The Sea Spider's Contribution to T.H. Morgan's (1866–1945) Development

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ABSTRACT   Over a century ago, T.H. Morgan helped found *The Journal of Experimental Zoölogy*, a series devoted to emerging investigations in development and evolution, variation and heredity, adaptation and ecology. T.H. Morgan initially encountered these topics in his graduate research on the ontogeny and phylogeny of the sea spiders. His Ph.D. thesis, written in 1891, reflects in interesting ways the conceptual shifts in evolutionary biology in the late 1800s. Embryology had become a major criterion in using morphological similarity to speculate on phylogenetic relationships. Yet, when Morgan studied the development of sea spiders to draw conclusions about their relatedness, he struggled with the incompleteness of knowledge about the role of inheritance and variation of ontogenetic processes. This can best be seen in his discussions of the properties of conservation during embryonic cleavage, varied development of supposedly homologous appendages, and the evolvability of larval stages. After his dissertation, Morgan never returned to phylogenetic analysis. He had been dissatisfied with the plethora of untestable phylogenetic hypotheses based on comparing complicated embryological phenomenon, and joined an experimental movement in which systems were explicitly chosen and constructed to test hypotheses about developmental processes. *J. Exp. Zool. (Mol. Dev. Evol.) 310B:203–215, 2008.*   © 2007 Wiley-Liss, Inc.

In the summer of 1890, Thomas Hunt Morgan (Fig. 1), age 24 years, delivered a lecture at the Marine Biological Laboratory at Woods Hole, Massachusetts, based on his dissertation research. Woods Hole was emerging as a center for scientific thoughts in the 1890s, and Morgan was in good company. His advisor, William Kenneth Brooks (1848–1908), a classical morphologist, was responsible for mentoring future cytologist, Edmund B. Wilson (1856–1908), embryologists Ross G. Harrison (1870–1959) and Edwin G. Conklin (1863–1952), and geneticist William Bateson (1861–1926) among others at Johns Hopkins (Maienschein, '91b). Brooks had, in turn, been a student of Louis Agassiz (1807–1873) and later Alexander Agassiz (1835–1910) at Harvard's Museum of Comparative Zoology. Brooks carried on his mentors' precise methods of descriptive morphology, without endorsing Louis Agassiz' creationist agenda. He was well known for encouraging his students to think independently and he did not expect that answers about evolutionary relatedness drawn from comparative zoology should come easily. Bateson ('10) would later

say of his mentor, "Variation and heredity had stood as axioms. For Brooks they were problems. As he talked of them the insistence of these problems became imminent and oppressive."

Morgan's dissertation on the evolutionary relationship of sea spiders (pycnogonids, the extant members of Pantapoda) among arthropods contains one of the few embryological accounts of pycnogonid development to this day. Yet, excluding a handful of sea spider specialists, few are familiar with the work, in part because Morgan's dissertation is an unexceptional outlier among his approximately 370 scientific manuscripts and 22 books. Using comparative anatomy and embryology to infer phylogeny was the traditional approach for an evolutionist in 1890, and these studies contrast to Morgan's later and more

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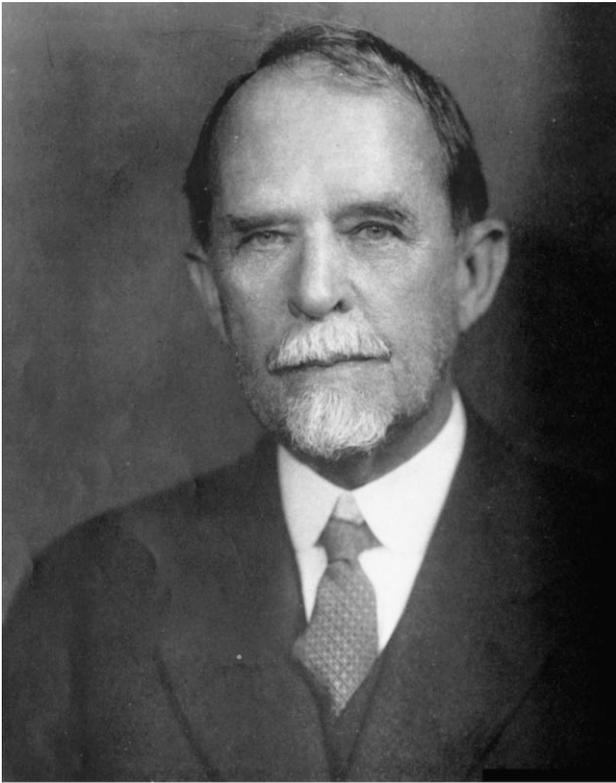E-mail: amaxmen@post.harvard.edu

Fig. 1. A photograph of Thomas Hunt Morgan from the frontispiece of *Journal of Experimental Zoölogy* (1945). Morgan published a manuscript in this volume 100, as well as in the first (1904).

famous experimental work for that he would win a Nobel Prize in 1933. His descriptive graduate work has been laid to rest in dimly lit library stacks and when it is acknowledged, it is given only a cursory analysis. For instance, the geneticist Sturtevant ('59), a former student of Morgan, and the historian of science, Maienschein ('91b) considered the thesis merely typical of a graduate student studying zoology in the late 19th century. Historian of science, Allen ('69, '78) discussed the dissertation in his biography of Morgan, but certain important details are obscured.

In this study, I critically evaluate Morgan's three manuscripts on sea spider phylogeny: *A Preliminary Note on the Embryology of the Pycnogonids* (1889), *The Relationships of the Sea Spiders* (1890), and his dissertation and *A Contribution to the Embryology and Phylogeny of the Pycnogonids* (1891). I argue that Morgan did not merely pass through the prescribed and schematic motions of using ontogenetic stages as evidence for relatedness; rather, Morgan struggles with the inevitable incompleteness of embryological knowledge culminating in an explicit skepticism about his own phylogenetic conclusions.

The manuscripts reflect a growing discontent with using embryology to deduce evolutionary relationships. In Morgan's (1889) first scientific publication, he is hopeful that embryological descriptions will reveal the phylogenetic relationships of the pycnogonids among arthropods. In Morgan's (1891) thesis this initial optimism has disappeared. In the thesis, most hypothetical evolutionary scenarios are removed and the topics more often than not include open-ended questions rather than ready answers. In some cases these changes in Morgan's writings are subtle. As historian of embryology, Oppenheimer ('67) observed, "It is one of the obstacles to an approach to certainty in intellectual history that the influence of one idea or pattern of ideas on the development of another is not indicated accurately by references either in texts or bibliographies" (p 13). Here, I pay particular attention to the tone, questions, and discrepancies within and between Morgan's graduate manuscripts to discover why Morgan was initially interested in sea spiders and comparative embryology, and why he eventually found his own results to be problematic.

