Insect Wings: The Evolutionary Development of Nature's First Flyers

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12.1 Introduction

Powered flight is one of the more spectacular evolutionary novelties to have come about during the 4-billion-year history of life on Earth. Flight bestows upon the flyer another dimension in which to experience life. Suddenly, new avenues are available for dispersal, escape and avoidance, locating a suitable mate, and reaching once unobtainable resources. Moreover, wings can be so much more than merely a means to fly. Properly adapted the wings themselves may play a role in courtship, camouflage and mimicry, thermoregulation, and protection and defence. Despite the profound significance of flight, it is a challenging feat to achieve and control. Powered flight has evolved independently at least four times, three of which occur among the Amniota, while the last is far flung across the branches of the animal tree of life. It is this last lineage that was also the first to evolve this singularly successful means of locomotion, rivalling in numbers of species all other forms of life combined. Insects took to the skies perhaps as long as 400 million years ago, and some 170, 250, and 350 million years before pterosaurs, birds, and bats, respectively (Engel and Grimaldi 2004). The pterygote insects (Insecta: Pterygota), Nature's first flyers, have dominated the Earth's skies since the dawn of terrestrial animal life, and their origins are so remotely removed from our world today that it is their evolution that remains one of the more

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A. Minelli et al. (eds.), *Arthropod Biology and Evolution*,
DOI: 10.1007/978-3-642-36160-9_12, © Springer-Verlag Berlin Heidelberg 2013

abominable mysteries in insect evolutionary biology.

Unlike the flight of vertebrates in which the homology of the wing with forelimbs is easily recognized and supported, the wings of insects are not merely a wholesale co-option of one or more legs. Indeed, the full complement of hexapodan legs is present and often unmodified, at least for purposes of flight, in all pterygotes just as it is in the primitively wingless insects. Thus, the question of wing origins in insects is more confounded than that of vertebrates. In addition to discovering for what purposes were wings or wing-like structures first employed or how they operated, we must also reveal from what morphological elements they were composed. The former questions regarding functional ancestry are seemingly simplistic to answer, but they are wholly dependent on first knowing from what wings were derived, yet this nature of critical reliance has evaded many in their quest for wing ancestry. Indeed, replies to these questions, both brilliant and ill-conceived, have abounded for more than a century, and the answers remain elusive. No satisfactory answer to the mechanical, behavioural, and physiological origins of insect flight will ever be produced until a conclusive answer is discovered regarding the morphological homology of the wing. It is in this context that the rise of evolutionary developmental biology offers one of the greatest opportunities to elucidate the homology of insect wings and, in turn, will permit a well-founded account of flight origins.

Wings arose once in insects, that is, the Pterygota are monophyletic and supported as such by abundant morphological and molecular evidence (Grimaldi and Engel 2005). This reality certainly simplifies the investigation of their origins, focusing our attention at a specific node representing the common ancestor of pterygotes as well as the associated transitional branch between that ancestor and its shared predecessor with the silverfish (Zygentoma). While wings have evolved a single time among insects, they have repeatedly been lost or become vestigial. Indeed, wings have been reduced or lost an innumerable number of times, even among close relatives within a single genus. In some lineages, the genetic architecture for developing wings has been turned off and on, resulting in a seemingly cyclical 'reevolution' of wings across the clade (e.g. among Phasmatodea). In all such instances, however, wings reappear wholesale with the same morphology, same arrangement of veins and crossveins (including the same arrangement of venational synapomorphies for the clade! and even in Phasmatodea when they are not well organized the same homologies can be recognized), and associated thoracic modifications belying the fact that these have not independently reevolved but instead have remained 'dormant' until such time as the entire genetic machinery has been reinitiated.

It is beyond the purposes of this review to provide a detailed account of pterygote comparative morphology and flight biomechanics and physiology in insects. For suitable reviews of these subjects, we refer the reader to Dudley (2000); Alexander (2002); Vigoreaux (2005); and Grimaldi and Engel (2005). Herein, we provide brief overviews of current developmental and palaeontological evidence for insect wing origins and diversity attempting to emphasize where present research has brought us and in what directions this field of inquiry might proceed to maximal benefit.

12.1.1 A General Word of Caution and Plea for Phylogeny

Given that wings have a single evolutionary origin among insects and that this event took place early in the hexapodan tree of life, wings, and their entire genetic architecture, are abundantly ancient. It is therefore all the more critical that any study be cognizant of phylogeny. The greatest insights will come from investigations as close to the base of the pterygote tree as is permissible with today's tools. Indeed, the most could be gleaned from suitably basal clades of the earliest extant winged insects, namely the mayflies (Ephemeroptera), and the dragonflies and damselflies (Odonata) (Grimaldi and Engel 2005). Of even greater interest are those stem-group Ephemeroptera from the Palaeozoic although they are unavailable for vital genetic and developmental work. Unfortunately, stem-group Pterygota remain unknown. Much fanfare and bravado have come from the study of stoneflies (Plecoptera), and yet these are by no means 'primitive' flyers and certainly not even close to being 'primitive' insects. Plecoptera may be relatively basal among extant lineages of Neoptera, but most evidence indicates that they are nested at the base of a subordinate clade within a monophyletic Polyneoptera or orthopterid group of orders (e.g. Haas and Kukalová-Peck 2001; Kjer et al. 2006; Ishiwata et al. 2011; Yoshizawa 2011; Trautwein et al. 2012). Even a cursory examination of hexapod phylogeny reveals the evolutionary distance between the extant Plecoptera and the stem of the pterygote node (Grimaldi and Engel 2005; Trautwein et al. 2012). All the more concerning it is then that virtually all of the model systems from which our knowledge of the developmental and genetic architecture of insect wings is derived are among the Neoptera and even derived species among highly derived families in highly derived orders of the holometabolan insects, themselves an apomorphic lineage of neopterans. Certainly, the homology of genetic systems for insect wing development is greatly conserved, but this architecture (genetic and morphological) still stems from a common ancestor nearly 400 million years removed from the extant species which we study. Deep insight into the developmental mechanisms of wings can be obtained, but we must temper our findings against phylogeny and, where possible, rely most heavily on truly comparative data, particularly those that come from independent comparisons with basal pterygote lineages. Naturally, model systems are used given the ease of working with them, and developing suitable models among mayflies, dragonflies, and the like is exceedingly difficult. Nonetheless, we must recognize that in terms of genetic systems, we are working with 'quaint' tools on less than ideal target organisms and should proceed cautiously and conservatively in our interpretations. In reviewing the developmental evidence for the origin of wings, it is important to remain neutral to any previous hypotheses which may bias interpretation of these data. As is often the case in discussions of the origins of developmental features, such as wings, if such data are not scrutinized under an unbiased approach, it is easy to reach conclusions that unfurl beyond context and overlook direct evolutionary implications. As many authors have stated and reiterated, and since we are working in the bounds of comparative evolutionary biology, it is crucial not to dismiss key concepts of homology and phylogeny, particularly when synthesizing diverse forms of data as morphology and developmental genetics over long periods of evolutionary time.

12.2 Development of Insect Wings

Of the contending hypotheses put forward regarding wing origins, the most influential in driving relevant research have been renditions of the paranotal (Crampton 1916), gill/exite, and 'epipodite' theories. The former hypothesis, in the strict sense, regards wings as a novel feature derived from extensions of the thoracic tergites. The latter hypothesis, which also appears to be given greater support from developmental studies, suggests that winged insects have evolved from a common ancestor that possessed dorsal limb precursors of wings, likely in the form of some exite from the coxopodite (i.e. an epipodite, such as a crustacean gill). Any comparison of the wing with a coxal endite can be excluded; however, given its podite of derivation, the coxa is a distinctive part of the hexapod telopodite. The styli found in Zygentoma and Archaeognatha can also be disregarded as precursors to wings, as the thoracic styli originate from the coxae and the abdominal styli are hypothesized telopodites. Furthermore, while such structures are present in extant (derived) taxa of these orders, it is unknown whether they were plesiomorphic for hexapods or derived features within those lineages.

From an anatomical viewpoint, wings are essentially appendages. They develop as outgrowths from the body and articulate with the body at their bases. Unlike traditional appendages such as legs, however, (yet similar to gills, exites, and other outgrowths from the pleural wall, itself originating from a basal appendage podite), muscles attach only to the base (axillary sclerites) and do not extend into the wing cavity. Genetically, wings are also definable as appendages, developing as a result of the expression of a basic set of gene networks involved in general appendage formation, while various other genes and gene networks are co-opted/induced to form the specific features that differentiate the wing from other appendages. Therefore, while it is clear that the wing is some rendition of an appendage, the nature of its development and genetic patterning has complicated attempts in formulating hypotheses of homology. However, in collating the evolutionary developmental data gathered thus far, it appears that a combination of the paranotal and exite theories may be most plausible for explaining the origin and evolution of the hexapod wing. In order to elucidate such a complex topic, it is necessary to examine how wings develop, determine what genetic mechanisms are responsible for wing formation, and make comparisons with other insect appendages.

12.2.1 Embryology and Tissue Development

It has been known since Malpighi (1687) that the wings of adult pterygotes can be observed in the larval stages; however, it was not really until Weismann's work (1864) on muscid fly metamorphosis that greater attention was devoted to studying wing development. In the late nineteenth century, it already had been discovered by many that the early wing primordium is already present in embryonic stages (Pratt 1900; Tower 1903). The cells of embryonic wing discs, in fact, are found occupying a very similar space to those of the meso- and metathoracic leg discs, as well as found among the epidermal cells that will form the main trunk of the longitudinal tracheae (Madhavan and Schneiderman 1977; Cohen et al. 1991; Williams and Carroll 1993; Held 2002). This close association between the early wing and leg primordia, though, appears to be a derived feature only of some groups that possess true imaginal discs (Jockusch and Ober 2004). By the end of the embryonic stages, however, the leg and wing rudiments are well differentiated. The early developing wing is most frequently characterized as dorso-lateral in origin during tissue differentiation, in which the epidermal cells of the disc begin to thicken (Tower 1903; Powell 1904; Murray and Tiegs 1935). It must be noted, however, that this position is purely a description of relative location on the body trunk and not a definitive statement of tissue origin. This position is also always just lateral to or slightly dorso-lateral to the longitudinal thoracic tracheal trunk. Following differentiation and during proliferation of the disc cells, the slight dorsal migration of the disc appears to be an artefact of the reorganization of the adult trunk, including expansion of the pleural region. Although most recent works highlight the prominent invaginated form of *Drosophila* wing discs, at least five distinct forms of wing discs (or fields/bodies of proliferating wing tissue) have been described from the Holometabola (Tower 1903). These types range from completely evaginated (such as the form of beetle horn tissue proliferation) to fully invaginated and stalked, including various intermediate forms of partially invaginated discs. In Coleoptera alone, several types of wing growth can be observed, from the invaginated to the fully evaginated (Fig. 12.1d–h) types (Powell 1904, 1905; Quennedey and Quennedey 1990). While the term imaginal disc is sometimes specifically applied to such invaginated pockets of ectoderm in the Holometabola from which certain imaginal structures are formed (mostly in regard to the observations made on *Drosophila*), this type of disc is apomorphic and appears to have evolved independently in several holometabolous lineages (e.g. Švácha 1992). In the broad sense, imaginal tissues (in this case, wings) that explicitly form as evaginations in holometabolous insects, therefore, should also be termed imaginal discs, though this terminology is avoided due to transparent ambiguities in delineation of wing growth types (Švácha 1992;

