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Restructuring the Traditional Suborders in the Order Scleractinia Based on Embryogenetic Morphological Characteristics

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The order Scleractinia includes two distinct groups, which are termed "complex" and "robust" as indicated by the molecular phylogeny of mitochondrial 16S ribosomal gene sequences. Since this discovery, coral taxonomists have been seeking morphological characters for grouping this deep division in the order Scleractinia. Recently, morphological characteristics during embryogenesis that facilitate grouping the two clades as "complex" and "robust" were reported, thus clarifying a deep division in the Scleractinia. In the present report, I establish two new suborders, Refertina and Vacatina, on the basis of the embryogenetic morphological characteristics, molecular data, and new observations of *Tubastraea coccinea* and *Cyphastrea serailia* embryogenesis. In particular, the embryo of *T. coccinea* has a possible fertilization membrane that was first observed in the phylum Cnidaria. The new suborder Refertina consists of the families that belong to the "complex" clade and have no or little blastocoel. The new suborder Vacatina is composed of the families that fall into the "robust" clade and have an apparent blastocoel.

Key words: coral, suborder, embryogenesis, hyaline layer, complex, robust

INTRODUCTION

Scleractinian corals are found in oceans around the world. The classification of these animals, including those in the fossil record, has been for a long time confused. The development of molecular and morphological tools developed now enables a better understanding of the evolutionary history of scleractinians. Our understanding of skeletal growth and homology is limited, because rampant convergent evolution limits the usefulness of morphological phylogenetics. Molecular phylogenetic analyses however have revealed the multi-level systematics of the Scleractinia, giving rise to new hypotheses regarding relationships among suborders, families, and genera that do not agree with those proposed on the basis of traditional classification. Moreover, many families of Scleractinia have not been established by molecular methods, and phylogenies often vary depending on the number of samples and which genes were used (Fukami et al., 2008; Huang et al., 2011; Arrigoni et al., 2012; Kayal et al., 2013). However, morphology is also very important, and has broad utility, especially for the field biologists.

Before launching a long debate between morphology- and molecular-phylogeny researchers, Romano and Palumbi (1996) found that the order Scleractinia includes two discrete lineages that originate in the early evolutionary history of the group, termed "complex" and "robust" on the basis of mitochondrial 16S ribosomal gene sequences. Coral taxonomists have for a long time been seeking morphological characteristics for grouping this deep division in the order Scleractinia, but morphological support for the robust and complex dichotomy was deficient (Kitahara et al., 2010). Recently, however, Okubo et al. (2013) have reported on a morphological characteristic during embryogenesis that facilitates grouping the two clades as "complex" and "robust", thus clarifying a deep division in the Scleractinia. Corals in "complex" clade have a blastocoel, while those in "robust" clade have no blastocoel during embryogenesis (Okubo et al., 2013). In addition, we have already found that gene expression patterns relating gastrulation are different between representatives in each group (Okubo, Hayward, Foret and Ball, in preparation).

Originally, "complex" corals were described as having comparatively porous and light-calcified complex skeletons with branching and various growth forms, while "robust" have relatively heavy-calcified ones with plate or massive growth forms (Romano and Palumbi, 1996). However, many studies have implied that the names "complex" and "robust" do not fit the morphological characteristics of the two groups; thus Veron (2013) mentioned "these two nicknames are somewhat inappropriate". Besides, molecular analyses suggest that more than half of the traditional suborders (Fungiina Verrill, 1865; Caryophylliina Vaughan & Wells, 1943; Astrocoeniina Vaughan & Wells, 1943; Dendrophylliina Vaughan & Wells, 1943; plus the Meandriina and Poritiina proposed by Veron, 1995) contain the suborders that belong to both "complex" and "robust" groups. In addition, the "robust" coral clade is a lineage that is embedded in the "complex" clade (Fukami et al., 2008; Kitahara et al., 2010).

In this paper, I propose two new suborders, Refertina and Vacatina, restructured from the traditional suborders, on the basis of molecular data and the key morphological characteristics of the type genus for grouping the two clades: the

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presence or absence of a coeloblastula and the mode of gastrulation. In addition, embryogenesis in *Tubastraea coccinea* from the "complex" clade and *Cyphastrea serailia* from the "robust" clade was described. In particular, in the current study, embryogenesis was first observed in the family of *T. coccinea*, namely Dendrophylliidae, as *T. coccinea* has been known as a brooding species. The new suborder Refertina consists of the families that belong to the "complex" clade and have no or little blastocoel. The new suborder Vacatina is mainly composed of the families, which fall into the "robust" clade and have an apparent blastocoel.

