

論文内容の要旨

Comparative histology of radula-supporting structures in Gastropoda; phylogenic and functional morphologic implications

腹足綱の歯舌支持構造の比較組織学的研究

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Mollusca is the second largest phylum in Animalia, and composed of Solenogastres, Caudofoveata, Polyplacophora, Monoplacophora, Bivalvia, Scaphopoda, Cephalopoda, and Gastropoda. Gastropoda especially has gained the most diversified anatomy and ecology among above classes of the Mollusca and are therefore an interesting taxon for comparative anatomy.

In the last two decades, gastropod phylogeny has been reconsidered drastically, and new systematic schemes have been proposed. The monophyly of each higher clade is almost supported by molecular phylogenetic analyses. The recent classification by Bouchet and Rocroi (2005) includes six higher gastropod clades, i.e. Patellogastropoda, Vetigastropoda, Cocculiniformia, Neritimorpha, Caenogastropoda, and Heterobranchia.

Mollusks possess some phylum-specific organs like the mantle which envelops the viscera from dorsal side and form the shell(s), plates and spine composed of calcium carbonate and proteins. The 'buccal mass' is feeding apparatus which is another unique character to Mollusca excluding Bivalvia. The components of the buccal mass are: 1) chitinous ribbon-like radula, being composed of the radular membrane and multiple transverse row of teeth, 2) radula-supporting structures with cartilaginous

tissue (odontophoral cartilage) or the complex of fibrous connective tissue and muscle fibers (radular bolster), 3) muscles operating the motion of buccal mass and radula, 4) plate-like chitinous jaw(s), 5) the radular sac which is a blind pouch forming the radular teeth, 6) the subradular membrane fixing the radula on to the buccal mass.

In this study, a comparative histological study was undertaken to reveal the morphological diversity and systematic characters of a radula-supporting structure of gastropods. Observations on 33 species, all from different families, revealed six major morphological characters, viz. (1) the number of odontophoral cartilages or radular bolsters: 0, 1 (fused), 2, 4, 5, 6 and 10, (2) histology categorized into 6 types based on the properties of cartilage matrix and cells, (3) the presence or absence of an enclosing membrane of the cartilages or radular bolsters, (4) the presence or absence of overlapping of the right and left cartilages or radular bolsters, (5) the closest position of the cartilages or radular bolsters to each other in cross section at ventral or dorsal side, (6) the insertion areas of the ventral approximator muscle connecting the cartilages or radular bolsters: ventral, medial, or outer lateral area.

Outgroup and ingroup comparisons based on recent phylogenetic hypotheses suggest the following evolutionary scenario for gastropod radula-supporting structures: The ancestral gastropod is assumed to have possessed two pairs of odontophoral cartilages with a thick matrix and ventrally connected by the approximator muscle. The cartilages have possibly independently increased in number in Patellogastropods and Neritimorpha, decreased into a one pair, single piece or lost in Caenogastropoda, and replaced by connective tissue and muscle fibers in Heterobranchia. Some taxa like Cypraeidae have gained a unique histology. The cartilages or radular bolsters are closest ventrally in cross section in the majority of gastropods but closest dorsally in part of the taenioglossate Caenogastropoda. Moreover, characters of radula-supporting structure are more diverse in Gastropoda than in other Molluscan classes.

A correlation between morphological types of the radula-supporting structures and ecology is clearly rejected. For example, various herbivorous gastropods belonging to Patellogastropoda, Vetigastropoda, *Aplysia* and *Siphonaria* have distinctive morphology and/or histology that are specific to each higher taxonomic category. Similarly, species in the caenogastropod Littorinimorpha share similar cartilage morphology and histology but show highly diverse modes of feeding such as grazing in *Littorina*, shell boring in Naticidae, deposit feeding in Strombidae, ciliary feeding in Calyptraeidae and carnivory in Ranellidae. Thus, there is no direct connection between odontophoral cartilage morphology or histology and feeding ecology in gastropods. In addition, major habitat selection is also unrelated to morphological diversification of

radula-supporting structures. It means the diversification of these character states in gastropods seems to be phylogenetically constrained.

Two types of strategy seem to be adopted to enhance the flexibility of radula-supporting structures at structural or tissue level: (1) multiple rigid cartilages connected each other with mobility, and (2) single pair of pliable cartilage or radular bolster. The insertion area of ventral approximator muscle is also important character for lateral rotation of radula-supporting structures. The observations in this study suggest that the characters of radula-supporting structures are under the control of phylogenetic factor. On the other hand, the condition of radula-supporting structures probably has affected the diversification of feeding habit. Gastropod feeding habit tends to diversify in Caenogastropoda and Heterobranchia, both of which possess pliable radula-supporting structure. The pliable radula-supporting structures seem to be related to the diversity of feeding habits by increase of the mobility of feeding apparatus.