I focus on those aspects of Morgan's graduate investigations that are relevant for today's discussions. Many of the problems Morgan grappled with predate the vocabulary we now use to describe them,[1] namely, process (or transformational) homology, homoplasy, and constraint (with respect to an ancestral larval or "phylotypic stage"). These topics implicitly arise in his discussion of embryonic cleavage, germ layer formation, appendicular homology, and the evolvability of the sea spider larva, respectively. One central problem for Morgan's interpretations involved the supposed polarization of concepts of heredity and variation in 1880. Morgan was familiar with Francis M. Balfour's comprehensive *Treatise on Comparative Embryology*,[2] in which heredity and variation are presented as interacting dialectical opposites. "There are, according to this theory, two guiding, and in a certain

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[1] Morgan rarely introduced new terms and discouraged the habit. "While giving the appearance of profundity, in reality often serve merely to cover ignorance and to make mystery out of a mechanism" (Morgan, '19; p 59).

[2] For evidence that Morgan was familiar with Balfour, please refer to the discussion in this manuscript on Larval Evolution.

sense, antagonistic principles that have rendered possible the present order of the organic world. These are known as the laws of heredity and variation'' (Balfour, 1880; p 2). The theory seemed to be straightforward but Morgan observed unaccountable variation at different points along a developmental trajectory in related species that made him question some of the fundamental assumptions about heredity and development.

PHYLOGENETIC POSITION OF SEA SPIDERS

It is quite understandable why Morgan was interested in the open challenge of sea spider phylogeny. Pycnogonids are bizarre arthropods, characterized by bodies too slender to house the gut diverticula and gonads, which are instead located in the four to six pairs of long legs. The head typically bears a snout-like proboscis, and a pair of clawed appendages (chelifores), palps, and specialized appendages (ovigers), which the male uses to carry embryos until hatching (Fig. 2A). They are exclusively marine, cosmopolitan, and most importantly for Morgan, certain species have been making their home on alga and hydroid beds nearby Woods Hole, Massachusetts, for over a century (Fig. 2B).

In the decade before Morgan's own graduate work, Hoek (1881; affiliated with the Challenger Expeditions), Dohrn (1881), director of the marine laboratory, *Stazione Zoologica* at Naples and a student of Ernst Haeckel, and Edmund B. Wilson (1878, 1881; Morgan's classmate at Johns Hopkins and a future leading cytologist) had all published manuscripts on sea spider evolution. Wilson's pycnogonids were collected by Alexander Agassiz in 1880. It is quite possible that Agassiz' pycnogonids had been given to Wilson by Brooks and later Wilson might have impressed Morgan with their potential for further phylogenetic analysis. Although all these scientists had put forth phylogenetic theories, the actual hypotheses changed from manuscript to manuscript.

But Pycnogonids were also an important taxon to understand. Sea spiders were considered primitive and thus they were paramount in understanding the origin and evolution of the Arthropoda. Sea spiders' affinity had affiliated with both crustaceans and arachnids and, in 1881, Dohrn and Hoek independently decided they were an entirely separate lineage of arthropods,
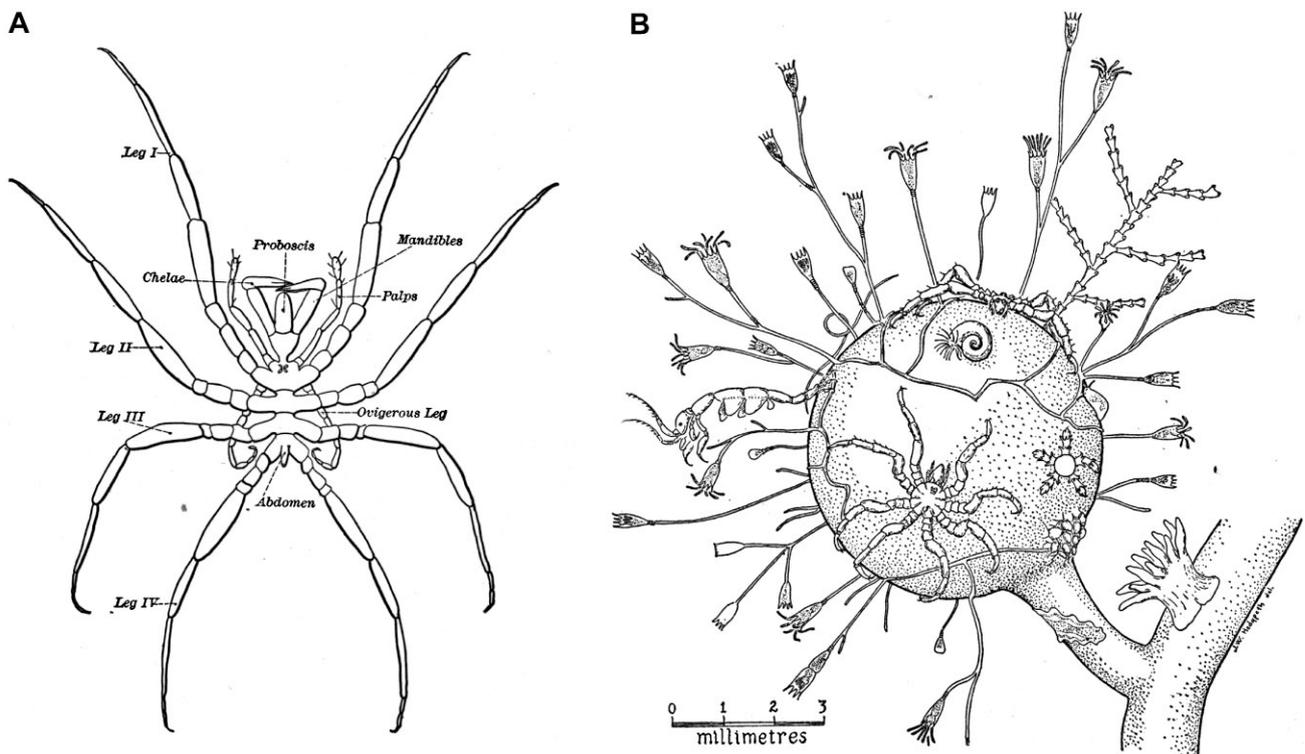

