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Living History of Physiology: Carl Gans

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Dudley, Robert, Raymond B. Huey, and David R. Carrier. Living History of Physiology: Carl Gans. *Adv Physiol Educ* 30: 102–107, 2006; doi:10.1152/advan.00023.2006.—In 2005, The American Physiological Society initiated The Living History of Physiology Project to recognize senior members who have made extraordinary contributions during their career to the advancement of the discipline and profession of physiology. Each Eminent Physiologist will be interviewed for archival purposes, and the video tape will be available from the American Physiological Society Headquarters. In addition, a biographical profile of the recipient will be published in *Advances in Physiology Education*.

PROFESSOR CARL GANS'S SELECTION for this honor from the American Physiological Society is well deserved. Professor Gans (Fig. 1) began his career in biological research in 1945 and continued to the beginning of the 21st century, when illness forced him to stop working. For more than one-half century, he has been a driving force in integrative biology. He also provided extraordinary service to the profession through editorship of the *Journal of Morphology* and of the monumental series *Biology of the Reptilia*. Through his courses and textbooks, he also contributed, and continues to contribute, to the education of countless numbers of students in comparative morphology, physiology, and biomechanics. His special genius derives from an extraordinary sensitivity to the natural history, evolution, and behavior of organisms, from his technical skills and innovations, and from his ability to integrate diverse approaches that are technically and conceptually elegant. Professor Gans has been doing integrative biology long before the field was formally recognized.

As refugees from Germany, Professor Gans and his family arrived in the United States in the 1930s. Before he became a professional biologist, Professor Gans was a practicing mechanical engineer, working primarily with the company Babcock & Wilcox. He graduated from New York University in 1944 with a Bachelor's of Mechanical Engineering and then spent 2 years in the Philippines and Japan in active service with the United States Army Corps of Engineers. After returning to the United States, he received a Master of Science in Mechanical Engineering from Columbia University in 1950. In 1955, he then returned to school at Harvard, graduating in 1957 with a Doctorate of Philosophy in Biology under the tutelage of Alfred Romer and Ernest Williams.

Professor Gans' impact on the field of physiology has been multifaceted and cannot be overstated. Below, we focus on aspects of his career (research, service, and education) that we see as being particularly significant.

Professor Gans' biology has always been grounded with deep sensitivity to the natural history and natural behavior of his study organisms. Among the community of workers in functional morphology and comparative physiology, Professor Gans has had few, if any, peers in this regard. He has made a career out of visiting diverse locales around the planet, where he invariably discovered and investigated superbly interesting and important questions in a number of taxa [e.g., see his article "All animals are interesting" (14)]. Professor Gans simply has an eye, nose, and ear for particular kinds of animals relative to the physiological problems that they present.

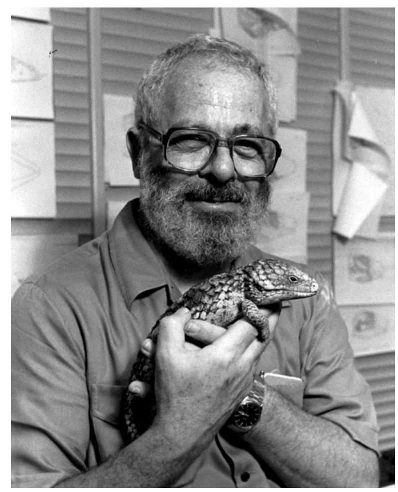

Fig. 1. Professor Carl Gans in ~1997.

Professor Gans' research is also firmly grounded with respect to the phylogenetic origins and evolutionary background of his study organisms. This perspective is perhaps not surprising, as he himself has contributed greatly to systematic revisions of diverse reptiles over the decades. In any case, Professor Gans was one of the first physiologists to incorporate phylogenetic thinking into the design of a research program in integrative biology, into his selection of research animals, and into his interpretation of experimental results. A delightful example here is his classic study "Respiration in early tetrapods: the frog is a red herring" (12). In the field of comparative biomechanics, there are still few workers who possess as clear of an understanding of the importance of phylogeny and evolutionary history as Professor Gans. In fact, he was implementing path-breaking research in evolutionary physiology long before the field was formally defined as such.

