EVOLUTION OF POLYEMBRYONIC DEVELOPMENT IN PARASITIC WASPS

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Major developmental innovations have been associated with adaptive radiations that have allowed particular groups of organisms to occupy empty ecospace. However, an understanding of the evolutionary forces and molecular mechanisms behind developmental novelties still remains tenuous. A little studied adaptive radiation in insects from the developmental perspective is the evolution of parasitism. The parasitic lifestyle has allowed parasitic insects to occupy a novel ecological niche where they have evolved a plethora of life history strategies and modes of embryogenesis, developing on or within the body of the host. One of the most striking adaptations to development within the body of the host includes polyembryonic development, where certain wasps form clonally up to 2000 embryos from a single egg. Taking advantage of well-established insect phylogeny, techniques developed in a model insect, the fruit fly, and a wealth of knowledge in comparative insect embryology, we are starting to tease apart the evolutionary events that have led to this novel mode of development in insects.

KEY WORDS: embryogenesis, evolution of parasitism, molecular mechanisms.

INTRODUCTION

Polyembryonic development represents the formation of multiple embryos from a single zygote. The accidental form of polyembryonic development, where an individual egg occasionally forms multiple embryos, has been described in almost all animal groups studied to date (Olsen 1962; Stansfield, 1968; Kaufman, 1982; Laale, 1984; Ashworth et al., 1998). This accidental form of polyembryony suggests that eggs of otherwise monoembryonic species have the regulative capacity to generate multiple embryos. On the other hand, obligatory polyembryonic development, where a single zygote of certain species invariably produces multiple embryos, is a relatively rare event in metazoans, but quite frequent in plants (Shaanker and Ganeshaiah, 1996; Carman, 1997). In metazoans, obligatory forms of polyembryonic development are present in both vertebrates and invertebrates. Species exhibiting polyembryonic development are scattered in multiple phyla including Cnidaria, Platyhelminthes, Arthropoda, Bryozoa, Echinodermata and Chordata (reviewed in Craig et al., 1997). It should be noted that in certain groups, the source of clones is not the embryo but the larva, as in all described cases of polyembryony in the phila Cnidaria and Echinodermata, and in Cestodea and Trematoda (Platyhelminthes) and Crustacea (Arthropoda) (Noble et al., 1989; Shostak, 1993; Glenn and Hoeg, 1995; Jaeckle, 1994).

The focus of this review is obligatory polyembryony in insects that arises by embryonic cloning. The term polyembryony denotes both the developmental process, and the form of reproduction. Developmental processes include complex cellular and molecular events whereby multiple embryos form clonally from a single zygote. In addition, polyembryony refers to a unique form of reproduction in which a single egg results in multiple progeny, maximizing the reproductive capacity of the species and increasing its fitness. Along with its ecological and reproductive ramifications, study of the phenomenon of polyembryony in insects has the potential for addressing one of crucial questions in the evolution of development: How do developmental novelties arise? Polyembryony in insects represents a developmental novelty whereby both precursor structure and evolutionary processes are basically unknown (type A novelty sensu Wilkins, 2001). In general, true developmental novelties are rare and often their evolution is not easily tractable. However, the combination of a relatively well-established insect phylogeny, embryological studies of insect polyembryony that span more than a century (Marchal, 1898), and techniques and concepts established in a closely-related model Arthropod, Drosophila melanogaster, demonstrate a promising system that could provide clues as to how complex developmental novelties are formed.
MULTIPLE EVENTS OF INDEPENDENT EVOLUTION OF POLYEMBRYONIC DEVELOPMENT IN WASPS