Fig. 2. (**A**) Figure from Morgan (1890) depicting an adult sea spider, or pycnogonid. (**B**) A sea spider, *Tanystylum orbiculare* Wilson, on a sargassum bladder in Woods Hole, Massachusetts (Hedgepeth, '48).

descendants of a common arthropod–annelid ancestor. On the basis of comparative studies of their anatomy, Wilson (1881) concluded that the first pair of appendages were significantly different between arachnids and pycnogonids, and used this character to separate the two groups. In Carl Gegenbaur's (1878) *Elements of Comparative Anatomy* pycnogonids were grouped beside another bizarre invertebrate, the water-bear or tardigrade, as an unsettled subgroup of arthropods. And in *A Treatise on Comparative Embryology*, Balfour (1880) suggested that pycnogonids are affiliated neither with crustaceans nor arachnids, and that they must have diverged very early from an arthropod ancestor. He recommends further investigation into pycnogonid embryology and appendicular innervation for future comparative studies.

EMBRYOLOGY IN PHYLOGENY

Morgan (1890) begins his lecture, *The Relationships of the Sea Spiders* by announcing that his "point of attack is to be largely from the side of the embryology of the groups" (p 145). E.B. Wilson had emphasized adult sea spider anatomy, A. Hoek and P.P.C. Dohrn emphasized the larval phase, but both had neglected pycnogonid embryology. Within the theoretical framework of evolutionary morphology comparative embryology was considered imperative for tracing the evolutionary history of different groups, offering a criterion independent from comparative adult anatomy for determining relationships. Early in the 18th century, the German anatomist, Johann Friedrich Meckel (1781–1833) put forward the theory that developmental stages revealed the progression of the organism from lower forms to its present state. Throughout the 19th century, morphologists acknowledged the similarity between embryonic stages among members of a group and promoted the ideas from the German embryologist Karl Ernst von Baer (1792–1876). Von Baer maintained that the tendency of change during development was from the undifferentiated and general to the specific and determined. In this way, likeness between animals during early ontogeny could be used as evidence for phylogenetic relationships. Furthermore, Darwin's theory of evolution by natural selection had provided an explanation for why earlier stages might be expected to be conserved across taxa— largely immobile and nonfeeding early stages did not seem to competitively interact with their environment and thus the struggle to adapt diminished.

Thus, if Morgan was interested in finding a challenging thesis project, adding comparative embryology to his pursuit of sea spider phylogeny would have been recommended as one such topic. In *A Treatise on Comparative Embryology*, Balfour notes that if early stages clearly followed the conserving laws of heredity as predicted by Darwin and Von Baer, phylogenetic reconstruction would be simple. He warns, however, that "the embryological record, as it is usually presented to us, is both imperfect and misleading (Balfour, 1880; p 3)." E.B. Wilson had noticed as well that trends in development and evolution were not simple to detect.

Every living being, at every period of its existence, presents us with a double problem. First, it is a complicated piece of mechanism, which so operates as to maintain, actively or passively, a moving equilibrium between its own parts and with its environment …. But in the second place, the particular character of this adaptation cannot be explained by reference to existing conditions alone, since the organism is a product of the past as well as of the present … Phenomena of the latter class may, for the sake of brevity, conveniently be termed 'ancestral reminiscences' (Wilson, 1878; p 1).

CLEAVAGE AND GERM LAYER FORMATION

Complications aside, Morgan began his work by observing and documenting the development of three pycnogonid species. In general, Morgan compared embryological processes rather than single structures during development, reflecting the fact that the developing embryo is hardly static, and therefore difficult to compare at a single point in time.

The initial series of mitotic cell divisions following the egg stage was called the segmentation or cleavage of the early embryo. Around 1890, cell lineage studies were still in their infancy, and so instead, it was common practice to compare the segmentation patterns across taxa. Morgan's problems began when he observed variation in segmentation between pycnogonid species. Outside of the variation attributable to yolk quantity there were no sound theories for

why one egg would develop differently from another. There seemed no adaptive advantage for variation and the species were all clearly derived from a common pycnogonid ancestor, thus possessing the same heritable "substance." Morgan (1891) suggested that mechanical forces, such as gravity and pressure, as opposed to heritable programs, could be factors during development, but available data could not discriminate among these possibilities:

> The embryo differentiates earlier in what corresponds to the anterior region of the adult than over the whole ventral surface, which suggests that the smaller cells may have adapted themselves to this early differentiation; but it seems equally possible that this differentiation may be due to phylogenetic laws in this particular case rather than to any mechanical connection with the micromere differentiation. So that for the present the question must remain unsettled until by actual experiment (which would not be difficult) the orientation of the segmentation planes be determined (p 22).

To observe variation at this early stage in development must not have been a complete surprise to Morgan. Other embryologists had already questioned the reliability of segmentation in divulging relatedness (Balfour, 1880). Although some cleavage patterns, such as spiral cleavage in which the orientation of cell spindles at mitosis is at a determined angle relative to the egg axis, held true for most mollusks and annelids, other groups, such as the crustaceans, cleaved irregularly. Balfour (1880) admitted that "... similarity or dissimilarity of segmentation is no safe guide to affinities. In many cases, it is true, a special type of segmentation may characterize a whole group; but in other cases very closely allied animals present the greatest differences with respect to their segmentation" (p 100). The "particles of inheritance" were a black box and it was not clear if the pattern of early cell division was a consequence of inherited material or if the characteristic features of the organism were resting in the initial cells as potential only to be expressed later in the development.

