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A tale of turns and cycles guiding to neural crest migration - an interview with Roberto Mayor

MIGUEL L. CONCHA*[,1,2,3]

[1]Institute of Biomedical Sciences, Faculty of Medicine, Universidad de Chile, [2]Biomedical Neuroscience Institute and [3]Center for Geroscience, Brain Health and Metabolism, Santiago, Chile

ABSTRACT Roberto Mayor is a prominent Chilean developmental biologist working in the UK and an advocate of the developmental biology discipline in Latin America. Roberto started as a preimplantation mouse developmental biologist during his undergraduate and graduate studies in Chile. Yet, he now uses *Xenopus* and zebrafish to elucidate the mechanisms that drive the directed collective locomotion of neural crest cells. What life events moulded the research career of Roberto across the years? This article addresses this question and provides a personal perspective on his scientific achievements. The story of Roberto is a mix of turns and cycles that ultimately guided him to the migrating neural crest. Turns that made him shift between model organisms and scientific topics. Cycles that drove him back and forth between Chile and the UK and which have connected his early studies as an undergraduate student with the most recent work of his lab. A big lesson that we can learn from the life of Roberto is that no matter how much you plan your life always serendipity plays a significant role. But you have to be alert and brave to take the opportunities that life offers you.

KEY WORDS: *Developmental Biology, collective cell migration, neural crest, Xenopus, zebrafish, Chile, UK*

Introduction

Roberto Mayor is an eminent scientist in the field of developmental biology that has significantly contributed to unravelling the mechanisms that drive the directed locomotion of neural crest cells. He is also a relentless promoter of the developmental biology discipline in Latin America. Roberto was born in Santiago, Chile. He cultivated his passion for this discipline throughout the years between Chile and the UK, where he is currently Professor of Cell and Developmental Neurobiology at University College London (UCL). This article is the result of conversations that took place between September and November 2019 and aims to provide a personal perspective on the scientific life and achievements of Roberto, exploring his motivations for science and digging into the circumstances that shaped his research career over the years.

Roberto is a logic and calm person that believes science is a cultural activity deeply connected to society. He loves transmitting his enthusiasm for science to young people and finds the interaction with students a source of inspiration. Roberto thinks science, and in particular developmental biology, is an opportunity to answer questions that have profound implications for the origin of us as humans. He realised the importance of science at an early age in Chile. Son of an office worker and an electric engineer specialist on generator sets (Fig. 1), Roberto was fascinated as a kid by all sorts of animals, keeping many of them at home, including canaries, thrushes, quails, fish and rabbits. He remembers that his mother used to tell him that as a child, he spent hours playing with corn worms that traders gave him at the street market. When he was around eleven years old, he came across a book that changed his life. The reading of Microbe Hunters by Paul de Kruif revealed him how a group of scientists, bacteriologists, doctors, and medical technicians discovered the microbes and invented the vaccines to counter them. Today, Roberto evokes this moment with joy:

> "*I was impressed by the dedication of these men of science, the difficulties that they had at some point and the sense of achievement at the end. All these characteristics were very appealing to me, so I believe that around that time, I decided to become a scientist in something related to biology.*"

Abbreviations used in this paper: MBL, Marine Biological Laboratory (University of Chicago); LASDB, Latin American Society for Developmental Biology; NIMR, National Institute for Medical Research (London, U.K.).

