CONCEPT OF COMMON BUD AND RELATED PHENOMENA IN BRYOZOA

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ABSTRACT

The *common bud* of Stenolaemata (Cyclostomata of authors), as understood by Borg (1926), is analogous to the buds of higher plants in its terminal position on branches of the Bryozoa and in its vital activities.

The common bud is truly common to all developing zooecia in a branch of a zoarium in a sense that its coelomic fluid remains undivided distally as long as a branch grows. As soon as a polypide bud originates, subtending to it, an oblique septum begins to rise proximally by fission (Borg's term) from the cylindrical wall of a branch; thus, a new zooecium with its own polypide is being initiated.

All polypide buds originate at the edge of a transverse membrane that seals the coelomic fluid terminally. As the branch continues to grow the developing polypide falls behind the growing edge of the membrane, which Borg named *growing zone*. Some biologists (including Hyman) erroneously consider growing zone synonymous with common bud— but the growing zone has the same relationship to the common bud as the meristem of plants has to their bud.

The walls and septa of a zoarium which possesses a common bud combine their calcareous layers into a single continuous structure, the colonial plexus (Elias' and Condra's term).

The Bryozoa possessing common buds attain a higher level of colonial individualization (*sensu* Beklemishev) than those without it, and the greater the transverse expansion and complication of the common bud, the greater the colonial individualization—such as attained in more advanced Stenolaemata.

Cheilostomata lack common buds, but in *Membranipora* and related crustose cheilostomes, whose colonies are built by contiguous rows of zooecia, each row develops by the means of its terminal *linear bud* (new term), with its own growing zone.

The Ordovician "graptolite" *Reticulograptus* closely resembles the extant stenolaemate *Stegohornera violacea* (Sars) Borg

INTRODUCTION

The idea of the common bud, by means of which the bryozoan colonies are developed, is an imaginative concept conceived by F. A. Smitt about a hundred years ago. As Borg briefly stated

(1926a, p. 254), Smitt believed "that in all Bryozoa the developing margin of the zoarium is to be regarded 'as a colonial bud, a common bud (*samknopp*), which separates [divides] itself by means

of fission, and develops into separate zoids [zooids]'" (SMITT, 1865, p. 6, translated by BORG). He erred, however, in his belief that all Bryozoa developed in this manner; and it was NITSCHE (1871, sep. 31 ff.) who explained that it was not the case with Cheilostomata and Ctenostomata. Accepting this correction, BORG worked out a revised concept of common bud, and established on the evidence of its presence a "new order for the Cyclostomata, co-ordinate with two old orders Gymnolaemata and Ctenostomata . . ." to "be termed Stenolaemata" (BORG, 1926a, p. 490). This taxonomic connotation ascribes to the common bud foremost significance in a natural classification of Bryozoa.

Whereas BORG described the stages of development of the modern Cyclostomata by the means of common bud, he noted that "certain differences between the various cyclostomatous forms present themselves even in the earliest developmental stages," although the common bud itself originates and develops in a similar manner from the "semispherical primary disc characteristic for all Cyclostomata" (1926a, p. 255). He also mentioned, in an unobtrusive way, his important discovery of an optical orientation of the minute particles comprising the calcified layer in the Crisiidae, which he examined in polarized light. He found that these particles "are located in a certain direction; namely parallel to the longitudinal [along the branches] axis of the [common] bud"; and, he noted, "the same is true also of the calcified walls of the zoids [zooids]." No observation of similar nature has ever been made elsewhere in the description of other groups of the Cyclostomata in this or other books by BORG, but greater biological and taxonomical significance to the optical orientation of the particles in the calcified layer in Crisiidae was added by the discovery of a similar optical orientation of the calcite in the unit-crystal primary skeleton in fenestrate bryozoans, hence suggestive of the presence in them of the common bud.[1]

BORG also clarified biological understanding of the "developing margin" in the Cyclostomata and indicated it to be *the growing zone of the common bud*. His most informative statement is quoted:
"At the edge of the terminal membrane the ectodermal cells are higher, very closely packed together without any intercellular spaces (pl. 3, fig. 12); their cytoplasm is densely granulated. The mesodermic cells are also placed considerably closer together. The [cellular] transition from this [marginal] zone to the remaining part of the terminal membrane and to the lateral walls of the common bud [below] is gradually effected. It is in this zone at the edge of the terminal membrane that the growth of the common bud mainly takes place. Here new cells originate; here new substance is stored in the cuticle, secreted from the ectodermal cells; here is also secreted calcareous matter (chapter 4); and, finally, it is here, too, and only here, that the rudiments of the polypides [polypide buds] first become visible. This zone in question may conveniently be termed the **growing zone** of the common bud" (BORG, 1926a, p. 321 [his underscoring]). It is obvious that in this statement BORG described the structure and activities of only a part—even if most essential—of the common bud: its growing zone. However, because he did not attempt a formal definition of the common bud and limited himself to specific descriptions of its occurrence in various cyclostomes, he left his concept exposed to misunderstandings and misinterpretations.

ACKNOWLEDGMENTS

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[1] I resolutely disagree with the speculative concept of growth in fenestellid branches by means of a "conveyor belt" principle, which was adapted for this purpose by TAVENER-SMITH (1969) in preference of the natural (for them) growth by means of common bud. It seems rather ridiculous to imagine that the same mechanism which was imaginatively conceived to explain the growth of certain brachiopod shells by ALWYN WILLIAMS (1966, 1968), would need to be proposed for explanation of the growth of a colonial organism. Even HYMAN (1959), who with the help of her academic redefinition of the well recognized concept of Lophophore, united into her "Lophophorate Coelomates" (1959, p. 228 ff.) the phyla Phoronida, Ectoprocta, and Brachiopoda, was avoiding any comparison of growth of the bryozoan colonies to that of brachiopod shells.

COMPONENTS OF COMMON BUD

The following components are present in the common bud of all stenolaemate bryozoan colonies:

1) *Terminal membrane* which stretches across and covers the bud cavity at the distal margin (or margins) in a developing colony. The terminal membrane consists (from outside inward) of a very thin cuticle, a one-cell thick layer of ectoderm, and a one-cell thick layer of diffusely spaced cells of mesoderm.

2) *Coelomic cavity,* which is filled with coelomic fluid, sealed by a terminal membrane above, and contained laterally and proximally by an outer wall and oblique septa or both.

3) *Colonial wall* and partitions (septa), all of which (from outside inward) consist of a very thin cuticle comprising a calcareous layer (precipitated by ectodermal epithelium), ectoderm, and mesoderm (Fig. 1).

4) *Growing zone,* a ringlike area along the contact of the terminal membrane and the colonial wall, where new cells of ectoderm and mesoderm originate and polypide buds make their "first appearance."

5) *Oblique calcareous septa,* which arise in the proximal part of the coelomic cavity by sending out from the colonial wall, as if by fission, oblique ingrowths (internal outgrowths) which ascend subparallel to the wall toward the terminal membrane. As the oblique septa rise, they elevate

and drag along their sides, as it were, the ectoderm and mesoderm, which cover the calcareous wall (or septum), from which they originate. Thus each septum consists of a central calcareous layer, which is flanked on either side by ectodermal and mesodermal layers. This manner of origin "by fission" makes all septa inherently possessive of a single primary calcareous layer, directly continuing from the calcareous layer of the zoarial wall, from which they originate. It is this uniform, one-layered, calcareous structure of all walls and septa which is highly characteristic of stenolaemates. And because it is a result of colonial development through mechanism of common bud, the definition of the latter must take this into account.

6) *Otherwise oriented calcareous septa,* which originate from the oblique septa, such as "median vertical" (Borg, 1926a, p. 270) septa rising along the linear coalescence of the two opposite oblique septa in Acamptostega (*Stomatopora, Tubulipora*), as explained below.

SPECIAL TERMS PERTAINING TO STENOLAEMATA (CYCLOSTOMATA) AND FENESTRATA

Proper understanding of special terms which indicate the peculiar processes in growth by means of the common bud is essential for its formal definition. These are fission and coalescence.

FISSION

The term fission was applied by Borg in two different, although closely related, senses. It was introduced as an English translation of the corresponding Swedish word in the citation of Smitt's original concept of the common bud, which was said to separate [divide][1] itself by means of fission" (Borg, 1926a, p. 254; translated from Smitt, 1866, p. 6). Borg continued sporadically to use "fission" in this same sense (p. 261, 273), but also, as inadvertently, transferred the term from "fission" of the bud to "fission" of the septa, which produces "separation." Thus initially he described "the first septum [which]
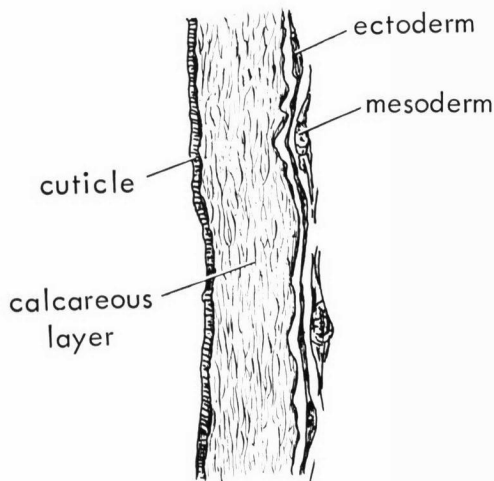
Fig. 1. Scheme of a calcified wall in Stenolaemata (after Borg, 1926b, fig. 1).

ectoderm

mesoderm

cuticle

calcareous layer

[1] The word "separate" is undesirable because Borg used it in a quite different sense in speaking of "the young primary zoids [zooids] [whose] distal part begins to separate itself by means of a joint from the proximal one" (Borg, 1926a, p. 358).

appears in it [bud] as an outgrowth from the calcified layer of the future basal side of the bud" (Borg, 1926a, p. 256). By basal side is meant here, in an upright colony, the side opposite that toward which the zooecial apertures are turned. In subsequent descriptions the term "fission" was employed exclusively for all dividing septa in the common bud, emphasizing this use particularly in an argument against employment by Barrois of the rival term **dichotomy** in describing the honey-comb-like serial arrangement of zooecia in *"Pha-langella flabellaris,* produced *à une march dicho-tomique"* (Barrois, 1877, p. 80). As Borg stated, this is not the case, since arrangement of the septa is produced by "fission of the septa, as well as [by] their *coalescence,* [which] always begins at the basal wall of the bud and continues gradually in the direction of the frontal wall (cf. text figs. 33 and 35)" (Borg, 1926a, p. 277; my italics) (Fig. 2).