Professor Gans' studies have also been deeply rooted in evolutionary theory. His many philosophical articles on the nature and causes of adaptation are classics and remain required reading. For example, in a 1979 study, Professor Gans tackled the long-standing paradox that the morphological and physiological capacities of organisms sometimes appeared to be "overdesigned" (15). Perhaps because of his engineering background, Professor Gans realized that "overdesign," while seemingly maladaptive in normal circumstances, would be adaptive during extreme or stressful situations. Thus he provided a fundamental criticism of the controversial concept of symmorphosis, long before that concept was formally proposed (5). Moreover, he saw how overdesign could promote "protoadaptation" (also known as "preadaptation").

Professor Gans' greatest contribution to comparative physiology is probably his pioneering research in the field of biomechanics. Much of his experimental effort was focused on major innovations in vertebrate feeding and locomotion. Right from the start of his studies on the mechanics of feeding, limbless locomotion, and lung ventilation in snakes, turtles, and frogs (from the mid-1950s to the early 1970s), Professor Gans set a standard for integrative biology that remains a challenging goal even today. He approached biomechanical questions from diverse perspectives of the study animal's ecology, behavior, and evolutionary history. Because of this and because of his engineering and technical expertise, he was able to ask and answer questions of broad comparative significance. Moreover, he had an innate ability to incorporate new technology into his work. In fact, he was one of the first investigators coming from a tradition of zoology and comparative anatomy to use the sophisticated electronics and recording technology that makes modern comparative biomechanics possible today. Professor Gans' technological expertise (e.g., Ref. 24) inspired other researchers in the fields of vertebrate morphology, herpetology, and zoology to follow in his footsteps.

Professor Gans was a pioneer in integrating biomechanics and physiology into the study of vertebrate evolution. Additionally, he dramatically altered our views of vertebrate evolution through the development of plausible evolutionary scenarios based on physiological processes and data. Most important in this regard was his collaborative research with Professor Glenn Northcutt on the origin and early evolution of vertebrates (see below). This synthetic work integrated insights from phylogeny, developmental biology, morphology, and physiology, and, in so doing, it revolutionized our understanding of vertebrate evolution. He also made significant contributions to our understanding of the evolution of ventilatory mechanisms in tetrapods, of the evolution of limbless locomotion, and of the effect of late Paleozoic changes in atmospheric oxygen and carbon dioxide on animal evolution (22).

One of Professor Gans' first biological interests was egg-eating snakes of the African genus *Dasypeltis*. His studies (7, 13) here provide clear insights into how Professor Gans thinks and how he is able to use engineering and evolutionary perspectives to draw major insights from a deceptively simple natural history observation (Fig. 2). These snakes are nearly toothless and specialize on eating "relatively large eggs, cracking them open within the esophagus, squeezing out their liquid contents, and regurgitating the shell (rolled up into a cigar-shaped mass)" (Fig. 3). Professor Gans began by describing the morphological and biomechanical adaptations that permit this dietary specialization of *Dasypeltis*, all of which appear to be obligate egg eaters. Moreover, perhaps because of his keen interest in geographic and taxonomic variation (8), Professor Gans noted that the color patterns of these species varied geographically but were always similar to those of sympatric and venomous carpet vipers. Realizing that he had found an example of Batesian mimicry, Professor Gans documented the similarity of color patterns and also striking behavioral convergence of *Dasypeltis* on the vipers (9). He then took it one step further and used this to develop the concept of "empathic learning," which helps resolve how mimicry can evolve even when the model is lethal (10). This set of studies is elegant and helped convince one of us (R. B. Huey) to pursue a career in functional biology rather than in medicine.

