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The comparative method of taxonomic study of Bivalvia used by Soviet malacologists [1])

With 9 Figures

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Tver
(With a supplementary note by Ya. I. STAROBOGATOV, Leningrad)

Presently the taxonomic system of freshwater molluscs is very various in the USSR and other European countries. It is explained by differences in methods of investigation. Soviet taxonomists use more diagnostic traits than our western colleagues. The present paper is an account of the methods of conchological studies which have been used in the USSR during the revision of some groups of molluscs and establishing a number of new species and re-establishing of some old ones. We believe that the acquaintance with these methods would help our foreign colleagues to estimate better the validity of taxa revealed by Soviet malacologists. We hope that this paper would promote mutual understanding between colleagues separated by state and linguistic barriers.

We express our heartful thankfulness to Dr. H. ZEISSLER (Leipzig). This paper has been resulted from her suggestion and she indicated some points which would be of interest for our colleagues. – The original figures have been made by E. V. SHIKOV.

The shells of freshwater molluscs are often very poor with diagnostic features. With wide range of intraspecific variability it creates considerable difficulties in developing the system of freshwater molluscs. In this connection, some Soviet malacologists have undertaken the search for new diagnostic features.

It is known that the contour of the frontal section of a shell valve across its apex may be considered as a segment of logarithmic spiral (STASEK, 1963; THOMPSON, 1959, and others).

Such spiral has some constant affinities. For instance the angle between radius vector and tangent line drawn into any point of the spiral is constant for each logarithmic spiral. This angle is called polar angle (fig. 1A). It is independent on the length of the spiral. Hence, if the contour of the transverse section of a shell is considered as a segment of the logarithmic spiral, then the polar angle of the curve of the shell transverse section is unchanged with the molluscan age. In 1967 A. F. ALIMOV showed on sphaeriids that the polar angles of the valve transverse section are rather constant in each species and markedly vary in different species. He proposed to measure polar angles in order to determine species.

[1]) (Ya. I. STAROBOGATOV, in litt. 17. I. 1990): The method proposed by me together with some of my colleagues is named "comparative" in western European literature (e. g. Malacological Review 18, 1985, p. 21–35). But it is not quite right. It is of most importance that the method is not a simple comparison but a comparison using the comparator (I use the camera lucida for matching the figures). Considering this situation, I name this method in Russian "comparatornyj" which perhaps may be translated into English more adequately by "comparatory" or "comparatorial".

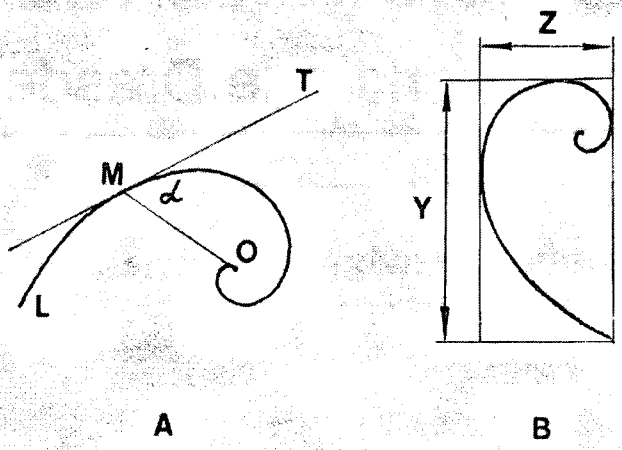

Fig. 1: Logarithmic spiral. A – polar angle, α = const. for $\sphericalangle$ M; B – measurements of the logarithmic spiral.

Further it was found that the species specifity of the polar angle is characteristic of other families of freshwater bivalvia as well. However, practical application of this systematic feature was inconvenient because of the complex measuring the polar angle value. In order to measure this angle we have not only to draw the valve transverse section but also carry out some graphical constructions (fig. 2).

B. M. LOGVINENKO and Ya. I. STAROBOGATOV (personal communication) have made an attempt to evaluate statistical standard deviations separately for the variability of the angle and for measurement of it. It is established on a material of 30 specimens of two forms of Caspian *Cerastoderma* and 5 repeating measurements of each specimen that the standard deviation of the variability of the angle is not significant by the presence of those of measurements of it. But they do not establish how many specimens must be studied in order to obtain significant standard deviation of the angle.

