

論文の内容の要旨

Systematic study of the order Elasipodida

(Echinodermata, Holothuroidea) in Japanese waters

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The order Elasipodida Théel, 1882 (Echinodermata: Holothuroidea) inhabits the worldwide deep sea floor ranging from 70 to above 10000 m in depth, including the polar region and hadal trench areas. Elasipodida is easily recognized by their gelatinous and often translucent body walls, conspicuous dorsal papillae or their derivatives, and large tube feet or fused into brims on ventrolateral edge. The order contains 171 extant species of 24 genera of 4 families, but the taxonomy is not well studied. The taxonomic research of Elasipodida prevented by their remote habitats with great water depths and the difficulty collecting specimen in good condition due to their easily damaged gelatinous body. Moreover, molecular analysis has been poorly applied to them. The purpose of the present study is the taxonomical revision of the order Elasipodida by molecular and morphological data mainly on the Japanese species. Based on the new taxonomic knowledge and phylogenetic relationships obtained, I discussed about the species richness of Elasipodida in the northwest Pacific Ocean, the categorization of body ossicles, and actual conditions of widely distributed elasipodid species.

In Chapter 2, I examined the detailed morphology of approximately 500 specimens and compared them with type specimens of 11 species to revise the species from Japanese waters based on the new systematics proposed by molecular phylogeny in the later chapters. I recognized a total of 42 species of 13 genera from 6 families in Japanese waters, including 3 new species and 6 newly recorded species. I also clearly defined terms of body ossicles of each family, which had been confusingly used in previous taxonomic literatures. Detailed description including clear photographs were given for taxonomically revised species.

For body ossicle observation, I used not only differences of shapes based on numbers and

presence or absence of specific ultrastructure that have been conventionally accepted, but also made a quantitative comparison of their shapes by SEM especially for genera *Benthogone*, *Laetmogone* and *Pannychia*. In particular in these genera, intraspecific variation in wheel ossicle morphology is very large, and they were successfully diagnosed by body ossicle characteristics observing maximum diameter of ossicles and the ratio of diameter of central connecting portion and entire ossicle diameter.

In Chapter 3, to evaluate the family and generic classification of the order Elasipodida, I carried out molecular phylogenetic analyses using a protein coding gene, cytochrome c oxidase subunit 1 (COI), and two ribosomal genes, 16S and 18S rDNA, gene for 97 holothurian taxa covering 35 species, 15 genera, 4 families in Elasipodida collected from the Pacific, Atlantic, and Antarctic Oceans. The monophyly of the current Elasipodida was highly supported in both maximum likelihood and Bayesian trees. Elasipodida was the second basal group after Apodida was firstly divided in the class Holothuroidea. The trees suggested that the paraphyly of Laetmogonidae, and the existence of six clades in Elasipodida. However, detected several clades and their relationships within Elasipodida were not obtained enough statistical supports. These trees confirmed the monophyly of four genera, *Laetmogone*, *Pannychia*, *Eynpniastes*, and *Psychropotes*, and showed the polyphyly of *Amperima* and *Ellipinion*, and the paraphyly of *Benthodytes* and *Peniagone*. The validity of monophyletic four genera were phylogenetically supported, but it was suggested that polyphyletic two genera and paraphyletic two genera need future taxonomic revisions.

To improve the basal resolution, family-rank relationships were analyzed using relatively conservative two ribosomal genes, 18S and 28S rDNA, of 15 representative species, which were selected two or three species from each clade of indicated six clades in the COI+16S+18S analyses. This concentrated analysis showed six distinct clades within Elasipodida. Among four current families, Elpidiidae, Pelagothuriidae, and Psychropotidae were monophyletic, while Laetmogonidae was paraphyletic with two separate clades. The monophyletic Elpidiidae contained two clades separated by large genetic distance. All six clades, including two of Laetmogonidae and two of Elpidiidae, were clearly distinguished by diagnostic morphological characters: arrangements of dorsal papillae, structure of calcareous ring, and type of body wall ossicles. I concluded that the six clades in Elasipodida should be treated as family rank taxa based on genetic distance between clades and morphological differences. Therefore, I established one new family and promoted one subfamily to family and classified the Elasipodida into six families to accord with the phylogenetic trees.

In Chapter 4, to evaluate the species diversity of the genus *Pannychia*, I sequenced COI gene and genome wide single-nucleotide polymorphism (SNP) sites using Multiplexed inter simple sequence repeat genotyping by sequencing (MIG-seq) for 221 individuals from the eastern and western Pacific, south Indian, and Antarctic Oceans. The phylogenetic analyses detected ten distinct clades within genus *Pannychia*. These ten clades were genetically divergent from each other. Currently only two species, *P. moseleyi* and *P. taylorae*, were valid in the genus, but I concluded that these ten clades

should be treated as species rank taxa of *Pannychia*. Based on the morphological observations of the specimens, five clades were identified to the two valid species, three synonyms of *P. moseleyi*, and other two Japanese clades were described as new species. The other two southwest Pacific and an Antarctic clades still need more morphological observations for taxonomic treatments because of sample conditions. Two clades had geographically isolated distributions from the other clades to the eastern Pacific and Antarctic Oceans, and five and three clades occurred in northwest and southwest Pacific Ocean, respectively. The western Pacific eight species had locally overlapping distributions each other, but show different geographical and bathymetrical distribution ranges.

In Chapter 5, I discussed about species diversity of Elasipodida in the northwest Pacific Ocean, the categorization of body ossicles in Elasipodida based on revealed phylogenetic relationships, and actual conditions of widely distributed elasipodid species, such as cosmopolitan species.

Out of 178 valid species in Elasipodida recognized in this study, 42 species distributed to Japanese waters. In the northwestern Pacific containing Japanese waters, 49 species was distributed and it surpassed 36 species in the North Atlantic Ocean, which is the most investigated region in the world. The habitats of elasipodid species spread a wide depth ranges from the continental shelf to the bottom of trench, and the northwest Pacific region including Japanese waters also contains various deep-sea environment from the upper bathyal to hadal zones. It is presumed that the diversity of the deep-sea benthic environments in this region provides suited habitats for various elasipodid species, and makes a high species diversity in this region.

Body ossicles have been used as the most important taxonomic character in Elasipodida likewise other holothurians. I reevaluated their categorization based on new family rank systematics. Body ossicles of Elasipodida were categorized into four types: rod, wheel, C-shaped and four-armed ossicles. Three types of ossicles, rod, wheel and four-armed ossicles, were shared by multiple families scattered in Elasipodida, and it was presumed that these three ossicles types might already differentiated before Elasipodida branched into six elasipodid families. In contrast, since C-shaped type ossicles occurred only in Elpidiidae, and it might be acquired in Elpidiidae after separated from other elasipodid families.

My molecular phylogenetic analyses revealed that *Pannychia moseleyi*, a typical widely distributed species regarded as a single species over the Pacific Ocean, was not a single species, but contained at least nine species. That suggested species diversity of *Pannychia* has been underestimated due to missing the species boundaries of closely similar species having partly overlapped distributions.