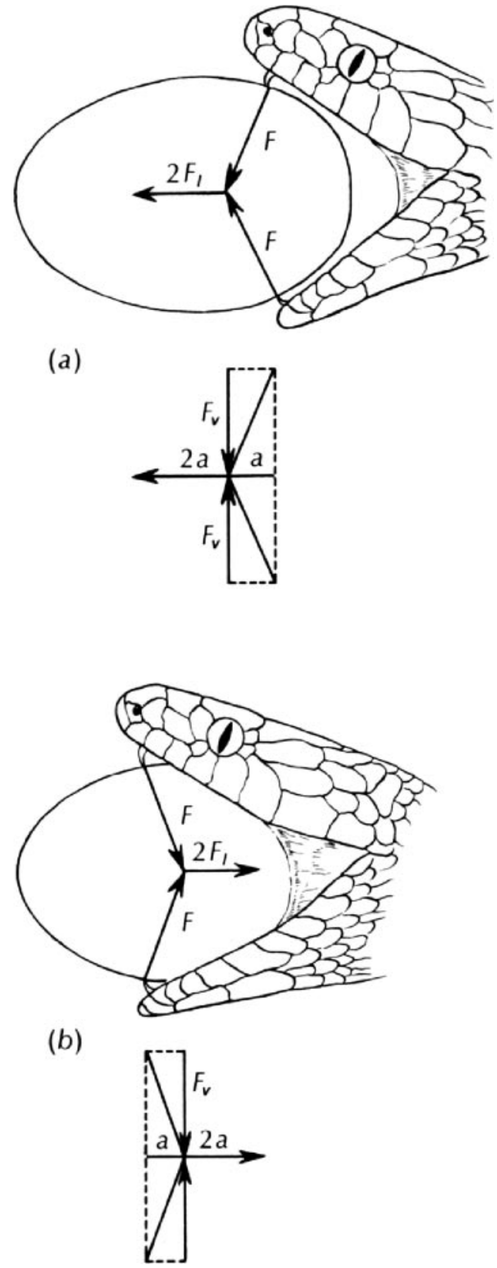

Fig. 2. Vector analysis of the forces applied to an avian egg during ingestion by the egg-eating snake *Dasypeltis*. *a*: Initiation of the bite. F_l, longitudinal force; F_v, vertical force; *a*, acceleration. *b*: Stage during the bite when net bite force propels egg into the throat. "Although the forward, 'out of the mouth' reaction forces–well known to those humans who have bobbed for apples–are thus reduced, they are not eliminated." [Reprinted from Ref. 13.]

Professor Gans' work on the mechanism of breathing in frogs illustrates his strategy of insisting that experimental research in biomechanics be guided by questions of general

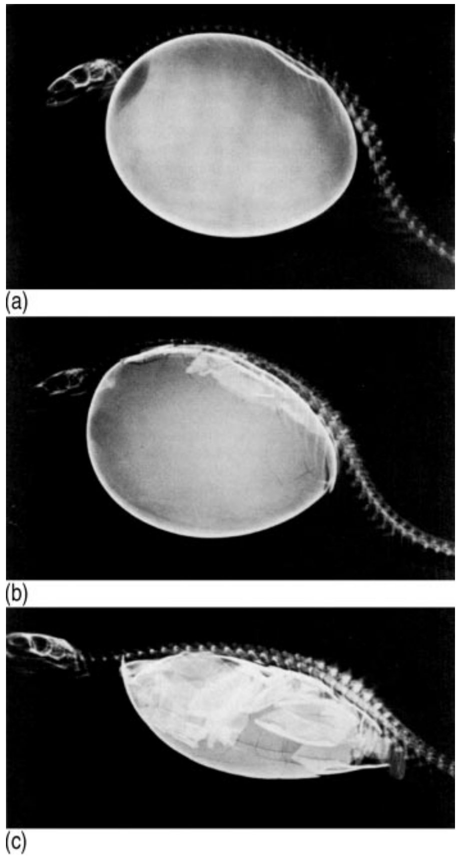

Fig. 3. X-rays showing the process of rupturing an egg in the esophagus of the egg-eating snake *Dasypeltis*. *a*: First rupture of the egg. *b*: Cracking and infolding of the dorsal shell region. *c*: Stage during which most egg contents pass down the esophagus. [Reprinted from Ref. 13.]

