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LETTER

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Giovanna Zaniolo: An inspiring scientist, teacher, mentor, and colleague. Active: 1967–2012

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Giovanna Zaniolo (Figure 1a,b) is a researcher who has made significant contributions to the study of the tunicate *Botryllus schlosseri* in Italy, as part of a flourishing national community with a rich history dating back to the eighteenth century (Manni et al., 2019). Born in 1942 in Vicenza (Italy), Zaniolo enrolled in Biological Science at the University of Padova (Italy) in the early 1960s. She graduated in 1967 with a thesis titled "Observations on the maturation, fertilization and first developmental stages of the *Botryllus* egg (Ascidiacea)" (Zaniolo, 1967; Figure 1c–e; Figure 2a–e). Her mentor during this period was Armando Sabbadin, professor emeritus of the University of Padova (Figure 1b). Shortly after completing her degree, Zaniolo joined the Comparative Anatomy Laboratory at the University of Padova, as a lab assistant. Within 2 years she advanced to the position of lab technician and in 1974 she became an assistant professor of Comparative Anatomy of Vertebrates. In 2002 she achieved the rank of full professor. Zaniolo primarily taught Comparative Anatomy of Vertebrates where she demonstrated her passion for the subject. She was a dedicated teacher, devoted and rigorous evolutionary biologist, and from the early days of her academic career she enthusiastically joined the budding field of Evolutionary and Developmental Biology (Evo-Devo).

During her scientific career, Giovanna Zaniolo has produced an impressive publication record covering 50 years of research activity with 55 publications (Table 1; Table S1). Her first publication, a short note written in Italian in 1971, examined the development of budlets of *Botryllus schlosseri* isolated or transplanted in the colonial matrix (Sabbadin et al., 1971). Her most recent publication, published in 2021, focused on the comparative transcriptomic and morphological analyses of sexual and asexual development of *B. schlosseri* (Kowarsky et al., 2021). Zaniolo's publications are predominantly centered on *B. schlosseri*, her favorite tunicate model. However, she has also made some sporadic digressions into other colonial ascidians.

B. schlosseri is a colonial tunicate characterized by small zooids grouped in star-shaped systems embedded in a common transparent tunic (Manni et al., 2007; Figure 1c–e). In this species, fertilization and embryonic development occur within the parental zooids (Kowarsky et al., 2021). Upon hatching, the mature larva selects a suitable substrate and metamorphoses in a sessile oozooid, which becomes the founder of a new colony. The larva possesses a small bud, representing the first asexual generation of the colony. Colonies display three generations of zooids developing synchronously, as buds (primary buds) give rise to an additional generation of small buds (secondary buds). During the phase called "takeover," colonies undergo the cyclical resorption of all adult individuals, which are then replaced in the filtering activity by their primary buds, thus becoming the new adult generation. Simultaneously, the secondary buds become primary buds and produce a new generation of secondary buds. Since a zooid usually produces more than a bud, this cyclical change of generations ensures the colony growth. Colonies can fuse together and form a larger chimeric colony if they share an allele in the histocompatibility locus (Voskoboynik et al., 2013). When fused, they can share, through the circulatory system, their hemocytes, as well as the somatic and germ stem cells that might invade the tissues of the partner colony, thereby parasitizing it (Stoner & Weissman, 1996). The coexistence of