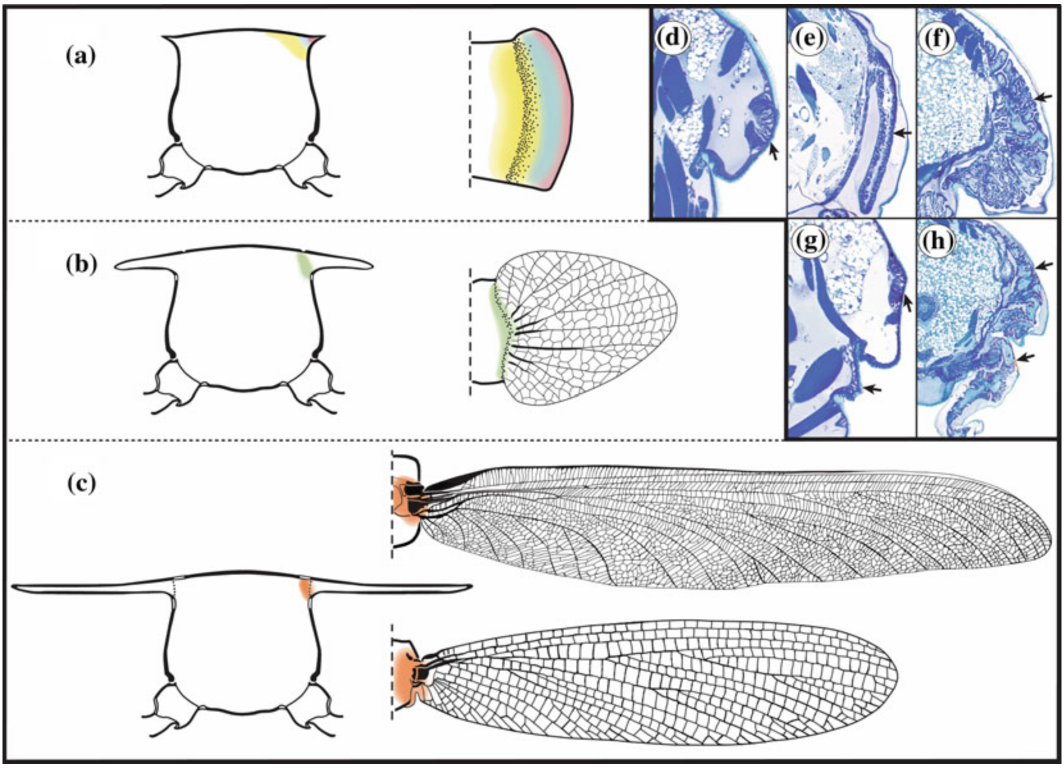


Fig. 12.1 Hypothesized pathway illustrating the origin of hexapod wings based on current knowledge of palaeontological, neontological, and development data. **a**–**c** *Left* side, cross-sectional views of mesothorax, illustrating wing development. *Right* side, dorsal views of mesothoracic wing development corresponding to cross-sectional views on *left* side. Colours highlight gene expression as follows: *yellow* = *ap*, expressed in tergum and paranotal margin; *blue* = *vg*, expressed along paranotal margin; *red* = *wg*, expressed along paranotal margin; together, *ap*, *vg*, and *wg* allow for paranotal extension and development of paranotal lobe/primitive wing; *green* = *hth* and *exd* (as well as possibly many other genes), expressed along paranotal margin and base of paranotal lobe to produce primitive joint/articulation; *orange* = *hth* and *exd*, as well as induction of other elements, giving rise to more derived wing articulations. **d**–**h** Growth of wing tissue in *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae), showing an evaginated type of wing growth. **d** Mesothoracic wing bud of last larval instar. **e** Mesothoracic wing of mid-prepupa ('pharate pupa'). **f** Metathoracic wing of late prepupa. **g** Last larval instar, showing metathoracic wing bud and differentiating leg tissue. **h** Late prepupa, showing metathoracic wing and leg. *Arrows* indicate developing wing, as well as developing leg (**g**, **h**). Photomicrographs are of semi-thin sections (6 μm) embedded in LR White and stained with toluidine blue

Jockusch and Ober 2004). Thus, although it is unknown how many groups actually possess imaginal discs outside of Diptera (Pratt 1900; Waddington 1941; Wehman 1969; Bryant 1975; Fristrom and Rickoll 1982; Cohen 1993), Lepidoptera (Mercer 1900; Tannreuther 1910; Dixey 1931; Nardi et al. 1985; Niitsu 2003; Niitsu and Kobayashi 2008; Niitsu and Lobbia 2010), and some Coleoptera (Tower 1903), imaginal discs only include the invaginated *Drosophila* type, composed of columnar epithelial cells on one side and a peripodial membrane on the other (Milner et al. 1984). All other late-developing tissues that evaginate in the Holometabola, in addition to all hemimetabolous pterygotes, should be categorized otherwise, as Anlagen, which has been used in the past, or in reference to wing Anlagen, possibly as wing buds or wing fields. A functional explanation for the development of diverse forms of wing discs is unclear, though it has been hypothesized that the form of disc growth most likely is related to the life histories of the larval stages (Tower 1903; Švácha 1992; Truman and Riddiford 1999). Since it is clear, then, that invaginated imaginal discs evolved far after the origin of wings, it can be hypothesized that the close developmental association between leg and wing primordia is a derived feature. Also, as wing discs (as well as other appendage discs) have evolved independently numerous times throughout Holometabola, it can be expected that differences exist in their development and gene expression patterns.

Comparisons of wing disc development have been made to that of gill development in Ephemeroptera, despite the derived phylogenetic position of this group in the Insecta. Arguments here lay mainly with comparisons of similar tergal positions with larval gills (and even gill covers) on the thorax and abdomen of this group and wings, as well as some similarities in muscle arrangements (Wigglesworth 1972; Matsuda 1981). While it might be desired to make such associations, any recognition of absolute homology between wings and ephemeropteran gills stops at these observed similarities and the appendage patterning genes co-opted to form such appendicular outgrowths. Also, because of such associations between similarity in position and misinterpreted morphological features of fossil taxa, an observed ancestral presence of wings on all trunk segments has been dubiously postulated and propagated in the developmental literature (Carroll et al. 1995). It should also be noted that the thoracic wing-like structures of primitive aquatic immatures are in fact the developing wing buds, and those on the abdomen are the gills. Although gills may utilize similar appendage patterning genes and pathways as wings, with notable exceptions (Niwa et al. 2010), since they are features only of immature aquatic pterygotes, they are independent features from wings. It is unwise, therefore, to hypothesize that wings first evolved in the aquatic immature stages of pterygotes, such as paleodictyopteran nymphs (Carroll et al. 1995), some of which may not have been aquatic at all. It may still be possible to hypothesize that wings and gills share some degree of serial and/or developmental homology (Jockusch et al. 2004), due to their sharing of similar developmental programmes; however, there is no evidence for gills and wings evolving together or during similar time periods, and it is more probable that gills arose independently, particularly considering that the earliest ephemeropteran immatures appear to lack gills (e.g. immature Protereismatidae: Grimaldi and Engel 2005).

12.2.2 Genes and Genetic Pathways

While traditional embryological studies have been able to determine that wing primordia first form in the embryo and that these ectodermal cells of the early wing disc are associated with the leg primordia, it was uncertain whether any of these cells are actually derived from the early leg disc. Together with developmental genetic techniques, it has become evident that in *Drosophila*, as revealed by early *vestigial* (*vg*) expression, the wing discs originate as a part of the leg discs and subsequently separate to migrate dorsally (Cohen et al. 1991, 1993; Williams and Carroll 1993). These data were used as further evidence that wings may be homologous to extensions from the coxal base (coxopodite/basicoxa), such as an epipodite or gill. Further studies outside of Diptera (in Hymenoptera) have shown, however, that this association between leg and wing primordia may yet be another derived feature in Diptera (Jockusch and Ober 2004), perhaps associated with the evolution of imaginal discs. Thus, as shared leg and wing primordia appear to not be the plesiomorphic state for Holometabola, they likely are not plesiomorphic for Pterygota. Although similar studies have yet to determine whether these primordia are also separate outside of Holometabola, it is intriguing that at least one holometabolous order (Coleoptera) shows such a pattern. Further support for this hypothesis of derived leg + wing primordia stems from observations in *Tribolium*, indicating that while there is anterior to posterior migration of early *snail* (*sna*) expressing wing primordia, dorsal migration of the wing primordia does not occur outside of Diptera (or perhaps outside of some other groups sharing wing disc development from a common ancestor) (Jockusch and Ober 2004). The hypothesis of the wing evolving specifically from a crustacean epipodite was first given evidential support by Averof and Cohen (1997), in which they demonstrated that *nubbin* (*pdm*/*nub*) and *apterous* (*ap*) appear to have similar expression patterns in insect wings as in the epipodite of *Artemia*. As Jockusch and Nagy (1997) explained in detail, such observations do not provide the evidence for such a precise conclusion (which explicitly excludes other hypotheses). It certainly demonstrates that appendages appear to require similar modes of development, but does not elucidate any differences in the targets that may be present downstream which differentiate various types of appendages.