B. M. LOGVINENKO and Ya. I. STAROBOGATOV (1971) have found the thing to be done. They showed that not only the polar angles of the shell frontal section contours but also the contours themselves were species-specific. From whatever part of area the

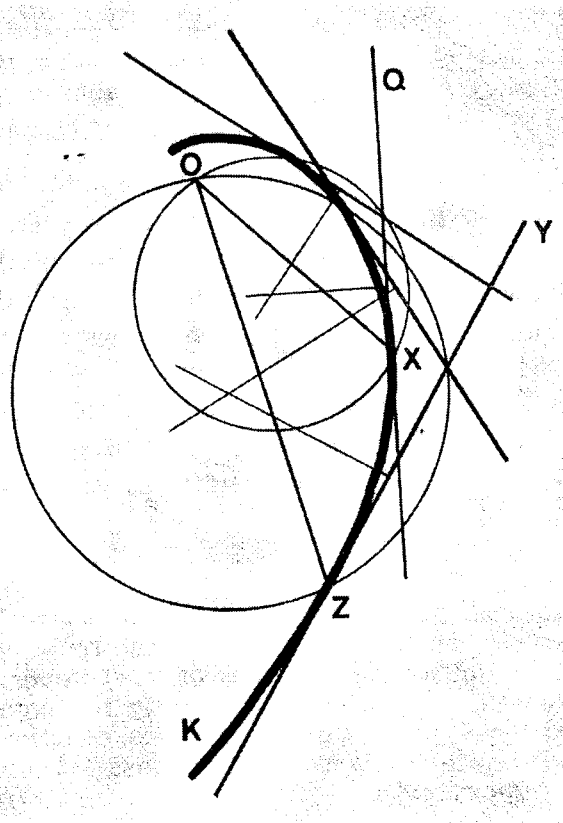

Fig. 2: Measuring of the polar angle on the frontal sections contour.

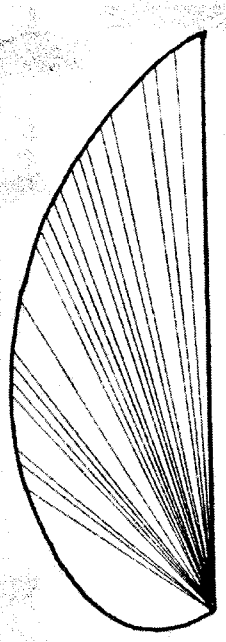

Fig. 3: Coincidence of the frontal section contours of 50 shells of *Pisidium amnicum* (O. F. MÜLLER) from different localities within its area (FRG to Baikal). (From LOGVINENKO & STAROBOGATOV, 1971, altered).

shells were taken, the contours of their sections were always identical. Moreover, pictures of transverse sections of the young specimen valves being matched with those of larger specimens look like smaller segments of the same logarithmic spirals tightened with chords (fig. 3).

In 1971 Ya. I. STAROBOGATOV, O. A. SCARLATO and B. M. LOGVINENKO have proved that the curvature of the shell valve frontal section can be used as an important systematic and diagnostic feature when investigating the families Cardiidae, Mactridae, Nuculidae, Nuculanidae, Pisidiidae, Scrobiculatiidae, Tellinidae, Unionidae, Veneridae (LOGVINENKO & STAROBOGATOV, 1971). Moreover, it appeared that the frontal section contour of shells of the same species was unchanged even in different varieties (fig. 4). Contours of frontal sections of some species may be considered as two logarithmic spirals (fig. 5B).

The shell transverse sections are uncomparable only in the following cases: 1) if the frontal section curve can not be interpreted as a logarithmic spiral (fig. 5A), 2) if homologous sections are uncomparable (this is characteristic for example of *Mytilus edulis* (L.) and *Dreissena rostriformis* (DESH.)).

In some cases the comparison of the shell transverse sections is seriously complicated though possible. Examination of the frontal section of forms with the constant spiral angle close to 0° (the shell is very flat) or to 90° (the shell section is almost circular) is especially difficult. In the former case one should draw as much as possible of the shell and in the latter one as little as possible.

In some cases the surface of frontal section is not a plane but is distorted (since this section should consequently cross points of shell which are the most moved off from the plane of symmetry). In this case the more curvature the frontal section surface has, the more is the possibility of an error. Such a case is observed in mussels and often takes place in *Dreissena*. In this case the smallest umbonal part of young specimens should be taken, i. e. such part that the frontal section plane curvature may be neglected.