importance to vertebrate evolution. Although the basic mechanism of respiration in frogs had been described in the late 19th century, considerable disagreement existed about the details even into the 1960s. Working with colleagues Hank De Jongh and J. Farber, Professor Gans completed a detailed set of measurements (Fig. 4) that included recordings of buccal and pulmonary pressure, electromyography of the relevant muscles, cinematography and cinefluorography, and monitoring of gas flow by placing frogs in atmospheres of variable argon and nitrogen content and recording the concentrations of the nostril efflux (18, 23). This experiment elegantly showed that frogs begin a breath by filling their buccal cavity with fresh air, that they then exhale pulmonary contents through the buccal cavity, and that they finally close their nostrils and pump the buccal contents into the lungs (Fig. 5). Professor Gans and his coworkers also demonstrated that the pulmonary efflux streams past the buccal contents with minimal mixing, allowing relatively pure air to be pumped into the lungs. Although there is debate in the literature about whether or not all species of frogs are able to exhale without significant mixing of the fresh air in the buccal cavity (29), the basic physiological patterns of ventilation in frogs that Professor Gans and Professor De Jongh described in 1969 remains accepted today.

Using these results on frogs and his associated investigations into the mechanism of ventilation in turtles (17, 21) as a starting point, Professor Gans then wrote two seminal reviews on the evolution of lung ventilation in tetrapods (11, 12). These reviews integrated information from three distinct fields, namely, respiratory physiology, comparative anatomy, and vertebrate phylogeny, in a way that clearly defined a set of unanswered questions and then presented a compelling set of hypotheses that inspired subsequent studies (1, 2, 3, 4, 6, 16, 26, 27, 30). Questions laid out in Professor Gans' review articles have remained central to the research careers of individuals such as Stephen Perry, Elisabeth Brainerd, and David Carrier.

One of Professor Gans' most important contributions arose out of team-teaching vertebrate biology to undergraduates at the University of Michigan with Professor Glenn Northcutt. As Professor Northcutt and Professor Gans developed their course together, an important scenario for the origin of vertebrates emerged. They realized that most derived aspects of vertebrates were additions to the basic protochordate system (19, 25). Adult vertebrates are characterized by a complex integument containing multiple sense organs, pigment cells, and a bony armor. Vertebrates are also characterized by a complex neural tube with numerous ganglia and many simple or complex sense organs. The perforated pharynx of protochordates has also been modified by the addition of gills with aortic arches, skeletal elements, and muscles for the pumping of water. Most importantly, vertebrates have a well-defined head, with sensory systems for the perception of chemical, light, mechanical, and electrical signals associated with enlargement of the anterior neural tube for processing sensory information.

These "new structures" transform from, or are induced by, three embryonic tissues: the neural crest, placodal tissues, and hypomeric muscle. Professor Northcutt and Professor Gans realized that these three embryonic tissues represent a set that arose at or close to the evolution of vertebrates from protochordates. Furthermore, they argued that the origin of vertebrates is essentially a story about the evolution of a new head. In the head, the neural crest functions as mesoderm and forms connective, skeletal, and muscular tissues. Together, the neural crest and epidermal placodes form specialized sense organs and associated neural structures. Muscularization of the hypomere brought new capacity and imposed new demands on the pharyngeal skeleton, involving a new cartilaginous skeleton that allowed an elastic recoil mechanism for buccal pumping. Dentine and enamel-like tissues first developed in association with electroreceptors, and the origin of bone appears to have been a secondary development, providing mechanical support to maintain fields of sensory receptors. Diffusional limits imposed by the integumentary armor necessitated pharyngeal modifications involving the development of a muscular-cartilaginous water pump and a "heart, aortic arch, and gill" system. These events in the evolution of a new head, Professor Gans and Professor Northcutt suggested, were associated with a shift from a filter-feeding mechanism to a mechanism that permitted active predation and made larger prey items accessible. The scenario that Professor Northcutt and Professor Gans developed has widespread appeal and has become a unified theory for the origin of vertebrates (Fig. 6).

