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Structure of the glandular stomach of the opisthobranchiate molluscs (Gastropoda, Opisthobranchia)

By Yu. S. Minichev

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Yu. S . MINICHEV , Stroyeniye zhelezistovo zheludka u zadnezhabernykh mollyuskov (Gastropoda , Opisthobranchia)

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The Structure of the Glandular Stomach in the Opisthobranchiate Molluscs (Gastropoda, Opisthobranchia).

BY

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SUMMARY

In this article the author studied morphology of the stomachs in the Opisthobranchia. In different orders of the Opisthobranchia the gastric adnexa are not homologous. The author showed the importance of the alimentary system in the solution of a number of problems relating to the systematics and phylogeny of the Opisthobranchia.

In recent times great importance has been ascribed to the peculiar features of the stomach structure for the clarification of different questions pertaining to the systematics and phylogeny of the Gastropoda (Graham, 1939, 1949; Johansson, 1941; Morton, 1952, 1953, 1955; Fretter & Graham, 1962; et alii). However, most of the works were carried out on the pulmonate and prosobranchiate molluscs. There are some works devoted to the study of digestive organs of single forms of the *Opisthobranchia* (Howells, 1936, 1942; Millot, 1937, 1938; Fretter, 1939, 1940; Forrest, 1953; Hurst, 1965; et alii), but so far no light has been thrown on the evolution of the stomach in different phylogenetic ramifications.

We give below some conclusions arrived at as the result of studies concerned with the morphology of the digestive organs in the opisthobranciate molluscs. The collections made by the expedition ship "VITIAZ" in the Pacific Ocean, and personal collections made by the author in the White Sea and in the Sea of Japan provided the material for this article.

Peculiar Features in the Structure of the Stomach in Different Groups of the Opisthobranchiate Molluscs.

The majority of the representatives of the *Cephalaspidea* - the earliest and most primitive order of the opisthobranchiate molluscs - are benthyc animals that feed on deposits, mainly of plant origin, arriving from the surface. In this respect they retained an early mode of life peculiar to the ancestors of the *Gastropoda* (Graham, 1955). With the type of nutrition based on food of plant origin (phytophagous or herbivorous nutrition) is associated an entirely singular structural plan of the digestive system, and of the stomach in the first place. On summing up the basic data pertaining to the structure of the stomach in primitive molluscs (Yonge, 1932; Graham, 1939, 1949; Morton, 1952, 1953; et alii) one may distinguish several most characteristic features. A greater portion of the stomach wall is lined with the ciliary epithelium; in specific areas there develops a solid cuticular lining, forming a singular gastric shield. A gastric diverticulum, which serves to increase the sorting area, arises not infrequently in various phylogenetic stems; the connective tissue surrounding the diverticulum is a site where the phagocytes, participating in the process of digestion, aggregate. The presence of the sac of the protostyle, which is adjacent to the groove running along the anterior portion of the gut, is a feature already found as a specific characteristic in the ancestors of the Gastropoda (Owen, 1956; Beklemishev, 1964). Through the differentiation of the sac of the protostyle from the gut, and, as the result of enhancement of the role played by various hydrolytic enzymes, the protostyle is transformed into the crystalline style (Johansson, 1941; Morton, 1952). The latter is present mainly in the phytophagous forms.

/ Insert here the Fig. 1 /

Translated caption for the fig. 1

Fig. 1. Schematic drawings of the structure of stomachs in different Gastropoda. Arrows indicate the direction of the process of morphological transformation.