MATERIALS AND METHODS

Collection of *Tubastraea coccinea* and *Cyphastrea serailia* embryos

Two colonies of *T. coccinea* were collected from Kagoshima prefecture, Japan, during December 2014. The colonies were cultured in aquaria for five months. *C. serailia* was collected from Wakayama prefecture, Japan, before the predicted date of spawning in 2013. Collected embryos were fixed in 10% formaldehyde and then embedded in glycol methacrylate (Technovit 7100; Heraeus Kulzer GmbH, Germany). Sections of 8-μm thickness were cut using a microtome (Leica RM2125; Leica Microsystems). All

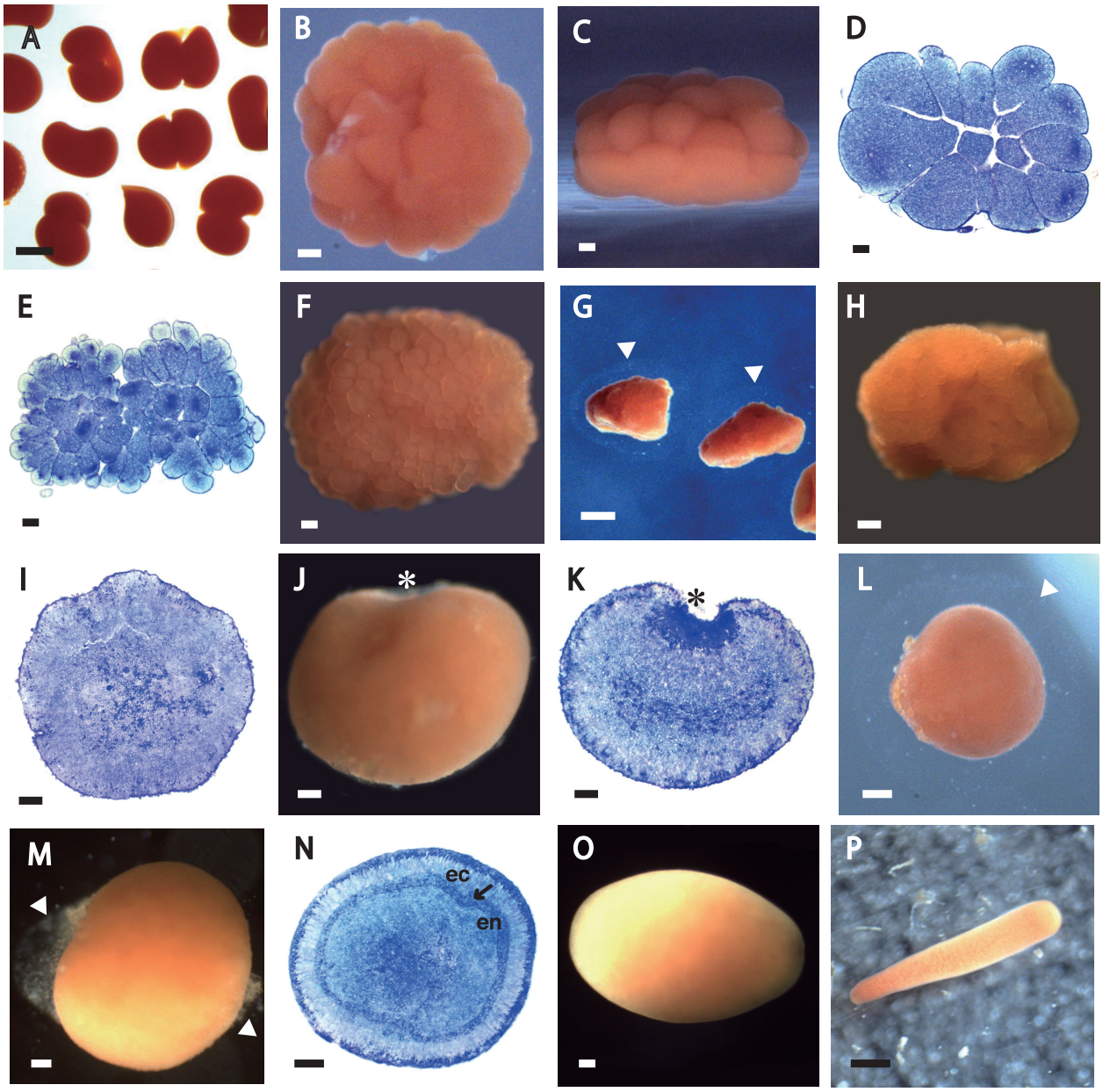


Fig. 1. Embryogenesis of *Tubastraea coccinea*. **(A)** First cleavage. **(B)** Morula stage. **(C)** Embryo has gradually flattened. **(D–F)** Cell cleavage has proceeded. **(G)** The embryo has an appearance of a rough stone. Arrowheads indicate possible hyaline layers. **(H)** The embryo has gradually swollen. **(I)** The outer cells surround an inner mass consisting of cellular fragments and cells. **(J)** Spheroidal embryo with a closing blastopore. **(K)** Section of **(J)**. **(L)** A round-shaped gastrula with a possible hyaline layer (arrowhead). **(M)** The embryo seems to have hatched out. **(N)** Mesoglea was formed (arrow), and distinct endoderm (en) and ectoderm (ec) layers were apparent. **(O)** Pear-shaped planula. **(P)** Elongated planula. Scale bar of **(A–F, H–O)** = 100 μm; **(G, P)** = 500 μm.