Professor Gans has been prolific in his research. His bibliography from 1945 to 1994 includes 677 references (28). Many of these papers fall into the categories of systematics of amphibians and reptiles and the zoology of amphisbenids (a

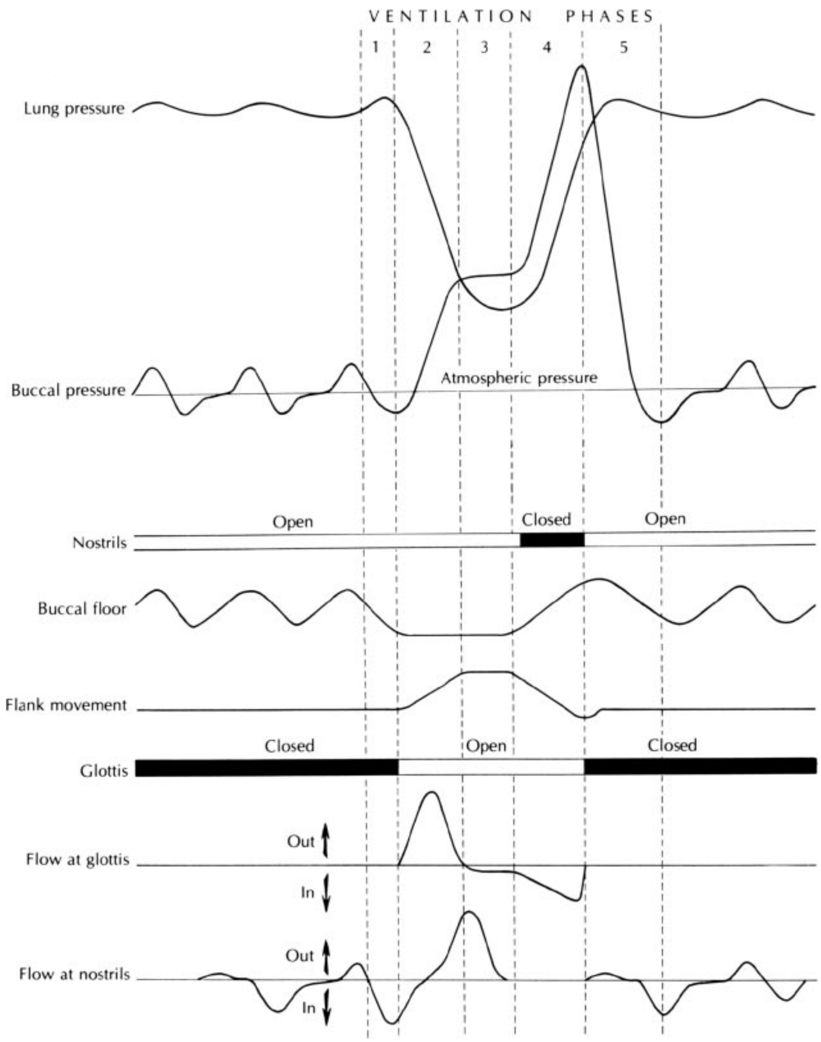

Fig. 4. Summary diagram showing the mechanics of breathing in the bullfrog *Rana catesbeiana* with simultaneous changes in pulmonary and buccal pressure during buccal oscillation and ventilation. Below the pressure changes are shown the movements of the nostrils, the buccal floor, the flanks, and the glottis as well as the magnitude and direction of flow between chambers and the exterior. [Reprinted from Ref. 13.]