1. - Lymnaea, 2. - Ophicardelus, 3. - Acteon, 4. - Bullacta,

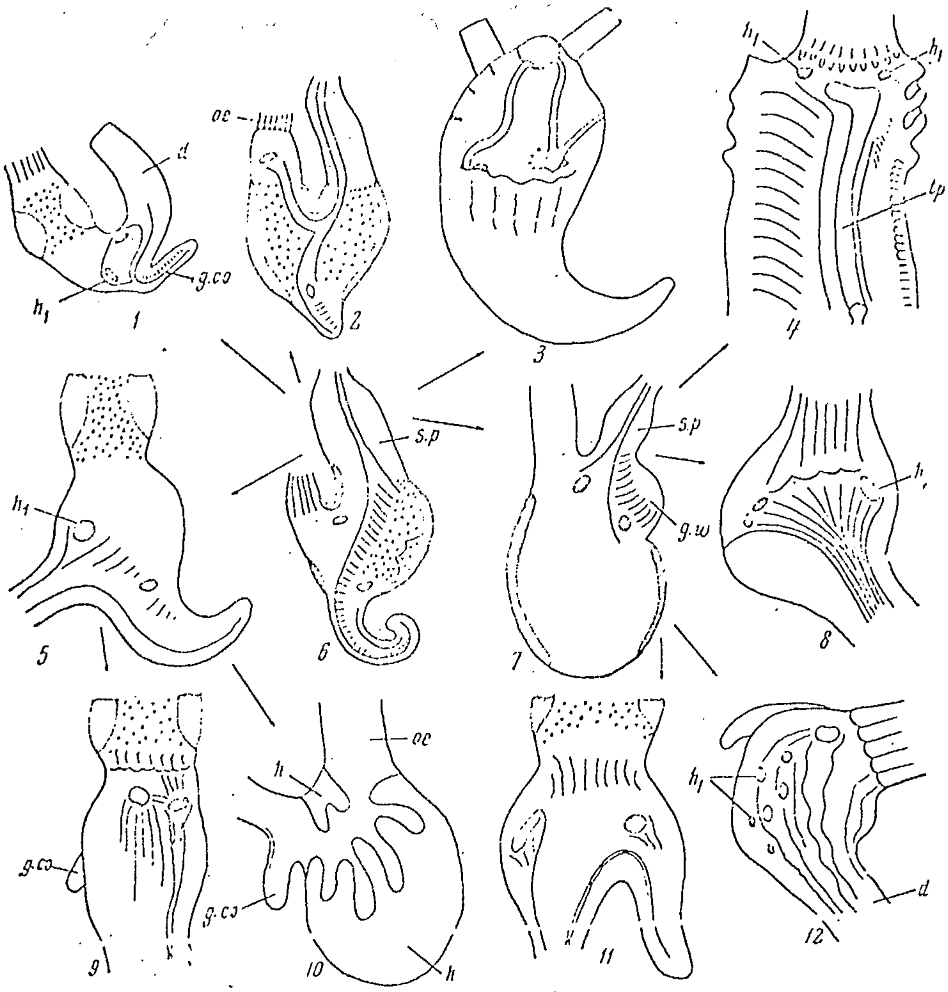

Рис. 1. Схемы строения желудков различных Gastropoda. Стрелками указаны направления морфологических преобразований

1 — Lymnaea, 2 — Ophicardelus, 3 — Acteon, 4 — Bullacta, 5 — Aplysia, 6 — Trochidae, 7 — Ringiculoides, 8 — Haminoea, 9 — Akera, 10 — Anopsia, 11 — Peracle, 12 — Bathydoris; d — кишка, g. co — гастрический вырост, h — печень, h_1 — проток печени, oe — пищевод, tp — тифлозоль, s. p — мешок протостиля (1, 2, 6 — по Morton, 1955; 3 — по Fretter and Graham, 1951)

5. - Aplysia, 6. - Trochidae, 7. - Ringiculoides, 8. - Haminoea, 9. - Akera, 10. - Anopsia, 11. - Peracle, 12. - Bathydoris; d-gut, g. co - Gastric diverticulum, h - liver, h_1 - Hepatic duct, oe - oesophagus, tp - typhlosole, sp - sac of the protostyle (1,2,6 - according to Morton, 1955; 3 - according to Fretter & Graham, 1954).

In Fig. 1 are depicted schematic drawings of the structure of the stomach in different Gastropoda. The Trochidae (Fig. 1, 6) occupy the central position, possessing, as they do, a complex of primitive traits in their stomach structure. From the Trochidae type of the stomach have developed (not in the sense of phylogenesis but in the sense of direction of the process of morphological transformation) the stomachs of the Pulmonata (Fig. 1, 1, 2) and the Opisthobranchia