***Address correspondence to:** Miguel L. Concha. Institute of Biomedical Sciences, Faculty of Medicine, Universidad de Chile, PO Box 70031, Santiago, Chile. E-mail: mconcha@uchile.cl - Web: http://www.ontogenesis.cl - https://orcid.org/0000-0003-3353-9398

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Fig. 1. Roberto Mayor with his parents and sister in Santiago, circa 1966. *Parents Isabel and Vicente and sister Liliana. Both parents encouraged Roberto interest in animals from his early infancy. Photo: family album.*

Training as a mouse developmental biologist (Chile, 1980-1990)

Roberto had no scientists in his family and only as a teenager discovered that Universities conducted science and that most of the active biologists in Chile came from a career called Biochemistry. He thus decided to study Biochemistry at Universidad de Chile, the most traditional public University in the country. However, he soon became disappointed as in the first years the career was too oriented to chemistry, mathematics and physics and almost nothing to biology. But something occurred that changed his initial frustration. The Faculty of Chemical Sciences and Pharmacy, which imparted biochemistry, was temporarily fused with the Faculty of Sciences, a small faculty that had some of the best biologists in the country. So, from one day to another, he started learning biology from Humberto Maturana, Herman Niemeyer, Mario Luxoro, Luis Izquierdo and Juan Fernández, among others. Thus, he was in the right place at the right time. As Roberto explains, "*it was at the Faculty of Sciences where I discovered developmental biology, and when I decided to become a developmental biologist.*"

Roberto had two influential mentors at the Faculty of Sciences. He was motivated by the excellent lectures of cell biology given by Juan Fernández, with whom he did a research rotation using a cell biology approach to study the cytoskeleton in leech embryos. But he then met Luis Izquierdo, a very impressive and friendly teacher interested in classical questions of developmental biology such as cell competence and pluripotency using mouse embryos (Concha and Signore, this issue). Roberto was deeply transformed by learning developmental biology from Luis Izquierdo and decided to do his undergraduate thesis, and then his PhD thesis, with him. Roberto studied the process of cell compaction in the preimplantation mouse embryo. He found unexpected cytoskeletal connections between cells of the early mouse embryo (Mayor *et al.*, 1989), an observation that has been "rediscovered" only recently (Fierro-Gonzalez *et al.*, 2013). This finding was intriguing and expanded his view of developmental biology, opening a personal cycle that was closed only three decades later (see details below at the section "Opening and close of a personal scientific cycle").

Switching from mouse to amphibian development (UK, 1990-1993)

The fact that Roberto spent six years in the laboratory of Luis Izquierdo, first as an undergraduate (1985-1986) and then as a PhD student (1986-1989), predicted that he would continue his developmental biology career in the mouse model. Indeed, when Roberto was about to finish his PhD, Luis Izquierdo offered him a position as a young principal investigator and suggested him to do a postdoc abroad and then return to Chile to take over his lab. Roberto was very grateful and happily accepted this exciting offer. Soon after, he secured a postdoc place in the lab of Martin Johnson, who was studying the molecular and cellular basis of preimplantation mouse development at the University of Cambridge. But the path that Roberto had carefully defined suddenly broke. Unforeseen reasons severely delayed the approval of his PhD thesis, and he lost his position in Cambridge.

The situation was uncertain. Yet, instead of being carried away by despair, Roberto took it as an opportunity to look for a new path. During his PhD, Roberto had attended a Workshop about the cytoskeleton (Fig. 2), where he met Bill Jeffery, former

Fig. 2. At a Cytoskeleton workshop in Santiago (1987). *From left to right: Veronica Tellez, David McClay, Nancy Olea, Joe Sanger, Horacio Vera and Roberto Mayor as PhD student. In this workshop Roberto met Bill Jeffery, former director of the MBL Embryology course in Woods Hole, who supported him to attend the course in 1988. Photo: Nancy Olea.*

director of the famous MBL Embryology course in Woods Hole. This fortuitous meeting in Chile helped him to attend the Embryology course in Woods Hole in 1988 (Fig. 3), where John Gerhardt and Mark Kirchner taught the *Xenopus* module. That experience opened his eyes to a more cell biology approach to understand development. Contrary to the predominant view of that time, Roberto though that gene activities could not explain all developmental process. He became fascinated by the "*beautiful experiments to investigate cytoplasmic movement performed in Xenopus by Jean Paul Vincent in John Gerhart lab"* (Vincent *et al*., 1986). And it was that critical experience that drove Roberto to shift to *Xenopus*. Luis Izquierdo was initially not very convinced, but in the end, he helped Roberto to find a *Xenopus* lab abroad. He contacted his friend Anne MacLaren in the UK who suggested Jim Smith at the National Institute for Medical Research (NIMR). He, in turn, put Roberto in contact with Mike Sargent. In a matter of weeks *"while the ink of the PhD thesis was still fresh"* Roberto was packing his things to do a postdoc in London (Fig. 4).