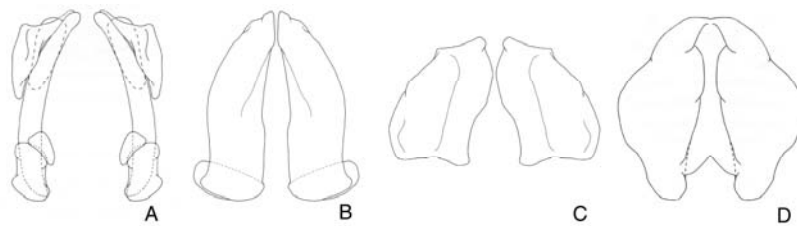


Fig. 1. The number of radula-supporting structures. A. 5 pair. B. 2 pair. C. 1 pair. D. 1 piece.

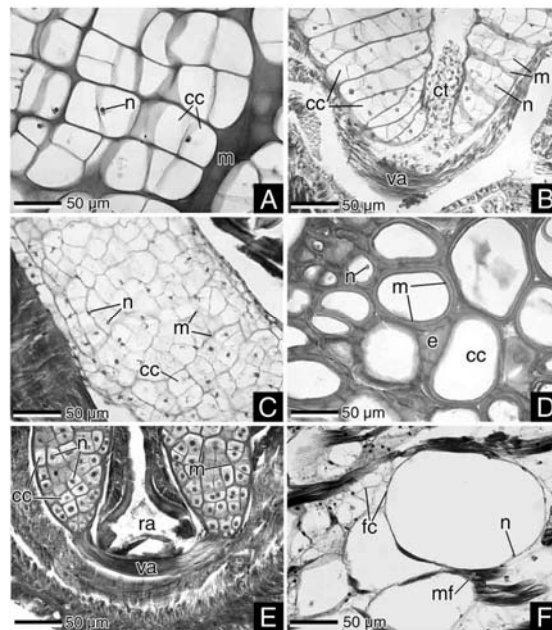


Fig. 2. The tissues of radula-supporting structure. A. Type 1. B. Type 2. C. Type 3. D. Type 4. E. Type 5. F. Type 6.

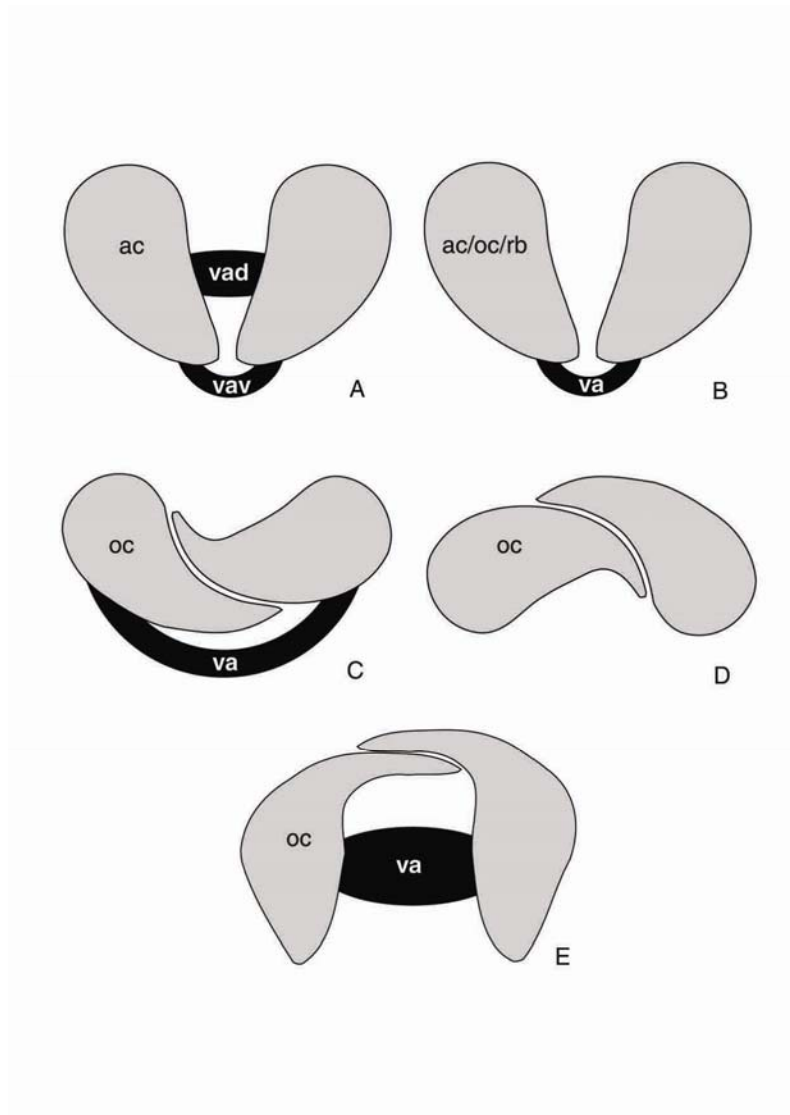


Fig. 3. Schematic diagrams about the right and left elements of main cartilages or radular bolsters. A. Ventrally close and connected by double-layered ventral approximator muscle inserting at ventral/medial side of the main cartilage. B. Ventrally close and connected by single layered ventral approximator muscle inserting at ventral side of the main cartilage or radular bolster. C. Ventrally close and connected by single-layered ventral approximator muscle inserting at outer lateral side of the main cartilage. D. Dorsally close and muscular connection absent. E. Dorsally close and connected by single layered ventral approximator muscle inserting at medial side of the main cartilage.