The primary embryological phenomenon that Morgan emphasizes in his studies is the formation of endoderm. Both in Balfour's (1880) *A Treatise on Comparative Embryology* and Gegenbaur's (1878) *Elements of Comparative Anatomy*, the formation of germ layers was considered phylogenetically important as opposed to the less understood and more variable process of embryonic segmentation. Organs could be observed forming from germinal layers, and therefore these layers were at the root of structural homology when anatomical comparisons were made between taxa. As a result of decades of emphasis on germ layer formation, Balfour's (1880, 1885) *Treatise*, includes a collection of case studies, summarizing what was known about germ layer formation across taxa. Two main processes that were distinguished at this stage are invagination (Fig. 3A), in which cells ingress at a single point to form the endoderm, and delamination, in which inner cells divide to form the endodermal layer and outer cells become ectodermal. Morgan describes the formation of pycnogonid germ layers as "multipolar delamination" (Fig. 3B). During multipolar delamination the sphere of cells comprising the early embryo divides simultaneously, and inner cells give rise to early endoderm. The process Morgan observed in pycnogonids appeared to be similar to what had been described previously in false-scorpions and spiders.[3] Multipolar delamination was treated as an important similarity (process homology in modern terminology) uniting arachnids and pycnogonids to the exclusion of crustaceans.

In his dissertation, Morgan (1891) expanded the discussion of multipolar delamination to include the alternative interpretation that such a process may be acquired independently. He notes that insects have been described as forming endoderm similarly, yet insects share little else with the pycnogonids that might indicate "special affinity," or rather, descent from a recent common ancestor. Morgan, however, was not the first to question the evolutionary significance of the germ layer process. Simultaneously, Haeckel's contemporary, the German anatomist Wilhelm His (1831–1904), was attacking germ-layer homology by demonstrating that the causes of germ-layer movements might be governed by the mechanics of cell growth (reviewed in Maienschein, '91a).

Even though these commentaries from Morgan's dissertation might seem to be subtle and disjunctive, at the time they posed substantial questions that would prove consequential in the future.

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[3] These reports refer to Metschnikoff, E. (Entwicklungsgeschichte des Chelifer. Zeit. f. wiss. Zool., XXI, 1871) and Balfour (Notes on the Development of the Araneina. Quart J. Micr. Sci., vol. XX, 1880).
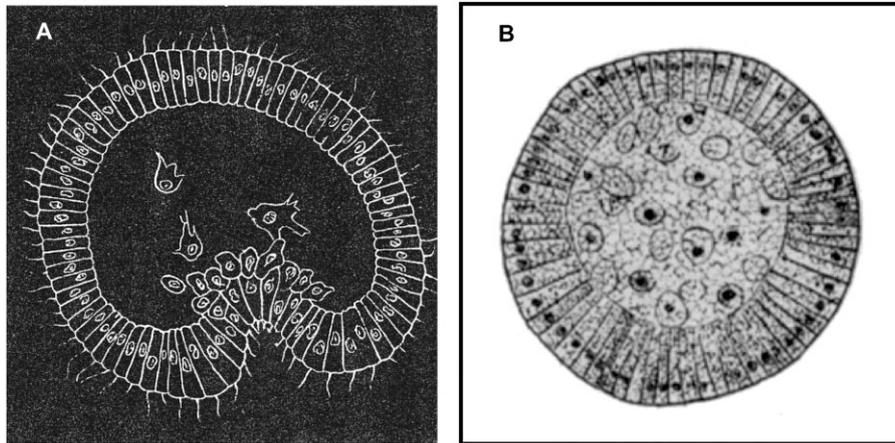
Fig. 3. (**A**) Figure modified from Balfour (1885) depicting an optical section during germ layer formation by the process of invagination in the sea cucumber, *Holothuria tubulosa*. (**B**) Figure from Morgan (1891) depicting a section of a sea spider (*Tanystylum)* embryo during germ layer formation by the process of multipolar delamination.

Uncertainty regarding ontogenetic flexibility shook the foundations of contemporary phylogenetics. Without understanding the mechanism behind cell specification and differentiation during multipolar delamination, the extent to which these embryonic processes were predetermined and heritable was speculative at best.[4] Morgan was undoubtedly aware of the movement toward experimental embryology called *Entwicklungsmechanik* (developmental mechanics) spearheaded by Wilhelm Roux (1850–1924) and others in Europe, who sought to understand the relative importance of external and internal factors in development. The basic premise of *Entwicklungsmechanik* was that embryonic development was difficult to understand simply by observation and that experimentation provided a way to answer questions about what was occurring within and between cells. Soon after his graduation, Morgan would travel to the *Stazione Zoologica* in Naples to investigate the role of the cytoplasm in the transfer of cellular information during development and regeneration. Morgan (1898)became one of the movement's leading advocates in the US, explaining its goals to a wider audience, "...in the definition of developmental mechanics as the study of the causal morphology of the organism, Roux means simply that the changes in form through which the embryo passes are the result of a series of causes, and these causes are what the new study proposes to investigate" (p 12).

HOMOLOGY OF APPENDAGES

Most studies in arthropod evolution discuss which appendages might be equivalent among taxa (Table 1). In *Elements of Comparative Anatomy*, Gegenbaur (1878) emphasizes the goal of using phylogeny to reveal anatomical homology and to infer adaptation "with certainty" based on variation between homologous structures (p 9). As Pycnogonid limbs are structurally dissimilar to the limbs of other arthropods the job of assigning appendicular homology is particularly complicated, and, to this day, remains in flux (Budd and Telford, 2005; Dunlop and Arango, 2005; Maxmen et al., 2005; Jager et al., 2006). Morgan regarded the problem off appendicular homology in the pycnogonids as the "stumbling block," repeating the phrase that Wilson (1881) had used earlier. On the basis of embryology, Morgan was uniting the pycnogonids with the arachnids, and following this hypothesis he aligned the appendages between the two groups. Initially it would appear that the four pairs of pycnogonid walking legs[5] correspond to the four pairs of legs observed in arachnids. Pycnogonids, however, also have three appendages associated with head segments (chelifores, palps, and ovigers), whereas arachnids have two (chelicerae and pedipalps). In his early work, Morgan (1890) assumed that pycnogonid and spider appendages correspond along the length of the body, and that the "extra"

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[4] For an evaluation of the role of experimental embryology in the emergence of the chromosomal theory of inheritance refer to Gilbert ('78).

[5] Some pycnogonids bear five or six pairs of appendages, complicating the problem further.