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sections were mounted on glass slides and stained using methylene blue.

RESULTS

Embryogenesis of *Tubastraea coccinea*

The release of buoyant eggs started at approximately 22:30 on 28 March (n = 40) and on 18 May (n = 3), and 22 May (n = 10) 2015. Planulae were released on 19 May (n = 1), 21 May (n = 1), and 23 June (n = 3), 2015. The water temperature was 22.5°C. Although only one colony spawned during each period, cell cleavage initiated at 1:50 on 29 March, 19 May, and 23 May 2015, indicating that internal self-fertilization or parthenogenesis had occurred. Microscopic analysis did not reveal sperms and polar bodies around the eggs. The early cleavage was holoblastic (Fig. 1A). Cleavage proceeded and the embryo entered the morula stage 6 h after spawning (Fig. 1B). The embryo gradually flattened (Figs. 1C–F) and then became a rough stone-shaped mass without a coelom by 12–16 h (Fig. 1G). At this stage, the presence of a fertilization membrane around the embryo (Fig. 1G, arrowheads) was observed. The embryo gradually thickened after 27 h (Figs. 1H). The outer cells surrounded an inner mass consisting of cellular fragments and cells (Fig. 1I), indicating that gastrulation had occurred. The surface of the embryo became smooth and a blastopore (asterisk) was observed (Figs. 1J, K). The possible hyaline layer was still apparent (Fig. 1L), but then the embryo appeared to have hatched out (Fig. 1M). The gastrula started swimming after approximately 140 h and the hyaline layer disappeared. The mesoglea formed (arrow), and distinct endoderm and ectoderm layers became apparent (Fig. 1N). By 6 April 2015, the gastrula formed a pear-shaped planula larva, which was actively swimming (Fig. 1O). By 16 April 16 2015, the planula had become elongated and displayed a slow, creeping motility (Fig. 1P).

Embryogenesis of *Cyphastrea serailia*

Spawning of egg-sperm bundles occurred at approximately 20:00 on 11 July 2013. The first cleavage started 2.5 h after spawning. Cleavage proceeded, forming a blastocoel (Fig. 2A, B). The embryo entered the cushion-shaped stage by 5 h (Fig. 2C). The embryo became further flattened after 7 h (Fig. 2D). A pseudo-blastopore (Okubo et al., 2013) then arose in the center of the disc-shaped embryo as it once again formed a spherical shape with an apparent blastocoel by 8–9 h (Fig. 2E–J, arrow head). After 10–11 h, the embryo was a completely hollow sphere (Fig. 2K). Gastrulation by invagination initiated after approximately 15 h (Fig. 2L). Invagination proceeded and the blastopore (asterisk) became smaller (Fig. 2M). Two germ layers, the ectoderm (ec) and endoderm (en), were formed and separated by the mesoglea at approximately 18–21 h (arrow, Fig. 2N). The endodermal layer ruptured and it's cells moved into the space formed by invagination. The gastrula started swimming by ca. 24 h (Fig. 2O). The blastopore became the oral pore (Fig. 2P).

DISCUSSION

Tubastraea coccinea from the "complex" clade has no blastocoel and becomes a stereogastrula. Prior to gastrulation, the prawn-chip stage, which is common in *Acropora*, *Montipora*, and *Galaxea*, is not found in this species. Instead, a rough stone-shaped *T. coccinea* embryo was observed, resembling that of *Porites cylindrica*, although the *P. cylindrica* embryo has little blastocoel (Hirose and Hidaka, 2006). The reason for this similarity may be that Dendrophylliidae, to which *T. coccinea* belongs, is more closely related at a molecular level to Poritidae than to Acroporidae (Fukami et al., 2008; Kitahara et al., 2010).

Surprisingly, a possible fertilization membrane was observed around the *T. coccinea* embryo, despite Cnidaria being the only known phylum in the animal kingdom to have no fertilization membrane (Dan, 2000). The observed layer was quite translucent; therefore, was not distinctly visible under the microscope until a part of the observation was complete. However, the layer could have been present when spawning occurred, because the embryos maintained a certain distance from each other at that time (Fig. 1A). The fertilization membrane is thought to prevent polyspermy, and the hyaline layer may play an important role in holding blastomeres together during cleavage. In this species, there is no evidence whether reproduction by self-fertilization or by parthenogenesis has occurred. In corals, self-fertilization was identified histologically in *Isopora bruggemanni* (Okubo et al., 2007), whereas parthenogenesis was suggested by Lively and Johnson (1994) on the basis of the observations of *Pocillopora damicornis* (Ward, 1992) and *T. coccinea* and *T. diaphana* (Ayre and Resing, 1986).