It has been found that *Scr* is expressed in the first thoracic segment (T1) not only in derived pterygote groups, but also in basal insects (Rogers et al. 1997; Angelini and Kaufman 2005). It is uncertain whether it is expressed in non-insect apterygotes (i.e. Entognatha); however, because it appears to be present in basal Hexapoda (which lack wings), it is quite possible that *Scr* may have been exapted for the repression of prothoracic wings (Hughes and Kaufman 2002), possibly in several different ways and to varying extents, particularly as large 'winglets' (or 'paranotal lobes' as many were not articulating, or the evidence for their articulation is lacking) have been found throughout the extinct Odonatoptera, Palaeodictyopterida, and many other groups (e.g. Wootton 1972; Carpenter 1992; Grimaldi and Engel 2005). This hypothesis is further supported in Coleoptera (*Tribolium*: Tomoyasu et al. 2005 and *Onthophagus*: Wasik et al. 2010), whereby RNAi *scr*$^{-}$ mutants essentially develop mesothoracic wings on the prothorax. Orthoptera (*Gryllus*: Zhang et al. 2005) also show a similar expression pattern of *Scr*, probably indicating that *Scr* functions to repress wing formation in T1 in Orthoptera as well. In Hemiptera (*Oncopeltus*: Chesebro et al. 2009), while RNAi *Scr*$^{-}$ mutants also develop some aspect of ectopic mesothoracic wings on the prothorax, there appears to be no indication of an articulation. A fascinating apomorphic derivation of this T1 pathway appears to have evolved in a different lineage of hemipterans (Membracidae). Here, *Scr* continues to be expressed in the ectoderm despite the formation of a dorsally derived appendage (Prud'homme et al. 2011). While this appendage likely is not homologous with meso- and metathoracic wings (Yoshizawa 2012), it is clear that it has co-opted portions of the wing/appendage patterning pathways as has similarly occurred in many other insect groups. Because of such observations in similar expression patterns, it certainly is possible that similar genes have acquired different functions, mainly through changes in the regulation of downstream targets. Such data may also indicate that *Scr*, or likely downstream targets of *Scr*, has changed since the origin of basal hexapods and, particularly so, since the origin of pterygotes. These changes appear to differentially affect wing development, such as eliminating points of articulation, eliminating or reducing the laminate (paranotal) extension, or various degrees of both. As many studies are beginning to conclude, it may not be so much that differences in expression domains give rise to morphological novelties; rather, it is the differences in regulation and deployment of these genes that produce change (Averof 1997; Grenier et al. 1997). Such differentiation is difficult to detect with gene expression data for several reasons, such as topological conservation in expression (Bolker and Raff 1996). It also is equally likely that other undiscovered genes may play large roles in such seemingly conserved pathways. Since developmental studies have progressed largely in the light of candidate-gene approaches, including comparing expression patterns and functions of similar genes, it is quite possible that unstudied genetic architectures or features may have significant effects in producing the different outcomes we see in similarly expressed genes. Such genes might represent cascades of targets, downstream of conserved networks such as Hox genes, and could be influential in morphogenesis (Hughes and Kaufman 2002).

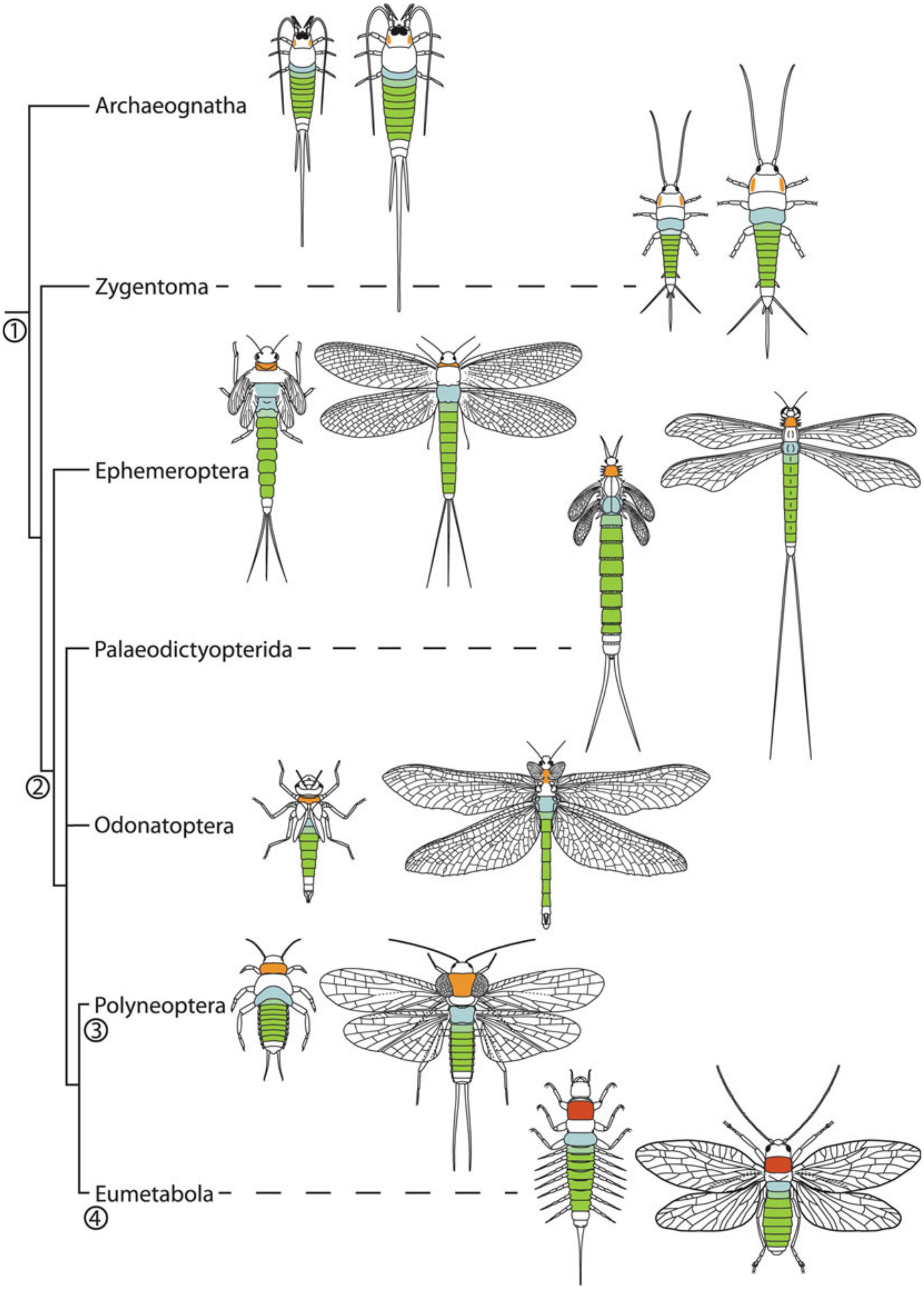
It is possible that the potential to develop embryonic wing primordia may be in every thoracic and abdominal segment; however, as defined by *snail* expression, since no definitive wings (or wing precursors) have been found on the abdomen of hexapods, it is incorrect to state that insects lost abdominal wings. This statement is at least consistent with the fossil record, because ancestrally, as said above, hexapods never had definitive wings on the abdomen. It is now evident that *Bithorax* complex (BX-C) genes have evolved the ability to regulate imaginal disc and imaginal tissue formation in segments, likely through various suites of target genes (Hughes and Kaufman 2002). Interestingly, while it appears that *Ubx* and *abd-A* have evolved the ability to repress abdominal wing (and leg) primordial development (i.e. to designate abdominal identity) (Simcox et al. 1991; Carroll et al. 1995), it has been demonstrated that *Ubx*$^-$ and *abd-A*$^-$ mutants of *Oncopeltus* (Hemiptera, hemimetabolous), although forming abdominal legs and dorsal pigmentation suggestive of early wing-pad development, have not been shown to form any definitive abdominal wing buds in the nymphs (Angelini et al. 2005). It is unknown in this case, however, whether embryonic wing primordia form. While RNAi studies have yet to be done in *Gryllus* (Orthoptera), the expression patterns of *Ubx* and *abd-A* are quite different from those in *Drosophila*, particularly with regard to *abd-A* during early and middle embryonic stages (Zhang et al. 2005). Interestingly, similar results are seen in *Tribolium* (Coleoptera) *Ubx*$^-$/*abd-A*$^-$ RNAi mutants as with those of *Drosophila* (Tomoyasu et al. 2005). In wild-type *Tribolium*, patches of cells expressing *sna* are observed not only in the thoracic segments, but also in nearly every abdominal segment (Jockusch and Ober 2004). Furthermore, as in *Tribolium*, it is fascinating that *Ubx* and *abd-A* knockouts of *Tenebrio molitor* have survived to the adult stage and demonstrate a homeotic transformation giving rise to the presence of wings (fore- or hindwing identity could not be confirmed) on all abdominal segments (Takahiro Ohde and Teruyuki Niimi, pers. comm.), though lacking signs of abdominal leg development. It should be noted, though, that *Ubx*/*abd-A* parental RNAi induces abdominal leg formation in the larva of *Tribolium*. These fascinating results demonstrate that the genetic network and potential to form fully developed wings, though of questionable function, can be deployed in most (if not all) abdominal segments. Such findings, perhaps, should not be considered too extraordinary given the serially homologous ground plan of insect segmentation. Indeed, in addition to the results of Tomoyasu et al. (2005), this extant ability to produce wing-like structures on the abdomen is quite interesting, but is far beyond providing conclusive statements for early wing evolution and origins. As already mentioned, while the abdominal segments appear to also have a capacity for various types of dorsal appendage development and short tergal extensions or lobes (in addition to ventral appendage development in immatures and ancestral ventral leg development), wings have thus far not been found to have occurred naturally on these segments. It must be emphasized that, given current understanding of the functions of *Ubx* and *abd-A*, while they appear to remain broadly expressed in the abdomen throughout Hexapoda, several forms of appendages have evolved (mainly in immatures) on the abdomen in different hexapod orders; (Fig. 12.2). Such diversity in development suggests mechanisms of developmental drift, changes in downstream targets, and/or changes in expression patterns (e.g. Warren et al. 1994), modes of development which could utilize various components of an underlying appendage (though not necessarily and specifically a wing) formation programme. In addition, while such expression patterns could indicate possible serial homology of dorsal appendages in the thorax and abdomen in hexapods, early appendage patterning markers, such as *dpp*, *sna*, *vg*, and *wg*, do not necessarily dictate downstream processes such as wing formation. Therefore, such data may support observations contrary to Kukalová-Peck (1978) (e.g. Boxshall 2004; Grimaldi and Engel 2005) that wings may not have been a ground plan of the pterygote abdomen and, similar to the case of *Scr*, may represent a derived feature in these advanced holometabolous groups. As indicated by expression patterns of BX-C genes in some crustaceans, while superficially similar expression patterns may exist in distantly related taxa, such as is seen in various Hox genes, such expression patterns may likely serve divergent functions (Abzhanov and Kaufman 2000a, b). More data outside of Holometabola are direly needed to create an improved comparative framework.