After these works, the method of comparing the shell frontal section contours began to be widely used by Ya. I. STAROBOGATOV and his numerous disciples. Subsequently, this method has been named comparative method and applied to gastropods (IZZATULLAEV & STAROBOGATOV, 1984).

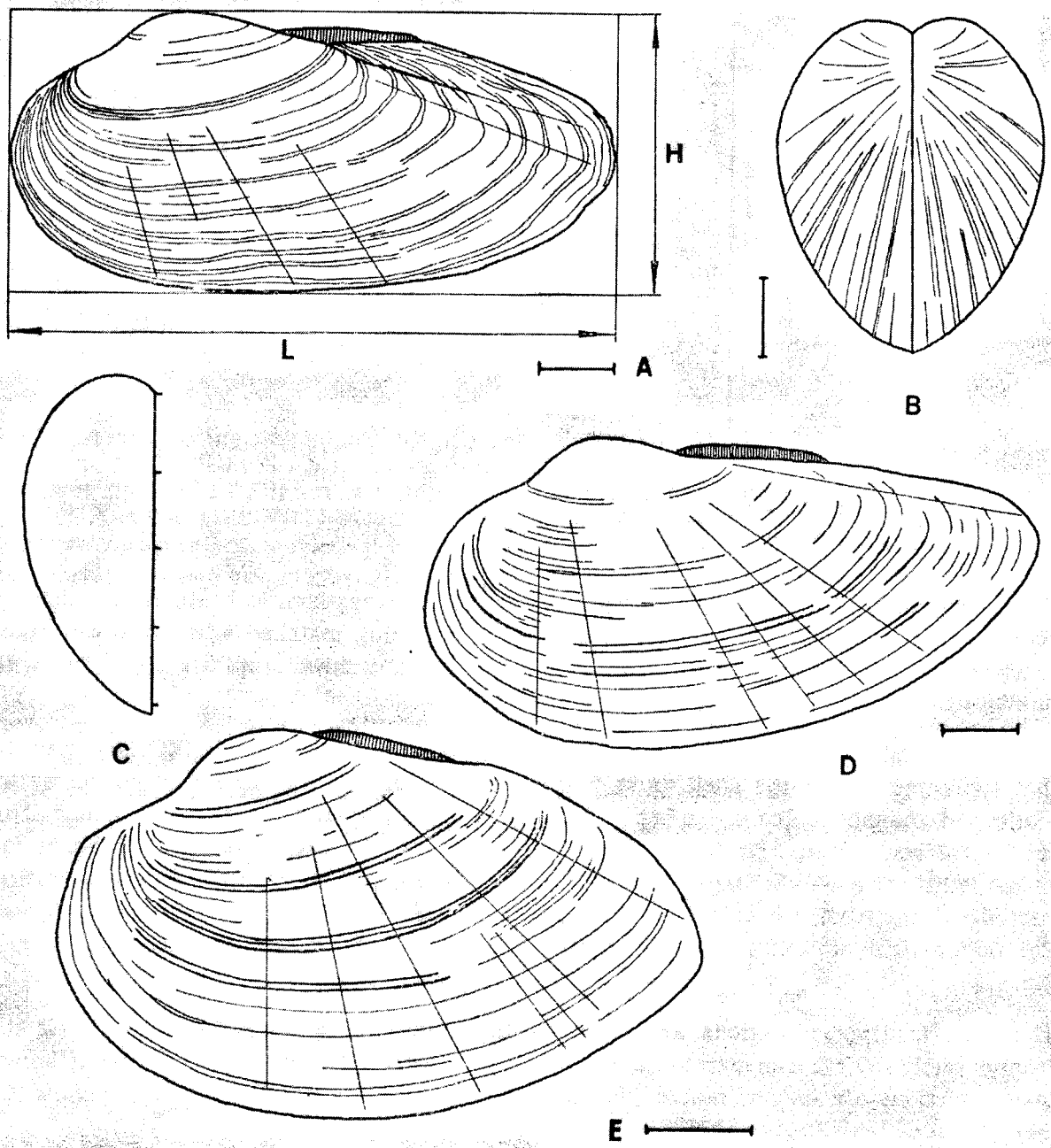

Fig. 4: *Unio tumidus* PHILIPSSON, different forms. A, B, C, D – *U. tumidus falcatulus* DROUET. A – lateral view, B – frontal view, C – the shell frontal section contour, L – length, H – height, E – *Unio tumidus* var. *minor* ROSSMAESSLER. (From STADNICHEN-
Scales: 1 cm