Hymenoptera (wasps) represents a holometabolous insect order that consists of two suborders. Suborder Symphita includes basal plant-eating groups, and Apocrita, an advanced group of parasitic species (Figure 1). Hymenoptera possess polytrophic meroistic ovaries (BUNING, 1994) and basal groups produce yolky eggs which undergo long germband embryogenesis (SPEICHER, 1936; FLEIG and SANDER, 1986, reviewed in SANDER 1976). Apocrita (parasitic wasps plus ants and bees) represents a monophyletic assemblage which includes ectoparasitic species (laying the egg on the surface of the host), endoparasitic species (ovipositing within the body of the host), and free-living pollinators including eusocial species (WHITFIELD, 1998). Basal species in all parasitic groups whose life histories are known appear to be ectoparasitic. They lay large yolky eggs, and undergoing long germband development, such as described in the honeybee (FLEIG, 1990; BINNER and SANDER, 1997) and the endoparasitic basal braconid *Bracon hebetor* (GRBIC and STRAND, 1998). This suggests that the basal state of embryonic development in parasitic wasps includes canonical long germband development associated with meroistic polytrophic oogenesis, where critical determinants are transcribed in nurse cells and transported to the oocyte in a manner described in *Drosophila*. However, many parasitic lineages contain parasitic species that have evolved a derived form of development within the body of the host (endoparastites). This switch in life history strategy subjects them to a different selection regime compared to other terrestrial insects. The evolution of endoparastism appears to be crucial for further evolutionary innovations, such as polyembryony. Polyembryony evolved independently four times in wasps: in Braconidae, Encyrtidae, Dryinidae and Platygasteridae (IVANOVA-KAZAS, 1972). The association of endoparasitic lifestyle with evolution of polyembryony is strengthened by the fact that the only other case of polyembryony in insects is displayed by endoparasitic Strepsiptera (NOSKIEWICZ and PÓLUSZYNISKI, 1935).

POLYEMBRYONIC EMBRYOGENESIS: EMBRYOLOGICAL INNOVATIONS

Independent evolution of polyembryony evokes several important questions. First, what is qualitatively novel in polyembryonic development relative to canonical insect embryogenesis? Second, which

Figure 1
Phylogeny of Hymenoptera (modified from Whitfield 1998). Families that display polyembryonic development are highlighted by gray shading. Drawing of the egg illustrates long germband development of more primitive basal Hymenoptera.
elements of the regulatory mechanisms were modified to result in a novel, obligatory form of embryo cloning? Finally, understanding such independently evolved, but similar novelties could inform us about evolutionary constraints and plasticity. For example, are there multiple pathways in the evolution of certain features, or are similar evolutionary innovations based on a common program?

Thus far, our model insect for polyembryonic development has been the polyembryonic encyrtid *Copidosoma floridanum* (Silvestri, 1906; Grbic et al., 1996; Grbic et al., 1998, Zurov et al., 2004). This wasp parasitizes noctuid moths and produces up to 2000 embryos from a single egg. However, a poor understanding of encyrtid phylogeny and a lack of knowledge of closest monoembryonic ancestors led us to initiate studies on another independently-evolved polyembryonic wasp, the braconid *Macrocentrus grandii*. A better understanding of the phylogeny of braconids could help us to determine the closest monoembryonic relatives, and to generate a hypothesis about transitory forms that may have led to polyembryonic development. In addition, studies of multiple forms of polyembryony could uncover common features and possible variations in polyembryonic development.

**Polyembryony in *Copidosoma*: A Challenge for the *Drosophila* Paradigm of Development**

*Copidosoma floridanum* is a parasitic wasp that parasitizes the eggs of the host, the moth *Trichoplusia ni* (Fig. 2). After parasitization, the host emerges and undergoes five host instars. During the process of host development *Copidosoma* undergoes embryonic development within the host body surrounded by the nutritive insect blood (hemolymph). As a result of embryonic proliferation, up to two thousand larvae are formed synchronously during the fifth host instar. These larvae pupate and emerge as adult wasps.