While gills and wings may share similar patterning genes (given that they are both, at least in part, appendicular) and require similar pathways to define their antero-posterior (A/P), dorso-ventral (D/V), and proximo-distal (P/D) axes, this observation does not necessarily define them to be serially homologous (Jockusch et al. 2004). In other words, while similar expression patterns may be present in taxa that share a common ancestor, the morphological features that develop in those groups are not homologous unless they evolved through modification of the same structures present in the common ancestor (Hall 1994). Thus, similarity in patterns of gene expression may reflect conservation of gene function from a distant common ancestor, but it does not equate to homology of the derived structures in which the expression is seen (Bolker and Raff 1996). Furthermore, as there are gills of immatures that arise from ventral, pleural, and tergal regions in pterygotes, it is quite likely that such appendicular structures are independent, as hypothesized for many of the epipods and polyramous structure of crustacean limbs (Boxshall 2004). It is understandable that the general gestalt of such nymphal gills resemble wings; however, not only are their articulations completely different (Dürken 1907, 1923), early patterning genes, such as *apterous* (*ap*), show different expression patterns (Niwa et al. 2010). If we were to continue to be motivated by similarities of gene recruitment and co-option in forming our hypotheses of homology, then beetle horns, aside from their different form and location on the body, could also be hypothesized as derivatives of epipodites, styli, or gills and in some regards appear to show more similar expression patterns to wings than do styli or epipodites. Appendage patterning genes, such as *dac*, *hth*, and *Dll*, show similar expression patterns in beetle horns to truly segmented appendages (Moczek and Rose 2009). Major signalling proteins for P/D patterning, such as *decapentaplegic* (*dpp*), which is required for leg outgrowth in most (but apparently not all; Jockusch and Ober 2004) hexapods, are also involved in horn formation, demonstrating recruitment of similar genes and pathways for apparently novel features (Wasik and Moczek 2011). In other words, aside from minor differences in gene expression and downstream targets, the main difference between ventral, lateral, and dorsal appendages is the site at which gene co-option/recruitment occurs.

12.2.3 Homologous Versus Novel: 'Epipodite' Versus Amalgamation

Although many structures that are said to be non-homologous to structures in ancestors may appear to be new, their formation and evolution typically originated from preexisting developmental architectures (Bowsher and Nijhout 2007; Prud'homme et al. 2007). For arthropods, this statement is now based on a wealth of developmental data on segmentation and appendage patterning. As already mentioned though, while expression of genetic pathways may be conserved (and the genes within them homologous), the deployment and functioning of these genes may be different and they may be expressed in non-homologous structures (Bolker and Raff 1996). Such differences in gene function serve only to further distort definitions of homology (Hall 2007), as may be the case in insect wing development.

Unlike the case for abdominal wings, the presence of definitive prothoracic wing-like structures has been documented (Crampton 1916; Ross 1964; Kukalová-Peck 1978; Grimaldi and Engel 2005), although evidence for articulations is lacking. As it has been demonstrated that nearly a full developmental programme for wing formation is present in the


Archaeognatha
Zygentoma
①
Ephemeroptera
Palaeodictyopterida
②
Odonatoptera
Polyneoptera
③
Eumetabola
④

◀ **Fig. 12.2** Phylogenetic hypothesis of insect relationships and wing development. Abbreviated phylogeny of Hexapoda, focusing on basal orders to illustrate the distribution of various morphological features (paranotal lobes, gills, styli, and wings) in representative immatures and adults. Representative taxa are as follows: Archaeognatha (Meinertellidae); Zygentoma (Lepismatidae); Ephemeroptera (Protereismatidae); Palaeodictyopterida (Megasecoptera); Odonatoptera (Eugeropteridae); Polyneoptera (Lemmatophoridae); Eumetabola (Sialidae). Colours represent gene expression as follows: *orange/red* = *Scr*, expressed in the prothorax; *blue* = *Ubx*, expressed primarily in the metathorax and first abdominal segment, but also in A2–8; *green* = *abd-A*, generally expressed in abdominal segments 2–8 (and partially in A1). Significance of numbers at nodes is as follows: **1** Origin of Hexapoda, loss of abdominal appendages through *Ubx*/*abd-A* regulation (although styli develop to various degrees on thorax and abdomen in Archaeognatha and Zygentoma), and expression of *Scr* along lateral margins of prothorax. **2** Appearance of wings on meso- and metathorax (Pterygota), broader expression of *Scr* in prothorax, and repression of wing formation on prothorax by *Scr* (though paranotal lobes begin to appear, indicating diverging functions of *Scr*; although *Ubx*/*abd-A* remains expressed in similar patterns throughout adult insects, gills, legs, and other such appendages develop on the abdomen in immatures of several orders. **3** Paranotal lobes remain in some lineages of Polyneoptera; however, they are lost in many other lineages, indicating diverging functions of *Scr* or induction of other genes/pathways. **4** While various abdominal gills (appendages) are present throughout pterygotes in the immature stages, more diversity appears in Eumetabola, including segmented gills and other abdominal appendages; diverging functions of *Scr*, and likely induction of other genes/pathways, also appear in Eumetabola, as modifications of the prothorax develop in various orders (e.g. wing-like appendages in Hemiptera)

prothorax of holometabolous and hemimetabolous insects, only it has been repressed at least by *Scr*, it appears more likely, at least given the results of developmental research thus far, that wings were a ground plan for the hexapods only in the thorax. Such a hypothesis is supported by expression patterns of the early limb induction module including the transcription factors *ap*, *wg*, and *vg* in taxa that are more representative of early pterygotes and hexapods (Niwa et al. 2010). These data also indicate that, contrary to popular citation, a wing is more likely an amalgamation of tergal and pleural outgrowths which develop according to the redeployment of limb patterning genes and portions of their pathways, as opposed to a modification of such structures as gills, epipodites, styli, or other limbs that share similar developmental modules. Contrasting expression patterns of these genes, while *ap* is expressed in a large dorsal area of the pterygote wing, it does not appear in ephemeropteran gills nor in archaeognathan styli. On the other hand, *wg* and *vg* were expressed in the gills and styli of the aforementioned taxa, as well as at their bases (as in wings), indicating regions of articulation (Buratovich and Wilder 2001; Niwa et al. 2010). From such investigations in early hexapod lineages, it is apparent that the interaction of at least *ap*, *wg*, and *vg*, as revealed through their expression at the tergal–pleural (coxopodite) boundary, functions as a module for paranotal extension (Ng et al. 1996; Niwa et al. 2010). Recent studies have also confirmed through RNAi that *vg* is involved in paranotal extension, in which adult *vg* knockdowns of *Tenebrio molitor* show paranotal extensions on all abdominal segments (Takahiro Ohde and Teruyuki Niimi, pers. comm.). Other major regulators of this outgrowth of the tergal margin may include *dpp* and *hedgehog* (*hh*) signalling, which are also important in later patterning of the veins (Celis 2003; de Celis and Diaz-Benjumea 2003), and possibly *scalloped* (*sd*). Subsequently, through the incorporation of existing appendage patterning genes (such as *dachshund* [*dac*], *exd*, *Distal-less* [*Dll*]), an articulating appendage (wing) is formed while also providing more refined patterning along the D/V, A/P, and P/D axes. As in legs, the complex of *homothorax* (*hth*) and *exd*, among their many functions, appears to play a role in defining the region of articulation (González-Crespo and Morata 1996; Azpiazu and Morata 2000; Casares and Mann 2000; Morata 2001) and patterning of the axillary sclerites, similar to the coxopodite of legs (Jockusch and Nagy 1997). It may be interesting, then, to hypothesize that the complex region forming the articulation of the wing may, in fact, involve a highly derived coxopodite (i.e.

the basal part of the appendage). Similar to how the ancestral basicoxa fragmented to form the areas of the insect pleuron, it may be possible that through recruitment of such coxopodite patterning genes, the primitive sclerotization surrounding the wing base in basal pterygotes also fragmented/fused to form the wing pteralia. While *hth* and *exd* are expressed at the margin of the base of the wing and extend onto the wing blade, *pdm* expression also extends into the area of the wing hinge, approximately covering its entire dorsal surface (Jockusch and Nagy 1997), as does the Iroquois complex (Iro-C) (Cavodeassi et al. 2002), *teashirt* (*tsh*) transcription factor, and *wg* signalling pathway (Klein and Martinez Arias 1998; Peterson et al. 1999; Klein 2001) and therefore also seem to function in axillary patterning (Ng et al. 1995), in addition to a number of other known and undescribed genes (Butler et al. 2003; Cho and Irvine 2004). This expression of *pdm* and the resulting mutant phenotype (which begins to resemble a paranotal lobe due to the near obliteration of the axillary sclerites), as well as its expression at leg joints, seems to provide further evidence that it may have been influential in providing the paranotal extension the needed articulation to produce a functional wing. Interestingly, extreme *pdm* mutants also lack nearly all venation (Ng et al. 1995).

As it has been observed in morphological studies, the wing not only is a paranotal extension, but it also appears to incorporate elements of the pleuron (coxopodite/basicoxa) (Grimaldi and Engel 2005; Hasenfuss 2008). While this observation has not been acknowledged with developmental data outside of Holometabola, it appears to be supported at least by *Drosophila* in the structure of the wing disc (Bryant 1975; Cohen 1993; Klein 2001). Since the dorsal elements of the pleuron are part of the wing disc, it is evident that some part of the coxopodite was integrated into the paratergal extension to give rise to the wing articulation. This observation provides support for the hypothesis put forward by Niwa et al. (2010), in which they postulated that the pterygote wing was formed through the intersection of two developmental modules, one which produced a dorsal limb-like process and the other which created a planar extension of tergite at the tergal–pleural boundary (Šulc 1927, Kukalová-Peck 1983). Kukalová-Peck's (1983) assertion that wings 'may represent a fusion between the epicoxal segment' and zygentoman paranotal lobes are perhaps not far from accurate in essence, although the above demonstrates that ad hoc exites are superfluous. Interestingly enough, as the wing disc also includes tissue for the adult tergum, this association likely indicates an inseparable developmental module (as indicated by the early, uniform expression of *ap*; Jockusch and Nagy 1997; Klein and Martinez Arias 1998). If we accept the hypothesis that the wing is largely a paranotal extension, separating the two early developing tissues (that of the notum from that of the upper pleuron) would therefore abolish formation of the wing. While this is interesting from *Drosophila*, one wonders what differences might be found if such a study were to be undertaken in a basal, living mayfly where the sclerotized pleural surface is dramatically dissimilar.