The term "fission" is considered more suitable than dichotomy, because it is befitting the lopsided origin of oblique septa growing at an acute angle to the cylindrical zooecial wall, thus making it appear that the latter is split asymmetrically in a terminal direction.

DICHOTOMY

Borg applied the term "dichotomy" exclusively to the manner of zoarial branching of zoaria in *Stomatopora* (1926a, text-fig. 31) (Fig. 3) and other zoaria, that is, in the same sense as accepted by all bryozoologists.

COALESCENCE AND VERTICAL SEPTUM

The term "coalescence" was used by Borg to indicate meeting of two symmetrical oblique septa along their distal rims, as observed in the earliest growth stage in the Tubuliporidae. Along the line of this coalescence "a median vertical septum [perpendicular to basal side] is formed, which grows forwards, . . . the two original septa also keep on growing, and gradually assume a more and more horizontal position (text-fig. 27-28) (Fig. 4-5). In this way three cavities have been produced in the common bud, an upper, median, which alone is connected with the cavity of the primary disc, and two lower, lateral ones (text-fig. 28) (Fig. 5). The first . . . constitutes the begin-ning of the primary zoid [zooid] (text-fig. 27, 28,
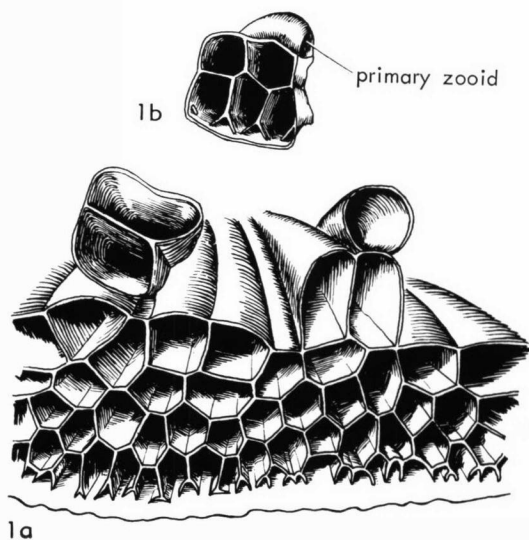

FIG. 2. *Tubulipora phalangea.*——*1a.* Part of common bud of well developed zoarium, ×40.——*1b.* Young com-mon bud, ×35 (after Borg, 1926a, fig. 33, 35, mod.).

FIG. 3. Distal end of zoarium of *Stomatopora granulata,* branching dichotomously, ×53. In the left bud growth has ceased prematurely (after Borg, 1926a, fig. 31, mod.).

p.z.). (Fig. 4-5), the other two [which] will give rise [as parts of common bud] to the rest of the zoarium. . . . [This initial] division of the bud thus obviously . . . deviates remarkably from the conditions existing in the Crisiidae." (BORG, 1926a, p. 270) (Fig. 6-7).

The combination of coalescence of the two oblique septa and subsequent rise of the vertical septum is highly characteristic for all Tubuliporidae throughout development of their zoaria, which are the most primitive among nonjointed Stenolaemata, the genus *Stomatopora* being simplest of all. It seems that the mechanism of their development, which clearly is bilaterally symmetrical, can be detected also in Paleozoic Cyclostomata and Fenestrata.

DOUBLE WALLS AND JOINED WALLS

The new term *"joined walls"* is suggested here for zooecial walls which originate through direct, surface-to-surface contact, as exemplified by the contact between lateral walls in adjacent rows of zooids in *Membranipora*. Such joined walls should not be called "double walls" (SILÉN, 1944, in explanation to text-fig. 47, p. 59), with or without hyphen, as the term double-wall (preferably with hyphen) should be restricted to the more com-
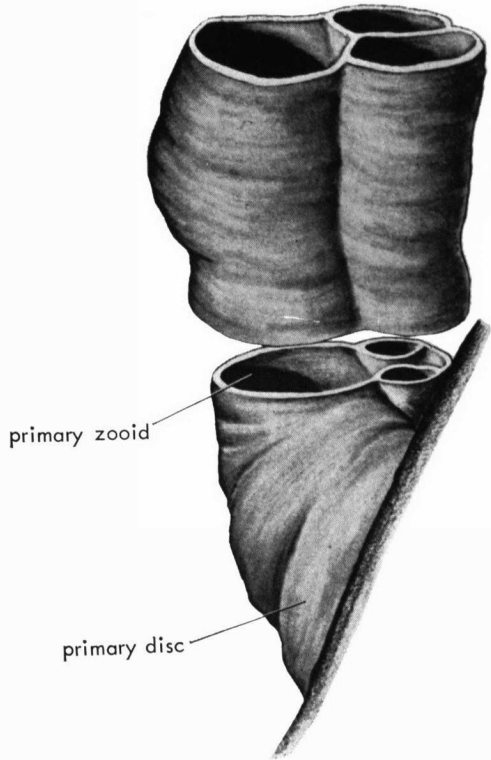

FIG. 5. Primary disc and beginning of zoarium of *Tubulipora phalangea* seen from right hand side, partly schematic, *ca.* ×195 (after Borg, 1926a, fig. 28, mod.).

FIG. 4. Primary disc and beginning of zoarium of *Tubulipori andersoni*, seen from frontal side, ×175 (after Borg, 1926a, fig. 27, mod.).

plicated Stenolaemata, where the double-walls are made by the inherent combination of two investments, one outer (gymnocyst) and the other inner (cryptocyst).

BUDDING REGION

The term "budding region" (=common bud, *sensu* BORG) apparently was applied for the first time by ROBERTSEN (1903, p. 117, ff.) in her description of the process of budding in *Crisia*. As previously mentioned, she observed that in the decalcified preparations of this cyclostome the "growing point . . . consists of two parts, (a) the layer of deeply staining cells, and (b), the budding region." In a comment on this observation, BORG (1926a, p. 324) noted that "from this and from other statements it seems as though she imagined that, in this genus, there was in the common bud [ROBERTSEN's "growing point"], partly a special growing zone composed of the ectoderm and mesoderm [ROBERTSEN's "deeply
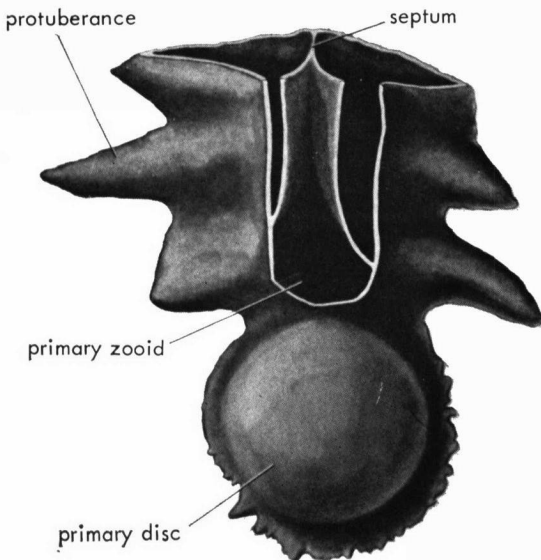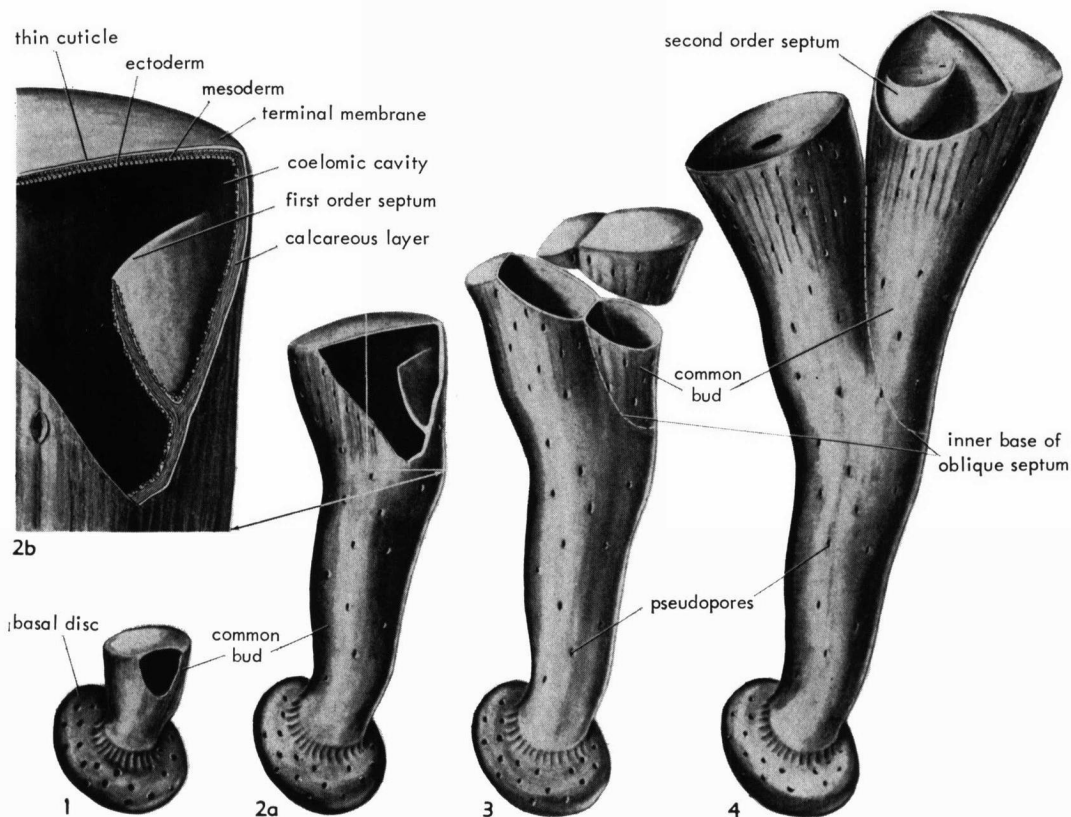
FIG. 6. Primary disc (*1*), common bud (*1,2a*), and development of primary zooid and first branch (*3-4*) of *Crisia eburnea*, ×145; *2b*, part of terminal portion of calcarous wall of common bud, seen from inside, *ca.* ×440. Upper part is growing zone (after Borg, 1926a, fig. 13, 15-17, mod.).

staining cells"] of the terminal membrane, partly another region, proximal to this, where the polypide-buds were formed. This is by no means the case. The growing zone is at the same time also the "budding region" [of the polypides].

