論文の内容の要旨

Taxonomy and Phylogeny of Anenthemonae (Cnidaria: Anthozoa: Actiniaria)

（変型イソギンチャク亜目（刺胞動物門：花虫綱：イソギンチャク目）の系統分類学的研究）

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Sea anemones are a well-known group of marine animals belonging to Actiniaria, one of the largest orders of the class Anthozoa of the phylum Cnidaria with approximately 1100 species, in 264 genera within 50 families. Although there have been many species described, the taxonomy and phylogeny of sea anemones are both still in need of research because there are few morphological taxonomic characters known from their soft flexible bodies. Additionally, there is still no reliable molecular marker for phylogenetic analyses due to the slow evolutionary rates of both the mitochondrial and nuclear genomes. These numerous problems have hampered the taxonomic and phylogenetic research of sea anemones.

The first comprehensive classification system of the order Actiniaria was proposed by Oskar Carlgren in 1949. This system had been used until recently, but the latest comprehensive molecular phylogenetic analyses in 2014 suggested this classification did not reflect the actual phylogeny. Subsequently, the classification system of sea anemones was thoroughly revised, and Actiniaria was classified into two suborders, Enthemonae and Anenthemonae. The suborder Anenthemonae consisted of two superfamilies, Actinernoidea and Edwardsioidea, and the latter superfamily was composed of only one family, Edwardsiidae. Species of Edwardsiidae have particular worm-like bodies and burrow into substrates. Anatomically, Edwardsiidae are strongly characterized by having only eight perfect mesenteries in the first mesenterial cycle even as adults, whereas almost all other actiniarians have twelve perfect mesenteries in the first mesenterial cycle.

Though the family Edwardsiidae is one of the most diverse taxa in the order Actiniaria and includes approximately 85 species of 11 genera, the knowledge of the fauna of this family in Japan is still poor: only ten species of four genera have been recorded from Japan. However, no comprehensive taxonomic survey has been conducted, and hence the number of edwardsiid species and genera present in Japan could be greater than that recorded. Moreover, Edwardsiidae is also considered by taxonomic researchers to be an important group for evaluating the evolution of Anenthemonae and Actiniaria as they are considered to retain ancestral characters of sea anemones. They have one of the simplest body plans in Actiniaria: worm-like bodies, fewer numbers of tentacles, and absence of several muscles and basal discs. Especially, the peculiar arrangement of only eight perfect mesenteries (macrocnemes) in the first mesenterial cycle has been traditionally regarded as a trace of an ancestral character among actiniarians because the development of all actiniarians involves a stage with a similar mesenterial arrangement to this family. This traditional hypothesis has been challenged recently by some taxonomists advocating that the simplified mesenterial arrangement of Edwardsiidae may be derived in the secondary adaptation to the infaunal life. However, no reliable study has been conducted to determine whether the species of Edwardsiidae retain the ancestral features of the order Actiniaria or have derived them from the secondary adaptation, because all preceding studies have examined only a few species of Anenthemonae.

In this study, I conducted comprehensive and wide sampling from Japanese waters and collected over 250 specimens of Anenthemonae. I identified 47 species, including 33 previously undescribed ones, in 15 genera. Six genera of Edwardsiidae were newly recorded in Japan.

Based on phylogenetic analyses using sequences of mitochondrial 12S and 16S rDNA, cytochrome oxidase III (COXIII) DNA, nuclear 18S, 5.8S, and

28S rDNA and internal transcribed spacers (ITS) 1and 2 DNA, I drastically revised the classification for Anenthemonae: Anenthemonae was rearranged to be monophyletic by excluding some species of the genus *Metedwardsia* (of Edwardsiidae), instead including *Halcampella maxima* and some similar species (of Halcampidae). In the suborder Anenthemonae, I classified the species into three monophyletic superfamilies, Actinernoidea, Edwardsioidea, and Halcampelloidea, the third superfamily of this suborder. In Actinernoidea, two families Actinernidae and Halcuriidae turned out to be para- and polyphyletic respectively, and thus I rearranged the inner classification of this superfamily by establishing the family Isactinernidae, into which *Isactinernus* and *Synhalcurias* were placed, and a new genus *Isohalcurias* to solve the paraphyly of Halcuriidae. In the superfamily Edwardsioidea, which included only one family Edwardsiidae, the genera *Edwardsia*, *Edwardsianthus, Paraedwardsia, Scolanthus,* and *Isoscolanthus* were included in a large monophyletic clade. Following the phylogeny, I synonymized the five genera into *Edwardsia* as species in these genera all had nemathybomes, the most characteristic features on the surfaces of edwardsiids. In addition, the genus *Tempuractis* was established in the superfamily Edwardsioidea. In the superfamily Halcampelloidea, *Halcampella maxima* and some similar species previously classified in the family Halcampidae were placed. However, the family Halcampidae was within Enthemonae; thus, I established a new family Halcampellidae for the species belonging to the new clade of Anenthemonae and two new genera *Hexactis* and *Pseudoedwardsia* in this family.

According to this study, there are now 11 species and six genera in three families of Actinernoidea, 36 species and five genera in family Edwardsioidea, and four species of three genera in family Halcampelloidea. In conclusion, my study revealed the diversity of Japanese Anenthemonae as 51 species, 14 genera, and five families in three superfamilies.

Several evolutionary trends of Anenthemonae were estimated from the constructed phylogenetic trees in the present study. Actiniarian taxa consisting of simplified worm-shaped species have evolved several times from the general columnar-shaped ancestral taxa in Actiniaria. The simple morphology of Edwardsiidae is estimated to have gradually evolved in the lineage of Anenthemonae in two steps: first, the body was transformed to the worm-like shape in the common ancestor of Edwardsioidea and

Halcampelloidea, and later the basal disc and four of eight macrocnemes degenerated in the lineage of Edwardsiidae. Thus, my study indicated that the worm-like simple body of Edwardsiidae was derived by an adaptation, and thus settled the dispute concerning the morphology of edwardsiids that had continued for a century. In addition, this study showed that nemathybomes were acquired monophyletically in the lineage of the genus *Edwardsia*. The protective function of nemathybomes was suggested by this study; hence, they would be advantageous to the anemones of *Edwardsia*. The species of this genus would become more adaptive for the burrowing lifestyle by nemathybomes, and thus might have remarkably diverged and consequently occupied approximately 87% of species number in Edwardsiidae and even 70% in Anenthemonae.