12.2.4 Developmental Implications for Wing Origins?

We must keep in mind that while much excellent work has been accomplished in developmental genetics, much of the progress has been made in *Drosophila*, a highly apomorphic taxon in Diptera. Since much developmental evidence for wing origins stems from literature on *Drosophila*, while it certainly demonstrates many interesting developmental features, it is still difficult to separate gene expression features that may suggest deep homology and be indicative of ancestral wing origins from highly derived features in a lineage that is far removed from basal hexapods and certainly from ancestral Arthropoda. Straightforward conclusions drawn from such developmental data, then, must certainly be analysed in great detail and in a much broader comparative framework. Also, as it is becoming more evident that, while expression patterns of complexes such as HOM-C are thought to be largely conserved in diverse lineages such as crustaceans and hexapods (Hughes and Kaufman 2002), the functions of these genes may have shifted, likely through changes in downstream targets/pathways or upstream regulators (Prud'homme et al. 2007) and developmental drift (Angelini and Kaufman 2005), to give rise to the morphological diversity we see today. If such is the case, then even greater stress is placed on sampling diverse lineages, as well as examining expression patterns and performing functional assays. In compiling all palaeontological, neontological, and developmental evidence thus far (Fig. 12.2), and following the results of Niwa et al. (2010) and building upon their hypothesis, it appears that there is evidence for a developmental ground plan in Hexapoda that produced paranotal extensions of the thorax (Fig. 12.1a, b). Subsequently, through the integration of appendage patterning modules (e.g. those present in gills, exites, legs, and c.), a functional articulation (hinge) developed integrating the dorsal elements of the pleuron, providing a functional wing and providing a basis for which further refinements of the pterygote wing could be made, such as in wing shape, venation, structure of the articulation (axillary sclerites), and c (Fig. 12.1c).

Important avenues for understanding the intricacies of morphological change (and wing origins and evolution) will include emerging tools of genomics and methods for examining specific developing tissue subsets, such as in transcriptomics and proteomics (e.g. Alonso and Santarén 2005). As many of the more general patterning pathways are being elucidated, as Angelini and Kaufman (2005) note, it will be of great significance to focus closer on understanding the genetics behind the plethora of subtle morphological changes that occur through signalling of downstream targets of major appendage patterning pathways for example (e.g. Butler et al. 2003). More attention should also be devoted to understanding the genetic control of tergal outgrowths, as well as the formation of the axillary sclerites. It may be of great utility if future research also includes examination of protein structure, which may provide insight into regulatory and functional changes that have occurred in such developmental genes.

12.3 Palaeontology of Insect Wings

We have purposely belaboured the point concerning phylogeny, and it is therefore of great interest to consider those taxa that are as close to the common ancestor of Pterygota as is possible. Naturally, any species living today is separated from this ancestral taxon by nearly 400 million years, and this creates several challenges. Palaeontological evidence is unique in its ability to bridge this gap, at least partially, and the investigation of phylogenetically relevant taxa from Palaeozoic deposits is of considerable interest in regard to the origins of flight. As critical as Palaeozoic insect fossils are, it must be admitted from the start that no fossil species of a stem-group pterygote with or without protowings has yet been recovered. Indeed, the pre-Late Carboniferous record of insects is amazingly sparse, and it is from the Devonian or earlier in which wings originated, meaning that the hunt continues for abundant, mid-Palaeozoic outcrops of completely preserved hexapods.

Insect wings are the most common source of data in palaeoentomology owing to their solidity and resistance to subsequent transportation and taphonomic processes. Generally, insect wings should be considered in conjunction with the remainder of the body for a reconstruction of the entire animal and comprehensive taxonomic and morphological treatment. However, in some cases, particularly for Palaeozoic taxa, isolated wings preserved as compressions or impressions provide the only evidence for past species richness [refer to Carpenter (1992) for the most recent comprehensive catalogue], and here, there is often a bias for well-sclerotized forewings modified for protection in certain clades, these being particularly durable for preservation. The use of these data in insect systematics varies dramatically by taxonomic group due to various adaptations, functional modifications, and polymorphisms and therefore must be reasonably evaluated by taxonomists and in a cladistic framework. Well-preserved insect fossils with complete body appendages and tiny morphological structures are known from amber inclusions, but such resin-entombed specimens are unfortunately unavailable prior to the Cretaceous except for a few fragmentary remains reported in Late Triassic amber from Italy (Schmidt et al. 2012). Admittedly, the fossil record of insects pales in comparison with the enormous numbers of Recent species, but the available evidence does highlight the dramatic number of lineages present in different epochs, serves as a reasonable proxy for diversity during these time periods, and gives a unique perspective on taxa with unique characters or character combinations, together reconstructing a profound understanding of insect evolution during its early phases. Grimaldi and Engel (2005) provide a cladistically framed overview of insect evolution and diversity, reflecting the available palaeontological evidence up to that date.

12.3.1 First Appearance of Winged Insects

The earliest hexapod fossils are known from the Early Devonian of Rhynie, Scotland, and preserved in chert formed in a silica-rich, volcanic spring and of Pragian age (ca. 407 million years old). Two definitive hexapods are known from the Rhynie chert, the first and most widely known being the collembolan *Rhyniella praecursor*, a species for which there is generally good knowledge of its overall morphology (Whalley and Jarzembowski 1981). The second, representing a true insect, is known only from the fragmentary remains of a head capsule and was dubbed *Rhyniognatha hirsti* (Tillyard 1928; Engel and Grimaldi 2004). The mandibles of *R. hirsti* were dicondylic, a synapomorphic trait placing them as more derived than the most basal order of wingless insects. Furthermore, the mandibles were of the typical metapterygotan organization, an apomorphic suite of traits found only among pterygote insects and in the Metapterygota (all winged insects exclusive of Ephemeroptera) in particular (Engel and Grimaldi 2004). This cladistic placement indicated not only that *R. hirsti* was assuredly an insect but that the species belonged to the winged insects and was from a lineage that diverged subsequent to the divergence of the mayflies, implying that wing origins and diversification took place sometime prior to the Pragian. This revelation pushed back the presumed origins of wings by nearly 80 million years and also the origin of insects as a whole, highlighting that insects perhaps stemmed from the Silurian and were among the earliest forms of terrestrial animal life (Engel and Grimaldi 2004). Unfortunately, *R. hirsti* was fragmentary and no wings were preserved with the fossil, leaving open numerous questions regarding the putative wings of the species. Remarkably, the age and phylogenetic placement of *R. hirsti* are roughly in accord with estimates of divergence based on molecular data alone, which suggested an origin of pterygote insects anywhere from the latest Ordovician to the Silurian, and a later origin of the more derived neopteran insects, perhaps as early as the Early to mid-Devonian (Gaunt and Miles 2002; Rehm et al. 2011). Fossil evidence of a metapterygotan insect from the Early Devonian implies the acquisition of wings at least in the earliest Devonian (Lochkovian) or latest Silurian corresponds with the formation of the first trophic relationships between terrestrial arthropods and vascular plants, the latter having invaded land slightly earlier (Edwards et al. 1995).

Subsequent to *R. hirsti*, there are only a couple of definitive insect remains from the Devonian, the first being a relatively complete compression from Famennian strata near Strud, Belgium (Garrouste et al. 2012). Like *R. hirsti*, *Strudiella devonica* possessed metapterygotan mandibles and emphasized that the origination and diversification of pterygotes, at least into the most basal lineages, had already occurred. Again, similar to *R. hirsti*, *S. devonica* also lacked wings, either because it was a nymph and did not yet possess them because it was secondarily apterous or perhaps as a result of preservation. The sole specimen is too poorly preserved to permit analysis of fine details of the thorax to determine whether minute sclerites representing a point of articulation might have existed, and again critical questions regarding the form of wings in the earliest fossils assignable to Pterygota were left unresolved. The only other Devonian evidence for insects is the mid-Devonian (Givetian) bristletail fragments (Archaeognatha) from Gilboa, New York (Shear et al. 1984). Putative Eifelian remains of a remarkably modern-looking bristletail from Gaspé Bay in Quebec, Canada (Labandeira et al. 1988) have been revealed to be a modern contaminant (Jeram et al. 1990). No other records of hexapods are known from the Devonian, a scant record at best and the greatest hindrance to understanding early insect evolution.

The first wings preserved in the fossil record are much younger than any estimate of the age of Pterygota as well as than the fragmentary remains of pterygotes from the Devonian. Indeed, the earliest wings are known from the transition period between the Early and Late Carboniferous, approximately 318 million years ago and nearly 90 million years younger than the very incomplete remains of *R. hirsti*. This considerable gap is partly the result of a scarcity of Early Carboniferous freshwater deposits worldwide. These earliest Late Carboniferous insects have been attributed to the orthopterid lineage and thereby clearly derived from the Neoptera (Prokop et al. 2005). The Namurian is the earliest stage of the Late Carboniferous with a sudden occurrence of diverse winged insects comprising stem groups of the major lineages, highlighting that the extensive diversification of Pterygota had already taken place; those clades became well established and radiated themselves (Hennig 1981; Kukalová-Peck 1991; Grimaldi and Engel 2005; Prokop and Nel 2007). In terms of the fossil record, the Late Carboniferous reveals a world in which winged insects and flight were already ancient and this lineage had radiated into all of the higher (superordinal) clades which would persist to the present day, as well as a few which would not last beyond the end-Permian Event at the close of the Palaeozoic (ca. 251 million years ago). From the Palaeozoic, the fossil record currently provides two perspectives—one that is too scant to permit much clarity (Devonian–Early Carboniferous) or one that is too late in regard to the window of time in which wings and flight originated (Late Carboniferous-Permian), a maddening situation for entomology and evolutionary biology.

12.3.2 Wing Flexion and Palaeoptery Versus Neoptery as Crucial Innovations

As mentioned previously, today's phylogenetic evidence universally supports a single origin for insect wings (e.g. Kukalová-Peck 1978, 1983, 1991; Boudreaux 1979; Hennig 1981; Kristensen 1991; Grimaldi and Engel 2005; Trautwein et al. 2012). At about the same time, Lameere (1922); Crampton (1924), and Martynov (1925) independently noted two fundamentally different means of wing flexion, this giving rise to the classificatory division between palaeopterous (those incapable of flexing the wing back over the abdomen) and neopterous (those capable of such flexion) insects. Those lineages with the palaeopterous condition were classified as the formal group Palaeoptera, the remainder in the Neoptera, and thus was born the debate over relationships between the basal orders of winged insects and whether or not the Palaeoptera are monophyletic and, if not, then which of its constituent groups were basal and which were more closely allied to the neopteran insects. In addition, the arrangement and form of the basal sclerites forming the wing base differ between the lineages in question. Indeed, the Odonatoptera differ notably from other pterygotes, something which led Matsuda (1970, 1981) and La Greca (1980) to reconsider pterygote monophyly. Despite the differences between odonates and other winged insects, the basal sclerites can be successfully homologized with those of Ephemeroptera and Neoptera (Ninomiya and Yoshizawa 2009). Furthermore, the thoracic musculature of the primitively wingless *Lepisma* (Zygentoma) and Pterygota was first established by Matsuda (1970) and again by Hasenfuss (2002). Hasenfuss (2002) provided a detailed comparative morphological study of the mesothorax of *Lepisma*, demonstrating the details of homology and transformation with the pterygote ground plan. The corresponding sclerites and muscles of three subcoxal leg elements present in lepismatids are recognizable in the pterygotan pterothorax (Hasenfuss 2008).