In making this comment Borg obviously was concerned with the restricted case of the "budding region" of polypides—not of zooids—and it was logical for him to deny the existence of a special place, distinct from the growing zone, where polypides supposedly originate in *Crisia* (or for that matter, in any other cyclostomes). As he observed, "the polypides always take their origin in the growing zone of the common bud and in no other place . . . [but] the polypide buds . . . in no case . . . keep their original position during the further development, but are gradually displaced . . . in the same direction as the distal parts of the developing cystids [sacs] (chapter 4),

the two processes keeping pace with each other, as is natural. Of course, it is not a question of an active migration of the rudiments of the polypides and cystids [sacs], but of a displacement owing to the constant activity of the growing zone" (Borg, 1926a, p. 323), that is, its invariable movement in a distal direction during colonial growth. No inconsistency is seen, therefore, in Borg's own subsequent use of "growing region" for a special kind of common bud in more complex divisions of the Stenolaemata (Borg, 1926a, p. 296, in *Domopora stellata*, text-fig. 49), and in connection with the Heteroporidae, he called it "the budding region proper" (1933, p. 353).

Because Robertsen's interpretation of "budding region" as the place of origin of polypide buds was not generally accepted by others and because no rule prevents putting new sense in old terms with advance of knowledge, use of "bud-

ding region" in the well-explained and consistently used sense of BORG can hardly be considered objectionable.

A single exceptional use by BORG (1933, p. 340) of "budding zone or common bud" (instead of "budding region or common bud," BORG, 1933, p. 274, 275, and others) should be considered a *lapsus calami.*

GROWING MARGIN

The term "growing margin" was used by BORG (1926a, p. 293, text-fig. 47) (Fig. 8) for the sharp edge of the "bilaminate zoarium" of *Diplosolen,* in which the zooids develop on either side of a common, flat median lamina. The growing margin (or edge) "protrudes quite a distance beyond the budding region"—the common bud, which is thus divided symmetrically by the edge.

A similar growing margin is developed in many unilaminate adnate zoaria of Stenolaemata, such as the distal edge in *Tubulipora phalangea* GRAY (BORG, 1926a, fig. 33-35) (Fig. 2), *Domopora stellata* GOLDFUSS (BORG, 1926a, text-fig. 49, p. 300), and others.

COLONIAL PLEXUS

Discovery of the colonial plexus (ELIAS & CONDRA, 1957, p. 26-29), and the coining of this term for description of fenestrate bryozoans was a principal result of investigating these fossils with polarized light. It was inspired by BORG's already-quoted discovery that, when viewed in polarized light, the "calcified layer" of the wall in extant Crisiidae "the minute particles [of calcium carbonate] composing it are located in a certain direction: namely, parallel to the longitudinal axis of the [common] bud. The same is true also of the calcified walls of the zoids [zooids]" (BORG, 1926a, p. 256). The latter statement is particularly significant in that it refers to the distal part of the zooid walls which grew subsequent to separation from the common bud (thus becoming free from it and also from the young zooids in the common bud, which originally were contiguous with them).

BORG (1933, p. 354, with reference to his 1926 paper, p. 255 ff.) subsequently stated that "the matrix of the calcareous wall is . . . a chitinous substance, between the fine fibres of which the particles of carbonate of lime are deposited."

second order septum

first order septum

joint

1

terminal membrane removed
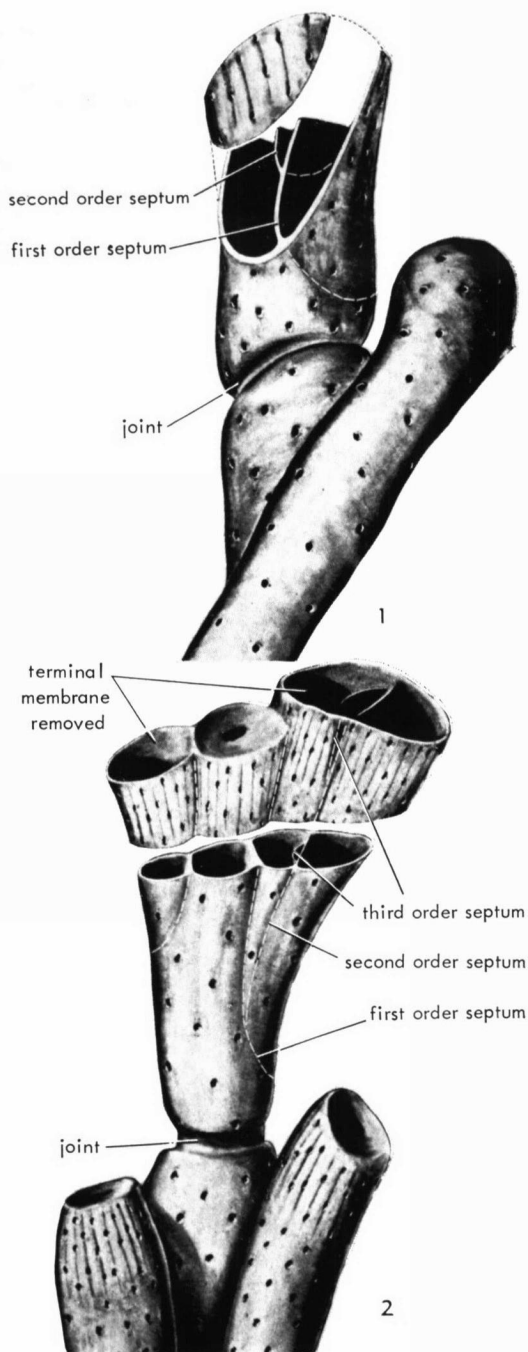
third order septum

second order septum

first order septum

joint

2

FIG. 7,1. Zooid and developing branch of *Crisia eburnea,* seen from basal side, ×150.——7,2. Same, seen from frontal side, ×120 (after Borg, 1926a, fig. 18, 19, mod.).

growing margin
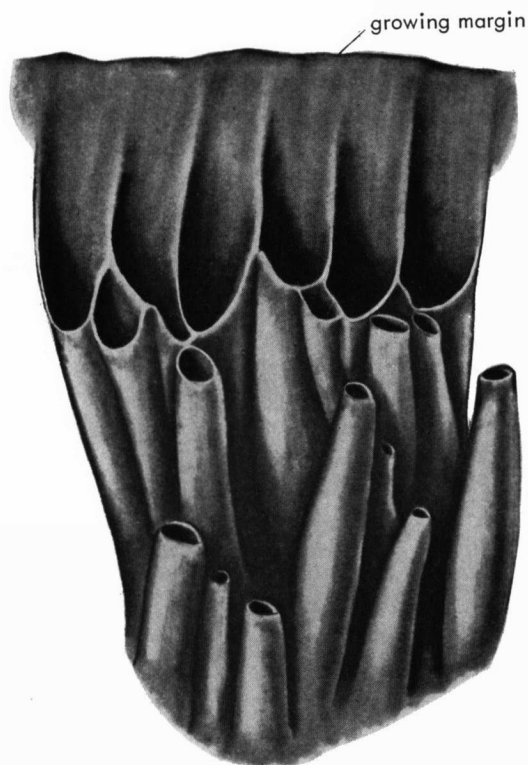

FIG. 8. Part of growing zone of zoarium of *Diplosolen obelia* seen from frontal side, ×60 (after Borg, 1926a, fig. 47, mod.).

The usefulness of these and other important observations by BORG for comparative analysis of Paleozoic Bryozoa and extant and fossil cyclostomes will be explained in a special paper on the order Fenestrata. It may be added here, however, that the term colonial plexus can be extended for use in the Cyclostomata, referring to older part of their zoaria behind the advancing common bud.

DEFINITION OF COMMON BUD

The following definition applies to all cases of the common bud development, including the stenolaemate colonies where secondary calcification results in an additional calcareous layer on one or both sides of the primary calcareous layer, and which differ from it in texture. As defined below, this primary layer is essentially the same in them all.

The common bud denotes a continuous existence, throughout colonial growth, of an undivided

coelomic cavity, shared by two or more developing zooids and located in the terminal part (or parts) of a bryozoan zoarium; the developing zooids are only proximally separated from each other by septa originating from colonial walls and from each other, their distal rims not reaching the terminal membrane. This mode of origin of septa assures unification of all walls and septa into an uninterrupted foil-like primary single—a single-layered calcareous structure in primitive forms or two-layered in advanced Stenolaemata.

In most primitive Stenolaemata (Camptostega) (BORG, 1926a, p. 474), the particles of crystalline calcite in this structure are optically oriented parallel to the longitudinal axis of the growing common bud (BORG, 1926a, p. 256).[1]

The common bud originates in the basal disc of a colony (zoarium) and constitutes the principal part of colonial growth. Its terminal part, the growth zone, continuously occupies the termini of all growing branches or all of the growing periphery in nonbranching colonies (as in Lichenoporidae).

