the
WINNOWER

BIOLOGICAL SCIENCES

Spiral cleavage, an oblique matter

BRUNO COSSERMELLI VELLUTINI

READ REVIEWS

WRITE A REVIEW

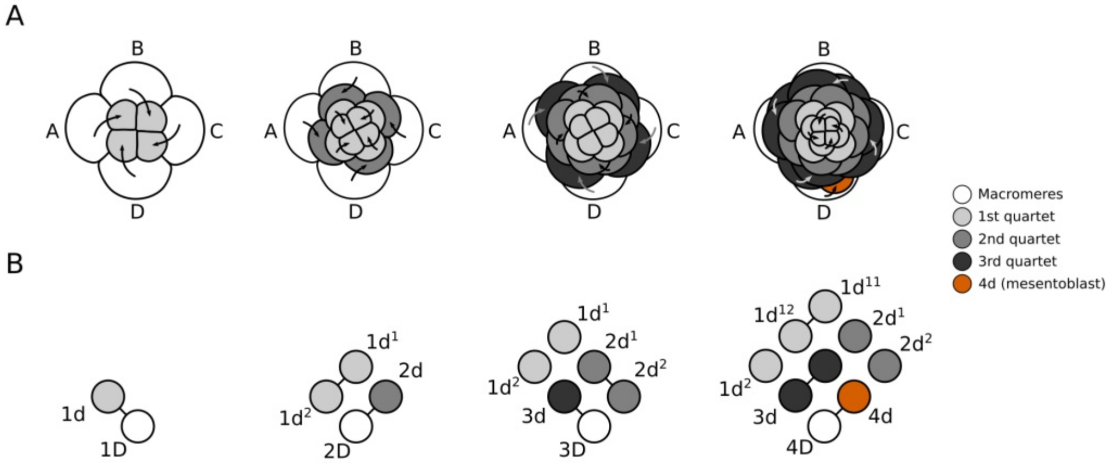
CORRESPONDENCE:
organelas@gmail.com

DATE RECEIVED:
April 17, 2016

,

By the end of the 19th century, a series of biologists had dedicated themselves to following and discovering the fate of individual cells of an embryo during ontogeny. These works, known as cell lineage studies[1], were critical to disambiguate the relationship between ontogeny and phylogeny, directly challenging the idea of recapitulation (Guralnick, 2002; Maienschein, 1978).

The detailed work of the cell lineage biologists Edmund B. Wilson, Edwin G. Conklin, Frank R. Lillie and others, revealed something remarkable. After carefully tracing the embryonic cells of different organisms, they discovered that animals such as molluscs, annelids, nemerteans and polyclad flatworms, whose adult stages are so different, actually share a similar embryogenesis[2] (Child, 1900; Conklin, 1897; Heath, 1899; Lillie, 1895; Mead, 1897; Wilson, 1892). Their embryos show the same cleavage pattern, in which cell divisions occur with the mitotic spindles oblique to the animal/vegetal axis, switching direction (clockwise and counterclockwise) at each division cycle (Costello and Henley, 1976; Hejnol, 2010; Henry and Martindale, 1999; Lambert, 2010). A quartet of vegetal macromeres sequentially gives rise to animal micromeres, and the resulting symmetry of these cleaving blastomeres, when viewed from the animal pole, was described as spiral. This developmental pattern thus became known as *spiral cleavage* (Wilson, 1892).



THE SPIRAL CLEAVAGE PATTERN. (A) ANIMAL POLE VIEW OF A GENERALIZED SPIRAL-CLEAVING EMBRYO. ARROWS INDICATE THE DIRECTION OF CELL DIVISIONS. DEVELOPMENTAL SEQUENCE BASED ON (CONKLIN, 1897). (B) SCHEMATIC DIAGRAM OF CELL DIVISIONS IN THE D QUADRANT IN A LATERAL VIEW (TOP: ANIMAL POLE, BOTTOM: VEGETAL POLE). CELLS ARE NAMED WITH THE STANDARD SPIRAL CLEAVAGE NOTATION(CHILD, 1900; CONKLIN, 1897; WILSON, 1892). REPRESENTATION BASED ON LAMBERT (2010).

Because the cell divisions are stereotypic, individual blastomeres can be followed and compared between spiral-cleaving taxa in a fairly consistent manner. The ability to compare blastomere fates at this unprecedented cellular-resolution uncovered a surprising similarity in the fate maps of spiral-cleaving embryos (=annelids, molluscs, nemerteans and polyclad flatworms). The iconic example being the 4d mesentoblast, a well-conserved mesoderm precursor (Lambert, 2008). Overall, despite having the oblique cell divisions as an idiosyncrasy, spiral cleavage is understood today as a complex of developmental characters (Costello and Henley, 1976; Hejnol, 2010; Henry and Martindale, 1999; Lambert, 2010).