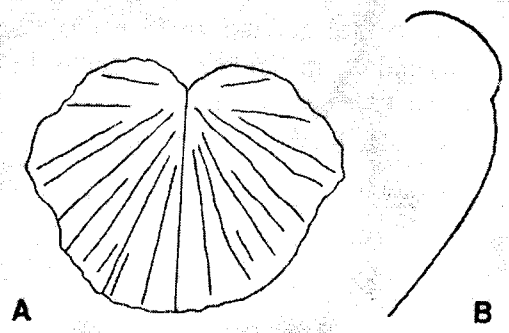

Fig. 5: Particular cases of the frontal sections of shells. A – *Pisidium ferrugineum* PRIME. Please note that the frontal section contour can not be interpreted as a logarithmic spiral. (From KUIPER, 1966). B – *Musculium morii* STAROBOGATOV & BUDNIKOVA. Please note that the frontal section contour can be interpreted as two logarithmic curves.

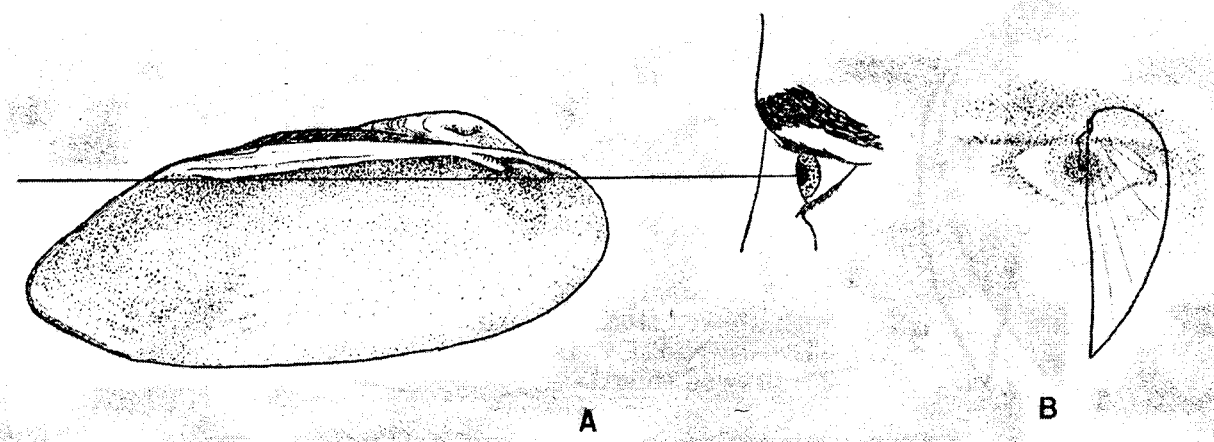

Fig. 6: Correct shell position in relation to the view axis during drawing the frontal section contour. A– lateral view, B – frontal view. (The original figures have been made by E. V. SHIKOV).

In 1975 A. I. KAFANOV has shown on sea-shells that the shell frontal section contours are not exact logarithmic spirals. The polar angle measured on the frontal section contour is not constant. However, these data did not prevent applying the comparative method. This is explained by the fact that, firstly, the frontal section contours are very close to logarithmic spirals and are slightly variable and, secondly, if they even are not exact logarithmic spirals they always preserve their species specifity.

As using the comparative method, the shell is drawn with biological stereoscopic microscopes MBS-9 (USSR), Opton DR, Opton SV-8 (BRD) and with respective drawing apparates (camera lucida). Before working, a square should be drawn under the microscope to be sure that the optical system gives no distortion. Then the shell valve should be placed on the microscope stand on plasticine in strictly standard position.

For molluscs with heterodont (pisidiids) and preheterodont (unionids) hinges, a position of valve is used in which the axis crossing tops of the interior cardinal (pseudocardinal) and interior lateral (pseudolateral) teeth is parallel to the optic axis while the anterior and posterior valve edges coincide in the field of view (fig. 6). Certainly another shell position may be used, especially in lifetime diagnostics, but the shell position should be strictly identical for all the specimens studied (LOGVINENKO & STAROBOGATOV, 1971).