Some interpreters claim that no differences distinguish concepts of the common bud and of its growing zone. Most outspoken is HYMAN in *"The Invertebrates."* Because HYMAN's well-earned authority on extant invertebates is widely recognized, it is essential to take into account her statement about possible lapses in her knowledge of Bryozoa, as expressed in the preface to volume 5 (1959, p. v): "The [preparation of the] present volume . . . was a laborious task. Especially the Ectoprocta proved exceptionally difficult. . . . To receive direct instruction in the Ectoprocta I spent some time at São Paulo, Brazil, where Professor and Mrs. Marcus showed me unlimited kindness and consideration; but unfortunately illness prevented me from taking advantage of the situation." This may explain, at least partially, the

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[1] The fact that BORG observed optically oriented particles of calcite in the calcified layer of the septa and walls in all of the Crisiidae, but not in the more advanced families of Stenolaemata is in itself no evidence for or against presence of common buds in them, but merely a more complex organic texture in the calcareous layer of the walls and septa in the latter. The growth of zoarium by the means of common bud assures uninterrupted continuity of the walls and the rising of septa from them (by fission). The optical orientation of the minute elongated crystals of calcite in their growth within the fibrous tissue of the calcified layer is a natural result of the parallel disposition of the fibers that forces the crystals to grow in the direction along the contacts between adjacent fibers. This would not take place wherever the fibers lose their parallel disposition which may have occurred in the advanced Stenolaemata. This supposition is a subject of verification by examination under polarized light of oriented thin sections prepared from them. No optical properties can be expected to be revealed by electron microscopes of any kind.

dubious contents of her cardinal statement, as follows:

"In more complicated types of cyclostome colonies, the colony expands distally by the simultaneous formation of a number of partitions cutting off new zooids. There is therefore present a peripheral growing zone, termed by BORG (unnecessarily) *the common bud"* (HYMAN, 1959, p. 358; her italics).

Because the term common bud is underlined, and the term is not mentioned anywhere else, HYMAN made it appear that BORG originated this term to be used exclusively for the peripheral growing zone in more complicated types of cyclostome colonies. As previously mentioned, the concept of common bud was introduced by SMITT (1865, p. 6), as explained by BORG (1926a, p. 254), who also clearly stated that the growing zone is a part of the common bud (*sensu* BORG). Furthermore, he did not use the term common bud for only the more complicated types of cyclostome colonies; on the contrary, he preferred to call the peripheral parts of these colonies a growing margin of zoarium (1926a, explanation to fig. 49, p. 300); or budding region (1926a, p. 306, 307), in *Diplosolen obelia* and *Hornera,* respectively; and he remarked that "it is scarcely necessary to speak of a common bud in *Hornera"* (1926a, p. 306). In fact, BORG used the term common bud judicially, and in some most complicated zoaria, such as *Lichenopora,* he cautiously stated that "the whole zoarium *can be thought of* as a greatly widened common bud" (1926a, p. 314; my italics).

HYMAN's misinterpretation of what is meant by common bud appears to be connected with her misunderstanding of cyclostome wall structure, which she describes thus:

"In cyclostomes the walls of contiguous zooecia are fused to form a common wall" (1959, p. 301; also p. 298, 299).

The use of the word "fused" is quite unsuitable, even as an abbreviated expression for a wall origin. No matter how loosely understood, the word fused indicates putting together of originally separated things. That this is not the case in cyclostome zooecia can be seen even by comparative observation of HYMAN's selected illustrations, which she has taken from various unimpeachable sources. Thus, in *Entalophora* (1959, text-fig. 108-E) (Fig. 9,*1*) the youngest centrally located, zooecia are considered by her "fused," but else-

where, quite inconsistently, the similarly located young zooids (zooecia) in a "higher cyclostome (*Pustulipora*)" (1959, text-fig. 136-K), very similar to *Entalophora* (Fig. 9,2) are called, quite correctly, "terminal growing zone with partitions for new zooids," obviously destined to grow into fully developed ones (which are shown below), each with its separate cylindrical wall.

The combination of the two illustrations demonstrates, therefore, that there is no such thing as "fusing," e.g., joining together of zooecial walls in cyclostomes, but, on the contrary, the "partitions for new zooids," which originate in the growing zone as common "walls" between the contiguously arising young zooids, grow eventually into individual distal cylindrical walls. These rise directly from the originally common partitions, and in the maturing stage become farther and farther separated from each other.

It seems logical and inevitable that morphologic and taxonomic work on advanced invertebrate colonial forms such as the Ectoprocta (Bryozoa) involves recognition of some correspondingly advanced concepts, which transcend the familiar, simpler concepts inherent in more primitive colonies, such as those of Hydrozoa. Thus a newcomer in the field of ectoproctan studies finds that special terms used by ectoproctologists, annoyingly lack relation to terms employed for other groups of animals, some of them "fantastic," others "superfluous,"—and some simply "bad" (HYMAN, 1959, p. 285-287). HYMAN substituted other terms and expressions for them, the most unsuitable of which is "fused," which she applied, as already mentioned, to the young zooecia partitioned in the common bud (1959, p. 301, text-fig. 108-E, 109-A).

In HYMAN's condensed descriptions of colony formation in cyclostomes, "exhaustively" (she admits) "studied by BORG (1926a)," HYMAN (1959, p. 358) deliberately avoided BORG's terms and made a shambles of it by stating that colony formation in cyclostomes "does not appear to differ fundamentally from the cheilostomes" (1959, p. 389), unknowingly repeating the fatal error by SMITT. Ironically, colony formation of the cheilostomes, which she treats before that of the cyclostomes, has been far less exhaustively studied by anyone than that of cyclostomes. This situation is inadvertently reflected in her statement that "nonstoloniferous colonies, which comprise the vast

majority of gymnolaemates [an oblique reference to cheilostomes] consist of a continuous succession of zooids more or less fused to each other" (1959, p. 288)—the favored word "fused" again, with no biological or structural meaning behind it.

The common bud (*sensu* BORG) was accepted

wall of zooid

growing zone

as a useful concept by SILÉN (1944, p. 49, ff.), BEKLEMISHEV (1952, p. 348), SHULGA-NESTERENKO (1949, p. 8), BASSLER (1953, p. G9—common bud properly understood and limitations of its use explained), ELIAS & CONDRA (1957, p. 1, 31-33, 38, 40); BRIEN (1960, p. 1305); and KLUGE (1962, p. 76).

The common bud was well defined in the Bryozoa volume of the *Treatise,* but the definition concerned only most primitive forms of the Cyclostomata (BASSLER, 1953, p. G9): "**Common bud.** In Cyclostomata, the protoecium [ancestrula] grows into a cylindrical tube with mouth closed by an uncalcified terminal membrane which by the growth of an oblique calcareous septum is divided into 2 parts. The smaller part becomes the common bud, and the larger the first zooecium. Further growth repeats the process with development of a new septum and so on until a zoarium is formed with the common-bud portion composed of chitinous fibrous substance extending throughout. First recognized in Cyclostomata, occurrence of the common bud now is reported by some students in Cryptostomata and Trepostomata."

With exception of Membraniporidae (whose colonial growth is analyzed below), which were originally considered by SMITT (1865) as exemplary colonies with growth by means of common buds, no colonial growing zone (meristem) can be recognized in the cheilostomes. This is the principal biological difference between the colonial growth of cheilostomes and cyclostomes. On the contrary, growing zones or meristems (BONNER, 1952, p. 121) occur in colonial hydrozoans and, in this respect, colonial growth in them, particularly in those with apical meristems, is akin to that in cyclostomes. It would be useful now to compare critically the data on morphogenesis in cyclostomes and in those organisms where growing zones or meristems have been customarily recognized.

FIG. 9,1. "Cyclostome *Entalophora* with zooecia fused (after Calvet, 1931)" (as interpreted by Hyman, 1959, fig. 108E, mod.).——9,2. "Branch of higher cyclostome (*Pustilipora*) showing terminal growing zone with partitions for new zooids (after Busk, 1886)" (after Hyman, 1959, fig. 136K, mod.). [NOTE.—In both illustrated forms the central part of zoarium consists of developing zooecia divided from each other by single-layered septa, which according to the concept of common bud *sensu* BORG were produced by fission and coalescence. The outer part of both zoaria consists of mature zooecia, whose free, single-layered cylindrical walls grew from the termini of the septa.]

BOTANICAL BUDS AND THEIR MERISTEMS

Seemingly, the fundamental difference between the common bud and growing zone in stenolaemate colonies would be easier to understand if our minds were refreshed on corresponding differences between their analogous botanical coun-
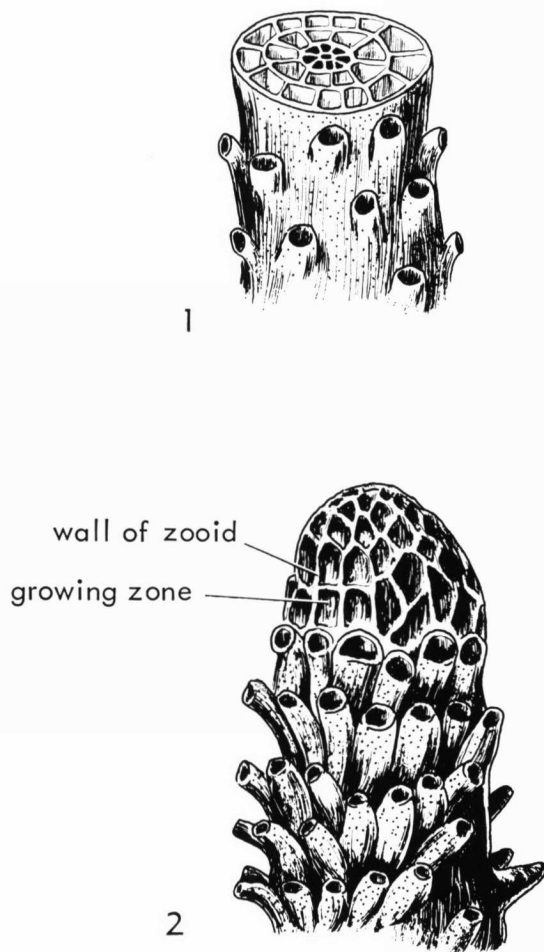
terparts—buds and meristems, the latter originally called growing points.

In a special chapter on buds SINNOTT (1923) has stated that in higher vascular plants "growth of the stem in length takes place only at a certain definite point, where the cells are thin-walled and capable of active division; . . . [and where] these growing points are protected by leaves or scales they are known as buds (fig. 43)" (1923, p. 88). "Within the buds are not only the beginnings of the stem but of the various structures which are borne upon it, such as leaves and flowers. The terminal bud governs the elongation of the stem, and, through the development of lateral buds, *branches* arise." (p. 89; SINNOTT's italics).