The fundamental debate has been over Palaeoptera monophyly. Palaeoptera was largely deconstructed for a long while. Börner (1904) arranged the basal winged orders with Ephemeroptera diverging from Metapterygota (all other winged insects), a position supported by morphology and molecular data sets (e.g. Staniczek 2000; Beutel and Gorb 2006; Cameron et al. 2006; Zhang et al. 2008). Schwanwitsch (1943) reversed this, with Odonata diverging first, establishing the Chiastomyaria hypothesis based on muscle arrangement (=Opisthoptera of Lemche 1940) and supported by initial phylogenomic data sets, albeit with understandingly limited taxon sampling (Simon et al. 2009). Palaeoptera monophyly was argued for by Kukalová-Peck (e.g. Kukalová-Peck and Brauckmann 1990; Kukalová-Peck 2009) in an expanded and revised system of Pterygota (although see Béthoux et al. 2008 for a discussion of some of her methods of character analysis). Palaeoptera has also been supported by limited molecular analyses (Kjer et al. 2006; Regier et al. 2010; Ishiwata et al. 2011) and by some morphological character systems (e.g. Blanke et al. 2012), although the most honest description of the available evidence is that there is ambiguity over relationships (e.g. Hovmöller et al. 2002; Ogden and Whiting 2003; Kjer et al. 2006; Whitfield and Kjer 2008). Kukalová-Peck (1997) proposed a strong convex brace ‘cup-aa1’ or a contact between AA and CuP (vein abbreviations used in text outlined in Table 12.1) as a putative synapomorphy of Ephemeroptera and Odonatoptera and subsequently proposed division of these groups into the ‘Hydropalaeoptera’ (=Ephemeroptera + Odonatoptera) and ‘Rostropalaeoptera’ (=Palaeodictyopterida) (Wootton and Kukalová-Peck 2000). Bechly (1996) proposed that the Ax0 in Odonatoptera was homologous to the subcostal brace ScA in Ephemeroptera, implying that it was another potential synapomorphy supporting the same arrangement of orders. Haas and Kukalová-Peck (2001) purportedly identified 65 differences between Palaeoptera and Neoptera based on wing characters traceable in extant species, although the homology of some of these is tenuous. Later, Kukalová-Peck (2009), when describing the first Carboniferous protodonate immature, reviewed what she interpreted as synapomorphies of Ephemeroptera and Odonatoptera based on wing articulation and venation. Assuming Palaeoptera monophyly, it has been argued that the neopterous condition is plesiomorphic and that the palaeopterous condition is derived (Hasenfuss 2008; Kukalová-Peck 2009) and that the wing bases of Ephemeroptera and Odonata are secondarily stiffened (Willkommen 2009). In addition, it has been argued that wing development of Palaeozoic Palaeoptera proceeds gradually through numerous moults of nymphal instars to several subimaginal instars bearing articulated wings in comparison with Recent members (Kukalová-Peck 1978); although as noted by Béthoux et al. (2008), the evidence for moulting subimagos in the fossil record is tenuous. During the course of development, the wings of young nymphs of these fossil taxa apparently arch backward (Fig. 12.3a, f) and gradually become straightened in each

Table 12.1 Abbreviations for major wing veins discussed in text

AA	Anal anterior
AP	Anal posterior
CP	Costa posterior
Cu	Cubitus
CuA	Cubitus anterior
CuP	Cubitus posterior
IN	Intercalary
M	Media
MA	Media anterior
MP	Media posterior
R	Radius
RA	Radius anterior
RP	Radius posterior
ScA	Subcosta anterior
ScP	Subcosta posterior

subsequent instar until the wings are fully outstretched, this putatively suggesting that palaeoptery in the adult was secondarily derived (Kukalová-Peck 1978; Hubbard and Kukalová-Peck 1980). Relationships between Ephemeropterida, Odonatoptera, Palaeodictyopterida, and Neoptera remain controversial and constitute a debate of lasting significance. Metapterygota (=Odonata + Neoptera) and Palaeoptera (Odonata + Ephemeroptera) are the most widely recovered suite of relationships, although many data are in conflict. Future work may well support a monophyletic Palaeoptera, and it must remain a viable alternative solution to the arrangement of the basal winged lineages.

As mentioned, Palaeoptera are known for their inability to flex their wings back over the abdomen. Insects exhibiting the palaeopterous morphological condition were remarkably diverse and abundant in Late Palaeozoic ecosystems, indicating to some that they were the first of the flying insects (i.e. that neoptery is derived relative to palaeoptery), and these insects were decimated by the Permian/Triassic mass extinction (Labandeira and Sepkoski 1993). There is a single exception to the rule of permanently outstretched wings among Palaeoptera, namely the extinct order Diaphanopterodea whose species were capable of wing flexion in a roof-like position (Fig. 12.3h) owing to a unique arrangement of eight rows of movable sclerites at the wing base (Kukalová-Peck and Brauckmann 1990; Kukalová-Peck et al. 2009). Based on other characters, the Diaphanopterodea clearly belong within a monophyletic Palaeodictyopterida and their wing flexion is not only independent from that observed in Neoptera but also not indicative of the basal condition for the Palaeodictyopterida as they are not a primitive grade of this superordinal complex (Kukalová-Peck 1978).

Of course, critical to the aforementioned discussions of relationships are the Palaeodictyopterida, a diverse lineage of Palaeozoic palaeopterous insects. Obviously, no molecular study has included representatives of this lineage (or for that matter, any of the extensive stem-group representatives of the Ephemeroptera and Odonatoptera known from the same time period), and it remains unclear what influence the inclusion of palaeodictyopterids might have on modern phylogenetic interpretations. The only means of ascertaining the influence of Palaeodictyopterida on cladistic studies of basal lineages is the combination of molecular data with an extensive morphological data set coded for a suitably rich number of extinct species. Such a study would require direct observation from the fossils as there appears to be some misinterpretation of these Palaeozoic taxa in the literature (e.g. Béthoux and Briggs 2008; Béthoux et al. 2008; Kukalová-Peck and Beutel 2012; Shcherbakov 2011), and data mining from such papers may conflate problems. The establishment of a robust phylogeny for basal pterygotes including all of the fossil taxa is one of the ripest challenges for future research.

Another challenge resides in the assumption that the basal condition observed for extant members of a lineage holds true for stem groups. For example, coding the earwigs as having trimerous tarsi, the same as stick insects and webspinners, fails to consider palaeontological evidence that the trimerous condition is not homologous between these orders. Stem-group earwigs share abundant synapomorphies with crown-group Dermaptera but have fully pentamerous tarsi, the presumed plesiomorphic condition for Neoptera, if not all Insecta (Grimaldi and Engel 2005). Similar evidence exists from stem-group stick insects that they independently arrived at the trimerous condition, and thus, any analysis treating these orders as possessing the same character state in their ground plans is based on faulty data. Such is also a challenge for the basal winged lineages. For example, there is a widespread assumption that all basal and extinct groups of winged insects are aquatic in their immature stages based on crown-group Ephemeroptera and Odonata. The putatively plesiomorphic appearance of stoneflies among the Neoptera has led some to postulate that the ground plan condition for this clade is similarly aquatic. Yet, there remains no convincing evidence that this is the case. Indeed, stem-group Odonata lack a clear indication of the


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)

◀ **Fig. 12.3** A Palaeozoic bestiary of early winged insects. **a** Nymph of *Idoptilus onisciformis* Wootton (Palaeodictyoptera). **b** Prothoracic articulated winglets of *Lithomantis carbonarius* Woodward (Palaeodictyoptera: Lithomanteidae). **c** Prothoracic articulated winglets of *Stenodictya pygmaea* Meunier (Palaeodictyoptera: Dictyoneuridae). **d** *Arctotypus sylvaensis* Martynov (Protodonata: Meganeuridae). **e** Nygmata in wing membrane of *Lithomantis bohemica* Novák (Palaeodictyoptera: Lithomanteidae). **f** Nymph of *Protereisma americana* Demoulin (Ephemeroptera: Protereismatidae). **g** Wing venation of *Protereisma permianum* Sellards (Ephemeroptera: Protereismatidae). **h** Habitus of *Permuralia maculata* Kukalová-Peck and Sinitshenkova (Diaphanopterodea: Parelmoidae). **i** Wing venation of the stem-group mayfly relative *Lithoneura lameeri* Carpenter (Ephemeropterida: Syntonopterodea). **j** Habitus of *Permohymen schucherti* Tillyard (Megasecoptera: Permohymenidae). **k** Habitus of *Kemperala hagenensis* Brauckmann (Neoptera: Paoliidae). **l** Wing venation of *Diathemidia monstruosa* Sinitshenkova (Dicliptera: Diathemidae). **m** Paranotal extensions of the prothorax of *Lemmatophora typa* Sellards (Lemmatophoridae). Images a, b © The Natural History Museum, London; images f, g, i, j, m © Museum of Comparative Zoology, Harvard University.

life history for their immatures, and quite interestingly, nymphs of stem-group Ephemeroptera of the family Protereismatidae (Fig. 12.3f) do not possess abdominal gills (or gills of any kind!), suggesting that they were not aquatic (Grimaldi and Engel 2005). The same can be said for putative stem-group stoneflies among families such as Lemmatophoridae (Fig. 12.3m). Immatures of Palaeodictyopterida are widely known (Fig. 12.3a), but again no obvious gill structures are present, and the morphology of many is convergent with immature beetles living in moist detritus layers on tropical forest floors. There is no overwhelming evidence that any of these lineages have aquatic nymphs in their ground plans when fossils are considered. This does not rule out the possibility that they could have been aquatic but merely emphasizes that the underlying assumption that they must have been is entirely ad hoc. We desperately require a modern, revised understanding of the immature stages of Palaeozoic insect clades.

Obviously, the resolution of these relationships and early life histories has significant consequences for the interpretation of wing and flight origins and the ground plan reconstruction of basal wing structure and articulation. The developmental studies outlined above seem to be converging on a consistent picture of wing formation and homology but cannot resolve which form of articulation and flexion (or lack thereof) is basal. Such a polarization of the alternative differences in articulation requires the integration of such comparative developmental evidence with a robust phylogeny for early Pterygota. Thus, any changes in reconstruction for the base of Pterygota will have profound influences on how we interpret the stages in wing origins as well as the associated scenarios proposed for the production of early powered flight. The phylogeny infused with palaeontological evidence will also permit a more precise timing for flight origins, the life history of those stem-group taxa involved, and those abiotic factors of the ancient ecosystem (one profoundly different from the world in which we live!) that influenced the evolutionary development of wings.