TABLE 1. The homologies of pycnogonid appendages to those of other arthropods alluded zoologists for over a century[†]

pedipalp
chelifore   chelicer   palp
                                                                                          chelicer
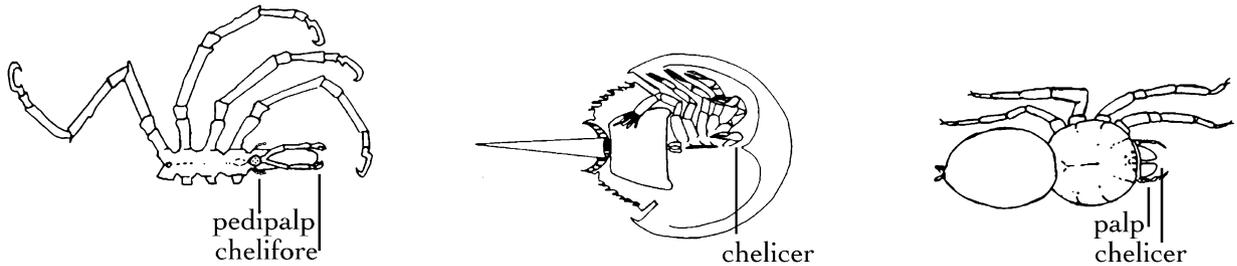
Tab. I. *A Half-century of homologies.*

Somite	CARPENTER, 1905			WIRÉN, 1918			FAGE, 1949			FERRIS & HENRY, 1949—53		
	Pyc.	Xiph.	Arach.	Pyc.	Xiph.	Arach.	Pyc.	Xiph.	Arach.	Pyc.	Xiph.	Arach.
1	*M O U T H* eyes	eyes	eyes	*M O U T H* dorsal antimere	rostrum	rostrum	Chelifores & dorsal antimere	Chelicera	Chelicera & labrum	*M O U T H* proboscis	rostrum	labrum
2	—	—	rostrum	chelifores	chelicera	chelicera	palpi & ventral antimeres (*ovigers*)*	*M O U T H* 1st leg	pedipalps	base of proboscis	base of rostrum	[absent]
3	chelifores	chelicera	chelicera	"pedipalp" & ventral antimeres	pedipalps	pedipalps	1st leg	2nd leg	1st leg	chelifores	outer carapace	chelicera
4	palpi	—	—*	palpi	1st leg	1st leg	2nd leg	3rd leg	2nd leg	palpi	pedipalps	pedipalps
5	ovigers	1st leg	pedipalps	oviger	2nd leg	2nd leg	3rd leg	4th leg	3rd leg	ovigers	2nd leg	1st leg
6	1st leg	2nd leg	1st leg	1st leg	3rd leg	3rd leg	4th leg	5th leg	4th leg	1st leg	3rd leg	2nd leg
7	2nd leg	3rd leg	2nd leg	2nd leg	4th leg	4th leg	abdomen	pregenital	[pregenital]	2nd leg	4th leg	3rd leg
8	3rd leg	4th leg	3rd leg	3rd leg	abd. 1	abd. 1		genital	genital	3rd leg	5th leg	4th leg
9	4th leg	5th leg	4th leg	4th leg	genital	genital	*(non-homologous)*			4th leg		
10	abdomen	pregenital	[pregenital]	abdomen						abdomen		
11		genital	genital									

*Vestigial in *Epeira*
[Items in brackets refer to condition in the scorpion]

[†]Wilson (1881) and Morgan (1891) referred to the problem as the "stumbling block" in pycnogonid phylogenetics. Table 1 is reproduced from Hedgepeth ('54: p 200) and figures of the pycnogonid, horseshoe crab (to represent Xiphosura), and spider (to represent arachnid) have been added by the author.

appendage is the final pair of pycnogonid walking legs, which, he explains, have been subsequently lost in other arachnids. To account for the appendicular transformation in the evolution of the lineages from a pycnogonid–arachnid ancestor, Morgan (1890) presents a hypothetical scenario, "We may imagine, if we like, that this took place at a time when the third pair of appendages [the ovigerous legs] appeared and began to carry the eggs, so that the body, by utilizing the first legs as egg carriers, retained a pair of the abdominal legs for purposes of locomotion" (p 156).

In contrast, hypothetical scenarios are conspicuously absent from Morgan's dissertation. Morgan ('05) would later denounce such unsubstantiated stories, "It seems to me that the method of the Darwinian school of looking upon each particular function or structure of the individual as capable of indefinite control through selection is fundamentally wrong" (p 57). Morgan's change in attitude can be seen when comparing his speculative scenario from 1890 on leg evolution between sea spiders and arachnids with a later statement on scientific methodology, "[Hypotheses] have been used…to hold together a body of isolated facts; as such they are in reality only fictions. They have been used in the reconstruction of supposed historical events, especially in

biology in the setting up of family trees'' (Morgan, '07; p 6).

A corollary of Morgan's hypothesis that appendages of pycnogonids and arachnids were homologous along the length of the body was that the first pair of appendages, pycnogonid chelifores and arachnid chelicerae, were homologous. Special homology, as defined by Gegenbaur (1878), required that the two structures be of similar descent and also develop from the same anlagen. For this reason, Wilson (1881) and Dohrn (1881) had rejected the homology of pycnogonid chelifores and arachnid chelicerae because of the difference in the origin of nerves targeting the first appendages. Balfour (1880) referred to their studies when he distinguished the pycnogonids, with anterior appendages innervated from the supraoesophageal ganglion, from horseshoe crabs whose appendages are all post-oral. In the early works, Morgan (1889, 1890) ignores the voices of dissent and supports correspondence of chelifores and chelicerae with simple, unillustrated descriptions of structural similarity, innervation from the brain, and a common developmental origin—both appendages arise heterolateral to the stomodeum. The conclusion remains the same in his dissertation, yet the discussion is expanded to include ontogenetic divergence in the formation of the first appendages (Fig. 4). According to Gegenbaur (1878; p 64), assigning ''special homology'' was the ultimate task of comparative anatomy, and it required corresponding structures to share a common origin as well as common descent. Morgan (1891) had already concluded that pycnogonids were related to arachnids based on embryological processes, and although he agreed that during development arachnid appendages are innervated at a more posterior point than in pycnogonids, he maintained that the two appendages remained homologs, ''Chelate appendages are innervated in the adults [pycnogonids] by supraoesophageal ganglia…though, all the appendages in the embryos of true arachnida are innervated by post-oral ganglia…the early innervation of this pair from the brain itself may be regarded as a more abbreviated condition than what was seen in spiders'' (p 30). Disparity during neurogenesis is noted, ''The absence of brain invaginations would be a more weighty objection against the relationship of the two groups [arachnids and pycnogonids]'' (Morgan, 1891; p 30). Ultimately, however, the disparity is dismissed, in that Morgan does not take this variation as necessitating reassessment of homology statements.
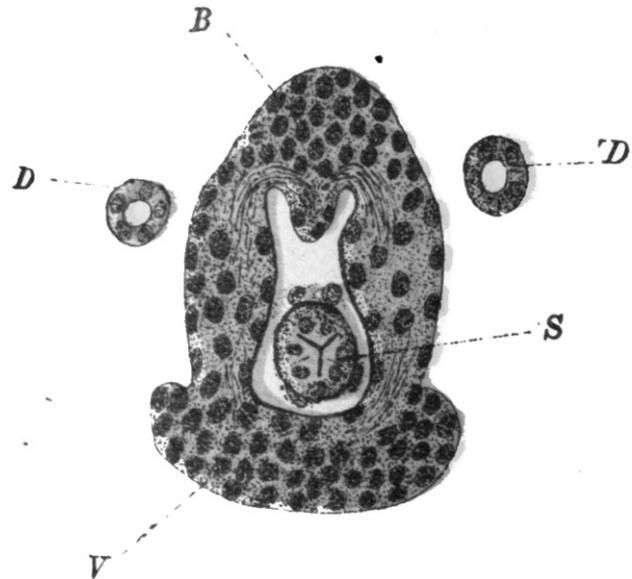
Fig. 4. Figure from Morgan (1891; Plate I, Fig. 14) depicting a section through the anterior portion of the pycnogonid larva of *Tanystylum orbiculare*. The section passes through the brain (B), the circumoesophageal ring, and a pair of ventral ganglia (V). On either side of the brain are a pair of diverticula (D, ′D) leading to chelifores that receive nerves from the brain.