The concept of growing points is defined by SINNOTT in a separate chapter on the subject in which he states that "In such organs as the root and stem, the continued production of new cells is accomplished through the activity of *growing points or meristems,* which are merely groups of cells remaining in an embryonic and undifferentiated condition. These groups of permanently young cells occupy regions where growth is to take place." (p. 142; SINNOTT's italics).

In the chapter on the "Structure of Bud," in the more modern "Plant Biology" of WEATHERWAX, the author stated (1947, p. 104) that: "the dormant bud of a woody plant ordinarily consists of a series of protective scales on the outside, a number of embryonic leaves, and an undifferentiated growing point. The growing point is the essential part."

ANALOGIES IN DEVELOPMENT OF PLANTS AND COLONIAL ANIMALS

Of course, the common bud in stenolaemate colonies has quite a different structure from that of the buds in plants. Its growing zone, which resembles the growing point or meristems of plants in position and function, consists of young cells, in which BORG recognized ectodermal and mesodermal cells, concluding that in this zone also originate rudiments of the polypides" (polypide buds). These peculiarities of the growing zone make it analogous not exactly to the meristems of plants, but more nearly to its combination with the nearest part of the surrounding tissue, where new cells, originating from the meristem,

begin to become differentiated. However, this consideration does not destroy general correspondence of the growing zone of cyclostomes to the active part of a plant bud where new cells originate (in meristem) and their differentiation (next to meristem) begins. Indeed, BORG nowhere indicated that the growing zone of cyclostome colonies corresponds to the growing point or meristem of plants; but ROBERTSEN described "the growing point" (1903, p. 117) in *Crisia* as having "two parts: (a) the layers of deeply staining cells, and (b), the budding region," where the polypide buds originate. BORG disagreed in that, according to his observations, only a single zone (his "growing zone") "is at the same time also 'the budding region'" (1926a, p. 324), which is where "the rudiments of the polypides first become visible" (1926a, p. 321).

The seeming discrepancy between the two statements about location of the polypide buds actually does not exist because, as BORG explained, whereas "the polypide-buds originate in the growing zone . . . in no case do they keep their original position during the further development, but are gradually displaced," in proximal direction, as it were, to the distally advancing growing zone (BORG, 1926a, p. 323).

The role of the common bud in cyclostomes is as dynamic as that of a bud in plants. Just as the meristem in a plant bud continuously produces new cells which become differentiated and furnish material for embryonic branches and leaves, so the new cells, which are incessantly produced in the growing zone of a cyclostomatous common bud, become the cells of ectoderm and mesoderm. Both the meristem and the growing zone move constantly in distal direction as the organisms grow. Behind them, and within a bud, new parts of the organism are developing, be it a plant bud or a cyclostomatous common bud.

PLANTLIKE COLONIAL GROWTH IN HYDROZOA AND CYCLO-STOMATA

In a biophilosophical essay on morphogenesis by BONNER (1952), which only recently attracted my attention, the author drew a parallel between the growth of higher angiosperms (and other plants) and the hydrozoans. Starting from the plants (1952, p. 101), he defined "a meristem,

[as] a specific region where cell division takes place" (1952, p. 101). BONNER further remarked that "it would appear at first glance that one of the unique features of plants is the meristem and that there is no real counterpart of this among animals. The fact is, however, that [some] animals have rather perfect meristems, although they are not normally called that by zoologists" (1952, p. 118-119).

He pointed out the presence of these "perfect meristems" in some of the simplest colonies among colonial metazoans, the colonial developments of which were found, as HYMAN expressed it, "in definite ways similar to those obtaining in plant growth. Their mode of growth is either monopodial or sympodial" (HYMAN, 1940, p. 403-405), the same as in the plants, from the use in whose descriptions these terms are borrowed.

It appears instructive that this was written in the first (1940) volume of HYMAN's ambitious treatise on "The Invertebrates" (by a specialist on the vertebrates); and that in this volume, in her description of "colony formation in Hydrozoa" she used the same three terms: bud, budding zone, and growth zone, terms already used in the same sense by BORG and other "ectoproctologists" who, in her later opinion, "seem to get themselves entangled in their own terminology" (HYMAN, 1959, p. 285). As written in 1940, in the "monopodial growth which prevails among the gymnoblastic [stoloniferous] hydroids, the main stem and all branches are permanently topped by terminal hydranths and continue to elongate indefinitely by the means of a *growth zone* just below each hydranth (Fig. 116E). Below the growth zone, lateral buds arise at intervals, and, since *each bud has a growth zone,* the stem elongates between successive buds, which thus come to be separated by a length (internode) of newly formed stem" (HYMAN, 1940, p. 405; my italics). Not only the terms, but even the relationship of a bud to its part, the growth zone, repeats the understanding by BORG (1926a, p. 321) of the relationship between the common bud and its growing zone in cyclostomes. The two cases of the same biologic relationship differ only in extent of the buds: a multitude of separate buds in the colonial hydroids, and only a single common bud in the massive, or several common buds in branching colonies of cyclostomes.

Equally instructive is HYMAN's description of the sympodial growth of Hydrozoa in which "the hydranth stems have *no growth zone* and do not elongate after being formed. Below the temporary last hydranth of the hydrocaulus [stem] or branch is a *budding zone* from which *a bud* arises laterally" (HYMAN, 1940, p. 405; my italics). It follows, as it were, that in HYMAN's 1940 terms, in sympodial colonial hydrozoans the "mode of growth" is by means of "budding zones," whereas the "mode of growth" in monopodial colonial hydrozoans is by means of "growth zones." In most primitive cyclostomes, on the other hand, the polypoid budding region or zone is also the colonial growing zone, according to BORG (1926a, p. 324).

BONNER formulated the same difference between sympodial and monopodial growth in hydrozoids in a shorter and different way than HYMAN, for he used consistently the term meristem synonymously with growing zone or growth zone. In his description of most advanced sympodial colonies he stated that "as the apical meristem advances [with the growth] it gives off buds that remain meristematic and these become the lateral branches which in turn give off hydranths. If the leaves [in plants] are considered to be analogous to the hydranths, the situation is quite parallel to that found in plants, again presumably because in both cases the growth is meristematic" (BONNER, 1952, p. 125).

Growth in cyclostomes may be also considered meristematic, with a terminal location of the meristem (the growing zone). However, the mechanism of the growth in them is unlike any meristematic growth in other animals or in plants. The distinction depends on the presence in cyclostomes of a unique combination of a terminal membrane at the top and oblique partitions at the base and internal sides of the common bud, with the growing zone occupying the rim of the terminal membrane. The rims of the oblique partitions do not reach the terminal membrane as long as the process of growth continues. Because of this, the coelomic fluid on either side of any partition retains free communication across it beneath the terminal membrane. It is this continued presence of the undivided coelomic fluid at the distal end in all ramifications of cyclostome colonies that biologically defines the presence in them of the common bud.

PHILOSOPHICAL IMPLICATIONS OF COMMON BUD

The presence in a colony of the common bud, and the ensuing unification of all its walls and septa into a colonial plexus have a profound philosophical significance.

Borg was on the right track in understanding its significance when he mentioned incidentally that in the very compact, wartlike zooaria of Lichenoporidae "the connection between the zoids [zooids] is more intimate than in any other Cyclostomata; a *Lichenopora* zoarium may well be regarded as an *individual of higher order* as considered as a colony" (Borg, 1926a, p. 472; my italics; also 1933, p. 377).

It is of interest to note that some botanists approach this same philosophical concept the other way around when viewing a tree as an individual of higher order, composed of the lower order individuals, the branches and branchlets. It is well known that the latter, when severed from a tree and transplanted, develop by budding into individuals of higher order, young trees.

A quarter of a century after Borg's casual remark on "an individual of higher order," the Russian zoologist Beklemishev (1952) advanced a broader theory of "individualization of a colony." In this he visualized a general hierarchy of organismic "ranks," the lowest represented by simplest cell-like "monoenergid" Protozoa, the next higher composed of "polyenergid" Protozoa, "which are somewhat analogous rather to Metazoa, particularly preempting the multicellular structure of the latter. Flowering plants and some metazoans (most hydroids, bryozoans and others) present units of higher constructional rank than an individual, that is a *cormus*" (Beklemishev, 1952, p. 38; free translation, his italics; compare botanical term Cormophyta).

Beklemishev (1952, p. 66) illustrated his theory by some examples, stating that: "the concept 'protozoan colony' is juxtaposed to 'polyenergid individual' of a protozoan, and here I call the colony a slightly individualized unification of monoenergid protozoans (for instance *Synura* of Chrysomonadina); whereas by 'polyenergid individual' (plasmodium or somatella) I mean such unification of monoenergid individuals, where the individuality of the latter is expressed more weakly than individuality of the total (for instance, *Pelomyxa* of Amoebina, or an adult *Opalina ranarum* of Protociliata). In all these cases the term 'colony' indicates a definite, even if comparatively lowest, stage of integration (Spencer's term) of units into an individual of higher rank. For indication of the higher whole formed by unification of multicellular individuals, irrespective of the level of integration reached by the whole, I shall use the term *cormus* or *zoarium"* (author's italics).

In view of Beklemishev's philosophical concepts, as quoted, it is not surprising to find that he grasped Borg's understanding of the common bud and of the growing zone better than most reviewers of Borg's research on Stenolaemata, even if Beklemishev avoided exact translation or transliteration of Borg's terms. Thus he wrote (1952, p. 348) that in Stenolaemata there is always, at the proximal edge, an undivided growing region, from which new "cystids" are divided by the development of oblique septa.