Cyphastrea serailia from the "robust" clade has an apparent blastocoel, and gastrulation occurred by invagination. The process of embryogenesis with a pseudo-blastopore is similar to the other "robust" corals (Okubo et al., 2013). In *C. serailia*, invagination occurred after a pseudo-blastopore disappeared, such that the relationship between the location of the pseudo-blastopore and invagination could not be determined. In *Favites abdita* and *F. pentagona*, invagination occurs in a different location from the pseudo-blastopore (Okubo et al., 2013).

In corals, there is no reported evidence on how mesenteries and mesenterial filaments are formed. Study of *C. serailia* may histologically show that the formation starts when the endodermal layer is ruptured and the endodermal cells move into the space formed by invagination during the "robust" mode of embryogenesis (Fig. 2N). Thereafter, vertical histological sections revealed that the moving cells formed a mesentery-like shape (figure not shown). In contrast, it could not be determined how the thin layer, which included a number of nuclei (Fig. 1N), had formed from the *T. coccinea* stereogastrula (Fig. 1K). It is unknown whether mesenteries and mesenterial filaments typically form from the cells in the thin layer or the cells gathered at the center of an embryo.

In conclusion, the observations in the present study, the initial wide analyses reported by Okubo et al. (2013), and the published literature all indicate that the order Scleractinia has two distinct groups based on its mode of embryogenesis: one consists of corals with no or little blastocoel, and the other consists of corals with an apparent blastocoel. These results clarified a deep division in the Scleractinia that facilitates grouping the two clades as "complex" and "robust" with one exception (see discussion below). In this paper, therefore, I establish two new suborders restructured from

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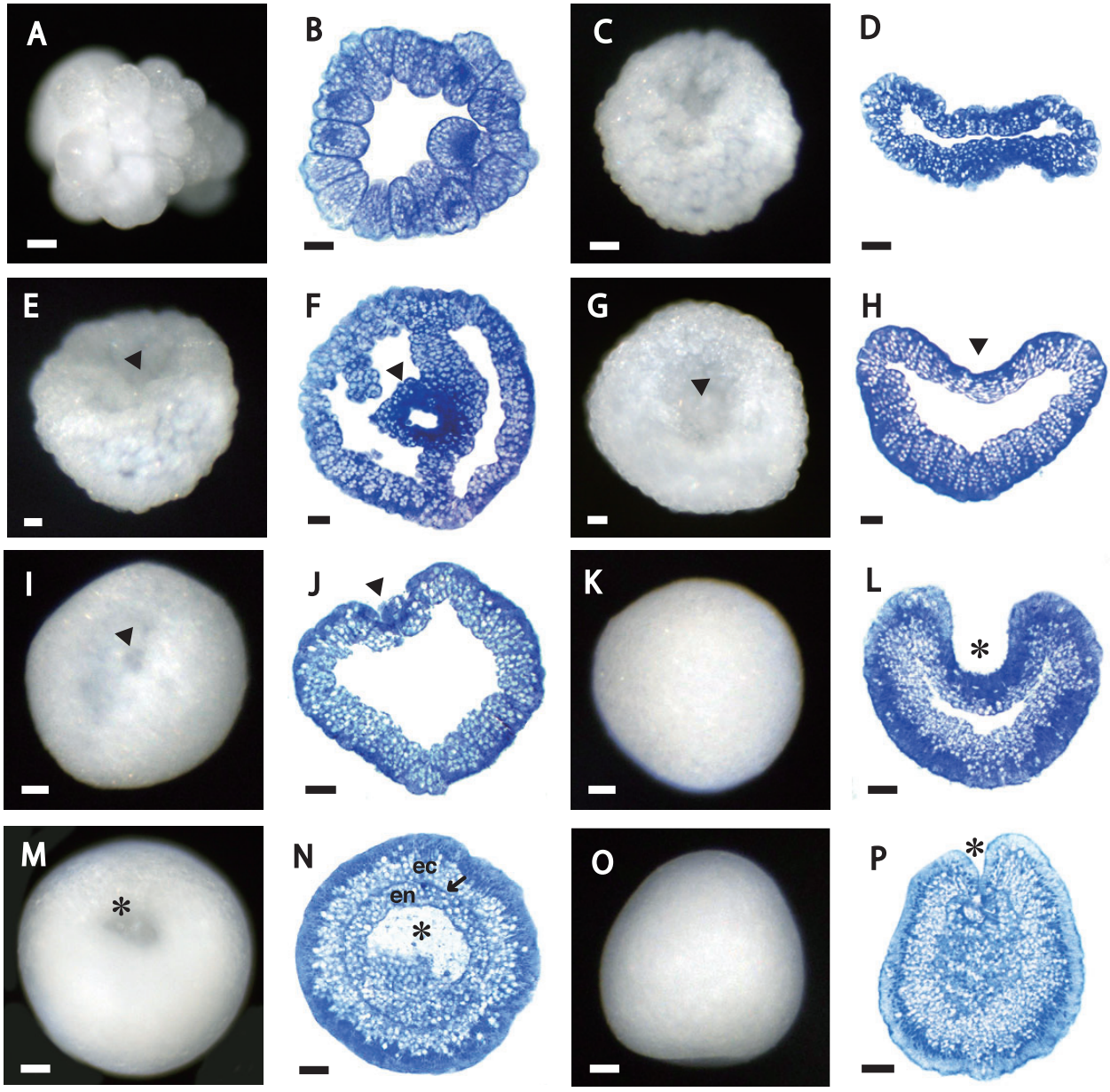