Likewise, Morgan (1891) describes and subsequently downplays a potentially important feature of neurogenesis relating pycnogonids to the onychophoran (''velvet worm''), *Peripatus*. Comparing ''ventral organ'' development in the pycnogonids with *Peripatus*,[6] ''a striking similarity is seen…Whether these structures are in any way related is impossible to say, but it is worthwhile to call attention to the close similarity both in position and structure between these organs in the two groups'' (p 24). Onychophorans were considered to be potential intermediates between annelids and arthropods, thus this character would support a separate lineage of pycnogonids. Yet, Morgan refrains from suggesting that the similarity in neurogenesis between pycnogonids and onychophans should override similarity of germ layer formation between pycnogonids and arachnids. There was no clear reason to favor one criterion over another.

In retrospect, a confounding problem was that phylogenetic methods were often circular prior to work by the systematist Willi Hennig (1913–1976). Homologous traits were defined by phylogeny, and those traits were then recycled for reconstructing

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[6] Morgan is referring to Sedgwick, A. (A Monograph of the Development of *Peripatus Capensis*. Stud. Morph. Lab., Camb., IV, Pt.I, 1888).

phylogenies. Morgan's comparative embryology had convinced him of a relationship between pycnogonids and arachnids, and so appendages of pycnogonids and arachnids simply had to be homologous. Not understanding the extent to which developmental trajectories were flexible undermined confidence in homology statements and this was a consistent source of conflict in phylogenetic reconstruction.

LARVAL EVOLUTION

A large portion of Morgan's attention was devoted toward establishing the relevance of the post-embryonic larval stage, the protonymphon, in phylogenetic reconstruction (Fig. 5A). Again, Morgan's emphasis follows precedence. As with other early stages, the observation of similar larvae between dissimilar adults had been used as proof of relatedness. For example, the trochophore larva united annelids and mollusks, and the nauplius larva had connected barnacles with other crustaceans. In *A Treatise on Comparative Embryology*, Balfour (1885) wrote, "There is a high chance of the ancestral history being preserved in the foetus or the larvae" (p 362). Pycnogonids were commonly grouped with crustaceans based on resemblance of their pelagic larvae, the protonymphon and nauplius, respectively. Each is arthropodian, small and roundish, has a median visual apparatus, and bears three appendages. During Morgan's graduate career, however, Hoek and Dohrn retracted their earlier ideas of crustacean affinity, and independently decided that the differences between the protonymphon and nauplius were significantly large. This led them to conclude that the protonymphon was a separate derivative of a trochophore-like ancestor. To this end Dohrn proposed a hypothetical transformation of the trochophore larva into the protonymphon. Although Morgan adamantly disagreed with this imaginative scenario, the hypothesis continued to receive attention well into the 20th century, perhaps best exemplified by zoologist Joel Hedgepeth's ('54; p 15) playful stanza:[7]

The pycnogonid leads a parasitic youth,and never grows a large abdomen;A precocious polychaete perhaps,of arthropods a paedomorphic omen.

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[7] Joel Hedgepeth's stanza was written in the style of Walter Garstang, whose delightful poems on larval forms were published posthumously in 1951.