The lab of Mike Sargent was interested in mesoderm development. It had recently cloned the *Xenopus* homologous of Snail, a gene initially identified in *Drosophila* as required for mesoderm development. Roberto performed molecular biology experiments and identified regulatory regions that controlled the expression of Snail in the mesoderm of *Xenopus*. But, he also realised that a group of cells located dorsal to the neural tube, which he later identified as neural crest cells, also expressed Snail. At the same time, a rotation student identified, by chance, a new gene that Mike Sargent would call Slug; it had a sequence similar to Snail and was also expressed in the neural crest. The discovery of Snail and Slug opened a new perspective on the study of neural crest development, especially with the advent of *in situ* hybridisation as a new technique to observe gene expression directly in the embryo. Researchers like Nicole LeDouarin had been working on the neural crest for ages. Still, they only were able to infer their position based on laborious grafting and labelling experiments. Roberto remembers that "*for the first time, you could see the location of neural crest cells within the embryo by performing in situ hybridisation for these genes. This was very exciting."*

Fig. 4. With Mike Sargent at the NIMR, Mill Hill London, 1992 during Roberto's postdoc. *Photo: Angela Nieto.*

By the end of the postdoc, Mike Sargent offered Roberto to extend his contract at the NIMR. But he could not accept due to his previous commitment with Luis Izquierdo in Chile. With the departure from London approaching, Roberto had to think about a topic for his future research in Chile. As Slug was an excellent neural crest marker, he talked with Mike Sargent, who generously allowed him to continue working on the neural crest in Chile. And this is how, from a series of concatenating events, Roberto began his research career in neural crest development.

Fig. 3. At the MBL Embryology course in Woods Hole in 1988. *Roberto is the fourth from left to right in the first row. Many students from this class became prominent developmental biologists. Photo: Marine Biological Laboratory (Woods Hole, Mass.). Digitised by: MBLWHOI Library, Embryo Project Encyclopedia.*

The start of neural crest research as an independent investigator (Chile, 1993-2003)

When Roberto returned to Chile in 1993, he inherited the lab of Luis Izquierdo who had just died a few months before from Creutzfeldt-Jakob disease (Concha and Signore, 2021). He established a new laboratory of molecular and developmental biology in a place that *"never saw a Gilson pipette before".* He was excited about the idea of beginning an independent research career studying the process of neural crest induction. But he soon felt isolated as the critical mass of developmental biologists in Chile was very short. "*I was the only devel-*

Fig. 5 (Left). Hosting John Gurdon in Chile in 1995. *Sir John Gurdon visiting the Faculty of Sciences, Universidad de Chile, after the Santiago Southern Summer Symposium organised by Jorge Allende and Eddy de Robertis. Nancy Olea, professor at the Faculty of Sciences is also in the picture.*

Fig. 6 (Right). Back in Chile circa 1996. *Roberto as an independent investigator in Chile in his office at the Faculty of Sciences, Universidad de Chile. Photo: Claudia Linker.*

opmental biology using molecular biology in the whole country", Roberto remembers. An exception to this isolation in Chile was a symposium on developmental biology organised by Jorge Allende, with the participation of prominent developmental biologists such as Sir John Gurdon among others (Fig. 5), but this last just a few days. He took some fresh air by visiting the lab of Robert Grainger at the University of Virginia in 1995 where he learnt *Xenopus* embryology and a few months later attended the lab of Judith Eisen at the University of Oregon to learn zebrafish development. Both visits ended up being fundamental for the scientific approach of Roberto, who started to integrate *Xenopus* and zebrafish research to unravel conserved developmental mechanisms (Fig. 6).