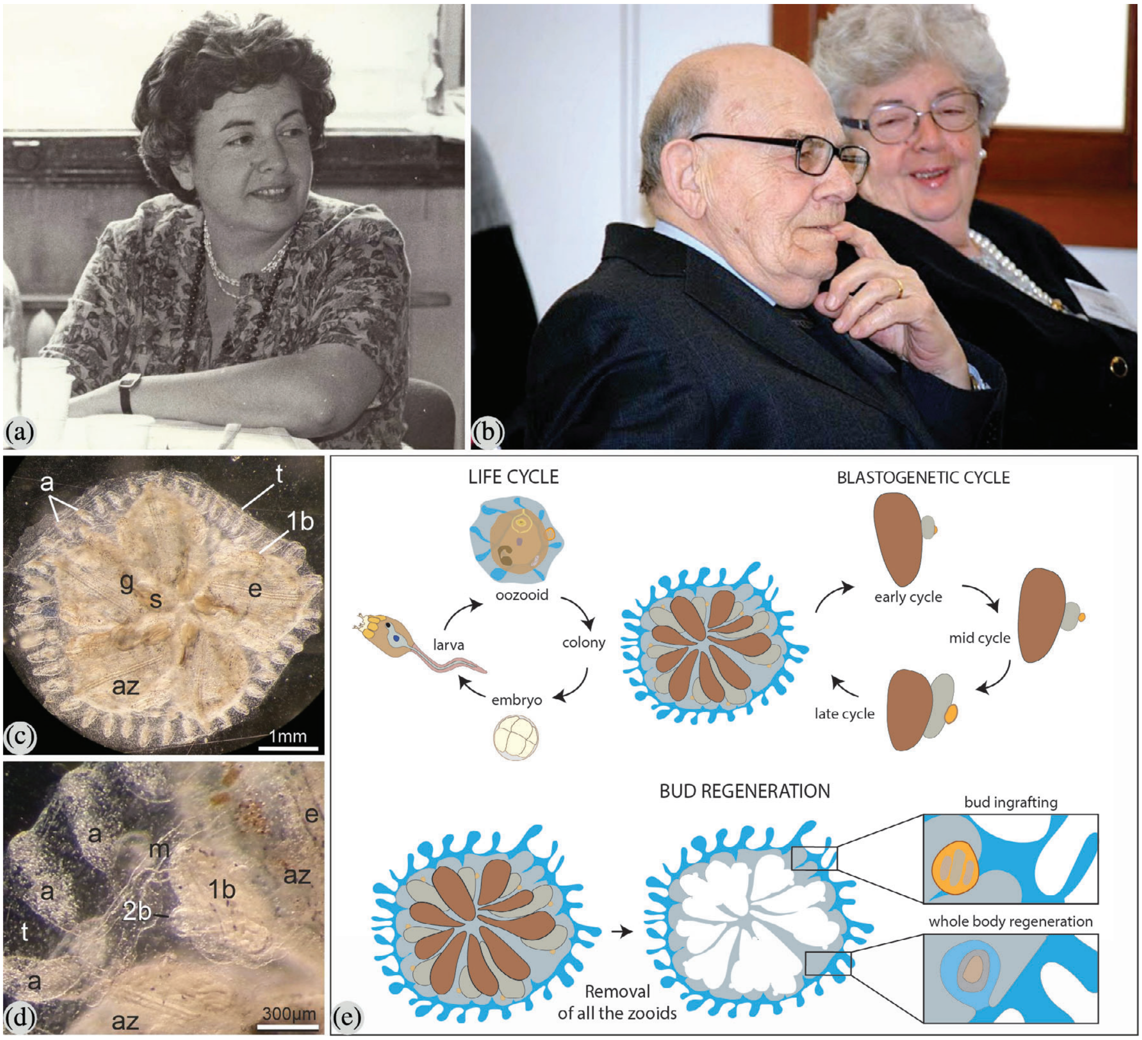

FIGURE 1 (a) Giovanna Zaniolo, photographed in 1984. (b) Giovanna Zaniolo and her mentor, Prof. Armando Sabbadin. Meeting of the Italian Association of Developmental and Comparative Immunobiology, held on February 18, 2011, Monteortone (Italy). (c, d) Ventral view of a colony of *Botrylloides schlosseri* (c) and detail (d) of a primary bud with a secondary bud. 1b: primary bud; 2b: secondary bud; a: ampulla; az: adult zooid; e: endostyle; m: marginal vessel; t: tunic. (e) At the top is an illustration depicting the life cycle of *B. schlosseri*. At the bottom, the illustration shows the remarkable regenerative ability of *B. schlosseri* following surgical removal of zooids. The two techniques used to induced regeneration from the colonial matrix and vasculature are ingrafting of palleal buds (buds generated through typical asexual reproduction from the primary bud lateral body wall, known as the pallium) and inducing whole body regeneration by stimulating budding within the colonial vasculature.

different stem cell-mediated phenomena (sexual and asexual reproduction) along with the extraordinary regenerative ability, make this organism a model for evo-devo studies in several research fields.

In *B. schlosseri*, Giovanna Zaniolo primarily studied sexual reproduction, asexual reproduction, regeneration, self- and nonself-recognition, and nervous system development (Table 1). These research topics remain relevant today, as evidenced by the ongoing work within the *Botryllus* community, which continues to explore these areas using innovative methodologies. Indeed, these themes are now expanding into the realms of stem cell biology, regenerative medicine, aging, and allorecognition.