After examining the evidence for both the trochophore and naupliar arguments of relatedness, Morgan (1891) wrote, "an answer is exceedingly difficult to give" (p 33). Excluding a priori phylogenetic expectations, the protonymphon is not affiliated clearly with any other larva. Instead he emphasized the uniqueness of the protonymphon. For one, the protonymphon lacks an anus, "not a trace of proctodaeum does the pantopod-larva possess...no reasonable account can, I believe, be given to explain how this posterior opening could have become lost in transition of the trochophore into pantopod-larva"(p 33). Pressured to speculate, Morgan argued that larvae may be generated de novo, and thus would reveal little about evolutionary relationships (Fig. 5B). Here, Morgan followed almost exactly a discussion from Balfour's (1885) *Treatise of Comparative Embryology* (p 363) distinguishing two evolutionary forms of larvae. One form represented a modified version of the adult ancestor of the group, and the second form was introduced as a larva early in the lineage, conserved among members, yet did not represent the ancestor. In a sense, the first form is reminiscent of recapitulationist theories and the second resembles Karl Ernst von Baer's ideas of similarity among the undifferentiated early stages before specialization of adult morphology. Finally, Morgan (1890) seems to have created a third larval type, not discussed by Balfour, and he suggests the pycnogonid protonymphon has evolved in this manner. In the third type "larval forms are affected by the new characters of the adult...we may suppose the newly acquired characters of the adult to be thrown back upon the larval form already present" (p 160). Once again, Morgan is skeptical about the constraint that is assumed to exist during organism development. He denounces the tradition of assigning primary importance to particular larval stages. "The necessity of believing that the young forms, in such groups as Annelids, Crustacea, more nearly resemble each other than do the adults seems to me an entirely unwarranted supposition." Morgan (1890) argues that because the death rate is far greater for pelagic larval forms than adults, selection acts more vigorously, and results in rapid adaptive responses at immature stages in animals with pelagic larva. Therefore, "...in such groups as the ones we are discussing,—Annelids, Crustacea, etc.,—we ought to expect....the reverse of what we find in such a group as the higher vertebrates; viz. that the young forms diverge
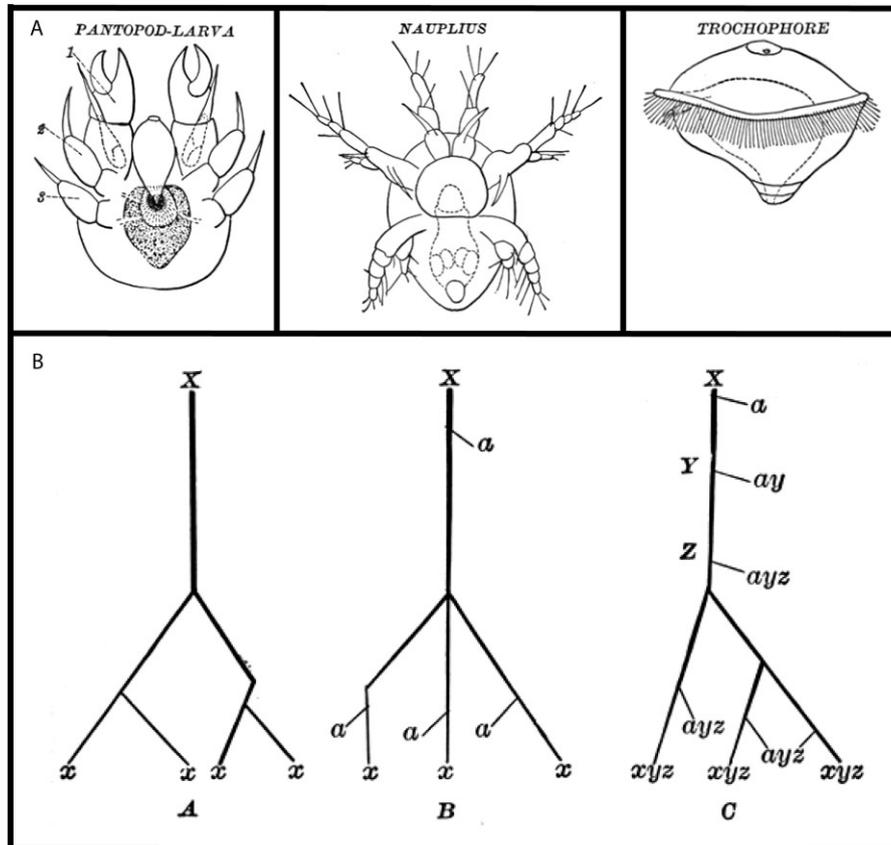
Fig. 5. (**A**) Figures from Morgan (1890) of the pycnogonid (= pantopod) larva, hypothesized to descend from the crustacean nauplius or the annelid trochophore larva. (**B**) Three models of possible mechanisms by which a larval form evolves within any group of animals. Morgan presents this diagram (1890) and explains that larva may not be important from a phylogenetic point of view. These conditions include: a primary larval form (*A*) in which the larva represents the ancestral condition, and the adult forms diverge; A condition (*B*) in which adults each share a similar larva *a* possessed by the ancestral adult *X* of the group; and (*C*) a condition in which the adults evolve and their corresponding larvae are subsequently changed such that *a* is changed to *ay* and *az* as the adult *X* changes into *Y* and *Z*.

far apart and the adults come nearer together'' (p 166).

In the chapter entitled *Criticism of Dorhn and Hoek*, his opinion remains unaltered: The protonymphon shares no significant similarity with either the trochophore or nauplius. Larval similarity previously had been the basis for comparison with annelids and crustaceans, respectively. Thus, after eliminating these possibilities Morgan presents the reader with a final option, pycnogonids have evolved independently or from an ancestor shared with arachnids. Hesitantly, Morgan (1890) places the pycnogonids nearer to the arachnids than other arthropods. ''The very great differences in the adult structure of the groups [pycnogonids and arachnids] indicated no very recent origin, but possibly they came in at a time when the Arachnids had the first pair of appendages chelate, and these were innervated from the

supraoesophageal ganglia'' (p 34). The troublesome protonymphon is discarded completely from analysis, ''After the divergence of the pycnogonids as a group from the general phylum of the arachnids, the pantopod-larva may have developed'' (p 34).

In the decade after Morgan's dissertation, larval evolution received a good deal of attention. Although some larvae reveal evolutionary relationships, the environmental pressures of aquatic life can result in convergent morphologies. As Wilson (1898; p 1) stated, ''many of the most interesting and hotly contested controversies of modern embryology have been waged in discussions of the possible ancestral significance of larval forms, such as the trochophore, the Nauplius, and the ascidian tadpole''. At the time, little was known about the basis of inheritance and the evolvability of ontogeny to thoroughly address

these questions. Among others, Morgan ('27) continued to think about that subject and would latter use genetic crosses to study the inheritance of larval characters.

CONCLUSION

In the end, Morgan's (1891) conclusion remains defeatist. He is skeptical about his own phylogenetic conclusions, "Whether future work supports or disproves such a hypothesis [pycnogonid and arachnid affinity], it is hoped that it may be useful, if only as furnishing another point of view for looking at the phylogeny of the Pycnogonids, or may lead to a more complete study of the embryology of the group" (p 35). During the same Marine Biological Laboratory seminar at which Morgan (1890) presented his findings, E. B. Wilson ended his relatively inconclusive discussion of annelid segmentation stating that "...the present need is for new facts, not for new theories. When the facts are forthcoming, the theories will take care of themselves" (p 78).

In the detailed manner characteristic of Morgan throughout his career, he identified the key issues pertaining to the role of inheritance and variation in ontogenetic processes, exemplified in his discussions of the properties of conservation during embryonic cleavage and germ layer formation, varied development of similar appendages, and the evolvability of larval stages. To fulfill the objective of his thesis topic, he was forced to overlook weaknesses in the current system. Had he explicitly attacked recapitulation or speculative biology in the thesis, he would have risked inciting influential people as a graduate student and perhaps his burgeoning scientific career would have been prematurely obstructed.