When the shell is placed, the valve contour is drawn from the very umbo with the drawing tube. Large shells may be drawn uncompletely but drawing of the frontal section should be always started from the umbo. Both valves should be drawn in the case of species with different valves. The resultant picture is traced with drawing ink and thus, a stencil is obtained which may be used with the same drawing tube and at the same magnification without fail (the magnification of this stencil should be indicated on the same sheet) for comparison with other shell contours (fig. 7). If the shell contour of another mollusc does not coincide with the stencil contour, a new stencil should be drawn. Thus, molluscs are divided into groups corresponding to one or another stencil. Respectively, the drawing apparatus is used here as comparator.

The increase of accuracy in comparing the frontal section curvatures (for instance by means of enhancing the magnification) immediately leads to revealing the species variability of the frontal section curvature. In this case the shell series is not divided into few groups (2–4) but almost every shell differs from another. Then the variability may be studied or the accuracy (i. e. magnification) may be decreased; so the variability is neglected.

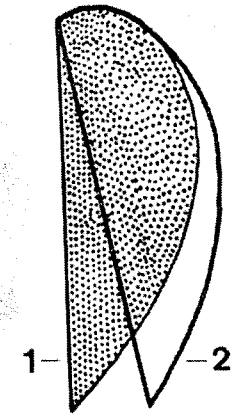

Fig. 7: Comparison of the shell frontal section contour with drawed stencil. (From LOGVINENKO & STAROBOGATOV, 1971, altered). 1 – shell, 2 – drawed stencil.

As it was shown in practice of many years of using the comparative method, the shell groups differing in character of the valve curvature always have clear differences also in other morphologic features: the shell form, the form and position of the hinge teeth, the main parameter ratios, etc. In result, the comparative method considerably facilitates the mollusc determination. After dividing the shells into groups, it is very easy to find characteristic morphologic features and to determine the species belonging to every shell group.

In all cases when molluscs differing in characters of their shell frontal section curvatures and in other features are found together without intermediate forms, malacologists believe it being a sufficient reason to consider molluscs of these forms as separate species. A concrete solution of this problem we shall illustrate by an example of shells belonging to subgenus *Tumidusiana*.

O. P. KODOLOVA and B. M. LOGVINENKO (1973, 1974, 1975) have examined the family Unionidae and showed that within the genera and subgenera *Unio, Tumidusiana, Anodonta* and *Pseudanodonta* all the forms do not differ in composition of their water-soluble muscle proteins. Basing on this facts, the conclusion has been made that each of above mentioned groups was represented in the European part of the USSR by a single species.

Using the comparative method, Ya. I. STAROBOGATOV (1977b) has analysed material of the *Tumidusiana* subgenus from the collection of the Zoological Institute of the USSR Academy of Sciences (Leningrad) and has established the following:

1. All the specimens of the *Tumidusiana* subgenus are represented by two forms. We shall conditionally name them form "A" and form "B". Morphologically these forms markedly differ from each other: in the valve frontal section curvature; in having different positions of external and internal pseudocardinal and pseudolateral teeth in relation to each other; in having different positions of the point most moved off from the valve closing plane of the shell etc.
2. Morphometrically both forms differ significantly from each other in the main parameter ratios.
3. In many water reservoirs both forms are found together in the same biotopes but they are also often found separately. There are no morphological intergradations in joint inhabitation of these forms.
4. Areas of the forms coincide in many respects. However, in the north of Europe only form "A" inhabits.
5. Ecologic differences appeared non-significant. Analysis of cases of the joint inhabitation showed that both forms really inhabit the same biotopes.