The empirical findings of cell lineage studies raised several important evolutionary questions regarding the evolution of development and the establishment of homologies (Guralnick, 2002). What are the underlying causes behind embryonic cleavage patterns—mechanical forces acting on the embryo or inherited historical factors? Are the events of early development necessary to build the adult characters? Is there an embryological criterion for homology? The ideas progressively moved towards a more evolutionary view of development, where ontogeny is not “a brief and rapid recapitulation of phylogeny” but an inherited product of evolution and subject to modification (Guralnick, 2002).

Even though most cell lineage biologists initially denied the systematic value of embryonic cleavage patterns, mainly in opposition to recapitulation (Guralnick, 2002), it was difficult to argue against the striking similarity between spiral-cleaving embryos, and dismiss their potential kinship[3]. Schleip (1929) was the first to propose a group to contain the animals displaying spiral cleavage—the Spiralia.

Recent metazoan-wide phylogenetic analyses corroborate the kinship between spiral-cleaving taxa, in a major protostome clade that is sister to the Ecdysozoa (e.g., insects) (Dunn et al., 2014). The latest works in protostome phylogenomics (Laumer et al., 2015; Struck et al., 2014) suggest that Spiralia (=Lophotrochozoa in some cases, see Hejnol (2010)) contains not only the typical spiral-cleaving groups, but several other taxa. Some spiralians (=animals that belong to the clade Spiralia) do not show any clear trace of spiral cleavage, such as bryozoans, brachiopods, gastrotrichs and rotifers, while others do exhibit spiral-like characters, such as gnathostomulids (Riedl, 1969), phoronids (Pennerstorfer and Scholtz, 2012) and entoprocts (Marcus, 1939; Merkel et al., 2012). What can we say about the evolution of these disparate cleavage patterns?

The spiral arrangement of embryonic blastomeres is present in the three main clades of Spiralia (Gnathifera, Lophotrochozoa and Rouphozoa), suggesting that this character is ancestral at least to the Lophotrochozoa-Rouphozoa clade. This implies the spiral cleavage pattern was lost during the evolution of gastrotrichs, brachiopods, bryozoans and maybe rotifers. How did these groups lose spiral cleavage? Which aspects of a typical spiral-cleaving embryo did they lose, in addition to the spiral arrangement of the blastomeres? Are there any remnants of spiral cleavage?

The comparison between clades that have lost spiral symmetry, like bryozoans and brachiopods, and typical spiral-cleaving clades such as annelids and molluscs, can identify the traits that were lost, or are still shared, among these groups. This comparative approach can reveal novel insights about the evolution of spiral cleavage itself, and give rise to a broader perspective of the evolutionary mechanisms underlying spiralian development.

[This text is a section of my PhD thesis]

REFERENCES

Bonner, J.T. & Bell, W.J., Jr., 1984. “What Is Money for?”: An Interview with Edwin Grant Conklin, 1952. *Proceedings of the American Philosophical Society*, 128(1), pp.79–84. Available at: http://www.jstor.org/stable/986495.

Child, C.M., 1900. The early development of *Arenicola* and *Sternaspis*. *Wilhelm Roux’ Archiv fur Entwicklungsmechanik der Organismen*, 9(4), pp.587–723. Available at: http://dx.doi.org/10.1007/BF02156195.

Conklin, E.G., 1897. The embryology of *Crepidula*, A contribution to the cell lineage and early development of some marine gasteropods. *Journal of morphology*, 13(1), pp.1–226. Available at: http://dx.doi.org/10.1002/jmor.1050130102.

Costello, D.P. & Henley, C., 1976. Spiralian Development: A Perspective. *American zoologist*, 16(3), pp.277–291. Available at: http://dx.doi.org/10.1093/icb/16.3.277.

Dunn, C.W. et al., 2014. Animal Phylogeny and Its Evolutionary Implications. *Annual review of ecology, evolution, and systematics*, 45(1), pp.371–395. Available at: http://dx.doi.org/10.1146/annurev-ecolsys-120213-091627.

Guralnick, R., 2002. A Recapitulation of the Rise and Fall of the Cell Lineage Research Program: The Evolutionary-Developmental Relationship of Cleavage to Homology, Body Plans and Life History. *Journal of the history of biology*, 35(3), pp.537–567. Available at: http://link.springer.com/article/10.1023/A%3A1021119112943.