Primitive features in the structure of the stomach may be found in different opisthobranchiate molluscs, and in the first place - in the representatives of the Cephalaspidea. In particular, the stomach of the Ringiculoides kurilensis Minichev is divided both morphologically and functionally into two chambers (Minichev, 1967). The posterior chamber (Fig.1,7) is lined with a cuticular layer, and exteriorly it is surrounded by broad muscular bands; the anterior chamber, with thinner walls, is formed by the ciliary epithelium. A similar structure of the stomach is also characteristic in the other members of the Ringiculidae and, possibly, the Acteonidae (Fig. 1, 3). The digestive diverticula (the liver) open out into the anterior chamber by two independent ducts. The orifice of the left liver is situated closer to the oesophagus, and the orifice of the right liver is located in the lower portion of the gut. The ridges formed by tall ciliary epithelium, and situated between the orifices of the liver and the gut, represent the major and minor typhlosoles. In the anterior portion of the gut, the typhlosoles border the little furrow of the gut which is a characteristic feature of the sac of the protostyle of the prosobranchiate molluscs. A series of transverse ciliary groovlets is associated with the major typhlosole. This area of the stomach, differentiated morphologically into a small chamber, corresponds to the ciliary sorting zone of the Archaeogastropoda. The anterior portion of the gut is widened and possesses all the features peculiar to the sac of the protostyle (the disposition of the typhlosoles, the presence of a sulcus in the gut, tall ciliary epithelium, etc.). The semi-liquid mass filling the anterior portion of the gut and projecting into the lumen of the stomach represents the protostyle of the most primitive type. In the Ringiculoides there is present, in the connective tissue surrounding the anterior chamber of the stomach, a great number of minute (with a diameter of about 7 microns) amoebocytes. Experimental data indicate that the region of the protostyle is the site where the most energetic phagocytosis occurs [observations on the nutrition of Diaphana globosa (Loven)]

Some primitive features may also be found in the stomachs of other Cephalaspidea. Thus, J. E. Morton (1955), referring to the data obtained by V. Fretter (1939), noted a great similarity in the structure of the stomach of the Haminoea to that of the primitive Pulmonata. In the stomach of some species of the Refusa are retained the major and minor typhlosoles, associated as they are, with a pair of the hepatic ducts. In the Acteon the posterior portion of the stomach is lined with the cuticula and yet retains the longitudinal sorting ciliary striplets (Fretter, 1939). The cuticular area of the stomach in the Ringiculidae, and particularly in the Acteonidae, resembles the gastric diverticulum in the primitive Prosobranchia. However, it may be said that this area rather corresponds to the gastric shield in the prosobranchiate molluscs.

A transition from the phytophagous mode of life to the predatory one occured in the Cephalaspidea fairly early in the course of their evolution. Apparently, it is only the Atyidae that retained in pure form the primary mode of feeding. Nevertheless, even in the latter one may observe a considerable change in, and simplification of, the stomach. This transformation is doubtless associated with the formation of the composite "masticatory" stomachs ("Gizzard"). The stomach of Bullacta exarata (Philippi) (Fig. 1, 4) underwent a particularly conspicuous change. In this form the oesophagus merges into the widened portion of the gut from which the former is separated by an annular fold with a series of thread like appendages. In the Bullacta occurred the morphological merger of the glandular stomach and the gut. Along the ventral surface of the stomach runs a high ridge, bent at its anterior portion, the typhlosole. The anterior end of the typhlosole, together with the two large dorsal projections, form the limits of a narrow chamber into which open the hepatic ducts. The left side of the stomach bears a series of obliquely placed folds which are furnished, in their turn, with transverse ridges. To the right of the typhlosole runs a deep ciliary sulcus associated in the region of the hepatic orifice with small transverse folds. The interpretation of all these structures is somewhat difficult; the primitive relationships are preserved only in so far as the presence of a pair of the hepatic ducts is concerned, and also in the presence of the major typhlosole. It is interesting to note that the connective tissue with the blood bearing lacunae - which is characteristic for the primitive forms - is absent in the *Bullacta*.

The majority of the *Cephalaspidea* are predators which as yet did not succeed, in the process of evolution, to acquire the crystalline style but have already lost the early features of the stomach of the phytophagous forms. K. Kubomura (1957) found the crystalline style in the *Philinidae*. The author's investigations in the case of *Philine argentata* Gould and *Philine scalpta* Adams confirmed the data furnished by Kubomura; however, we consider that these species possess a sac of the protostyle. The presence of the carbohydrases in the mucous mass filling the initial portion of the gut has not been proved. Moreover, this mass does not show the concentric series of layers, a characteristic of the crystalline styles in other molluscs. The stomach of the Philinidae is indeed a rudimentary organ the main function of which is a temporary accumulation of food particles prior to their entrance into the diverticula of the liver.