Giovanna Zaniolo's expertise focused on in vivo manipulation of *Botryllus* colonies, as reviewed in Manni et al. (2019) (Figure 2). She dedicated considerable efforts and time to rearing colonies and conducting experiments involving colony transplantation. She created chimeric colonies that allowed her to study germ cell transfer between compatible colonies and to study histocompatibility (Sabbadin & Zaniolo, 1979). In her laboratory, she maintained pure genetic lines of *B. schlosseri* that could be distinguished for their pigmentation, enabling controlled crosses. This involved collecting the newly developing larvae directly from the parental colonies and attaching them to glass slides to observe the outcomes of her crosses. During that period, molecular genetics had not yet been applied to ascidians, therefore classic genetics experiments were the only available tool for assessing the transmissibility of traits and cells. Furthermore, she conducted various experiments of bud extirpation and isolation to investigate colony homeostasis, regeneration, and the crosstalk between generations (Gasparini et al., 2014; Sabbadin et al., 1975). To do that,

TABLE 1 Research fields covered by Giovanna Zaniolo's main publications. See supplementary S1 for more references.

Publication	Species	Research field: Sexual reproduction	Asexual reproduction	Allorecognition	Regeneration	Nervous system & sensory organs
Sabbadin et al. (1971)	*Botrylloides schlosseri*		x		x	
Sabbadin et al. (1975)	*B. schlosseri*		x		x	
Zaniolo et al. (1976)	*B. schlosseri*		x		x	
Sabbadin and Zaniolo (1979)	*B. schlosseri*	x	x	x		
Zaniolo (1981)	*B. schlosseri*			x		
Zaniolo et al. (1987)	*B. schlosseri*	x				
Sabbadin et al. (1991)	*B. schlosseri*	x	x	x	x	
Sabbadin et al. (1992)	*B. schlosseri*			x		
Zaniolo, Manni, & Burighel (1994a)	*Botrylloides leachi*	x				
Zaniolo et al. (1998)	*Botrylloides violaceus*	x				
Manni et al. (1999)	*B. schlosseri*					x
Manni et al. (2001)	*B. schlosseri*					x
Zaniolo et al. (2002)	*B. schlosseri*					x
Burighel et al. (2003)	*B. schlosseri*					x
Manni et al. (2004)	*B. schlosseri*					x
Manni et al. (2007)	*B. schlosseri*	x	x	x	x	
Caicci et al. (2010)	*B. schlosseri*					x
Gasparini et al. (2014)	*B. schlosseri*				x	
Manni et al. (2019)	*B. schlosseri*		x	x	x	
Kowarsky et al. (2021)	*B. schlosseri*	x	x			x

she worked with meticulous precision at the stereomicroscope using handmade tungsten needles. Even today, these experiments continue to inspire research on the effect of cell transplantation and stemness in normal and regenerating colonies (Vanni et al., 2023).

In 1979, Giovanna Zaniolo published a very impactful paper titled "Sexual differentiation and germ cell transfer in the colonial ascidian *Botryllus schlosseri*" (Sabbadin & Zaniolo, 1979) focused on sexual reproduction. In this study, she used genetically pure (e.g., colonies with opposite genotypes AAbb and aaBB to the two Mendelian pigmentation genes) compatible colonies that fused together to create chimeric colonies. After a while, the two original colonies were separated and the resulting offspring was examined on the basis of their pigmentation. The authors demonstrated that the fused colonies were capable of exchanging germ cells, as the offspring from a colony could exhibit the pigmentation of the partner colony for many following generations. These experiments revealed, for the first time, that colonies undergo sexualization and achieve maturity after a number of asexual generations. Additionally, the authors discovered the asymmetry of gonad development in zooids. The gonads were found to be more developed on the left side of the zooids compared to the right side; vice versa, the budding ability was greater on the right side than on the left one. Importantly, they proved the longevity of the germ cell: germ cells can leave the bud gonad rudiment and circulate in the hemolymph for several generations before homing and differentiating into the gonad rudiment of a newly formed bud. These findings were later confirmed and further investigated using techniques such as cell transplantation, live imaging, and genetic assays (Laird et al., 2005; Rinkevich et al., 2013; Voskoboynik et al., 2008).