Elsewhere he (Beklemishev, 1952, p. 348) indirectly referred to Borg's accomplishments thus: "The most characteristic feature in the colonial development of the Stenolaemata is their peculiar method of budding. The colony in these forms invariably possesses an *all-colony growth zone,* which may be single, or, when a branching colony is formed, a separate growing zone may be segregated at the terminus of each branch. The *common growth zone* invariably includes the terminal membrane, and the growth takes place at the edge of the latter"; my italics indicating author's terms for the common bud. He added further that ". . . the growth zone is uninterruptedly advancing at one [distal] end, and at its other [proximal] end are formed septa and individual zooecia." This is, in fact, a compact definition of the common bud *sensu* Borg; and in an explanation to Borg's 1926a, text-fig. 55 (Beklemishev's 1952, fig. 175-1) Borg's "common bud" is explained as "all colony zone of growth" (obstchekolonialnaia zona rosta). All quotations from Beklemishev (1952) are free translations from Russian.

DIFFERENT DEVELOPMENTS OF COMMON BUD

Different developments of the common bud, in different divisions, families, genera, and species

of Stenolaemata result in greater or smaller differences in the morphology of their colonies and may also be considered to indicate the degree of their colonial individualization. The least individualized are colonies of the two most primitive divisions—Camptostega, with jointed colonies (single family Crisiidae), and Acamptostega, with colonies not jointed (Tubuliporidae, Diastoporidae, and other more complex families). The most primitive of these colonies are most diffuse and delicate, their slender branches with fascicles of a few zooids each and their small terminal common bud in each branch capable of generating only two or three developing zooids at a time.

CAMPTOSTEGA

Comparatively simple colonial development, exemplified by that of *Crisia eburnea,* well described and illustrated by BORG (1926a, p. 255-259; text-fig. 13-20), frequently has been reproduced in modern compendia on living and fossil bryozoans. The common bud is not generally mentioned, however. A few of these illustrations are shown here, modified to emphasize extent of the common bud and growing zone and their relationship (Fig. 6-7). Thus, more advanced divisions of the Stenolaemata, Pachystega (Horneridae, Crisinidae, and other families), and Heteroporina (Heteroporidae), have a more compact grouping of the zooecia into relatively few and solid branches, thus having a less diffused common bud. Finally, in the fifth division, the Caliptrostega (families Lichenoporidae and Disporellidae), the colonies never branch at all, remaining discoidal or cushion-like, covered by a single terminal membrane. In this division, as BORG (1926a, p. 472) stated, "the fully developed zoarium can be regarded as a common bud which has been widened and, through the development of a great many septa, strongly complicated."

ACAMPTOSTEGA

BORG (1926a, text-fig. 26-32 on p. 271) (Fig. 3-5) combined his observations on *Stomatopora granulata* with those on *Tubulipora phalangea.* Because of the well-known similarity of the species of *Stomatopora* to each other, their zoarial development is much the same in both (BORG, 1926a, p. 272); also in numerous species of *Tubulipora,* the development of the zoarium is similar, and "the first common bud is formed as in *Stomato-*

pora and the primary zoid [zooid] separates itself from it in the same way as in this genus" (BORG, 1926a, p. 275). Just as in the case of *Crisia* and all Camptostega, the colony in Acamptostega starts from a primary disc.[1] The "young common bud" (also called the "first common bud") rises from the disc as a tube (Fig. 4), and the first two oblique septa rise symmetrically from opposite sides of it by "fission" of the cylindrical wall. The two septa coalesce at an angle in the middle of the bud at a distance (from the disc) about equal to the bud's diameter. It would be appropriate to mention here that besides difference from *Crisia* (and all Crisiidae) in the development of two opposite septa instead of a single septum, and the beginning of a new septum at their coalescence, a difference in the orientation of the first common bud also occurs in Tubuliporidae (where *Stomatopora* belongs): it does not grow straight upward but almost at once turns at an angle of about 45 degrees to the substratum, and in its further growth gradually becomes subparallel to it. As the bud turns, the pair of the oblique septa "meet in the median line of the bud (cf. text-fig. 27). As yet neither septum reaches the terminal membrane. When the two septa meet [coalesce] a medial vertical [in relation to the horizontal substratum] septum (text-fig. 27, *s*) is formed, which grows forward . . . [and] the two original septa also keep on growing and gradually assume a more and more horizontal position (text-fig. 27, 28) (Fig. 4-5). In this way three [coelomic] cavities are produced in the common bud, an upper median, which alone is connected with the cavity of the primary disc, and two lower lateral ones (text-fig. 28). The first-named cavity of the three constitutes the beginning of the primary zooid (text-fig. 27, 28, *p. z.*). The other two will give rise to the rest of the zoarium. The three cavities are connected with one another beneath the terminal membrane (1926a, p. 270, text-fig. 27) (Fig. 4).[2] The organization of septa in more advanced zoaria of Acamptostega (e.g., *Tubulipora,* Fig. 2), and development of the growing margin in a

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[1] Subsequently termed proancestrula by BORG (1933, p. 271); it is homologous to *protoecium* in fenestrate bryozoans (Fenestrata), as established by CUMINGS (1905, p. 173).

[2] Because the schematic line drawings by BORG do not seem in all cases to convey to the eye the morphologic concepts which he described—as for instance in his figure 27, where no terminal membrane is shown at all—the sketches which are here appended and referred to in the text are modified from his figures for the purpose of making them more illustrative, without detracting from what he put into them, but with addition of what he mentioned in text without illustration, such as the terminal membrane and contents of the common bud.

bilaminate zoarium of *Diplosolen* (Fig. 8) have been described above (p. 4, 7).

ADVANCED STENOLAEMATA

Borg found that all three advanced divisions of the Stenolaemata—Pachystega (hornerids), Heteroporina, and Calyptrostega (lichenoporids)—possess a common bud. However, they "develop their zoaria along other lines than the Cyclostomata *s. str.,* their body-wall is double, and there are several other characters uniting them, but distinguishing them sharply from the Cyclostomata *s. str."* (Borg, 1944, p. 18). By "double wall" he meant the existence of two investment layers, an inner (cryptocyst) and an outer (gymnocyst), adding that "on the other hand, they have structures common with the Trepostomata . . . [the latter] have developed their zoaria in such a way that their body-wall must have consisted of two layers just as in the Divisions just mentioned" (ibid., p. 18), a matter of conjecture.

Whereas segregation of the more primitive divisions Acamptostega and Camptostega into Cyclostomata *s. str.* seems logical, the classification of the three remaining divisions of Cyclostomata *s. lato* with Trepostomata may be disputed. The Heteroporidae (division Heteroporina) indeed bear substantial resemblance to many ramose Trepostomata, and the Lichenoporidae generally resemble some disclike hemispherical trepostomes. However, the division Pachystega (hornerids) is externally more nearly like some of the massive, dissepiment-less Permian Fenestrata (*Thamniscus, Acanthocladia*) (Fig. 10).

PACHYSTEGA (CANCELLATA)

Borg admitted that his material did not permit him "to trace the development of the zoarium in *Hornera* from the very earliest stages in order to find out how the structure of the body wall described in Ch. 1 originates"; but he was certain that "development of the primary zoids [zooids] from the primary disc does *not* take place in the same way as in the Tubuliporidae; . . . [but] is rather as in the Crisiidae" (Borg, 1926a, p. 305).

It is peculiar for Pachystega that their zoarium is "fixed to the substratum by means of a 'supporting disc' . . . [which is] composed of a number of [small] tubes representing a kind of kenozoid [kenozooid—abnormal zooid without polypides] . . . Sections through young zoaria parallel to
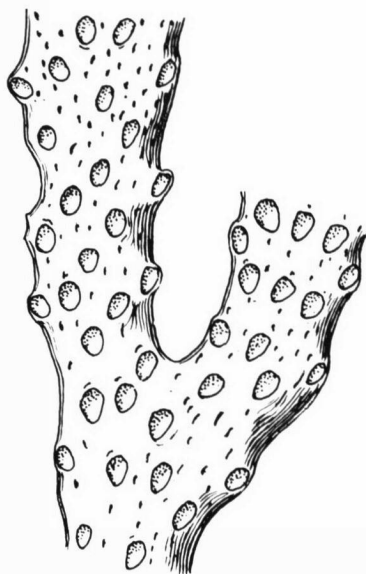

FIG. 10. Part of old zoarium of *Hornera antarctica* seen from frontal side, ×19 (after Borg, 1926a, fig. 54).

the longitudinal axis of the autozoids [autozooids—normal individuals] show that the tubes of kenozoids [kenozooids] take their origin from quite near the place where the primary zoid [zooid] originates from the pre-ancestrula. From here they radiate at all sides along the substratum. At the edge of the disc thus formed new tubes come into existence in the same way as in a common bud., i.e., by the fission of the partition-walls, or septa between those already existing. . . ."

"The mode of formation of said kenozoids [kenozooids] implies, I think, the explanation of the structure of the zoarial wall characteristic of all Pachystega. A young developing zoarium probably should be regarded as a greatly widened common bud, the basal wall of which is in contact with the substratum all around the proancestrula, while just inside this wall and parallel to it . . . the autozoids [autozooids], close together in the central portion of the bud, are gradually lengthening upwards, new ones being formed occasionally by fission of the interzoidal [interzooidal] walls. If this assumption is correct . . . the terminal membrane of the bud obviously would cover like a transparent veil the upper side of all the [small] tubes forming the disc as well as the ensemble of the outer walls of the autozoids [autozooids]; and . . . this is exactly what hap-

pens in the zoarium" of *Hornera antarctica* WA-TERS. BORG (1926a, pl. 8, fig. 49) illustrated a longitudinal section of very young zoarium of this species and partly on this evidence sketched a diagram (BORG, 1944, text-fig. 23, p. 176) (Fig. 11,*1*). In this diagram he distinguished the terminal membrane as part of the all-enclosing gymnocyst.

BORG (1944, p. 177) eventually concluded that the zoarial wall in the Pachystega "is formed by the following strata: (i) a gymnocyst, consisting of cuticle, ectoderm and mesoderm, and (ii) a cryptocyst, viz., a calcareous layer surrounded on both sides by ectoderm and mesoderm; between the gymnocyst and the cryptocyst is a slit-like 'hypostegal' coelomic cavity (cf. BORG, 1926b, p. 198).