Fig. 2. Embryogenesis of *Cyphastrea serailia*. **(A)** 32-cell stage. **(B)** Section of **(A)**. The blastocoel was formed. **(C)** Embryo flattened to become the cushion-shaped stage **(D)** Cushion-shaped embryo with a smooth surface further flattened. **(E–H)** Cushion-shaped embryo has gradually swollen with a pseudo-blastopore (arrow head). **(I)** A pseudo-blastopore gradually disappeared. **(J)** Section of g with an apparent blastocoel. **(K)** Embryo has become a hollow sphere. **(L)** Gastrulation has started by invagination. The asterisk in this and succeeding panels shows a blastopore. **(M)** The blastopore has become smaller. **(N)** Mesoglea (arrow) formed, and distinct endoderm (en) and ectoderm (ec) were becoming apparent. **(O)** The blastopore/oral pore began to close. **(P)** The endodermal layer ruptured and its cells moved into the space formed by invagination. Scale bar = 50 μm.

the traditional suborders, on the basis of morphological embryogenetic characteristics and molecular data.

Taxonomy

Phylum Cnidaria Verrill, 1865
Class Anthozoa Ehrenberg, 1834
Subclass Hexacorallia Haeckel, 1896
Order Scleractinia Bourne, 1900
Suborder Refertina new suborder

Definition.—The embryo has no or little blastocoel. After spawning and fertilization, the cleavage proceeded and the embryo became the prawn-chip or the rough stone-shape stage (Fig. 3a). The embryo resulted in smooth surface due to continued cell division, as the cells elongate to the flattened disc, and it became spherical as the sides of the bowl fold inward to form the blastopore (Fig. 3b, c). Simultaneously, cells, yolk granules and zooxanthellae (in the case of zooxanthellate corals) are released from the inner side of the cell membrane into the central cavity to

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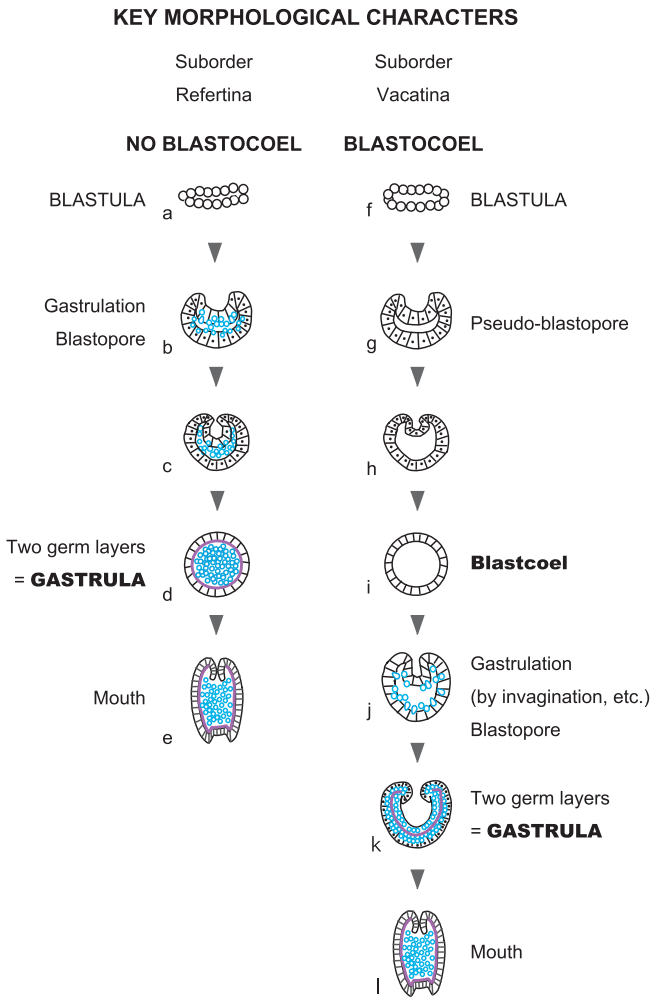


Fig. 3. Embryogenesis of the new suborders Refertina and Vacatina.

form a stereogastrula (Fig. 3d). The outer cells formed a single layer of epidermis and a central area contained cellular fragments and lipid bodies. The boundary between the inner and outer germ layers becomes clear, forming mesoglea (Fig. 3d). The oral pore (mouth) is formed by invagination (Fig. 3e). Corals in this suborder belong to the "complex" clade.