group of limbless squamates). Nevertheless, much of Professor Gans' research was focused on comparative physiology, particularly on biomechanics. Physiological topics in which he invested heavily include the mechanics of lung ventilation [15 peer-reviewed papers (PRPs)], the mechanics of limbless locomotion (25 PRPs), the functional significance of muscle architecture (15 PRPs), the mechanics of tetrapod feeding (34 PRPs), the mechanics of hearing and sound production (11 PRPs), the evolutionary basis of adaptation (20 PRPs), the physiology of snake venom (20 PRPs), and the evolutionary origin of vertebrates (9 PRPs). Many of these studies, such as those on egg-eating snakes, the mechanics of ventilation in tetrapods, and the origin of vertebrates, represent classics that form the foundation of much contemporary research. His later publications on mechanisms of adaptation and evolutionary constraint have also been highly influential.

Professor Gans is unusual in the degree to which he has facilitated and maintained international collaborations. He has personally collaborated with researchers in Australia, Belgium, France, Holland, Great Britain, Israel, Russia, Iran, Philippines, South Africa, Kenya, Nigeria, Argentina, and Brazil. Professor Gans also carried out extensive herpetological collecting and fieldwork in Brazil, Kenya, India, Sri Lanka, and Australia. He was one of the organizers of the nascent International Congress of Vertebrate Morphology in the early 1980s, which is now an energetic international society that grows in membership each year.

Professor Gans has also made an unusually significant and unselfish contribution to the dissemination and publication of scientific research. Most important is his founding and subsequent chief editorship of the influential series *Biology of the Reptilia*, now in its 20th volume. This beautifully edited, scholarly, and monumental series has no equivalent for any taxon. The series addresses all aspects of the biology of reptiles from ecology to endocrinology, development, physiology, and neural anatomy. Professor Gans also served as editor of the *Journal of Morphology* for a remarkable period of 25 years. In this role, as a graduate student, one of us (D. Carrier) watched him dedicate huge amounts of time to the translating and editing of manuscripts written by individuals for whom writing in English was inherently difficult. This investment of his limited time derived from a deep personal sense of duty and commitment to science.

Those who have worked with Professor Gans have rapidly learned to appreciate the deep thinking that underlies his sometimes laconic but penetrating statements. Professor Gans'

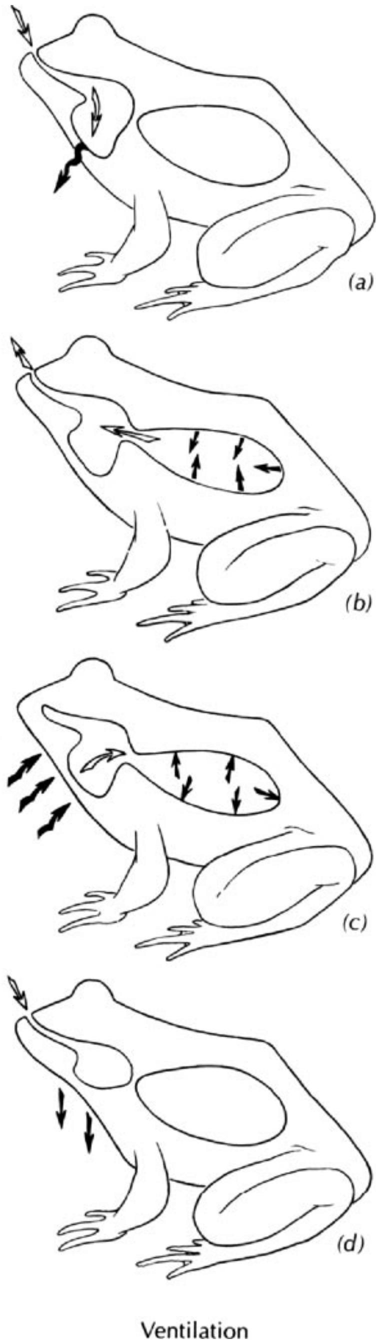

Fig. 5. Illustration of the ventilatory cycle in *Rana catesbeiana*. *a*: Inspiration into the buccal cavity. *b*: Pulmonary expiration. *c*: Filling of pulmonary volume through action of the buccal pump. *d*: Repetition of the cycle. "The ventilatory cycle of the bullfrog takes less than one second and is powered by the muscles of the floor of the mouth." [Reprinted from Ref. 13.]