12.3.3 Principal Lineages of Palaeozoic Pterygota

The attribution of particular fossils to higher-rank taxa has been challenging, particularly given the apparent presence of convergent characters in wing venation across unrelated clades. For example, the Syntonopteridae (Fig. 12.3i) were first attributed to the Palaeodictyoptera and later considered as Ephemeroptera based on the presence of Y-shaped intercalary veins (Edmunds and Traver 1954; Edmunds 1972; Wootton 1981; Kukalová-Peck 1985; Carpenter 1992; Willmann 1999; Prokop et al. 2010). However, the presence or absence of intercalary veins cannot be considered a unique autapomorphy of the so-called Hydropalaeoptera since this also occurs in Palaeodictyoptera such as the families Calvertiellidae and Namuroningxiidae (Béthoux et al. 2007; Prokop and Ren 2007). In addition to many convergences, the wings across these lineages are clearly plesiomorphic. The wing venation of palaeopterous insects has a prominent alternation between convex and concave longitudinal veins including prominently developed convex MA and stem of M always present. Further putative plesiomophies in venation are veins ScP and RA terminating at the wing apex and RA and RP beginning as separate stems (Lameere 1922; Kukalová-Peck 1991). Thus, there are significant challenges to properly placing particular fossils, exacerbated by the abundance of isolated wings which must be interpreted in the absence of body characters. Here, we outline the principal lineages as they are presently understood in the hope that this characterization will fuel future cladistic treatments of both molecular and morphological (including palaeontological!) data.

The mayflies (Ephemeroptera) are considered a basal lineage of winged insects with wings bearing a full set of deeply corrugated main veins, intercalary veins universally present, and a prominent arched subcostal brace ScA at the wing base as synapomorphies. Several stem groups are allied to the Ephemeroptera to form the superorder Ephemeropterida. The fore- and hindwings of Palaeozoic species were nearly homonomous in comparison with most Mesozoic, Tertiary, and modern taxa whose hindwings are much smaller or completely reduced (as with the exception of the Jurassic families Mesephemeridae and Mickoleitiidae). Nymphs of Permian taxa attributable to the Protereismatidae exhibit wings freely articulated with the thorax and a venation pattern similar to adults (Fig. 12.3f, g) (Kukalová 1968; Hubbard and Kukalová-Peck 1980). Syntonopterodea are the oldest and most plesiomorphic members of the Ephemeropterida and are known from the Late Carboniferous to the Middle Permian. Syntonopterodea share with other mayflies the presence of a distinct anterior curve or ‘zigzag’ of AA1 + 2, constituting a potential synapomorphy for the clade (Kukalová-Peck 1985, 1997; Willmann 1999). The systematic position of this group is critical for the resolution of phylogenetic relationships between major pterygote lineages (e.g. Edmunds and Travers 1954, Kukalová-Peck 1985; Willmann 1999; Grimaldi and Engel 2005; Prokop et al. 2010). The most prominent diagnostic features are the constriction of the area between AA1 + 2 and AA3 + 4 in the hindwing, the presence of a concave longitudinal vein IN (intercalary) between them, and a constriction of the area between AA3 + 4 and the first branch of the concave AP at the same point (Prokop et al. 2010). Unfortunately, most syntonopterids are based on isolated wings, but *Lithoneura lameeri* (Fig. 12.3i), known from a siderite nodule from Mazon Creek, Illinois, is an exceptionally preserved fossil with exquisite details also of body structures in addition to wing venation (Carpenter 1938, 1987; Kukalová-Peck 1985; Willmann 1999). Another ‘keystone’ fossil that has at times been included here is *Triplosoba pulchella* from the Late Carboniferous of Commentry, France. *Triplosoba* had an unusual wing venation for mayflies such as the basal connection of MA with R and RP in the forewing, and MA remote from RP and basally fused with MP in the hindwing. Prokop and Nel (2009) transferred this taxon to Palaeodictyopterida as suggested by earlier authors (Forbes 1943; Willmann 1999). Nevertheless, doubt remains about the inclusion of *Triplosoba* in Palaeodictyopterida (Staniczek et al. 2011). Bechemeyer and Engel (2011) followed Prokop and Nel (2009) and excluded the Triplosobidae (their Triplosoboptera) from what they considered to represent a monophyletic Ephemeropterida, admitting that the former might be a stem group to Palaeodictyopterida or Metapterygota.

Odonatoptera, comprising the Recent dragonflies and damselflies along with the extinct griffenflies and others, are one of the most peculiar groups owing to their strikingly different wing articulation relative to other pterygotes. Odonatopterans are readily recognized by the presence of two large plates (costal plate and radio-anal plate), rather than an arrangement of multiple axillary sclerites, the former representing a unique synapomorphy for the clade. The lineage was abundant and diverse and their morphology stable over evolutionary time, with the earliest species known from the earliest Late Carboniferous (Namurian) (Riek and Kukalová-Peck 1984; Bechly et al. 2001; Ren et al. 2008). Wings of Odonatoptera have a strongly reduced anal area, especially in the forewings; ScP reaching the costal margin well before the wing apex, and an anal brace with a Z-like kink in CuP at the point of fusion with AA. Prothoracic winglets present in Eugeropteridae were probably articulated and movable, whereas in Erasipteridae, the articulation is not apparent (Bechly et al. 2001). Both of the latter groups represent the most basal lineages known from the Late Carboniferous. Geroptera, with the single family Eugeropteridae, is known only from Argentina and possess a rather coarse meshwork of simple crossveins and a short ScP reaching the costal margin at about wing mid-length, this being convergent with Erasipteridae, Paralogidae, and Odonatoclada (Riek and Kukalová-Peck 1984). Erasipteridae are known from the early Late Carboniferous of central Europe and retained a partially dense pattern of crossveins (the so-called archeodictyon) and a long median stem lacking the arculus and nodus (Pruvost 1933; Bechly 1996; Bechly et al. 2001). The Palaeozoic griffenflies of the Protodonata (Fig. 12.3d), also widely known as the Meganisoptera (a name which implicates their former common name as 'giant dragonflies' despite the fact that they are in no way 'dragonflies'), are famous for having given rise to the largest wingspans among insects. *Meganeuropsis permiana* from the Early Permian Wellington Formation of central Kansas and northcentral Oklahoma had a wing span around 710 mm, well exceeding that of any living insect (Carpenter 1939, 1947). Insect gigantism, known particularly from the Late Carboniferous, occurred also in other groups such as the stem-group mayfly *Bojophlebia prokopi*, with a wingspan reaching almost 500 mm (Kukalová-Peck 1985). One of the favoured hypotheses for the presence of such giant insects (and other massive arthropods) at this time is the corresponding hyperoxic atmospheres, thereby permitting the passive transfer of more oxygen via tracheae to metabolically active tissues (Graham et al. 1995). However, these insect giants coexisted together with even more diverse normal- to small-sized relatives (Nel et al. 2009). Another explanation of Palaeozoic insect gigantism assumes that the increase in body size of some insects was a result of an evolutionary race in body size between aerial predators such as griffenflies and their putative prey among the Palaeodictyopterida (Hasenfuss 2008). While the latter is an enticing hypothesis, it is entirely ad hoc as there is no evidence for what griffenflies fed upon nor any phylogenetic evaluation of relationships for these lineages which demonstrate such an arms race. Similarly, Nel et al. (2008) also considered other factors such as the absence of flying vertebrate predators at this time, but again it is not immediately clear why this alone should lead to such a dramatic increase in size. A comprehensive and conclusive explanation for Palaeozoic insect gigantism remains to be seen.

The Protodonata, or Meganisoptera, are known entirely from the Late Palezoic and are currently considered as a stem group to true Odonata, differing mainly in wing venation by the absence of a nodus, discoidal cells, and a pterostigma (Nel et al. 2009). Wings of these species consist of hundreds to thousands of small polygonal cells, especially numerous in the Meganeuridae (Fig. 12.3d). A true odonatoid nodus with more or less oblique nodal and subnodal veinlets at about wing mid-length first appears in Nodialata, a clade comprising Protanisoptera and Discoidalia (Bechly 1996). The Upper Permian family Lapeyriidae has been considered to be the most basal group of Nodialata (Nel et al. 1999). The Protanisoptera were a widely distributed group of Permian Nodialata that had a partly developed nodus, the hindwings as long or even slightly longer than forewings, the brace formed by ScA uniquely oblique, and a special form of pterostigma crossed by RA, the latter considered as convergent with Dicliptera (Fig. 12.3l) (Palaeodictyopterida) and among modern Diptera.

The extinct superorder Palaeodictyopterida (=Dictyoneuridea) represents a widely diverse group of Palaeozoic insects ranging from the earliest Late Carboniferous to the Late Permian, with a peak in abundance in the Late Carboniferous (Sinitshenkova 2002). Triassic records of *Thuringopteryx gimmi* and *Paratitan reliquia* putatively suggesting the existence of palaeodictyopteridans after the Permian/Triassic mass extinction have been revised and unambiguously excluded from the superorder (Willmann 2008; Shcherbakov 2011). Palaeodictyopterida have a number of wing venation symplesiomorphies for pterygotes such as a pronounced CP and ScA and a convex ridge formed by stiffened membrane in conjunction with basal portions of AA (homologous to the anal brace in Ephemeroptera and Odonatoptera) (Kukalová-Peck 1991, 1997). Kukalová-Peck (2009) supposed palaeoptery as derived based on fusions between basivenalia and fulcalaria in the subcostal to jugal rows putatively visible in various palaeodictyopterid groups, but this requires confirmation. The Palaeodictyopterida were most remarkable for their haustellate mouthparts (Fig. 12.3b), their sucking beaks making them among the earliest of specialized herbivores. The classical divisions of Palaeodictyopterida recognize four main orders Diaphanopterodea, Palaeodictyoptera, Megasecoptera, and Dicliptera (Grimaldi and Engel 2005).

Palaeodictyoptera are the largest and most diverse group and are known from the earliest Late Carboniferous to the Late Permian, with a few giant species like *Mazothairos enormis* attributed to Homoiopteridae (Kukalová-Peck and Richardson 1983; Prokop et al. 2006). The fore- and hindwings were either similar in form, or in some families, the hindwings were distinctly broader, for example as in Spilapteridae. The wing venation had a complete set of main veins including MA and MP, a prominent corrugation of convex and concave veins, and usually lacked fusion between these systems. Intercalary veins were sometimes present, as in the families Calvertiellidae and Namuroningxianiidae (Prokop and Ren 2007), while the main longitudinal veins were frequently connected by numerous crossveins forming a dense pattern of irregular networks (=‘archeodictyon’) and were well developed in families such as Dictyoneuridae. Articulated prothoracic winglets were putatively present in some members of Palaeodictyoptera such as in *Lithomantis carbonarius* (Lithomanteidae) and *Stenodictya pygmaea* (Dictyoneuridae) (Fig. 12.3b, c) (Kukalová-Peck 1978). However, most of the known lateral prothoracic extensions lacked any observable articulation with the prothorax, much like those in neopteran insects such as Lemmatophoridae (Fig. 12.3m) from the same deposits (Kukalová-Peck 1978, 1991). Nygmata-like structures were present in the wing membrane (Fig. 12.3e), observable as circular spots or punctures in distinctive positions principally alongside RP and the medial veins of various groups (e.g. Novák 1880, Carpenter 1963). However, the homology of these with similarly named structures present in different holometabolan orders like Neuroptera, Mecoptera, and Hymenoptera has never been elaborated (Forbes 1924, 1943), and they are assuredly of different evolutionary origins. Palaeodictyoptera are likely paraphyletic with respect to other palaeodictyopterid orders, lacking any distinctive synapomorphies and principally recognized by their exclusion from the other groups.