Etymology.—The name Refertina is derived from the Latin word *refertus*, meaning "filled". The name refers to the inner side of an embryo filled with cells and yolk granules.

Remarks.—At present, this suborder is composed of Family Acroporidae Verrill, 1902, Family Agariciidae Gray, 1847, Family Astrocoeniidae Koby, 1890, Family Dendrophylliidae Gray, 1847, Family Euphylliidae Alloiteau, 1952, Family Flabellidae Bourne, 1905, Family Fungiacyathidae Chevalier, 1987, Family Gardineridae Stolarski, 1996, Family Guyniidae Hickson, 1910, Family Micrabaciidae Vaughan, 1905, Family Poritidae Gray, 1842, Family Siderastreidae Vaughan and Wells, 1943, Family Turbinoliidae Milne-Edwards and Haime, 1848.

Suborder Vacatina new suborder

Definition.—The embryo has an apparent blastocoel. Cleavage proceeds after fertilization and a depression appeared in the side of the sphere, becoming a flattened or a cushion shape (Fig. 3f). Then, the embryo became swelling (Fig. 3g, h), formed an apparent hollow sphere, i.e., the formation of an apparent blastocoel (Fig. 3i). Cell fragments then start to move into the blastocoel by invagination (Fig. 3j), which leads to formation of the endoderm. As invagination proceeds, the blastocoel gradually disappeared (Fig. 3k). Ectoderm and endoderm are separated by mesoglea, and the blastopore becomes the oral pore/mouth (Fig. 3l). Corals in this suborder belong to the "robust" clade.

Etymology.—The name Vacatina is derived from the Latin word *vacatus*, meaning "empty". The name refers to the blastocoel of an embryo.

Remarks.—At present, this suborder is composed of Family Caryophylliidae Dana 1846, Family Pocilloporidae Gray, 1842, Family Fungiidae Dana, 1846, Family Meandrinidae Gray, 1847, Family Oculinidae Gray, 1847, Family Rhizangiidae d'Orbigny, 1851, Family Merulinidae Verrill, 1865, Family Mussidae Ortmann, 1890, Family Diploastreidae Chevalier and Beauvais, 1987, Family Anthemiphylliidae Vaughan, 1907, Family Montastraeidae Yabe and Sugiyama, 1941, Family Psammocoridae Chevalier and Beauvais, 1987, Family Stenocyathidae Stolarski, 2000, Family Lobophylliidae Dai and Horng, 2009, Family Coscinaraeidae Benzoni et al., 2012, Family Deltocyathidae Kitahara et al., 2013.

Incertae sedis: Family Montlivaltiidae Dietrich, 1926, Family Schizocyathidae Stolarski, 2000, Family Trochosmiliidae.

Restructuring the traditional suborders in the Scleractinia

The new suborder Vacatina corals formed a hollow coeloblastula at the morula stage at the time when the new suborder Refertina corals, such as *Acropora* had formed a so-called prawn chip, with little or no space between the two layers of which the embryo was composed (Fig. 4). The families Montlivaltiidae, Schizocyathidae and Trochosmiliidae, whose positions are equivocal, were placed in *incertae sedis* because there is no information on their molecular composition or sufficient information about their morphology.

It has recently been suggested that the families Gardineriidae and Micrabaciidae have a basal position in corals (Kitahara et al., 2010; Stolarski et al., 2011). The clade was termed "basal" (Stolarski et al., 2011), and Huang (2012) follows this grouping. In this paper, however, the two families could remain in the "complex" clade as the genetic distance between basal and complex is relatively short compared with that between complex and robust (Kitahara et al., 2010). Thus, the two families have been grouped in the new suborder Refertina.

