
		Expected Count	7,7	**5,3**	13,0
Total		Count	33	23	56
		Expected Count	33,0	23,0	56,0

Note: a combination of two categories of characteristics is favourable when the Count is larger than the Expected Count. The Expected Count are numbers based on no association at all (the crossed characteristics are called mutually independent). Theoretically the association is zero. Differences between Count and Expected Count mean more or less favourable combinations. These differences are important when the association is significant! For example (see last table): Opercula without a pustulous callosity are found more often in nerites with centered columellar teeth (Count = 31; Expected Count = 25.3).

Appendix 9: Overview of the species satisfying significant correlations between the characteristics of the operculum and the shell

Species are given which satisfy the significant correlation.

- curvature of the columellar area opposite to curvature of the operculum (36 cases):
Nerita articulata (2), Nerita ascensionis chlorostoma (2), Nerita atramentosa (1), Nerita balteata (2), Nerita chamaeleon (2), Nerita costata (3), Nerita erythrostoma (2), Nerita funiculata (2), Nerita grayana (2), Nerita helicinoides (2), Nerita incerta (2), Nerita insculpta (2), Nerita lirellata (2), Nerita longii (2), Nerita luteonigra (2), Nerita magdalenae (2), Nerita maxima (2), Nerita morio (2), Nerita nigrita (2), Nerita ocellata (2), Nerita olivaria (2), Nerita orbignyana (2), Nerita peloronta (1), Nerita planospira (2), Nerita plicata (3), Nerita quadricolor (2), Nerita scabricosta (3), Nerita semirugosa (3), Nerita senegalensis (1), Nerita spengleriana (3), Nerita squamulata (1), Nerita tessellata (1), Nerita textilis (2), Nerita undata (2), Nerita versicolor (3), Nerita yoldii (1).
With: (1) convex operculum, concave columellar area; (2) flat operculum, flat columellar area; (3) concave operculum, convex columellar area.

- ribbed shell and granulated operculum (29 cases):
Nerita albicilla, Nerita articulata, Nerita ascensionis, Nerita ascensionis chlorostoma, Nerita balteata, Nerita chamaeleon, Nerita costata, Nerita exuvia, Nerita filosa, Nerita fulgurans, Nerita funiculata, Nerita grossa, Nerita helicinoides, Nerita incerta, Nerita insculpta, Nerita longii, Nerita luteonigra, Nerita nigrita, Nerita oleagina, Nerita olivaria, Nerita patula, Nerita quadricolor, Nerita semirugosa, Nerita signata, Nerita spengleriana, Nerita squamulata, Nerita tessellata, Nerita textilis, Nerita undata.
Only species are mentioned that satisfy the relationship in question.

- well developed apex and obtuse angle apophysis (9 cases):
Nerita ascensionis chlorostoma, Nerita aterrima, Nerita grayana, Nerita grossa, Nerita luteonigra, Nerita oleagina, Nerita peloronta, Nerita quadricolor, Nerita spengleriana

- (well) developed ruff and (well) developed medial tooth (16 cases):
Nerita adenensis, Nerita aterrima, Nerita balteata, Nerita chamaeleon, Nerita fulgurans, Nerita grayana, Nerita longii, Nerita ocellata, Nerita oryzarum, Nerita patula, Nerita quadricolor, Nerita senegalensis, Nerita spengleriana, Nerita squamulata, Nerita textilis, Nerita undata.

- not centered columellar teeth and with presence of pustulous callosity on base apophysis (11 cases):
Nerita argus, Nerita aterrima, Nerita filosa, Nerita grossa, Nerita longii, Nerita maxima, Nerita oleagina, Nerita planospira, Nerita quadricolor, Nerita scabricosta, Nerita spengleriana