Thus, both the above examined forms may be considered as separate species. The form "B" has retained its name *Unio tumidus* (PHIL.) (fig. 4) while the name *Unio conus* (SPENGL.) has been re-instated for the form "A" (fig. 8). Similarly, Ya. I. STAROBOGATOV has also analyzed specimens from other groups (subgenus *Unio*, genera *Anodonta, Pseudanodonta)* and concluded that each examined group is represented by a few species. The

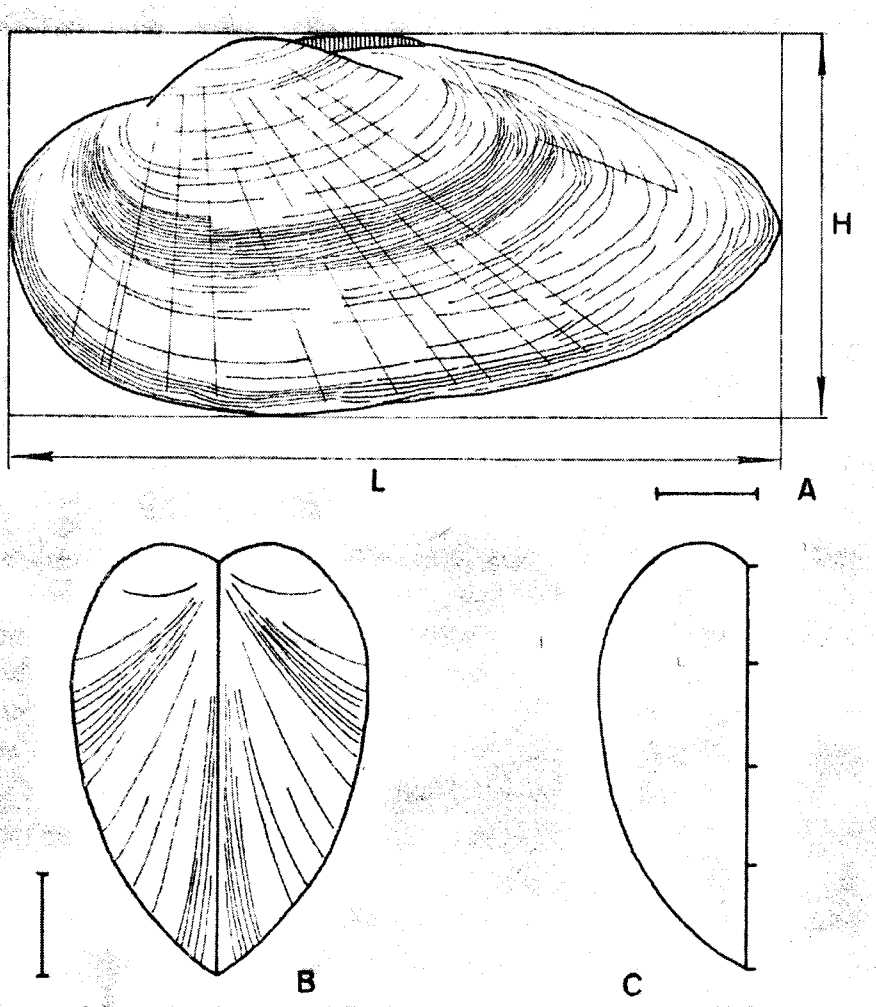

Fig. 8: *Unio conus borysthenicus* KOBELT. A – lateral view, L – length, H – height; B – frontal view; C – frontal section. (From STADNICHENKO, 1984, fig. 8A altered).
Scales: 1 cm

Unio genus (according to STAROBOGATOV, 1977a) has 4 species in *Unio* subgenus and 2 in the *Tumidusiana* subgenus; later M. N. ZATRAVKIN (1983) has found one more species of the *Unio* genus, *U. kalmykorum*. This species had been known before only as found in Pliocene deposits of the southern Russian steppes (Sal river, the tributary of the Don lower reaches, Rostov region). Thus, in the USSR the *Unio* genus is represented by 7 species distinctly differing from each other by the frontal section curvature. The indirect confirmation of some independent species of *Unio* s. str., *Tumidusiana*, *Anodonta*, *Colletopterum* and *Pseudanodonta* is the evident difference in the morphology of their glochidial shells and their attaching apparates (ANTONOVA, 1986; ANTONOVA & STAROBOGATOV, 1989).

Essentially, application of the comparative method directed the taxonomists' attention to many new and almost forgotten features. For instance, the analysis of Unionidae shells divided into groups by the comparative method showed that good diagnostic features are such features as the lengths of projected parts of pseudocardinal teeth position of the largest shell sections in relation to the ligament or to the shell height, etc.