Roberto remembers that the Chilean academic system of that time was rather hierarchical. The authorities of the Faculty of Sciences observed with some suspicion that a young researcher like him had no supervisor to mentor his career. They tried to *"solve this problem"* by hiring a senior professor (Edward - Eddy - De Robertis, among them) but did not succeed. Then Roberto had a brilliant idea. He proposed the authorities to hire two promising young investigators instead of a single senior professor, to build a group of young researchers that could create a critical mass investigating developmental biology. This plan was accepted, and Roberto contacted Miguel Allende, who was working in the US at that time. Also, Jose Luis Gómez-Skarmeta was finishing his PhD in Spain and was interested in doing a postdoc in Roberto's lab in Chile. These connections resulted in the appointment of Miguel Allende, presently Professor at the Faculty of Sciences, and Jose Luis Gómez-Skarmeta, who later returned to Spain and became an investigator at the Centro Andaluz de Biología del Desarrollo in Sevilla. Together, Roberto, Miguel and José Luis formed a promising developmental biology group that soon started to train a new generation of developmental biologists in Chile. When Roberto decided to leave Chile (see below), he advocated hard for the University to fill his position with two promising developmental biologists: Alvaro Glavic and Verónica Palma. Consequently, Miguel, Alvaro and Verónica form the current group of Developmental Biologists at the Faculty of Sciences.

Prolific years of research in neural crest migration (UK, 2004-today)

After nearly a decade as an independent researcher in Chile, the career of Roberto was flying (Fig. 7). He was publishing in relevant journals and receiving frequent invitations to give lectures in scientific meetings abroad. He was also named International Scholar of the Howard Hughes Medical Institute (HHMI), obtained a Human Frontiers Grant and a prize for the best Young Scientists in Chile. Yet, despite these achievements and the wish to continue research in Chile, he decided to leave the country and moved to London (Fig. 8). Claudio Stern played a significant part in the transition to London as he offered Roberto a position at UCL, where he was the director of the Anatomy and Developmental Biology Department. *"Claudio was extraordinarily supportive. I am incredibly grateful to him for his offer and support".*

Roberto always considered that neural crest migration was a fascinating process. He started to study this topic in Chile, but the poor microscopy infrastructure hindered the possibilities of making significant advances. But from one day to another, with the new appointment at UCL, Roberto had access to all sorts of modern microscopes. Also, London presented the opportunity to interact with a variety of colleagues holding similar interests but from different disciplines like physics and mathematics. He, therefore, started to study cell migration with no technological limitations and a more multidisciplinary perspective. At the core of Roberto's approach was

its ability to ask simple questions. Roberto emphasises that *"if your question is too complicated, you need to deconstruct it into simple ones. The simple question that I had about neural crest was how the direction of its migration is determined. In the end, the answer to this simple question has proven to be much more complex than initially imagined. But the only way to reach this answer was by asking simple questions once at a time."*

When Roberto started working on the neural crest, the dogma assumed that these cells had to transform from epithelial into individual mesenchymal cells to migrate. However, Roberto found that neural crest cells required cell-cell contact to direct their migration. So how could he reconcile these conflicting observations? The answer to that puzzle came from a new concept that was put forward among others by Peter Fridle in which cells could migrate as collectives. But this idea referred only to epithelial cells and explicitly excluded mesenchymal cells. According to Roberto "*it was a long battle to convince the scientific community that mesenchymal cells can also migrate collectively. Just by chance, I meet Peter Fridle in a meeting in Japan in 2008, and during one of the breaks, I showed him a movie of migrating Xenopus neural crest. His immediate conclusion was that neural crest could indeed migrate collectively! Since then, neural crest cells, but more importantly, mesenchymal cells were recognised as undergoing a form of collective cell migration."*