The embryonic development of this endoparasitic insect differs dramatically from the development of other insects. First, *Copidosoma* oviposits tiny yolkless eggs (50mm in size, a size similar to mouse eggs) that are surrounded by a thin chorion. The first cleavage of the egg is total, and leads to the formation of two posterior blastomeres (which will give rise to the embryo proper) and an anteriorly localized polyploid cell (Fig. 2 gray) that results from the fusion of polar nuclei (Grbic et al., 1998). This cell will form the polyploid syncytial extraembryonic membrane (gray). The second embryonic cleavage creates one small blastomere and three equal-size blastomeres. The small cell (Fig 2 red) is different from the other cells as it retains an injected fluorescent tracer, and is thus dye-uncoupled from other cells (Grbic et al., 1996). Embryonic blastomeres then undergo cleavages and become enveloped by the syncytial extraembryonic membrane, and embryos emerge from the chorion into the host haemolymph and form primary morula. The primary morula implants in the host tissue and initiates the proliferative phase of development that increases cellular mass many fold (Grbic et al., 1998). In monoembryonic animals, developmental progression from that point in embryogenesis would include a transition from morula-stage
embryo to gastrulation and segmentation leading to a completely segmented animal. In contrast, «insertion» of the proliferative phase in the canonical monoembryonic developmental program represents the developmental novelty responsible for clonal production of thousand embryos in *Copidosoma*. The proliferative phase is initiated by the split of the primary morula and creation of the polymorula, which consists of many proliferative morulae. Each proliferative morula at this stage consists of hundreds of round, apparently non-differentiated cells (Fig. 2), surrounded by the extraembryonic membrane (GRBIC et al., 1998). These packages of cells become subdivided by the ingressing extraembryonic membrane into progressively smaller clusters of cells. When the number of cells per cluster reaches about 20-30 at the fourth host instar larva, these cells undergo a change in cell shape from round to fibroblastic. The establishment of cell contacts results in cell compaction and simultaneous de novo formation of 2000 embryonic primordia (GRBIC et al., 1998). Following compaction, each embryo undergoes gastrulation and segmentation to form larva. Thus, polyembryonic embryogenesis in *Copidosoma* shows similarities to mammalian embryonic development, including early separation of embryonic and extraembryonic lineages, morula morphology, implantation, compaction and most importantly the net increase of the embryonic mass that is unique to mammals (DAVIDSON, 1990; GURDON, 1992). These evolutionary changes apparently represent convergent evolution driven by the similar developmental environment: placental development in mammals and nutritive host environment in *Copidosoma*. Obligatory polyembryony evolved in mammals (armadillo) (FERNANDEZ, 1909) and insects (parasitic wasps), but while in mammals polyembryony is conceptually compatible with the regulative development of the mouse embryo, polyembryony in insects is in sharp contrast with maternal pre-patterning of the *Drosophila* embryo.

**MATERNAL PRE-PATTERNING IN *Copidosoma*: SPECIFICATION OF THE GERM-LINE**

The germ line is one of first developmental fates specified in many organisms (SAFFMAN and LASKO, 1999). The RNA helicase *vasa* is the ubiquitous germ line marker in metazoans involved in the specification of the primordial germ cell (PGC) lineage. PGCs represent the first cells that give rise exclusively to germ cells by clonal mitotic divisions (NIEUWKOOP and SUTASURYA, 1979). PGCs are progenitors of germ line stem cells (GSCs) that undergo self-renewal, differentiate into gametes, and ultimately produce all of the cell types in future offspring.

Isolation of the *Copidosoma vasa* mRNA (*Cfvas*) homologue and examination of its pattern of expression showed that *Cfvas* is transcribed in nurse cells in *Copidosoma ovaries* (ZHurov et al., 2004). Vasa protein localizes in the structure called oosome (ZHurov et al., 2004), which was proposed to be homologous to the *Drosophila* germ line pole plasma (nouage). Thus, in *Copidosoma* at least one asymmetrically localized maternal determinant is deposited in the forming egg. After oviposition Vasa protein is invariably localized into the dye-uncoupled small cell, showing that this early cellular asymmetry is also paralleled by a molecular asymmetry. In the primary morula this asymmetry is perpetuated in several cells that express Vasa protein (Fig 2, red). Following the initiation of the proliferative phase Vasa-positive cells are scattered in individual proliferating morulae (Figure 2). During the process of division, the daughter cells all inherit Vasa protein, suggesting that they represent cell lineage. Following the entrance into the morphogenetic phase each reproductive embryonic primordium receives two Vasa-positive cells. These cells remain localized at the posterior and give rise to the embryonic gonads (Fig. 2). Thus, maternal cellular asymmetry marked by the expression of Vasa protein perpetuates throughout the proliferative phase and becomes continuous with the germ line, suggesting that *Copidosoma* specifies the PGC maternally.