The Megasecoptera had homonomous wings that were typically slender and petiolate (Fig. 12.3j), with a complete set of main longitudinal veins and frequent coalescence of MA and MP (e.g. Mischopteridae), or more rarely fusion to partial connections between MA and RP and MP with CuA (e.g. Sphecopteridae or Corydaloididae). The costal margin was usually straight with closely parallel veins ScP and R and had a generally denser pattern of crossveins relative to the remaining orders. Overall, the wing venation was considerably similar to Palaeodictyoptera (Carpenter 1962; Sinitshenkova 1980), although these similarities are largely symplesiomorphic. It is not entirely clear what subgroup or families of the paraphyletic Palaeodictyoptera might be more closely allied to Megasecoptera.

As mentioned above, Diaphanopterodea had homonomous wings that could be held roof-like over the abdomen when at rest (Fig. 12.3h). In addition, species had markedly curved stems of R and M running closely parallel, with the stem of R subsequently diverging from the separation of MA and MP; otherwise, the pattern of wing venation frequently resembled that of Megasecoptera, likely symplesiomorphically.

The last clade of Palaeodicyopterida is the Dicliptera. This was a small group known strictly from the Permian, with the hindwings strongly reduced in Diathemidae or completely lost in Permothemistidae (Fig. 12.3l). The forewing had a well-developed and sclerotized pterostigma, a strong reduction in the crossveins to a single rs-m vein, a large anal area, and fusion near the wing base between M + Cu and AA + Cu + CuP as a double anal brace (Kukalová-Peck 1991; Grimaldi and Engel 2005).

Wootton and Kukalová-Peck (2000) utilized available morphological data from palaeopterous Palaeozoic insects to interpret the flight abilities and techniques for various groups. Their interpretations indicated that there existed marked differences in flight abilities among Carboniferous and Permian ephemeropteridans by comparison with Recent taxa, while Palaeozoic odonatopterans exhibited a similar wing construction and shape to modern dragonflies and damselflies as well as an apparent early adaptation to aerial predation. The palaeodictyopterid groups exhibited a broad spectrum of flight techniques and patterns, indicative of the diversity and various peculiar specializations within the lineage.

Lastly, the Neoptera are, of course, well known for their ability to fold the wings over the abdomen due to a unique organization of the axillary sclerites, particularly the Y-shaped third axillary, this suite representing one of the strongest synapomorphies. The Neoptera comprise the vast majority of all pterygote insects in the Recent fauna as well as the fossil record. The wings of neopterans are characterized by the separation of the anterior remigium from a posterior vannus by the claval furrow and the subsequent subdivision of the neala (jugum) from the vannus by the jugal furrow, particularly visible in the hindwing. The wing venation of Neoptera has lost the strong pattern of corrugation; the stem of M is basally concave; vein MA is not clearly convex and frequently hardly identifiable when fused with RP or completely suppressed. The course of MA and MP is the most controversial issue among authors. Forbes (1943) supposed that MA is connected to R or RP, and there is a free MP in all Neoptera, while Sharov (1968) and others considered that MP was fused with CuA and only the basal part is retained as crossvein m-cua (='arculus'). The course of the medial and cubital veins close to the wing base and the orientation of the arculus play a role in the elasticity and function of the wing and have been utilized for phylogenetic interpretations of larger groupings among Pterygota. Neoptera is traditionally subdivided into three units: Polyneoptera, Paraneoptera, and Holometabola, the latter two united as the Eumetabola (Grimaldi and Engel 2005). Haas and Kukalová-Peck (2001) proposed a split between two major neopteran clades 'Pleconeoptera' + 'Orthoneoptera', both with a full anojugal lobe and 'Blattoneoptera' + (Paraneoptera + Holometabola) (although using the names Hemineoptera and Endopterygota for the latter two) with a partial anojugal lobe and reduced anterior anal sector (AA) as putative apomorphies. These divisions have not received support from more extensive morphological and molecular studies on insect relationships (e.g. Trautwein et al. 2012). The Neoptera are abundantly represented in the Palaeozoic, many of which were historically dumped into a wastebasket group called the 'Protorthoptera'. Handlirsch (1906) established the group for insects with orthopteroid affinities and 'Protoblattodea' for insects with blattoid affinities, although even he was unable to attribute several genera to either group (e.g. *Distasis*), and the groups overlapped in their characters as recognized. Martynov (1938), followed by Sharov (1961), attempted to separate Protoblattodea, Protorthoptera, and Paraplecoptera as stem groups to Blattaria, Orthoptera, and Plecoptera, respectively. Hennig (1981) supported the notion of a close relationship between Protorthoptera and Protoblattodea with the modern orders Orthoptera and Blattodea, respectively. By contrast, he noted difficulties with Paraplecoptera as it had been conceived, noting that it appeared to be based strictly on plesiomorphies. Carpenter (1966, 1992) took a conservative position and, in a retrograde classificatory scheme, merged Paraplecoptera and Protoblattodea with Protorthoptera pending future study. Sharov (1968) agreed that Protoblattodea and Paraplecoptera were inseparable and should be combined into one order. There are distinctive groups among these early Neoptera, such as the Paoliida (Fig. 12.3k) (a.k.a., Protoptera) and Caloneurodea, but retention of the remainder in 'Protorthoptera' obscures phylogenetic relationships, thereby serving no good purpose and is assuredly polyphyletic as constituted by Carpenter (1992) (e.g. Béthoux and Nel 2005; Béthoux 2007; Prokop and Nel 2007). While it is beyond the scope of the present work to summarize the entire geological history of insects, these taxa are of interest for wing origins as they factor into the reconstruction of basal character states for Neoptera. As such, a clarification of their relationships relative to extant neopteran orders, their implications for understanding the living clades, and certainly whether any may represent stem groups to Neoptera as a whole, is of vital importance to insect phylogenetics. For the moment, there is no robust phylogeny that comprehensively treats all 'protorthopteran' families alongside the full diversity of non-Eumetabolan insect orders, and this hinders any meaningful interpretation of primitive character states for Neoptera.

12.4 Conclusions

Mounting evolutionary developmental data is giving us a robust and greatly revised perspective on the homology of insect wings, thereby providing an immense leap towards answering the first of those questions posed in the introduction. There is a growing body of developmental evidence that the wing is largely a paranotal extension that integrated appendage patterning modules to develop a functional articulation incorporating portions of the upper pleuron. Unfortunately, there remains significant debate regarding the basal lineages of Pterygota, rendering it difficult to distinguish between competing interpretations of polarity relative to the form of the wing articulation. Palaeontological studies have advanced significantly during the last 25 years, particularly with a large number of critical reevaluations of taxa in a cladistic framework and by pushing back the timing of wing origins from the Early Carboniferous into the earliest Devonian, perhaps latest Silurian. Coupled with this has been the steady accumulation of new taxa from diverse time periods and deposits throughout the globe. While the recovery of an abundance of interpretable remains from the Devonian has not been forthcoming, work on clarifying the identity and relationships between Late Palaeozoic taxa has continued at a significant pace such that the principal lineages important for resolving basal relationships can be characterized and difficulties with particular taxa recognized (e.g. placement of *Triplosoba*, monophyly of Palaeodictyoptera). The currently expanding body of developmental work must unite with a newly invigorated study of insect palaeontology (including the reconstruction of life histories for immature Palaeozoic insects) and phylogeny. Once these elements are resolved and meaningfully united into a comprehensive picture of the early stages and ecologies of wing evolution, only then will we have a solid stance from which to build a consistent model for the origins of powered flight.

What we do know is that the ancestral pterygote lived in a seemingly barren world, quite foreign to anything we are familiar with today, and in which plant life was never far from a shoreline and the climate was generally warm with a moderately high O_2 level. Arborescence had not yet developed, and flight may have been a significant aid to reach nutritious sporangia at the apices of branches in early plants and/or for dispersal. Wings originated as paranotal extensions much like those observed in silverfish, suggesting that gliding may have been the initial stage in developing flight. This would have been followed by the integration of a hinge at the base and some early form of controlled flight. Beyond these few, overly simplified statements, we can say little else with certainty, and to speculate on elaborate adaptive scenarios is fruitless. Anything else about Nature's first flyer remains, for the moment, up in the air.

Acknowledgments We are grateful to A. Minelli for the invitation to contribute this brief chapter concerning wing origins and evolution. Much appreciation is given to R. Ward for his comments on an earlier draft of the section on development, to I.A. Hinojosa-Díaz and A. Nawrocki for general discussion of hexapod morphology and homology, to N.P. Kristensen, A. Nel, and A. Minelli for their comments, and to T. Ohde and T. Niimi for sharing and discussing their recent findings. Illustrative figures were executed by S. Taliaferro under the direction of M.S.E. and S.R.D. and supported by the Engel Illustration Fund, University of Kansas College of Liberal Arts & Sciences. We thank the President and fellows of Harvard College for permission to use MCZ copyrighted material. We are grateful to P. Perkins for permission to study and take photographs of type specimens from F.M. Carpenter's collection housed in the Museum of Comparative Zoology, Harvard University; C. Mellish and A.J. Ross for access to collections and permission to take photographs of *Idoptilus onisciformis* and *Lithomantis carbonarius* in the Natural History Museum, London; A. Nel for access to collections and permission to take photographs of *Stenodictya pygmaea* in the Museum national d'Histoire naturelle, Paris; L. Schöllmann for access to collections and permission to take photographs of *Kemperala hagenensis* in the LWL-Museum für Naturkunde, Münster; A.P. Rasnitsyn for access to and permission to photograph specimens in the Laboratory of Paleoentomology, Russian Academy of Sciences, Moscow; and T. Nichterl for permission to take photographs of *Lithomanthis bohemica* in the Naturhistorisches Museum Wien, Austria. Partial support for this work was provided by US National Science Foundation grants DEB-0542909 (to M.S.E.) and DEB-1110590 (to M.S.E., P. Cartwright, and S.R.D.), and the Grant Agency of the Czech Republic No. P210/10/0633 (to J.P.). This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

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