In the 1980s and 1990s, Giovanna Zaniolo focused on studying other aspects of sexual reproduction in ascidians. She described the ovulation strategy and the relationship between embryo and parent in colonial ascidians that exhibit different degrees of ovoviviparity, including *B. schlosseri* (Figure 2f,g), *Botrylloides leachii*, and the viviparous *Botrylloides violaceus* (Zaniolo et al., 1987; Zaniolo et al., 1998; Zaniolo, Manni, & Burighel, 1994a; Zaniolo, Manni, Martinucci, & Burighel, 1994b). Her research included comparative analysis of placentation modalities, revealing that ovoviviparity occurs in different ways and involves different degrees of integration between maternal and embryonic tissues. During those years, she became an expert in electron microscopy. Her laboratory possessed a Hitachi H-600 electron microscope that she used for her observations. This imaging technique allowed her to delve into detailed structural investigations of the organisms that were being studied.

Giovanna Zaniolo's ability to produce genetically pure lines of *B. schlosseri* and create chimeras enabled her to extend her studies to self- and nonself-recognition. She made pioneering contributions to the field by conducting research on the role of the tunic in fusion and non-fusion reactions, as well as exploring cytological and genetic bases of histocompatibility (Sabbadin et al., 1991; Sabbadin et al., 1992; Sabbadin & Zaniolo, 1979; Zaniolo, 1981); see for review: (Manni et al., 2007; Manni et al., 2019).

One of her notable publications focused on asexual reproduction is titled "Determination of polarity and bilateral asymmetry in palleal and vascular buds of the ascidian *Botryllus schlosseri*" (Figure 2h,i; Sabbadin et al., 1975). In this study, after removing all zooids from a colony, the tunic matrix was used to induce whole-body regeneration through circulating stem cells (vascular budding) or by engrafting isolated buds. In both extreme conditions, the regenerating buds were capable of reconstituting a new normal colony, complete with germ