**DEVELOPMENT OF THE PRECOCIOUS EMBRYOS: DIFFERENTIAL DISTRIBUTION OF PGC SPECIFIES THE REPRODUCTIVE POTENTIAL**

While it was known that the reproductive larvae give rise to adults and have a reproductive function, the reproductive potential of the precocious larvae in *Copidosoma* was uncertain. They do not molt and become consumed by their reproductive sibling. This poses the question of whether they have a reproductive potential that is simply not realized due to their premature death or they entirely lack potential for the reproduction. In social hymenoptera, workers are sterile in contrast to fertile queens. However, this sterility is often conditional. Both queens and workers have germ line progenitor cells, but in queens the reproductive apparatus become hypertrophic while in workers ovarioles degenerate (SCHMIDT CAPELLA and HARTFELDER, 2002). However, in some cases workers can restore their reproductive potential and...
become reproductives (NIJHOUT, 1999). During the proliferative phase in *Copidosoma* it was noticed that some proliferative morulae do not contain Vasa-positive cells (Fig. 2 blue). These morulae undergo differentiation and give rise into the precocious embryos that do not inherit PGCs. Thus, the mechanism based on segregation of PGC lineage in reproductives, and the failure of the precocious embryos to inherit PGCs represents novel cell-sorting mechanism that specifies the caste fate. This mechanism specifies in all-or-none fashion a different reproductive capacity in genetically identical embryos.

**FUNCTION OF PGCs IN COPIOSOMA: CASTE FATE AND PROLIFERATION**

In contrast to *Drosophila*, where PGCs undergo migration through the embryo to reach their position in future gonads (UNDERWOOD et al., 1980), *Copidosoam* PGCs undergo a complex journey which includes cell parcelling during the proliferative stage, differential segregation to two castes and final localization at the embryonic gonads (ZHUROV et al., 2004). Clearly PGCs must be involved in the formation of the germ-line, but their complex ontogeny poses the question of whether they have other functions in polyembryonic development? Besides Vasa, these cells likely contain many other determinants that may have a role in embryo germ cell specification, proliferation or caste fate. One possibility is that these cells have a cell-autonomous function in specifying the germ-line as in *Drosophila*. This scenario predicts that the removal of PGC progenitor cell will result in formation of the reproductive larvae without gonads. Alternatively, this cell could have non-cell autonomous function(s) so that the germ line specification is coupled with other developmental processes. Laser ablation of Vasa-positive cell at the four cell stage (red Fig 1) has revealed that it has multiple functions (ZHUROV et al., 2004, DONNELL et al., 2004) As a consequence of ablation *Copidosoma* reproductive embryos did not proliferate as detected by lack of formation of the reproductive embryos (ZHUROV et al., 2004). However, the precocious larvae development was not affected, resulting in normal numbers. Laser ablation of the Vasa-positive cell reduced 95% of polyembryonic proliferation. In contrast, ablation of any of the large blastomeres at the same stage (Fig. 2 white cells) restores the development and proliferation of reproductive embryos (ZHUROV et al., 2004). This suggests that the PGC progenitor has a dual function: it regulates proliferation and the reproductive caste fate.