In many Opisthobranchia the stomach is furnished with special blind diverticula the homology and function of which has not been completely cleared up. In the Anaspidea a blind diverticulum, lined with the ciliary epithelium and furnished with a longitudinal epithelial fold, leads out from the posterior portion of the stomach (Fig. 1, 5, 9) (Howells, 1942; Morton & Holme, 1955). In the Stylochelus the diverticulum is bent or twisted spirally and contains fecal masses shaped like a mucous cord. A rudiment of a similar diverticulum is also present in the Anopsiidae (Fig. 1, 10) a family which is connected phylogenetically with the Anaspidea. These formations may be likened to either the sac of the crystalline style or the gastric diverticulum of the pulmonate and the prosobranchiate molluscs. The gastric diverticula of the Anaspidea, and especially of the Aplysiidae, resemble greatly those in the Ellobiidae, the Turbinidae and others (Morton, 1955, 1955a). A characteristic feature of the gastric diverticulum in the Pulmonata and the Prosobranchia is the projection into it of the posterior portion of the major typhlosole with an area of the sorting ciliary z one, as well as the presence in its orifice of the posterior opening of the liver. The same peculiar features are a common occurrence in the representatives of the Anaspidea . According to the observations of J. E. Morton and N. Holme (1955), the gastric appendage in the Akera shapes the segments of the fecal cord and propels it into the gut. The blind diverticula of the stomachs of the Anaspidea are comparable, morphologically and functionally, to the gastric adnexa of the lower Prosobranchia, but are not entirely homologous with the latter.

We arrive at dissimilar conclusions on examining the blind gastric diverticula in the pelagic Thecosomata. In the representatives of the Peraclidae is revealed the presence of the most primitive relationships (Fig. 1, 11). In the majority of the Thecosomata the diverticulum opens into the hepatic duct (Meisenheimer, 1905; Howells, 1936), but in the Peracle it communicates directly with the stomach. The cavity of the diverticulum is incompletely sub-divided by two folds into two compartments which are histologically similar to the sac of the crystalline style. Inside the diverticulum there is present a solid mucous cord, showing a concentric linear pattern, the anterior point of which is bent toward the gut (Fig. 2).

[Insert here the Fig. 2]

Translated caption for the Fig. 2

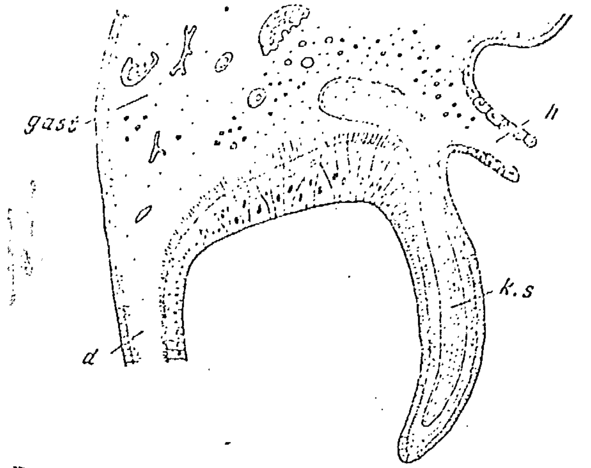

Рис. 2. Разрез через желудок Peracle reticulata (Orbigny)

d — кишка, *gast* — желудок, *h* — печень, *k.s* — кристаллический стебелек

Fig. 2. Section through the stomach of the Peracle reticulata (Orbigny) d-gut, gast - stomach, h - liver, k.s - crystalline style

C. Yonge (1926, 1932), while discussing the function of the stomach, put forward a suggestion that blind diverticula in the Thecosomata are the neoplastic formations which arose as the result of the molluscs effecting a transition to the phytophagous mode of nutrition. The alimentary system of the Thecosomata went through a singular evolutionary process. In particular, the essential food distributing mechanism in these molluscs is associated with their fins (Yonge, 1926). Yonge assumed that the "masticatory" stomach ("gizzard") in the Thecosomata was preserved as a feature common to their carnivorous ancestors and is now a functionally rudimentary organ. We consider that the ancestors of the Thecosomata were phytophagous forms; the author's observations and the data given by H. Howells (1936) indicate that the gizzard of the Thecosomata is a highly efficient organ ensuring the trituration of different food animals with the hard outer skeleton (radiolaria, foraminifora, diatoms, etc.). Apparently, the Thecosomata and the Cephalaspidea share a common origin from the early prosobranchiate molluscs which possess a primitive protostyle. The latter is retained in some of the Cephalaspidea and is transformed into the crystalline style in the Thecosomata.