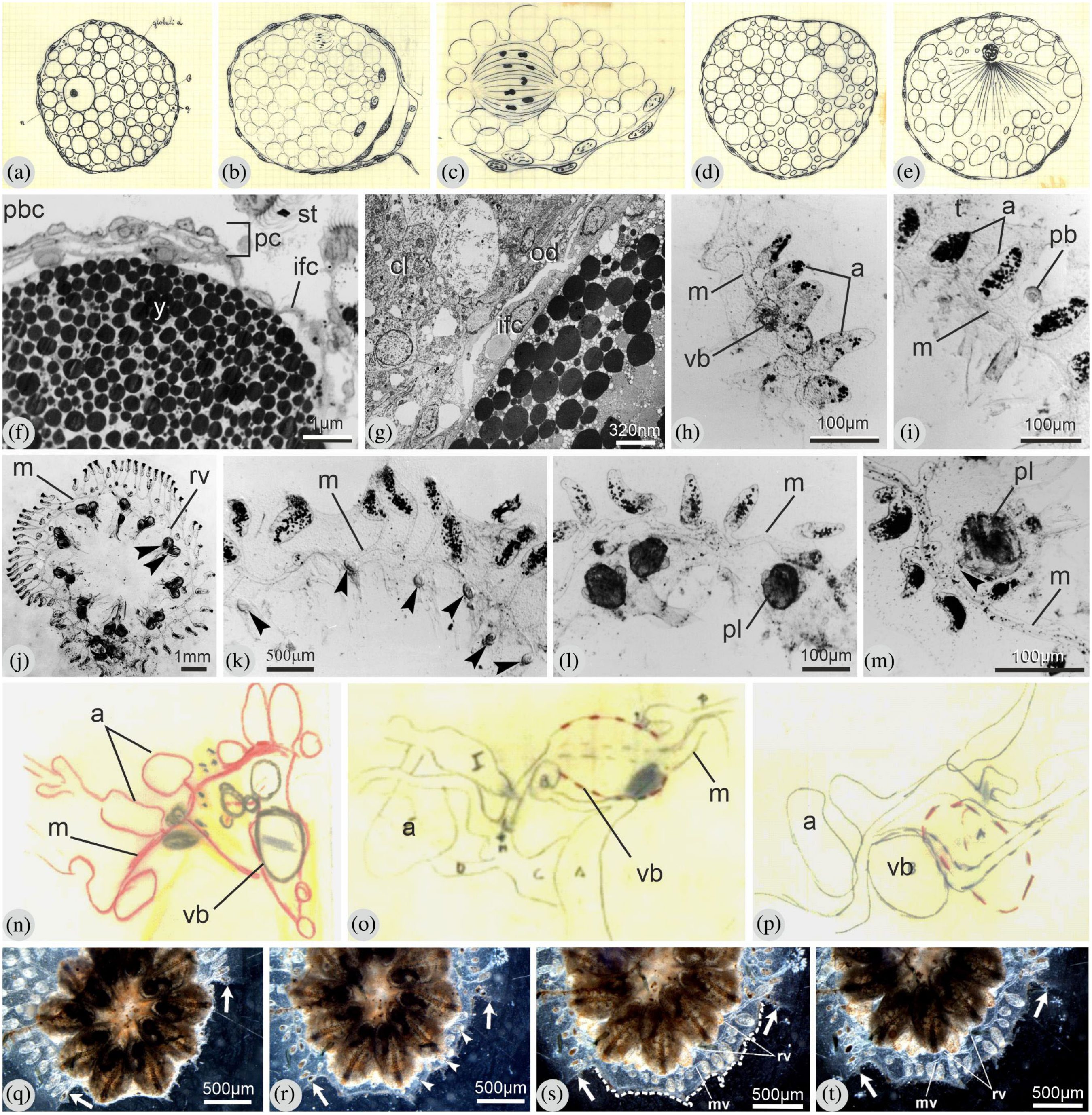

FIGURE 2 Legend on next page.

cells. The regenerated vascular buds developed within the vasculature from the aggregation of hemoblasts, also known as lymphocyte-like cells at the time, which are now considered stem cells (Manni et al., 2019). Giovanna Zaniolo and collaborators also observed that, in some cases, the regenerating buds exhibited an unusual configuration, likely due to the dramatic surgical manipulation that impaired the normal development. This phenomenon was referred to as "*situs inversus viscerum et cordis*" (Latin for "reversed location of viscera and heart"), where buds exhibited a reversed type of bilateral asymmetry. The abnormal buds had their gut located on the right side and the heart on the left side, representing a reversed position compared to normal buds. These and other papers illustrate Giovanna Zaniolo's manual abilities in surgical dissection of colonies (Figure 2j–m). Her laboratory notebooks attest to her way of following the dissected colonies under the microscope, taking note daily of the position of the colonial elements relevant for her experiments (such as the position of ampullae, marginal vessel, and regenerating buds; as well as the dynamics of hemolymph circulation within these elements; Figure 2n–p). Zaniolo's experiments had a breakthrough value and continue to be used by laboratories worldwide to obtain mechanistic insights into stemness and the interplay between generations of zooid (reviewed in Manni et al., 2019).

In addition to these studies on whole-body regeneration, Zaniolo published papers focused on the regeneration of the tunic and circulatory system of the colony (Figure 2q–t; Gasparini et al., 2014). In these investigations, she induced tunic and vessel regeneration by removing them around a few zooids of the colony. She then described the regeneration process, which involves the sprouting of new vessels from preexisting ones.

Toward the end of her career, Giovanna Zaniolo delved into the study of the nervous system, which became a research focus at the Padova *Botryllus* laboratory in the late 1990s. The lab made significant contributions to understanding the development of the nervous system in both embryo (Caicci et al., 2010; Manni et al., 1999) and in bud (Manni et al., 2001; Zaniolo et al., 2002). In 2003, this research group described a previously unknown sensory organ in *B. schlosseri*, called the coronal organ, whose cells are homologous to the hair cells of the mammalian ear (Burighel et al., 2003). This discovery opened up new frontiers in the study of the evolution of mechanoreception, leading to a reevaluation of certain embryonic territories, now recognized as neurogenic placodes. This contributed to a revision of the vertebrate evolutionary theory that considered the neural crests and the neural placodes vertebrate innovations (Manni et al., 2004). This field of research continues to flourish in the Padova *Botryllus* laboratory. More recent studies have expanded on the aspects related to neurodegeneration and evolution of human neurodegenerative diseases (Anselmi et al., 2022; Anselmi et al., 2023).