Following his initial observations, Roberto published several papers that demonstrated the ability of neural crest, as mesenchymal cells, to migrate as a collective (e.g. Carmona-Fontaine *et al.*, 2008; Theveneau *et al.*, 2010; Theveneau and Mayor, 2011). He also dissected critical mechanisms that guide the collective locomotion of neural crest *in vivo* (see below) and identified the first chemoattractant for neural crest cells (Carmona-Fontaine *et al.*, 2011; Theveneau *et al.*, 2010). More recently, he showed that mechanical forces play a crucial role in the onset of neural crest migration (Barriga *et al.*, 2018) and presented the concept of supra-cellular contraction in cell migration *in vivo* (Shellard and Mayor, 2019; Shellard *et al.*, 2018).

Fig. 7. Roberto's group in Chile in 1977. *From left to right: Roberto, Lorena Marchant, Alvaro Glavic, Florencio Espinoza, Néstor Guerrero, Juan Silva, Claudia Linker, Carlos Martinez, Jaime Cofré. Photo: Victor Monasterio.*

Bringing back some of Abercrombie's forgotten ideas

When Roberto was asking the question of what controls the directional movement of neural crest, the obvious answer was that cells followed a gradient of chemoattractant. He and others thus searched for a chemoattractant but failed to find one. But Roberto realised that cells exhibited some kind of repulsion when making contact and though that this behaviour could be the answer. From the literature, he became aware of the seminal work by Abercrombie, who showed that fibroblasts dispersing from confronted cultured explants redirected their movements upon collision following a process that he termed contact inhibition of locomotion (CIL) (Abercrombie and Heaysman, 1954; Roycroft and Mayor, 2018). The surprise was that since the initial description in the ninety fifties the attention to CIL vanished through the years to become almost invisible to the scientific community. Just by coincidence, Graham Dunn, one of Abercrombie's disciples, was working nearby at Kings College London. Roberto visited him, and after watching one of Roberto's movies of migrating neural crest, Graham unquestionably confirmed that these cells exhibited CIL. Roberto was on the right path and soon published a paper that he thinks is his most significant contribution to the field (Carmona-Fontaine *et al.*, 2008). Importantly, this story was an example of many in science history, in which pioneer work made by exceptional scientists in the past fall into oblivion but then are reborn when a new generation of researchers study the same idea with new technologies and perspectives.

Opening and close of a personal scientific cycle

When Roberto was an undergraduate student in the lab of Luis Izquierdo, he made an intriguing observation: cytoskeletal elements connected mouse embryonic cells during compaction at the 8-cell stage (Mayor *et al.*, 1989). This finding suggested that the mouse

Fig. 8. Roberto's group in the UK in 2010. *(Back row, from left to right) Rachel Moore, Mae Woods, Eric Theveneau, Roberto, Roger Singleton, Scott Curran and Ben Steventon. (Front row, from left to right) Manuela Melchionda, Carlos Carmona-Fontaine and Maria Kotini. Photo: Carlos Carmona-Fontaine.*