**TRANSITIONAL STEPS PRECEDING POLYEMBRYONIC DEVELOPMENT**

In order to address the question of evolution of the polyembryonic development it is necessary to turn to the system that preceded the evolution of polyembryonic development and to look at the development in the closest monoembryonic ancestor. The putative ancestor has to be an endoparasitic wasp. Second, it should undergo total egg cleavage. Finally, it should emerge from the chorion into the host hemocoeal, and should utilize the polar body-derived cell to form the extraembryonic membrane surrounding the embryo.

The braconid endoparasite *Aphidius ervi* exhibits the predicted features of the hypothesized ancestor of polyembryonic wasps. This wasp lays tiny transparent eggs that undergo total cleavage. Its embryo emerges from the egg shell into the host hemocoeal and remains enveloped by the polar body-derived extraembryonic membrane. Following the emergence from the chorion, morphogenesis is initiated by the formation of an embryonic primordium that consists of a solid ball of cells, similar to the *Copidosoma* embryonic primordium. The embryo of *Aphidius* initially forms just the anterior structures of the embryo. The rest of the trunk is formed by sequential proliferation, exhibiting characteristic short germband development. Since basal braconids display long germband development, *Aphidius* development represents secondarily derived short germband embryogenesis.

The embryogenesis of polyembryonic parasitic braconid *Macrocentrus grandii* wasps could help us to understand how polyembryony evolved in a defined phylogenetic context of braconids. Eggs of this species is also transparent, surrounded by tiny chorion and in contrast to those of their basal, ectoparasitic relatives, contain almost no yolk. Initial cleavage events in these tiny eggs differ from the canonical type of insect syncytial cleavage. Both wasps undergo total (holoblastic) cleavage in which nuclear division is immediately followed by cytoplasmic division, forming individual cells (blastomeres). This novel type of early cleavage appears to be common also in polyembryonic platygasterids (IVANOVA-KAZAS, 1972), and its general presence in all polyembryonic species suggests that it represents a prerequisite for the evolution of polyembryonic development.

Following early cleavages, *Macrocentrus* embryos emerge from the tiny chorion into the host hemocoeal and enter the proliferative phase of development. In this phase, the number of cells increases and cells become subdivided by the extraembryon-
ic membrane into several independent spatial domains. The proliferative stage in *Macrocentrus* results in a smaller rate of proliferation than in *Copidosoma* to form ultimately up to 20 embryos. Finally, initiation of the morphogenetic phase results in the formation of the embryonic primordium. In both species embryonic primordia are formed from the very beginning as cellularized structures. However, in *Copidosoma* the embryonic primordium is solid, without the blastocoel (GRBIC et al., 1996), while the *Macrocentrus* primordium consists of single layer of cells that surrounds the hollow space of the blastocoel. These species also differ in the type of germ band. *Copidosoma* embryogenesis was hard to classify. It more resembled long germ band development by its proportional growth and expression of molecular markers (GRBIC et al., 1996). On the other hand, *Macrocentrus* embryogenesis is clearly of a short germ band type. The initial primordium consists of anterior structures and the remaining trunk is generated by posterior growth.

The comparison of development in two independently evolved polyembryonic species and their putative monoembryonic ancestor suggests that evolution of polyembryony is compatible with meroistic ovarian apparatus present in basal monoembryonic wasps. On the other hand, innovations that are conserved in both polyembryonic species include a novel type of cleavage, and the proliferative phase responsible for creation of multiple embryos. It appears that in both polyembryonic wasps the proliferative phase has been simply «inserted» into the monoembryonic developmental program without any consequences for the later phases of development. Even though the proliferative phase seems to be similar in specific embryological events but different in the amount of proliferation, the late morphogenetic phase displays two completely different trajectories. In *Copidosoma* three-dimensional tissue specification proceeds from the morphogenesis of a solid ball of cells, resembling the long germ band type of embryogenesis (GRBIC et al., 1996). In contrast, the *Macrocentrus* primordium forms a single cell layer, and extension of the embryo trunk represents a form of short germ band development, as described in primitive insects. Even though short germ band development is considered to be a primitive remnant of insect ancestors, its secondarily-derived development in *Macrocentrus* indicates that the evolutionary trajectory can be inverted: short germ band development can evolve from a long germ band ancestor.