Throughout her career Giovanna Zaniolo collaborated with colleagues who made significant contributions to the tunicate community research: in addition to her mentor, Armando Sabbadin (founder of the tunicate laboratory in Padova), she shared the daily laboratory life with Paolo Burighel, Giambruno Martinucci, and Riccardo Brunetti. Among her younger close collaborators were Loriano Ballarin, Francesca Cima, and Lucia Manni (the latter mentored by Giovanna Zaniolo, together with P. Burighel). Alumnae following in Giovanna Zaniolo's footsteps are Dr. Chiara Anselmi (Stanford University, USA) and Dr. Virginia Vanni (Oxford Brookes University, UK).

At the national level, Giovanna Zaniolo was very active in professional organizations such as the Italian Embryology Group (now GEI-SIBSC, Italian Embryology Group—Italian Society of Development and Cell) and in the Italian Zoology Union. She regularly participated in their annual meetings, serving as an elected member of coordination committees and even organizing some of the meetings in Padova.

FIGURE 2 (a–e) Giovanna Zaniolo's original illustrations from her master thesis (Zaniolo, 1967). (a) Oocyte section at the level of the germinal vesicle; G and g: two different types of yolk granules; *globuli d*: yolk granule; *n*: nucleolus in the germinal vesicle. (b, c) Oocyte (b) with mitotic spindle tetrads (enlarged in c), equatorial view. (d) egg modifications at fertilization. (e) Male pronucleus aster and female pronucleus chromatin ball in a just fertilized egg. © G. (Zaniolo, 1967), published under a CC BY SA License. (f, g) Placentation in *Botrylloides schlosseri*. Histological section (f) showing the edge of the placental cup (pc) and part of the developing embryo, rich in yolk (y). ifc: inner follicle cells (derived from the egg envelope); pbc: peribranchial chamber; st: stigma. Toluidine blue. (g) Image at transmission electron microscopy by Giovanna Zaniolo showing the oviduct epithelium (od) and the inner follicle cells (ifc). These cells sustain the embryo development in the peribranchial chamber. The corpus luteum (cl) is derived from the outer follicle cells discharged in the mantle at ovulation. (h–m) Experiments of zooid ablation/transplantation performed by Giovanna Zaniolo. (h) Vascular bud (vb) developed in the marginal vessel (m) after the removal of all zooids (adults, primary buds, and secondary buds) from a colony leaving intact the marginal vessel and ampullae (a). (i) Palleal bud (pb) grafted into a hole made in the tunic (t) peripheral to the marginal vessel (m), to study bud polarity after connection to the vasculature. (j) Colony used to study the fate of isolated buds in the tunic. Right and left primary buds (arrowheads) were left in place in the colonial tunic after the ablation of the parental zooids. Buds are connected to the marginal vessel (m) by means of their radial vessels (rv). (k, l) Secondary (arrowheads in K) and primary (pl in l) palleal buds isolated from both the parent and the marginal vessel (m), which was left intact. (m) Vascularization of an isolated palleal bud (pb), reached by a collateral vessel (arrowhead) of the marginal (m) one. (n–p) Original illustrations from Giovanna Zaniolo's notebooks on experiments of vascular budding. Regenerating vascular buds (vb) are close to the colonial circulatory system (red line in n). a: ampulla; m: marginal vessel. © G. Zaniolo 1974, published under a CC BY SA License. (q–t) Images from Gasparini et al., 2014, published under CC BY. (q) shows part of a colony (in vivo, ventral view) in which the tunic and circulatory system facing four zooids were ablated by Giovanna Zaniolo to study its regeneration. Photo taken 2 h after the ablation; arrows: lateral cut edges. (r) The same colony of (q), injected with Phosphate Buffered Saline (PBS), one day after ablation. Small ampullae (arrowheads) are in the newly formed tunic. (s, t) The same colony showed in (q), two and three days after ablation. The dotted line highlights the regenerated tunic in which the marginal vessel (mv) and the crown of ampullae appears almost fully regenerated. rv: radial vessel.

Despite her retirement in 2012, her passion for *B. schlosseri* and her deep connection to the laboratory remain vibrant. She continues to actively engage in social and cultural activities as a member of Soroptimist International, an association of women dedicated to educating and empowering other women to improve their lives. Additionally, she holds the distinguished position of the first woman president of the Accademia Galileiana (the Galilean Academy), a prestigious academy of sciences, letters and arts located in Padova, further highlighting her influential role in academia.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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