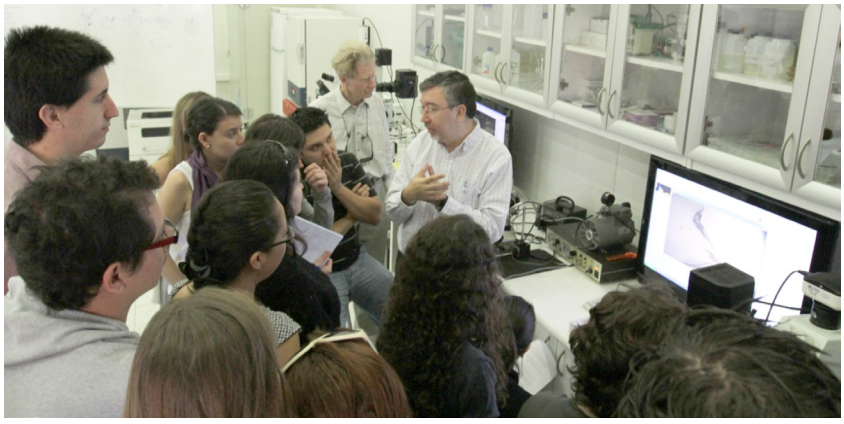

Fig. 9 (Left). Teaching in Quintay in 2012. *Roberto is showing how to perform neural crest grafts to a group of students at the Practical Developmental Biology course in Quintay-Chile in 2012. John Gurdon looks attentive from the background. Photo: Ariel Reyes.*

Fig. 10 (Right). Receiving the LASDB prize in 2013. *Roberto receiving the prize from the president of LASDB, José Xavier Neto. Cancun, Mexico, June 2013. Photo: LASDB.*

embryo behaved as a unit and not merely as a collection of individual parts. This idea was appealing and started to incubate inside Roberto's mind until it crystallised into a holistic concept of embryo development. This idea was reinforced after meeting Francisco Barbieri, an Argentinian developmental biologist much admired by Roberto.

"I was doing my PhD under the supervision of Luis Izquierdo, and one morning Izquierdo received a visit from this Argentinian scientist working on frogs. He talked with Izquierdo all morning, and in the afternoon, he met with a group of PhD students. Francisco Barbieri had a sharp mind and was extremely humble. I remember one question that he asked us: how we could compare the cytoplasmic movements that take place in a single cell during ooplasmic segregation in ascidia with the cellular movements during epiboly in gastrulation. This was a bit of a rhetoric question, as he answered it himself by proposing that both events could be considered similar. I was intrigued by the idea, especially as I was studying mouse embryo compaction, in which the eight cells merge into a single unit. Would it be possible to consider an embryo as a single unit, instead of a unit composed of cells? "

Almost 30 years later, Roberto published a paper showing that cranial neural crest cells of *Xenopus* and zebrafish migrate as a "supracell" (Shellard *et al.*, 2018). In this mode of locomotion, neural crest develops supra-cellular polarisation, actomyosin dynamics and internal cellular flows that resemble the behaviour of single 'swimming" big ameboid cell. Roberto argues that this recent finding of his lab has completed a cycle that started three decades ago as an undergraduate in Chile.

An advocate of developmental Biology in Latin America

Although Roberto does not work in Latin America, he has a special connection with scientists of the region. He is proud of the science performed in Latin America under the most challenging conditions. He also believes that young scientists have energy and commitment difficult to find in the rest of the world. Indeed, Roberto declares that *"every time I have the opportunity, I transmit the message in international forums that the Latin American students are amongst the best in the world."* His commitment to foster the developmental biology discipline in Latin America has reflected in the training and organisation of several practical courses of developmental biology in Latin America since 1999 (Fig. 9) (see Mayor in this issue). Roberto also played an active role in the origin of the Latin American Society of Developmental Biology (LASDB) (Fig. 10). He remembers that the idea of generating the LASDB evolved from a group of students that attended some of the first practical courses of developmental biology he organised almost twenty years ago. The course students created strong links between them and with

Fig. 11. Roberto's group in 2019. *(Back Row, from left to right) Delan Alasaadi, Branda Canales, Soraya Villaseca, Oliver Cameron and Matyas Bubna-Litic. (Front row, from left to right) Adam Shellard, Roberto, Melisa Turan and Oliver Beaven. Photo: Delan Alasaadi.*

the course faculty, and they demanded to establish some kind of developmental biology network for Latin America. Roberto though it was an excellent idea and asked advice to Eddy De Robertis, president of the International Society of Developmental Biology (ISDB) at that time. Eddy immediately replied to him that instead of a network, they should create a Society. Eddy and the ISDB were incredibly supportive, and the Latin American society was established in 2002 and had the first meeting in 2003 (see Wappner and Zurita in this issue).