The mode of gastrulation of *Pavona decussata*, a member of the family Agariciidae, is "robust" (Okubo et al., 2013). However, the molecular analyses strongly suggest that *P. decussata* should be classified as a "complex" coral (Fukami et al., 2008); therefore, I placed the family Agariciidae in the new suborder Refertina as an exception. Kitahara et al. (2010), with their more recent phylogenetic analyses of a larger number of species, based only on the mitochondrial CO1 gene, concluded that the "robust" coral clade originated

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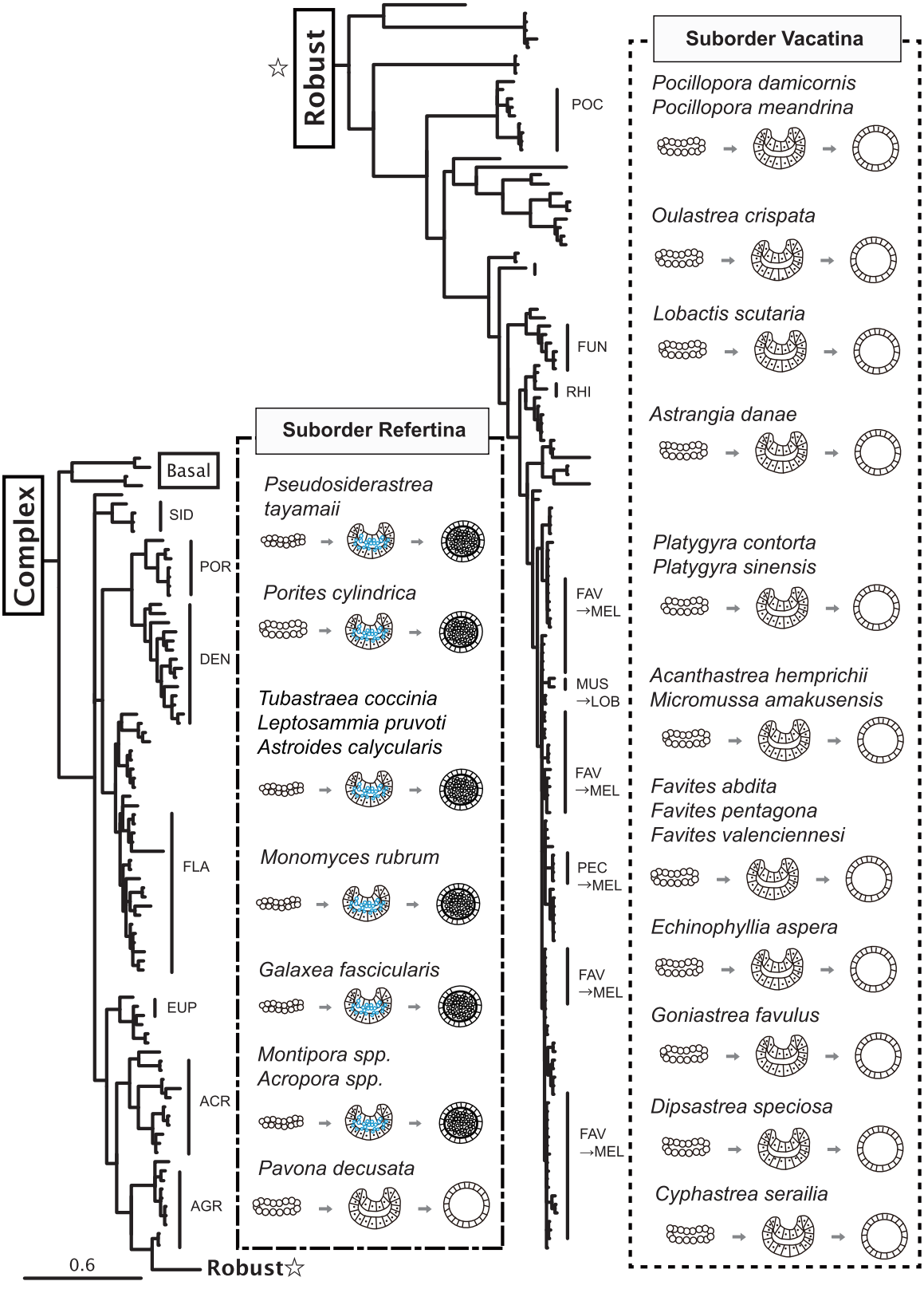


Fig. 4. Phylogeny and the presence of blastocoel from the results of the past studies. The studied species are overlaid onto the coral phylogeny of Kitahara et al. (2010), which is based on the sequence of the mitochondrial CO1 gene. See also other phylogenies that show each complex and robust clade is monophyletic from the analyses using various different genes (Stolarski et al., 2011; Huang, 2012). The family names revised in recent (Budd et al., 2012; Huang et al., 2014a, b) are explained using arrows. ACR: Acroporidae, AGA: Agariciidae, CAR: Caryophylliidae, DEN: Dendrophylliidae, EUP: Euphylliidae, FAV: Faviidae, FLA: Flabellidae, FUN: Fungiidae, LOB: Lobophylliidae, MEL: Meruliniidae, MUS: Mussidae, PEC: Pectiniidae, POC: Pocilloporidae, POR: Poritidae, RHI: Rhizangiidae, SID: Siderastreidae.