It is interesting to note that the blind stomach diverticula are present in some nudibranchiate molluscs - including the carnivorous forms - the most highly organized group among the Opisthobranchia. In the Anthobranchia [formerly the Doridacea which the author classified as an independent order (Minichev, 1968)], the blind diverticulum is usually located at the base of the gut and is lined with the tall epithelium without the cuticle and the cilia. In a number of cases this organ has a glandular character and is histologically similar to the liver. As is known, in the doridid larvae two lobes of the liver are laid down, but one of them disappears in the process of metamorphosis (Thompson, 1958), or is retained in the form of the so-called "gall bladder". Doubtless, the blind diverticulum is - at least in some species of the Anthobranchia - the homologue of the right lobe of the liver in the lower Opisthobranchia. Of interest is the supposition of N. Millot (1938) that gastric adnexa in the Anthobranchia and the Anaspidea are functionally similar. If this supposition be true, we have here a good example of the substitution of functions, i.e., the transformation of the secretory organ (the liver) into the excretory and distributing organ (an analogue of the gastric diverticulum).

Traces of the primitive structural plan may be revealed, in the main, only in the stomachs of the lower Opisthobranchia. Already in the Cephalaspidea one may observe the reduction (anatomical) of the structure associated with the preliminary treatment and distribution of food. The stomach becomes a site where the food accumulates for a short period of time, whereas the basic role in the process of digestion is acquired by the oesophagus. Indeed, it is in the oesophagus that food undergoes mechanical treatment and is subjected to the action of enzymes. Into the gizzard (which is formed ontogenetically from the lower portion of the oesophagus) are secreted the enzymes from the liver, the enzymes that hydrolyse starch, glycogen, proteins, etc. (Fretter, 1939). The oesophagus acquires the ability to perform peristaltic movements; and in it the food particles may remain for a long time. The dissolved substances and small food particles enter the liver where their absorption and phagocytosis take place. Larger particles from the oesophagus and the undigested material from the liver are ejected into the gut.

A further simplification of the stomach occurs in many evolutionary forms. In some instances one may observe a complete substitution of the stomach by the liver. This process begins already in the higher Cephalaspidea. Thus, in the Gastropteron rubrum (Raf.) the two primary hepatic ducts are sub-divided into 8 - 10 secondary ducts; and, in this species, a greater portion of the stomach wall assumes glandular character. In the Enotepteron flavum Minichev only insignificant areas of the stomach remain, those furnished with the ciliary epithelium, located among the numerous hepatic ducts.

Substitution of the stomach by the liver is very characteristic for the representatives of the Gymnosomata order. In particular, in the Anopsia the oesophagus opens into a chamber which is almost completely formed by the hepatic epithelium (Fig. 1, 10); in other forms the stomach becomes completely reduced (anatomically). Doubtless, the reduction of the stomach in the Gymnosomata is conditioned by the mode of nutrition: they suck out the soft tissues of the shelled Pteropoda molluscs. Substitution of the stomach by the liver in the Gymnosomata fully resembles a somewhat similar phenomenon observable in the parasitic Prosobranchia (Ivanov, 1945). Reduction of the stomach and its replacement by the liver in the Gastropoda molluscs is doubtless associated with feeding on food of high calory value, needing no preliminary mechanical treatment (trituration) or a special method of distribution along the alimentary tract.

D I S C U S S I O N

The primitive representatives of different phylogenetical branches of the Opisthobranchia retained basic features of the structure of the alimentary tract of the ancestral forms. The presence of intracellular digestion, of the ciliary sorting mechanisms in the stomach, the primitive form of the protostyle, participation of the blood elements in the processes of digestion, etc., all are early peculiar features common in some lower opisthobranchiate molluscs. The change in the functions of the anterior portion of the digestive tube, an increased role played by the digestion occurring in the alimentary tract cavities, a decreasing role of the phagocytosis, and substitution of the stomach by the liver, all are the principal paths followed by evolution of the alimentary tract in the Opisthobranchia.

The lower Cephalaspidea possess, in one or another combination, the following distinctive features of the stomach: the ciliary sorting zone with groovelets and ridges converging upon the intestinal sulcus; a zone with the cuticular lining; a sac of the protostyle adjacent to the intestinal sulcus; and paired hepatic ducts. On comparing the digestive system of the Opisthobranchia with that of the Prosobranchia, one may note a very great resemblance of the stomach structure in the Cephalaspidea and the Archaeogastropoda (Graham, 1949; Morton, 1953, 1955a; et alii). The other sections of the digestive system of the Cephalaspidea likewise indicate that this group is closely related to the early primitive Prosobranchia. In particular, the Acteon has a broad non-specialized radula (Fretter, 1939; Gabe et Prenant, 1952; Fretter & Graham, 1954; Hurst, 1965) which has the following characteristic features: a very large number of small radular plates (teeth?) of a single type, but not differentiated into the lateral and central plates; the weakly differentiated odontoblasts; and the odontophore occupying the central and lateral walls of the pharynx. These specific features do not allow us to trace the descent of the Acteonidae from a type of the present day Prosobranchia. Even in the extremely primitive forms of the prosobranchiate molluscs there are present several groups of radular plates differing in form, size and their location. It is possible that the Acteon retained its pharyngeal armament, which originated at the primary sources of the formation of the class of Gastropoda.