Collectively, descriptions of embryogenesis in these wasps illustrate the surprising level of plasticity and modularity of developmental programs. First, meroistic polytrophic ovaries that synthesize determinants for syncytial cleavage and long germ band development in *Drosophila* are compatible with specification of determinants for polyembryonic development. Second, innovations in the cleavage type and proliferative phase which should theoretically scramble *Drosophila* localized maternal determinants and diffusion-based action of the transcription factors are perfectly compatible with *de novo* formation of thousands of embryonic axes many days after oviposition. On the other hand, these multiple independent evolutionary events of polyembryony suggest that evolution of such a complex developmental program could have a relatively simple genetic basis that includes changes in very few genes.

**Scenarios for evolution of polyembryony**

An analysis of multiple independent events of polyembryony in wasps within the phylogenetic framework suggests that it consists of a complex and stepwise processes. The ancestral type of development in all polyembryonic lineages included an ectoparasitic life history strategy and a large yolky egg, exhibiting long germ band embryogenesis. With the evolution of endoparasitism, wasp embryos gained the advantage of exploiting the nutritive environment of the host not only for larval feeding, but also for embryo development. This shift resulted in several changes in egg architecture. First, the chorion which consists of elaborate structures in ectoparasites and other terrestrial insects protecting them from dessication, decreased in its complexity once the embryo evolved emergence from the chorion into the host nutritive haemolymph. In addition, because host nutrients were utilized for embryo development it was not necessary to stockpile a large amount of yolk in the eggs. Consequently, endoparasitic egg size decreased. In smaller eggs evolution favoured a new type of cleavage: total cleavage, immediately forming individual cells.

It is unique that in many endoparasitic wasps polar nuclei do not degenerate as in other terrestrial insects (TREMBLAY and CALVERT, 1972). Instead, they participate in the formation of extraembryonic membranes that completely surround the embryo. It appears that this structure evolved many new functions in contrast to the extraembryonic membranes in terrestrial insects. In many endoparasitic wasps, at the completion of morphogenesis the extraembryonic membrane fragments into individual polyploid cells called teratocytes. In
some endoparasitic wasps teratocytes circulate in the host hemolymph and synthesize proteins which are secreted, altering host physiology in support of endoparasitic development (Rana et al., 2002). However, in the polyembryonic embryogenesis of Copidosoma, the extraembryonic membrane is involved in the proliferative phase of development, separating proliferative cells into spatial domains. It never fragments to form the teratocytes and continues to surround both embryos and larvae. Even though endoparasitic embryos can take advantage of the host nutritive environment, they must first evolve a defense against the host immune system. Findings by Corley and Strand (2003) that the extraembryonic membrane in Copidosoma protects the larvae from the host immune system may provide a clue as to the primary reason for the evolution of this structure. In addition, it has been proposed that the polar cell-derived extraembryonic membrane plays a role in the uptake of nutrients from the host haemolymph (Koscielski and Koscielska, 1985). Analyzing the expression pattern of genes in the proliferative phase of development, it was determined that all cells of the extraembryonic membrane in Copidosoma express alkaline phosphatase mRNA (Terzin and Grbic, unpublished). This enzyme is involved in nutrient absorption and transport mechanisms in insects and vertebrates (Eguchi, 1995), suggesting that the extraembryonic membrane actively absorbs nutrients from the host haemolymph. Thus, the primary role of the extraembryonic membrane initially was probably to protect the emerged embryo of monoembryonic endoparasites against the host immune system, and to absorb nutrients. Later on, the existing structure was likely co-opted to the proliferative phase of embryogenesis in polyembryonic insects to organize proliferative growth.