Basing on application of the comparative method and complex of many other features, Ya. I. STAROBOGATOV and the malacologists of his school have revised species of freshwater Bivalvia inhabiting the USSR and adjacent regions. They revealed substantially more species in freshwater bivalvian molluscs that it had been believed before. For instance, in the European part of the USSR (except for the Crimea and the Caucasus) the fauna of Unionidae is represented by 23 species (STADNICHENKO, 1984; STAROBOGA-

TOV, 1977a; ZATRAVKIN, 1983), not 9 ones (SHADIN, 1952). Nowadays this system is accepted by the majority of the experts in the USSR. However, B. M. LOGVINENKO and the malacologists of his school have other opinions. They constate the most of species were chosen by Ya. I. STAROBOGATOV and his followers without sufficient reasons (LOGVINENKO & KODOLOVA, 1983; LOGVINENKO, KODOLOVA & KURASHEV, 1987; and others).

Discussion

The comparative method of conchologic studies is serving by the Soviet malacologists for just about 18 years. The popularity of the comparative method is explained by its simplicity. Using it only practically, everybody can divide into groups more than 100 any shells within an hour. It permits us also to compare real shells with photograph or precise drawing of the type-specimen when present in literature.

The shell frontal section contours were compared for systematic aims as well earlier (EHRMANN, 1933; FAVRE & JAYET, 1938; GEYER, 1927; ZEISSLER, 1971; and others). However, nobody has ever attached such great importance to this feature, and the method has never been applied so widely. The fact is that drawing the frontal section contour was carried out earlier in not strictly standard position. Because the contours of shells of the same species greatly vary, it led to the impression that the frontal section contour is a variable feature being not useful for taxonomic purposes. Really, the frontal section contour is a very stabile feature.

The comparative method is universal. Unlike other conchologic features, the shell frontal section contour can be applied to almost all species of the studied families. The advantage of the comparative method is also that it allows the lifetime determination of molluscs. It is possible even in the cases when external diagnostic features of species are very limited and when it is very difficult to separate species visually by the shell.

A shortcoming of the method is the difficulty or even impossibility of determining the shells with heavily corroded beaks. The second shortcoming is the impossibility of verbal description of the frontal section contours, so they are not included in current keys. Nevertheless, from our point of view there is a way out. In 1975 A. I. KAFANOV has shown that the ratio of shell valve convexity to the height is simply related to the polar angle of the logarithmic spiral. Hence, when using the rational geometrization of the Bivalvia shells in keys, one should slightly change the way of measuring the shell heights.

Presently malacologists measure the shell heights near the umbo and the ligament (fig. 4A, 8A). If measuring, the shell height is produced perpendicularly to the line by which the valve is placed during drawing the frontal section contour (fig. 6), then this height (MN in fig. 9) would correspond to the "Y" value in fig. 13. This inclined height/convexity of one shell valve ratio is related to the polar angle of the frontal section contour to indicate the extent of the curvature of the latter. This ratio can be apparently used in keys.

It appeared impossible to finish this account with an universal common evaluation of the field of the comparative method applicability. Points of view of the authors are quite different and, on the whole, they reflect the difference in opinions of Soviet malacologists in relation to the comparative method.

E. V. SHIKOV: The comparative method should not be absolutized. The frontal section contour is only a feature like the tooth pecularities, umbonal sculpture, etc. Like all other features it is a subject of intraspecific variability. The determination should not be carried out only by comparing the frontal section contours. The frontal section contour should be used together with other features.

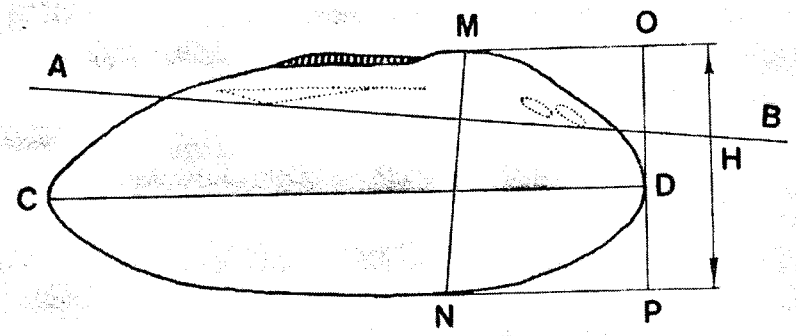

Fig. 9: Measuring height of the shell. H – traditional measuring, CD perpendicular OP; MN – incline height, AB perpendicular MN.