"As has just been mentioned the gymnocyst does not belong to each of the individual zoids [zooids] but is rather to be regarded as of zoarial origin, being derived [developed] from the terminal membrane of the original common bud. In most genera within the group there is no calcareous matter deposited in the cuticle of the gymnocyst but in *Stegohornera* this is the case to some extent.[1]

No further particulars on *Stegohornera* were given, and it would be interesting to learn more about the calcification of the gymnocyst in *S.violacea* (SARS) (Fig. 12,*2a-b*) and in what respect it differs from that in the cryptocyst.

BORG (1944, p. 177) described the calcareous layer of the cryptocyst thus: "The ectodermal cells secrete one chitinous stratum after the other; and in these layers calcareous matter, mainly carbonate of lime, is deposited simultaneously. Now as there are living tissues, capable of secreting chalky matter, not only inside the calcareous cryptocyst but outside it as well, a secondary thickening of the zoarial wall can be effected from both sides. . . . A thickening of the inside of the walls of the cystids [sacs] . . . is rather inconsiderable [but] a thickening from the outside . . . in the Pachystega . . . assumes a really enormous thickness. . . . The secondary thickening is a process extremely characteristic of the Pachystega." Another characteristic of the Pachystega is the absence in them of any pseudopores, but there exist only real pores piercing the cryptocyst.

HETEROPORINA

In Heteroporidae "there develops from the proancestrula a small funnel-shaped zoarium attached to the substratum by means of its basal surface. New zoids [zooids] must be assumed as being formed at the edge of the funnel around its entire periphery. As a consequence of this, the funnel widens more and more until the young zoarium has altered its shape from a funnel-like to a wart-like. . . . The budding region proper [a part of the growing zone] encircles the wart-like colony and occupies its peripheral zone; but as a consequence of its mode of formation, the entire zoarium can evidently be considered as a greatly widened and much complicated common bud."

"From this stage onward the development of the zoarium must have continued along diverging
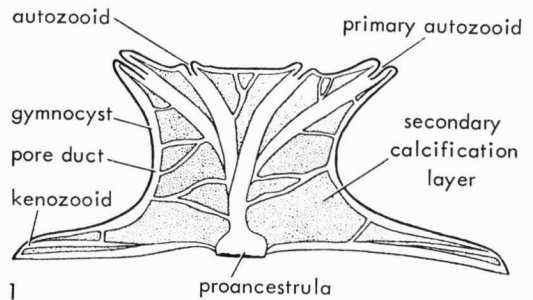
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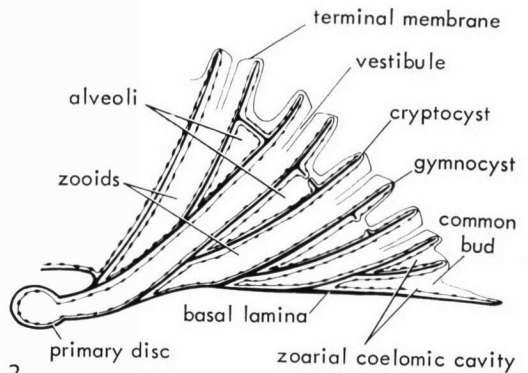
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FIG. 11,*1*. Diagram showing sagittal section through young zoarium of *Hornera, ca.* × 48 (after Borg, 1944, fig. 23).
——11,*2*. Diagram showing longitudinal section through part of zoarium in *Lichenopora, ca.* ×58 (after Borg, 1926a, fig. 55).

[1] "To this genus *Hornera violacea* SARS is referred on account of the structure of its body-wall and the loacation of its gonozoids. The fam. Stegohorneridae is instituted for it."
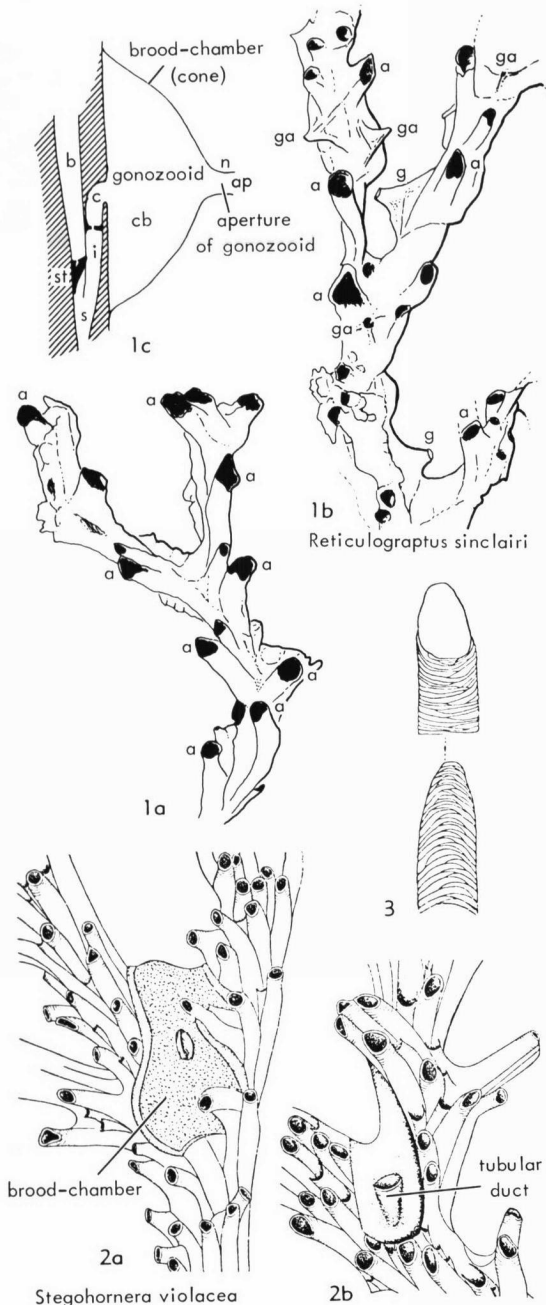
lines for the different species or groups of species" (BORG, 1933, p. 353-354). These species, branching or not branching, are commonly massive and are invested by a cuticle that "covers uniformly the whole surface of the colony. It does not seem to be fastened to the underlying calcareous layer [of the closely packed zooecia], though it often comes here and there, very near to it" (BORG, 1933, p. 355-356). Similarly, "the existence of a gymnocyst and a cryptocyst, and of a hypostegal coelomic cavity separating them can be demonstrated in all species of the Heteroporidae; that is, *the surface of the zoarium exhibits, in the present family* [Heteroporidae, subsequently elevated to the status of division], *the same structure as in the Horneridae and the Lichenoporidae"* (BORG, 1933, p. 357).

BORG (1933, p. 267) noticed on the surface of some species certain elevated spots similar to "the so-called 'monticuli' described in Trepostomata," and he illustrated numerous kinds of microstructure of the calcareous walls not unlike those in Trepostomata, for instance, a kind that has a "distinctly beaded appearance" (BORG, 1933, p. 338-339).

CALYPTROSTEGA (RECTANGULATA WATERS)

BORG stated that for this division he had abundant zoaria at different stages of development in which "the common bud originates from the primary disc in the same way as the Tubuliporidae, thus as a funnel-shaped formation directed to one side. . . . The formation of the zoids [zooids] takes place through the origin of calcareous septa in the common bud, and the division and coalescences of these septa according to the same laws as those valid for the Tubuliporidae and related families, as Smitt (1867) correctly mentions . . . in *Lichenopora* the zoids [zooids] are never sepa-

FIG. 12.——*1. Reticulograptus tuberosus sinclairi* WHITTINGTON & RICKARDS (1968); *1a,b,* front view, interpreted as stenolaemate bryozoan, ×20 [*a,* autozooid; *g,* gonozooid; *ga,* aperture of gonozooid] (after Whittington & Rickards, fig. 2,e,f); *1c,* schematic section of "conothecae" as understood by WHITTINGTON & RICKARDS, interpreted here as brood chamber of stenolaemate bryozoan, *ca.* ×100 (after Whittington & Rickards, fig. 1, no scale indicated).——

2. *Stegohornera violacea* (Sars) BORG (1944), parts of zoaria, seen from frontal side; *2a,* with brood chamber intact; *2b,* with brood chamber removed, so that the tubular duct is seen, ×14 (after Borg, 1926a, fig. 96, 98). [Described by BORG, 1926a, as *Hornera violacea;* generic name changed to *Stegohornera* in BORG, 1944, p. 5, 177.]—— 3. *Tubidendrum bulmani* KOZŁOWSKI, 1948 (1949) (caption of fig. 50, p. 163), terminal part of microtheca, dorsal and ventral views, ×40 (after Kozłowski, 1948). Transverse cross-bedding-like "fusellar" structure, typical for graptolites, not observed in *Reticulograptus sinclairi.*

rated from the common bud, and the reason for this fact is that they are set apart from its wall all round and forced inwards through new zoids [zooids] developing close to this. A result of this is that all round its entire circuit the edge of the common bud remains intact and undivided." In Lichenoporidae "the whole zoarium can be thought of as a greatly widened common bud" (Borg, 1926a, p. 314).

DOES MEMBRANIPORA POSSESS A COMMON BUD?

The species *Membranipora (Flustra) membranacea* (Linné) has played an important role in the development of the concept of common buds. When Smitt introduced the concept he claimed that all bryozoans possessed such buds, and prominently mentioned *Membranipora* among them. In criticizing Smitt, Nitsche (1871) assumed that *Membranipora* was considered by him as a particularly typical case of colonial development by means of common bud. Smitt denied this, however, explaining the particular way in which Nitsche had misunderstood his idea about the common bud (1872). On the other hand, Borg (1926a, p. 254) tacitly accepted the validity of Nitsche's observations, and in his memoirs made abundantly clear that a true common bud, as he understood it, exists only in the Cyclostomata *s. lato* (including Stenolaemata), and not in the Cheilostomata.