Evolution of small egg size, total cleavage, and novel, multifunctional extraembryonic membranes were the prerequisites for the evolution of the novel proliferative stage. This stage represents the true developmental innovation (Type A) because it was derived from novel structures (the extraembryonic membrane) and a cleavage type that does not have a known precursor in ancestral, ectoparasitic, insects. It is hard to conceptualize the evolution of a novel stage that disrupts one of the crucial paradigms of Drosophila development, maternal specification of the embryonic axis, while at the same time creating de novo 2000 independent embryonic axes! If the syncytial environment of the Drosophila pre-blastoderm embryo has created complications in understanding how pattern formation proceeds in the cellular milieu of short and intermediate germ band insects (Wilkins, 2001), then polyembryonic development represents a real challenge for the Drosophila paradigm. One of first prerequisites for such an event appears to be the uncoupling of posterior patterning and germ cell specification. The second step should include the initiation of the proliferation mechanisms to generate at least 40,000 cells necessary for initiation of 2000 embryonic primordia (Grbic et al., 1998). There are several relatively simple possible means how to initiate proliferation. In the monoembryonic ancestor cleavages must generate enough cells for the formation of the single embryonic primordium. At this point proliferation has to stop and become coupled with axial patterning. Thus, a simple change in the regulatory region of the mitogenic signal could extend the period of proliferation necessary for polyembryonic development. Another avenue generating the same effect would be to produce a mutation in the putative suppressor of proliferation that terminates early proliferation and regulates entry into the blastoderm stage of the monoembryonic ancestor. Both of these changes are relatively simple and could involve existing genes without requiring new gene recruitment (Wilkins, 2001). In a likewise manner, removal of the mitogenic signal by a similar mechanism at the completion of proliferation could regulate the exit from the proliferative stage.

It is hard to conceptualize how is the proliferative stage integrated with de novo establishment of embryonic axes. All 2000 embryo axes appear to form independently with random axial orientation relative to each other (Grbic et al., 1996). This favours an independent specification of the axial polarity within each embryo rather than a global mechanism specifying simultaneous polarity in 2000 embryos.

CONCLUDING REMARKS

Evolution of developmental novelties is a complex phenomenon that requires understanding of both the ecological processes and developmental mechanisms responsible for its creation. Analysis of the evolution of polyembryonic development within the phylogenetic context, and studies of multiple independent events of polyembryony have been important stepping stones toward beginning to understand the processes and mechanisms shaping the evolution of this novel form of development. As stated by Wilkins (2001), there is no general analytical method that can be applied to all developmental novelties. However, clues derived from a
broader phylogenetic context suggesting the polarity of states and an examination of possible ancestral hypotheses.

RIASSUNTO

EVOLUZIONE DELLO SVILUPPO POLIEMBRIONICO DELLE VESPE PARASITE

La comparsa di nuovi ed innovativi meccanismi di sviluppo embrionale è stata associata a radiazioni adaptative che hanno permesso a gruppi particolari di organismi di occupare ecosistemi nuovi. Tuttavia, le forze evolutive ed i meccanismi molecolari responsabili dell’origine di queste nuove modalità di sviluppo sono poco studiati o ancora del tutto sconosciuti. L’evoluzione del parasitismo negli insetti, ad esempio, è un meccanismo adaptativo molto interessante ma poco approfondito nel campo della embriogenesi. Gli insetti parasiti, svilupPADO su o dentro il corpo dell’ospite, hanno evoluPPATO una pleota di strategie di vita e modalità di sviluppo embrionale. Uno dei più affascinanti adattamenti allo sviluppo che avviene all’interno del corpo dell’ospite è rappresentato dalla poliembrionia presente in alcune vespe in cui, da un singolo uovo, si formano clonalmente fino a 2000 embrioni. Traendo vantaggio dalle tecniche sviluppate in un insettino modello, la Drosophila melanogaster, e da una grande quantità di conoscenze sulla embriologia comparata degli insetti, stiamo cercando di affrontare gli eventi evolutivi che hanno portato a questa nuova modalità di sviluppo negli insetti.

LITERATURE