In the opinion of Roberto, scientific discovery in Developmental Biology is relevant for the ordinary citizen of Latin America. *"The transformation of a single cell into a complex organism is one of the most captivating problems in biology. And us, as developmental biologists, have the duty to transmit this fascination to the ordinary citizen. The ordinary citizen of Latin America is not different from the ordinary citizen of Europe or Africa. We have similar heads, arms and hearts and all our bodies form by the same developmental mechanisms. It is in our human nature the aim to understand our origins, and one aspect of our origins is how we develop. How our embryonic brain transforms from a mass of cells into one of the more complex and fascinating structures of the entire universe? Why is my nose so similar to the nose of my parents? These are fundamental questions that development can answer. And if the development goes wrong, it could have devastating consequences for the embryo, newborn and family. We need to understand how malformations are generated during development to create therapies to fix them or even cure them before they appear"* (Fig. 11).

References

ABERCROMBIE, M., AND HEAYSMAN, J.E. (1954). Observations on the social behaviour of cells in tissue culture. II. Monolayering of fibroblasts. *Exp Cell Res* 6: 293-306.

BARRIGA, E.H., FRANZE, K., CHARRAS, G., AND MAYOR, R. (2018). Tissue stiffening coordinates morphogenesis by triggering collective cell migration in vivo. *Nature* 554: 523-527.

CARMONA-FONTAINE, C., MATTHEWS, H.K., KURIYAMA, S., MORENO, M., DUNN, G.A., PARSONS, M., STERN, C.D., AND MAYOR, R. (2008). Contact inhibition of locomotion *in vivo* controls neural crest directional migration. *Nature* 456: 957-961.

CARMONA-FONTAINE, C., THEVENEAU, E., TZEKOU, A., TADA, M., WOODS, M., PAGE, K.M., PARSONS, M., LAMBRIS, J.D., AND MAYOR, R. (2011). Complement fragment C3a controls mutual cell attraction during collective cell migration. *Dev Cell* 21: 1026-1037.

CONCHA, M.L. and SIGNORE, I.A. (2021). Developmental Biology in Chile: historical perspectives and future challenges. *Int. J. Dev. Biol.* 65: 29-47.

FIERRO-GONZALEZ, J.C., WHITE, M.D., SILVA, J.C., AND PLACHTA, N. (2013). Cadherin-dependent filopodia control preimplantation embryo compaction. *Nat Cell Biol* 15: 1424-1433.

MAYOR, R., PEY, R., AND IZQUIERDO, L. (1989). Development of cytoskeletal connections between cells of preimplantation mouse embryos. *Roux Arch Dev Biol* 198: 233-241.

ROYCROFT, A. and MAYOR, R. (2018). Michael Abercrombie: contact inhibition of locomotion and more. Int. J. Dev. Biol. 62: 5-13 (https://doi.org/10.1387/ijdb.170277rm)

SHELLARD, A., AND MAYOR, R. (2019). Supracellular migration - beyond collective cell migration. *J Cell Sci.* 32: jcs226142

SHELLARD, A., SZABO, A., TREPAT, X., AND MAYOR, R. (2018). Supracellular contraction at the rear of neural crest cell groups drives collective chemotaxis. *Science* 362: 339-343.

THEVENEAU, E., MARCHANT, L., KURIYAMA, S., GULL, M., MOEPPS, B., PARSONS, M., AND MAYOR, R. (2010). Collective chemotaxis requires contact-dependent cell polarity. *Dev Cell* 19: 39-53.

THEVENEAU, E., AND MAYOR, R. (2011). Collective cell migration of the cephalic neural crest: the art of integrating information. *Genesis* 49: 164-176.

VINCENT, J.P., OSTER, G.F., AND GERHART, J.C. (1986). Kinematics of gray crescent formation in *Xenopus* eggs: the displacement of subcortical cytoplasm relative to the egg surface. *Dev Biol* 113: 484-500.

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