Whereas Borg did not directly discuss the colonial development in *Membranipora*, Silén (1944) discriminated differences between colonial development in this genus and the Stenolaemata. After a brief summary of Borg's observations on the common bud, Silén (1944, p. 56-57) called attention to the timing in development of the polypide buds and the septa in Stenolaemata versus that of analogous elements in "Cheilo-Ctenostomata," and *Membranipora membranacea* in particular: ". . . polypid-bud of a new zoid [zooid] is, in the Cyclostomata, always formed before the cystid [sac] (Borg, 1926, ch. V). It is formed as an invagination from the terminal membrane of the common bud. When it has reached a certain stage of development, the corresponding septum originates and finally separates the part containing the polypid-bud from the remaining common bud" (Silén, 1944, p. 57) (Fig. 13).
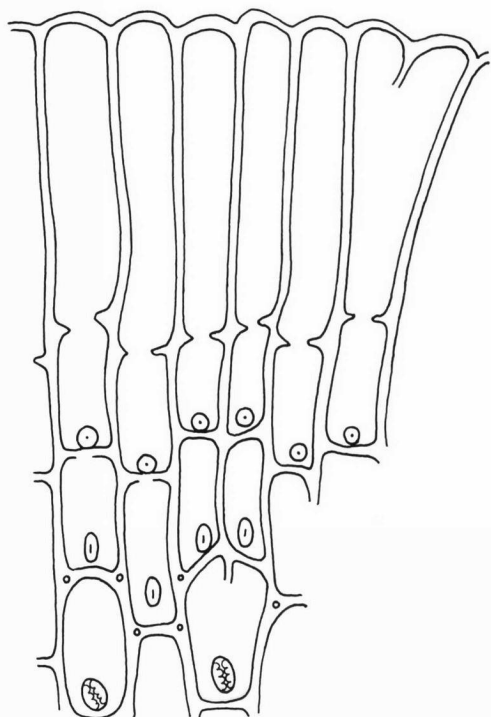

Fig. 13. *Membranipora membranacea*, with linear growing zone along distal edge, *ca.* ×50. Leucocites and line of contact between lateral walls of contiguous zooecial rows omitted (after Lutaud, 1957, fig. 1, p. 149, mod.).

In Stenolaemata, on the other hand, Borg found "that the polypides always take their origin in the growing zone of the common bud and in no other place." Next he mentioned some differences in the precise location of the polypide buds within the growing zone. In some genera they are closer to the terminal membrane, whereas in others they are closer to the wall around the common bud; in some they are "near the median line of the growing zone," and in others they are "all around the entire circuit of the common bud." Then he added that: "Wherever the polypide-buds originate in the growing zone, however, in no case do they keep their original position during the further development, but are gradually displaced in the same [retreating] direction as the distal parts of the developing cystids [sacs] (ch. IV), the two processes keeping pace with each other, as is natural. Of course, it is not a question of an active migration of the rudiments of the polypides and cystids [sacs], but of a displacement owing to the constant activity [the distal growth] of the grow-

ing zone. Thus the young polypides and cystids [sacs] are gradually forced away from the growing zone, while fresh ones are incessantly produced in it. There is yet another fact that should be strongly emphasized: as far as I have found, it seems as if the origin of a polypide-bud in the Cyclostomata gave the signal, as it were, for a fission of a septum in the common bud, by means of which ensue the two septa, intended to enclose the future polypide. In the Cyclostomata one can never speak of a polypide being formed [originated] in a young cystid [sac], . . . Thus, in this respect, the Cyclostomata differ decidedly from the Cheilostomata and the Ctenostomata where, as is well known, the cystid [sac] appears first, the polypide afterwards within this" (Borg, 1926a, p. 323-324).

Silén (1944, p. 58-59; my italics) distinguished in Cheilostomata two types of colonial development: "One type is chiefly represented [by the] encrusting zoaria or erect zoaria with broad and compact branches (text fig. 44 *a-c*)." In an early stage of colonial development "a number of chambers are formed around the ancestrula. Each chamber increases in size . . . . Then its distal end is cut off by a *transverse* wall. The individuality of the zoids [zooids] is evident . . . each zoid [zooid] has its own longitudinal, vertical walls (text-fig. 47). Thus the zoid [zooidal] rows are entirely independent of each other" (combined from the text and expl. to text-fig. 47, p. 59).

In the second type of colonial development, typified by *Membranipora membranacea* (Linné), one "may confuse the concept of the individuality of the zoid [zooid]. In rapidly growing zoaria only the proximal parts of the zoid [zooidal] rows are divided into zoids [zooids] whereas distal parts are undivided (text-fig. 45). The appearance of such zoaria induced Smitt (1865) to assume that also in the Cheilo-Ctenostomata the zoaria were formed by means of a common bud. The simple explanation [is] that owing to the rapid growth of the zoid [zooidal] rows, no *transverse* walls have time to develop [until] . . . the bud has [attained length] up to several times the zoid [zooidal] length" (Silén, 1944, p. 59; my italics). By the expression "the bud," Silén obviously meant the distal part of each single row of zooids, whereas Smitt apparently considered the combination of the distal parts of the adjacent rows; these rows are, however, independent from each other (Fig. 13).

An interesting revival of Smitt's understanding of the common bud has been advanced by Brien (1960), who described its activities thus: "A new polypide zooecium individualizes itself by partitioning of an initial ecto-mesodermic cystid [sac] cavity, the *common bud*. It represents the growing zone in all Bryozoa, the level at which new polypide cystids [sacs] are isolated. This growing zone belongs in the frontal edge of Phylactolaemata, in the anterior of the basal wall in Eurystomata (of Marcus, equals Cheilo-Ctenostomata of Silén). The common bud of the Cyclostomata is also located at the base of the anterior edge, as in Phylactolaemata, where the origin of septal partitions, which isolate new cystids [sacs], appears to be induced by the origin of the rudiments of a polypide. It does not precede it as in Eurystomata, but occurs in the same consecutive order as in Phylactolaemata" (Brien, 1960, p. 1305, Brien's italics, my translation).

Contrary to the similar decision to equalize the meaning of the common bud and the growing zone by Hyman (as quoted above), Brien preferred the term common bud, which of course has an obvious historical priority over the term growing zone, as applied to bryozoans by Borg.

The biological advantage of applying the two terms to two different concepts, as originally suggested by Borg, has already been emphasized by indicating their analogy to well-known botanical concepts. This analogy can be extended easily to elements in the development of *Membranipora,* which was described in detail by Lutaud (1957). Here a small terminal area occurs in each zooidal row where, according to Lutaud, new cells originate, just as in the growing zone of Stenolaemata and meristems of plants. This area is stippled in Lutaud's (Fig. 13) drawing (reproduced by Brien, 1960, fig. on page 1247) (Fig. 13), and the termini of each zooidal row, so indicated, are shown unequally advanced distally, which precludes their consideration as parts of a single colonial growing zone. Behind each terminal growing area transverse partitions are shown, each starting its development as a pair of prongs which grow toward each other from opposite sides of the zooidal row. The polypide buds originate next, always singly, in the middle of the distal side of each transverse partition, either after its

prongs have met each other or, less commonly, before they meet.

Both position and timing in appearance of the elements in this development are quite different from those in the common bud of Stenolaemata. The partitions (septa) are transverse, instead of oblique and each is made by the meeting in the middle of two originally independent prongs, instead of oblique septa rising as units and multiplying by fission. The polypide buds appear next in the growing area, but far behind its terminus, and singly rather than in groups. They develop not before but after initiation of the corresponding septa. Besides, as already mentioned, the longitudinal walls separating the contiguous rows of zooids in *Membranipora* are double, each consisting of two parallel, independently originating lateral walls of the longitudinal rows.

Finally, whereas multiplication of zooidal rows in *Membranipora* is accomplished by intercalation of a new double wall, in Stenolaemata it is accomplished by bifurcation (=dichotomy) of the equivalents of the zooidal rows, the branches. A typical process of bifurcation has been described and illustrated by Borg in *Stomatopora granulata,* the slender branches of which are very similar to the zooidal rows of *Membranipora:* "When a branching is to occur—in such a case the stem as a rule holds only one zoid [zooid]—the vertical septum in the [common] bud increases in length, so that it reaches the terminal membrane and coalesces with it. Thus the bud is divided into two halves which are situated alongside each other. These grow further, each in its own direction, diverging more or less from each other (text-fig. 31). Two septa are as a rule soon formed in each of these buds, one from each side (text-fig. 31, right bud, *s*). The two septa gradually meet in the median line of each bud, just as was the case in the first [initial] common bud" (Borg, 1926a, p. 274).

It may be noted also that the transverse septa in the alveoli of *Lichenopora* (Fig. 11,*2*), grow from their walls in the same perpendicular orientation as the transverse walls of *Membranipora*.

In view of some resemblance of zoarial growth in *Membranipora* to that by means of the common bud in Stenolaemata, it seems desirable to indicate that in the former the growth is by the means of linear buds—a new term.

RETICULOGRAPTUS SINCLAIRI NOT A GRAPTOLITE

The excellent illustrations of *Reticulograptus tuberosus sinclairi* (Fig. 12,*1a-c*), a description of which has been published recently by Whittington & Rickards (1968), provide sufficient information on this exceedingly well-preserved, delicate fossil to classify it outside of graptolites. Against the latter classification is the absence of any trace of transverse, "fusellar" (Fig. 12,*3*) structures, the presence of which in the graptolites was considered by Kozłowski "such as to exclude the graptolites from either the Coelenterata or the Bryozoa but to relate them to the Pterobranchia of the hemichordates" (Shrock & Twenhofel, 1953, p. 745). Coupled with this negative evidence (against classification with graptolites) is the presence in *Reticulograptus* of so-called conothecae (Fig. 12,*1c*), which never have been observed in any graptolites. On the other hand, the conothecae are in all respects similar to the brood-chambers in extant cyclostomes, and their shape and disposition, presence of an apical aperture, and combination with two kinds of bunched tubes (autothecae and bithecae), simulate point by point, including scale, the fertile zoaria of *Stegohornera violacea* (Sars), as illustrated by Borg (Fig. 12,*2a-b*). This remarkable resemblance does not mean biological or taxonomic identity but indicates the similar character of colonial development, which in *Stegohornera* is due to the presence of the common bud.

Because it is no longer possible to classify *Reticulograptus sinclairi,* and possibly *R. tuberosus* (Wilman) as well, as graptolites, it is logical to consider them as representatives of a bryozoan family nearest to the family Stegohorneridae Borg (1944), both belonging to the division Pachystega of the order Stenolaemata Borg (1926).

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