attention to nuance and precision of linguistic expression is even more remarkable given that his native language is not English. Capable in a diversity of European languages, Professor Gans has also brought to bear on his research a remarkable memory and extensive reading of diverse academic literature. His internationalist perspective on science has been mirrored by a deep knowledge of and respect for the vast panoply of human culture, talents that have served him well in his travels, fieldwork, and numerous collaborations.

Professor Gans' contributions to teaching (both undergraduate and graduate) have also been profound. Perhaps most importantly, he taught comparative anatomy to generations of undergraduate students and always emphasized evolutionary and functional perspectives. But he had an impact even on those students who took comparative anatomy at other universities: for example, his photographic atlas illustrating details of shark anatomy (20) brought triply injected dogfish sharks almost to life.

Professor Gans can often be demanding and critical, but he has been remarkably encouraging to a variety of students, most of whom were not his own. To illustrate this point, we end by retelling an event that profoundly influenced Dr. Bob Full, now Chancellor's Professor at the University of California (Berkeley, CA). As an undergraduate, Professor Full was attending his first meeting of the American Society of Zoologists. He was sitting alone in an overstuffed chair in the hotel lobby feeling badly out of place and discouraged that his presentation at a poster session had attracted little attention. An older man sat down beside him and struck up a conversation. They talked about the research for about 90 minutes. The undergraduate and professor-to-be left the conversation inspired and convinced that he was going to be a physiologist. Only later did le learn that the man who had shown such an interest in him and his work was the highly respected Professor Carl Gans. It was close to a decade, however, before Professor Full came to fully appreciate the significance of that conversation on his professional life.

In leadership, innovation, original research, support and dissemination of original research, international collaboration, and mentoring of young researchers, Professor Carl Gans has had a tremendous impact on the field of compar-

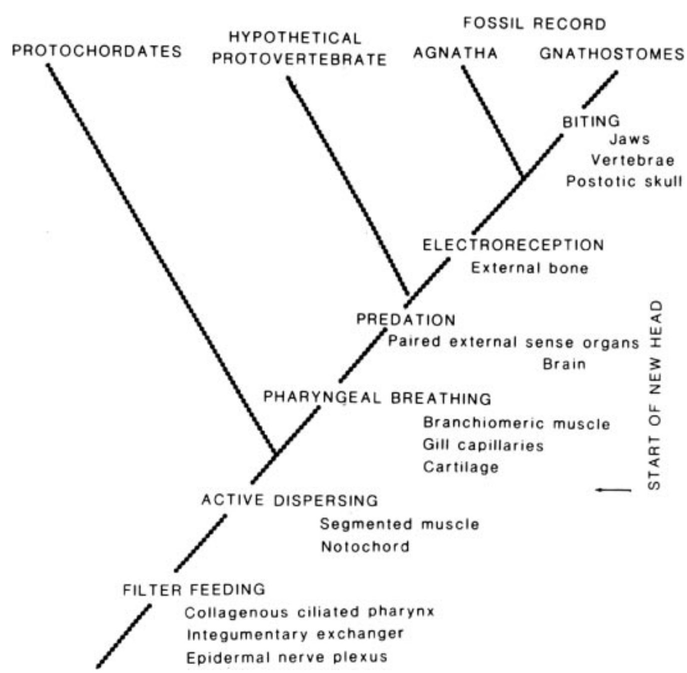

Fig. 6. Evolutionary scenario for major structural and functional transitions in vertebrate evolution. Proposed functional states (in capital letters) precede the modified structures (in lowercase letters) associated with them. [Reprinted from Ref. 25.]

ative physiology. To him, we send our heartfelt thanks and congratulations, and we join all of his colleagues in saying “Mazel tov!”

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