Thus, in the structure of the alimentary system, we bring to light one more proof of the origin of the Cephalaspidea - and therefor, of all the Opisthobranchia - from the very early prosobranchiate molluscs.

First stages in the evolution of the stomach were doubtless similar in the Opisthobranchia and the Pulmonata. Yet, as time went on, a sharp divergence became discernible: in the opisthobranchiate molluscs there occurred a gradual morphological and functional simplification of the stomach; whereas the pulmonate molluscs, while retaining many primitive features, developed along the path of enhancing the role of musculature in the function of the stomach. The presence of muscular stomach (gizzard) is a characteristic trait of the digestive tract in the Basommatophora and several other groups of the Pulmonata. Many Opisthobranchia possess the so-called "gizzard", a muscular chamber, often furnished with the chitinoid teeth, located in front of the glandular stomach. This chamber is of the ectodermal origin and is not homologous to the muscular stomach of the pulmonate molluscs. It must be noted here that in the Ringiculidae, the Ellobiidae and the Trochidae (the "primitive" families of the three sub-classes of the Gastropoda) the glandular stomach has a muscular envelope. In the Opisthobranchia this musculature becomes reduced and is functionally replaced by the muscles of the oesophagus; whereas it is retained in the pulmonate molluscs and its role is progressively enhanced.

The "masticatory' stomach of the Cephalaspidea takes shape fairly early in the course of phylogenesis, but, already in the representatives of higher families (which have become actively predatory), it disappears. In the phytophagous Anaspidea it is retained in a modified form. It is interesting to note that the chitinoid plates of the "masticatory" stomach may contain cellulase (Hashimoto et alii, 1951; a revue of digestive enzymes in molluscs vide Stone & Morton, 1958), which fact is doubtless connected with the progressively increasing role of the body cavity food digestion in this portion of the alimentary tract.

In so far as its function is concerned the evolution of the digestive system followed a similar pattern in the pulmonate and the opisthobranchiate molluscs. In particular, in the primitive forms the phagocytic function of the amoebocytes of the blood - the cells that seize and digest food particles from the stomach - is displayed very prominently. In the higher forms - for example, in the nudibranchiate molluscs - the role of wandering phagocytes in the process of digestion becomes diminished, but there appears the so-called process of "fragmentation of the phagocytes" from the epithelium of the glands of the alimentary tract (Millot, 1937; Forrest, 1953). Such a change in the phagocytic mechanics doubtless occurs fairly frequently in different phylogenetic stems of the *Opisthobranchia* and the *Pulmonata*.

Distinctive structural features of the stomach may acquire great importance in the solution of a certain number of problems in systematics (taxonomy?). Thus, the structural singularity of the stomach in the *Bullacta* (morphological unification of the stomach and the gut, development of the secondary sorting structures, etc.) bears witness to profound functional changes of the entire alimentary tract in this genus. The causes of these changes are not clear,but they are not conditioned by the type of feeding, for the *Bullacta*, as well as the typical *Alvidae*, are the unspecialized phytophagous forms. Tchangsi (1934), who studied in detail the organization of *Bullacta*, placed this form in the *Scaphandridae*, basing his decision on the similar structure of their radulas. Yet, the distinctive features of the "masticatory" stomach, of the nervous system, and of their shells indicate a close relationship between the *Bullacta* and the *Atyidae*. J. Thiele (1926) placed the genus in the *Atyidae*, as a sub-family. The original structure of the stomach and of the ctenidium, and of the sex organs enable one to separate the *Bullacta*, as an independent family, under the name the *Bullactidae* Thiele, 1926.

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THE STRUCTURE OF THE STOMACH OF THE OPISTHOBRANCHIATE MOLLUSCS (GASTROPODA, OPISTHOBRANCHIA)

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Summary

The morphology of stomachs in Opisthobranchia has been studied. Gastral outgronths of stomachs are not homologous to each other in different orders. The importance of digestive system for the solution of some questions of systematics and phylogeny in opisthobranchiate molluscs has been shown.