Heath, H., 1899. The development of *Ischnochiton*. *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere Abteilung für Anatomie und Ontogenie der Tiere.*, 12, pp.567–656. Available at: http://biodiversitylibrary.org/page/11552455.

Hejnol, A., 2010. A twist in time—the evolution of spiral cleavage in the light of animal phylogeny. *Integrative and comparative biology*, 50(5), pp.695–706. Available at: http://dx.doi.org/10.1093/icb/icq103.

Henry, J. & Martindale, M.Q., 1999. Conservation and innovation in spiralian development. *Hydrobiologia*, pp.255–265. Available at: http://www.springerlink.com/index/T2607273211U1557.pdf.

Lambert, J.D., 2008. Mesoderm in spiralians: the organizer and the 4d cell. *Journal of experimental zoology. Part B, Molecular and developmental evolution*, 310(1), pp.15–23. Available at: http://dx.doi.org/10.1002/jez.b.21176.

Lambert, J.D., 2010. Developmental patterns in spiralian embryos. *Current biology: CB*, 20(2), pp.R72–7. Available at: http://dx.doi.org/10.1016/j.cub.2009.11.041.

Laumer, C.E. et al., 2015. Spiralian phylogeny informs the evolution of microscopic lineages. *Current biology: CB*, 25(15), pp.2000–2006. Available at: http://dx.doi.org/10.1016/j.cub.2015.06.068.

Lillie, F.R., 1895. The embryology of the Unionidae. A study in cell-lineage. *Journal of morphology*, 10(1), pp.1–100. Available at: http://dx.doi.org/10.1002/jmor.1050100102.

Maienschein, J., 1978. Cell lineage, ancestral reminiscence, and the biogenetic law. *Journal of the history of biology*, 11(1), pp.129–158. Available at: http://link.springer.com/article/10.1007/BF00127773.

Marcus, E., 1939. Bryozoarios Marinhos Brasileiros III. *Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo, Zoologia*, 3, pp.113–299.

Mead, A.D., 1897. The early development of marine annelids. *Journal of morphology*, 13(2), pp.227–326. Available at: http://dx.doi.org/10.1002/jmor.1050130202.

Merkel, J. et al., 2012. Spiral cleavage and early embryology of a loxosomatid entoproct and the usefulness of spiralian apical cross patterns for phylogenetic inferences. *BMC developmental biology*, 12(1), p.11. Available at: http://www.biomedcentral.com/1471-213X/12/11.

Pennerstorfer, M. & Scholtz, G., 2012. Early cleavage in *Phoronis muelleri* (Phoronida) displays spiral features. *Evolution & development*, 14(6), pp.484–500. Available at: http://dx.doi.org/10.1111/ede.12002.

Riedl, R.J., 1969. Gnathostomulida from America. *Science*, 163(3866), pp.445–452. Available at:

http://www.ncbi.nlm.nih.gov/pubmed/5762393.

Schleip, W., 1929. *Die Determination der Primitiventwicklung, ein zusammenfassende Darstellung der Ergebnisse über das Determinationsgeschehen in den ersten Entwicklungsstadien der Tiere,* Leipzig: Akademische Verlagsgesellschaft m.b.h. Available at: http://www.worldcat.org/title/determination-der-primitiventwicklung-ein-zusammenfassen\nde-darstellung-der-ergebnisse-uber-das-determinationsgeschehen-in-den-ersten-entwicklungsstadien-der-tiere/oclc/15205929.

Struck, T.H. et al., 2014. Platyzoan paraphyly based on phylogenomic data supports a noncoelomate ancestry of Spiralia. *Molecular biology and evolution*, 31(7), pp.1833–1849. Available at: http://dx.doi.org/10.1093/molbev/msu143.

Wilson, E.B., 1892. The cell-lineage of *Nereis*. A contribution to the cytogeny of the annelid body. *Journal of morphology*, 6(3), pp.361–466. Available at: http://onlinelibrary.wiley.com/doi/10.1002/jmor.1050060301/abstract.

1. Also nicknamed *cellular bookkepping*, as recalled by E.G. Conklin: "…I followed individual cells through the development, followed them until many people laughed about it; called it cellular bookkeeping." (Bonner and Bell, 1984, p. 81).↩
2. "What a wonderful parallel is this between animals so unlike in their end stages! How can such resemblances be explained?" (Conklin, 1897, p. 195).↩
3. "…if these minute and long-continued resemblances are of no systematic worth, and are merely the result of extrinsic causes, as is implied, then there are no resemblances between either embryos or adults that may not be so explained." (Conklin, 1897, p. 195).↩