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from within a clade that includes the agariciids and the caryophylliid genus *Dactylotrochus*. There are thus at least two possibilities regarding the "*Pavona* exception". One possibility is that only *P. decussata* and a few other species in the family Agariciidae have the "robust" embryogenesis mode, and the rest of the species mainly have the "complex" mode; in this case, it indicates that "robust" embryogenesis may have been secondarily acquired in Agariciidae. The other possibility is that all members of the family Agariciidae have the same embryological "robust" mode. In this case, the "robust" embryogenesis mode acquired before separating robust clade and Agariciidae. Then, the taxonomic validity that the new suborder Refertina includes the family Agariciidae will be discussed, considering other potential taxonomic characters such as reproductive modes (Baird et al., 2009).

The oculinids were polyphyletic (Romano and Cairns, 2000; Le Goff-Vitry et al., 2004), with *Galaxea* falling into the "complex" clade (Kitahara et al., 2010). Budd et al. (2012) moved *Galaxea* and *Ctenella* into the family Euphylliidae, so I assigned the family Euphylliidae including these two genera to the new suborder Refertina. Accordingly, the family Meandrinidae becomes monophyletic and thus I assigned the family Meandrinidae to the suborder Vacatina. The family Guyniidae is grouped in the new suborder Refertina based on the results of Romano and Cairns (2000). So far in the family Astrocoeniidae, *Stephanocoenia* and *Stylocoeniella* have been molecularly analyzed and the former falls into "complex" group and the latter into "robust" group. *Stylocoeniella* is related to pocilloporids (Kitahara et al., 2010), but the type genus for the family is a fossil genus (*Astrocoenia*) could be morphologically similar to *Stephanocoenia* (Fukami et al., 2008), so that I grouped this family in the new suborder Refertina.

The family Siderastreidae is assigned to the new suborder Refertina based on the results of Benzoni et al. (2012). The families Acroporidae, Dendrophylliidae, Flabellidae, Fungiacyathidae, Poritidae, Turbinoliidae are grouped in the new suborder Refertina, and the families Anthemiphyllidae, Fungiidae, Merulinidae, Mussidae, Pocilloporidae, Rhizangiidae, Stenocyathidae in the new suborder Vacatina based on the results of Kitahara et al. (2010) and Okubo et al. (2013). The families Coscinaraeidae, Deltocyathidae, Diploastreidae, Lobophylliidae, Montastraeidae and Psammocoridae are grouped into the suborder Vacatina based on the results of Benzoni et al. (2007), Huang et al. (2011), Benzoni et al. (2012), Kitahara et al. (2010), Dai and Horng (2009), Budd et al. (2012) and Okubo et al. (2013).

The family Caryophylliidae is assigned to the new suborder Vacatina based on the result of molecular position of *Lophelia pertusa*, which should be close to the type genus *Caryophyllia* (Le Goff-Vitry et al., 2004), and its embryogenesis, which has hollow blastula (Larsson et al., 2014). Goffredo et al. (2012) reported on the embryogenesis of *Caryophyllia*, and they described the embryo has no blastocoel and gastrulation occurs by delamination. However, the early cleavage stages, especially between the morula stage to the blastula, which are the important stages to find the blastocoel, are not shown in their paper. In Fig. 6B of Goffredo et al. (2012), they describe the early embryos, however, the surface of embryos, which they show, is very smooth and no cellularization was observed from the picture. The embryos seem to be at the early gametogenesis stage, or even if they are embryos as they describe, the early cleavage stage including morula has already finished. So it is difficult to say that *Caryophyllia* has no blastocoel. I look forward to further studies on the early cleavage stages before delamination starts in *Caryophyllia*. It is very interesting if delamination occurs in *Caryophyllia* because *Pocillopora damicornis* and *P. eydouxi* also show delamination (Hirose et al., 2000) and they are close in the molecular phylogeny (Kitahara et al., 2010).

While the classification of corals remains in flux, several additional hypotheses flow from the results of embryogenesis. First, it would conclude that patterns of early development and gastrulation do make phylogenetic sense, rather than being correlated with other factors such as habitat or mode of reproduction. Second, it would appear that the mode of gastrulation in the new suborder Refertina is the original mode of gastrulation within the Scleractinia. Having discovered this apparent correlation between the pattern of embryonic development and the robust/complex clades, I turned to the literature to see whether this apparent correlation held up to broader scrutiny. The results are summarized (Supplementary Table S1 online). For some of these papers, the data are inadequate for unequivocal assignment to either a robust or complex pattern but Okubo et al. (2013) made the best predictions based on text descriptions plus figures. Some of the descriptions strongly support the correlation between phylogeny and pattern of development. So, in an era when scleractinian systematics is still in flux, patterns of embryonic development can supplement data as a tool for determining systematic and taxonomic position. Gastrulation mode such as delamination, invagination, ingression etc. could be used for grouping at the family or genus level, because the gastrulation mode is different at least among genera (Okubo et al., 2013). Also, in the early stages of polyp formation, the beginning of skeletogenesis might be useful as the morphology is different among families (Okubo unpublished).

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