M. N. ZATRAVKIN: I believe that only by using of the comparative method one can determine almost all species of freshwater Bivalvia. Only in complicated cases, for example, in corrosion of beaks, when curvatures of the frontal section of two species are very close etc., one should use other diagnostic features.

Supplementary note by Ya. I. STAROBOGATOV (in litt. 17. I. 1990): To my great sorrow, two scientists who have taken part in working out of this method died in 1988: my dear friend B. M. LOGVINENKO and my richly endowed student M. N. ZATRAVKIN. The discussed method permits to compare independently all four RAUP's (1966) [2]) parameters and also the fivth: the dimension of the upper base of the truncated cone of shell-tube. It is most applicable to gastropods with conispiral shells where we may see all whorls simultaneously (which is briefly discussed by IZZATULLAEV & STAROBOGATOV, 1984 and KRUGLOV & STAROBOGATOV, 1985). Studying the frontal section of bivalve shells or the position of suture in planorbispiral (i. e. secondary planispiral) shells, we may study only one or two of RAUP's parameters. This method is also important because linear dimensions and their relations can not adequately express the spiral growth of a shell. For example, *Lithoglyphus naticoides berolinensis* WEST. from NW Europe does not differ by linear dimensions and by their relations from *L. apertus* (KÜST.) from Danube drainage, but both forms easily differ by whorl expansion rates. The usefulness of this method is proved by experimental crossing of *Lymnaea stagnalis* (L.) and *L. fragilis* (L.) which can not be distinguished by all methods except the comparatory one, and are regarded by all malacologists as one and the same species. The experiments have demonstrated that after crossing they can not give rise to normal progeny (KRUGLOV & STAROBOGATOV, 1985) [3]). I regard this fact as that there are no absolute taxonomic differences. On the other hand, the comparatory method is not an absolute one. We have often observed variation in the whorl translation along the axis of shell (e. g. *Viviparus viviparus* (L.), *Lymnaea stagnalis* (L.)), respectively, *Lymnaea glabra* (MÜLL.) and *Aenigmomphiscola kazakhstanica* KR. et ST. coincide completely in comparison by the comparatory method, in spite of great differences in their reproductive systems (KRUGLOV & STAROBOGATOV, 1981) [4]). Consequently, this method is only an eurystic one, and in order to prove the species validity we have to use direct or indirect consequences of the Biological species concept, i. e. low viability or absence of hybrids, differences in the caryotypes, or absence of transition when two forms coexist together. I may also add that our flattest *Unio* s. str. is not *U. kalmykorum* but *U. protractus* BOG.: this follows from the study of type-specimens. In conclusion, I thank E. V. SHIKOV and M. N. ZATRAVKIN for the propagation of this method.

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Summary

DIE KOMPARATIVE METHODE DES TAXONOMISCHEN STUDIUMS DER BIVALVIA, ANGEWANDT DURCH SOWJETISCHE MALAKOLOGEN

In der gegenwärtigen Zeit sind die Auffassungen zur Systematik der Süßwassermollusken (Bivalvia, aber auch Gastropoda) zwischen Malakologen aus der UdSSR im Vergleich mit ihren Kollegen aus Mittel- und Westeuropa sehr verschieden. Bedingt durch die überwiegende Anwendung der komparativen Methode zur systematischen Klassifizierung von Mollusken (eingeführt durch B. M. LOGVINENKO und Ya. I. STAROBOGATOV im Jahre 1971), nehmen viele sowjetische Malakologen die Existenz von wesentlich mehr Arten an als ihre westeuropäischen Kollegen. Die komparative Methode beruht auf dem Vergleich des frontalen Querschnitts der Molluskenschalen in streng standardisierten Positionen, in der Form, daß davon Schablonen angefertigt werden, mit denen die Schalen anderer Formen verglichen werden können. Solche Vergleiche wurden zwar schon früher getroffen, ohne jedoch auf eine Standardisierung der Methodik des Vergleiches zu achten. Auf diese Weise kann relativ schnell auch umfangreiches Material systematischen Gruppen zugeordnet werden. Innerhalb solcher Gruppen können dann weitere morphologische Merkmale zur Differenzierung der Arten herangezogen werden.

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