After graduation, Morgan abandoned the practice of using comparative morphology to uncover phylogeny, joined the experimental movement, and sought out new methods of obtaining data that would directly test hypotheses about variation during ontogeny. A transition from descriptive/comparative to experimental/mechanistic approaches was taking hold in the younger scientific community in the decade after Morgan's graduate research. Morgan himself traveled several times to the *Stazione Zoologica* at Naples (1890, 1894–5, 1900) and allied himself with those studying embryological problems for their own intrinsic merit rather than as a means for phylogenetic reconstruction.

Almost 40 years after his dissertation, Morgan would again emphasize the methodological problems inherent in applying embryological data to draw phylogenetic conclusions. "It goes without saying that little or nothing has been contributed by such a procedure [embryology] to the study of heredity partly because the problems involved are too complex" (Morgan, '27; p 594). Just as he later argued that heredity had to be separated from embryology for science to progress,[8] in his graduate research he emphasized that embryology had to be first disengaged from phylogeny before it could be understood in its own right.

At several times, Morgan ('19) reflected back critically on the phylogenetic tradition: "[The biologist] gets confused and thinks that he is explaining evolution when he is only describing it" and he referred to morphologists as philosophical anatomists[9] and historians (Morgan, '09). Needless to say, Morgan never returned to his graduate work on the pycnogonids, nor to phylogenetic studies. He did, however, continue to work on embryology each summer and for most of his final years.[10] He never grew tired of observing embryos develop, only of presumptuous and speculative answers. He emphasized continuously that only through careful observations of the diversity of forms new avenues for research would emerge. For him the big questions, such as the role of ontogeny in phylogeny, had to be broken down into operational units and approached as components of a larger problem. Following this prescription, Morgan's pursuits would eventually return to problems of evolutionary theory. On the way, he and his associates laid the foundations for genetics, developing an operative approach to the study of inheritance and variation (Sturtevant, '59).

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[8] For an analysis of the role of embryology in the development of genetics refer to Gilbert ('78, '87) .

[9] "The morphologists, or philosophical anatomists, form the second great group of students whose activity is a direct outgrowth of Darwinism. The determination of the relationships of the great classes of animals on the principle of descent has occupied much of their time. Two other important fields of labor have also fallen to their share. The study of development or embryology has been almost exclusively pursued by morphologists inspired in large part by the theory of recapitulation. Systematists and morphologists alike have been evolutionists, but it is a curious fact of zoological history that until very recently there has been no body of students whose interests have been directed *primarily* toward the problems of evolution...Is it not strange, therefore, with all the real interest in the theory of evolution, that so few of the immediate followers of Darwin devoted themselves exclusively to a study of that process?" (Morgan, '09; p 372).

[10] In his later years, Morgan developed a marine laboratory at the California Institute of Technology. In the outline of his plans for the department, Morgan ('27) wrote, "Life began in the sea and there lie some of the greatest historical problems of biology" (as cited in Allen, '78; p 335).

EPILOGUE

Over a century after Morgan's dissertation, pycnogonids have lost none of their original mystique, their affiliation with other arthropod classes (Chelicerata, Myriapoda, Crustacea, and Hexapoda [including the insects]) remains ambiguous. In recent morphological and molecular phylogenetic analyses pycnogonids are placed as either sister taxon to the chelicerate (Wheeler and Hayashi, '98; Regier et al., 2005) or as a separate class, basal to all remaining extant arthropods (Zrzavπ et al., '98; Giribet et al., 2001). Today, if a doctoral student looking for work referred to zoologist Claus Nielsen's (2001) *Animal Evolution: Interrelationships of the Living Phyla*, a respectable resource on comparative zoology, they would find the embryology of pycnogonids and the ontogeny of the pycnogonid brain listed among topics in the concise section entitled ''interesting subjects for future research.'' As zoologist Wilhelm Fahrenbach ('94) wrote, ''Pycnogonids display a hybrid array of fine structural features that variously serve to relate them to some arthropod subphyla and distance them from others'' (p 44).

Taking Fahrenbach's statement a step further, it is not merely a problem of the array characters pycnogonids exhibit, but also that those characters are not discreet. Defining the head, for example, remains controversial. During development the head includes three pairs of appendages and as an adult it would appear to include those three along with the first pair of walking legs. Thus, similarity of structures *between* taxa has been complicated to define. Adding to the complexity of using similarity as criteria for homology, evidence of dissociation at different levels of organization is manifest in both Morgan's work as well as in recent investigations. Morgan questioned whether or not similar embryonic processes (e.g. mesoderm formation) that he observed were necessarily indicative of common descent. Likewise, today there is evidence of similar embryonic processes, controlled by orthologous genes, that result in the construction of nonhomologous structures, such as with the development of fly and mouse eyes. Morgan also observed that the first pair of pycnogonid appendages, chelifores, arose at a different position than the supposedly homologous first pair of arachnid appendages, chelicerae. The question is whether or not this finding was significant enough to negate the correspondence of chelifores and chelicerae. Cases demonstrating varied development of homologous structures have mounted over the century. For example, the same skull bones in various amphibians can be found to arise from different germ layers (Hanken and Gross, 2005).

Ideally, the homology of structures is corroborated at multiple levels (i.e. gene, embryology, position, structure). The correspondence of pycnogonid chelifores with the appendages of other arthropods has received considerable attention owing to the complexity of the problem (Maxmen et al., 2005; Jager et al., 2006). Evidence drawn from different levels is discordant. Chelifores share some structural similarity to chelicerae, but the structures are in other ways different. For example, pycnogonid chelifores bear excretory organs, whereas the excretory organs in chelicerates only occur posteriorly on the body (Fahrenbach, '94). The origin and points of cheliforal innervation differ from that of chelicerae (Maxmen et al., 2005; Morgan, 1891), yet the two structures appear to share some similarity at the level of gene expression (Jager et al., 2006).

To Morgan, as to the modern evo–devo community, the nonlinear processes of development are most enticing. As Morgan ('07) said, ''The most distinctive problem of zoological work is the change in form that animals undergo, both in the course of their development from the egg (embryology) and in their development in time (evolution)''.

ACKNOWLEDGMENT

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