Chapter 6

The Early Evolution of Biting–Chewing Performance in Hexapoda

Alexander Blanke

Abstract Insects show a plethora of different mandible shapes. It was advocated that these mandible shapes are mainly a function of different feeding habits. This hypothesis was tested on a larger sampling of non-holometabolan biting–chewing insects with additional tests to understand the interplay of mandible function, feeding guild, and phylogeny. The results show that at the studied systematic level, variation in mandible biting–chewing effectivity is regulated to a large extent by phylogenetic history and the configuration of the mandible joints rather than the food preference of a given taxon. Additionally, lineages with multiple mandibular joints such as primary wingless hexapods show a wider functional space occupation of mandibular effectivity than dicondylic insects (= silverfish + winged insects) at significantly different evolutionary rates. The evolution and occupation of a comparably narrow functional performance space of dicondylic insects is surprising given the low effectivity values of this food uptake solution. Possible reasons for this relative evolutionary "stasis" are discussed.

6.1 Introduction

Insecta *sensu lato* (= Hexapoda) display a high diversity of mouthpart shapes within the early evolved lineages which started to radiate approximately 479 million years ago (Misof et al. 2014). These shape changes were described qualitatively and were often stated to relate mainly to the type of food consumed (Yuasa 1920; Isely 1944; Evans and Forsythe 1985; Chapman and de Boer 1995). To the knowledge of the author, this and related statements regarding mouthpart mechanics being shaped by functional demands have never been tested in a quantitative framework.

Here, available evidence for mouthpart function and biomechanics in the early branched lineages of Hexapoda will be reviewed followed by an analysis of biomechanical performance changes of the mandibles across several non-holometabolan lineages. The analytical part of this chapter is restricted to the mandibles due to the

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paucity of knowledge regarding maxilla motion and its biomechanical parameters as will be outlined below. The biomechanical role of the labium during food uptake is even less known and difficult to compare between entognathous hexapods where the labium is fused with the pleural folds and Ectognatha, displaying a freely moveable labium.

6.2 Mouthpart and Muscle Configurations in Primary Wingless and Early Evolved Winged Hexapoda

As already stated in Chap. 2, a general difference in hexapod mouthpart configuration are the entognathous mouthparts of Protura, Collembola, and Diplura and the ectognathous mouthparts of Insecta *sensu stricto* (Chapman 1998; Grimaldi and Engel 2005).

Entognathous mandibles and maxillae are hidden within the head, lying in so-called gnathal pouches formed by a fusion of the enlarged subgenae and the labium (François 1970; François et al. 1992; Ikeda and Machida 1998). The gnathal pouches are mainly thin cuticular sheaths, enclosing mandibles and maxillae. In being sheathed into sack-like pouches, the movements of both the mandibles and the maxillae are mainly restricted to piercing motions (protraction) through the comparably narrow functional mouth opening, supplemented by a rotation and, to a minor degree, chewing motions (Koch 2001). Although the comparably narrow functional mouth opening in entognathous Hexapoda principally restricts larger mouthpart movements and wide gape angles, the diversity of different mouthpart articulations, muscle equipments, and thus movement types is remarkable and deserves further attention in order to understand the principal evolutionary transitions towards the prevailing (dicondylic) mouthpart configuration observable in more derived insects.

6.2.1 Protura

Protura (coneheads) have prognathous stylet-like mandibles and maxillae which are used for piercing into plant roots or fungal hypha by repeated protraction and retraction (Dunger 1983). The mandibles are approximately ten times longer than wide and have an elongated mandibular orifice half the length the mandible at their posterior part (Fig. 6.1). Although it is frequently stated that proturan mandibles articulate posteriorly with parts of the gnathal pouch and are thus non-permanent monocondylic (François et al. 1992), deduction of possible mandible movements based on the muscular equipment suggests that the gnathal pouch is rather used as a guiding structure in order to prevent lateral evasions of the mandibles during protraction and retraction. It remains to be tested whether the mandibles really articulate in a joint-like manner at their posterior end with parts of the gnathal pouch. The mandibular musculature is composed of several muscles, some of

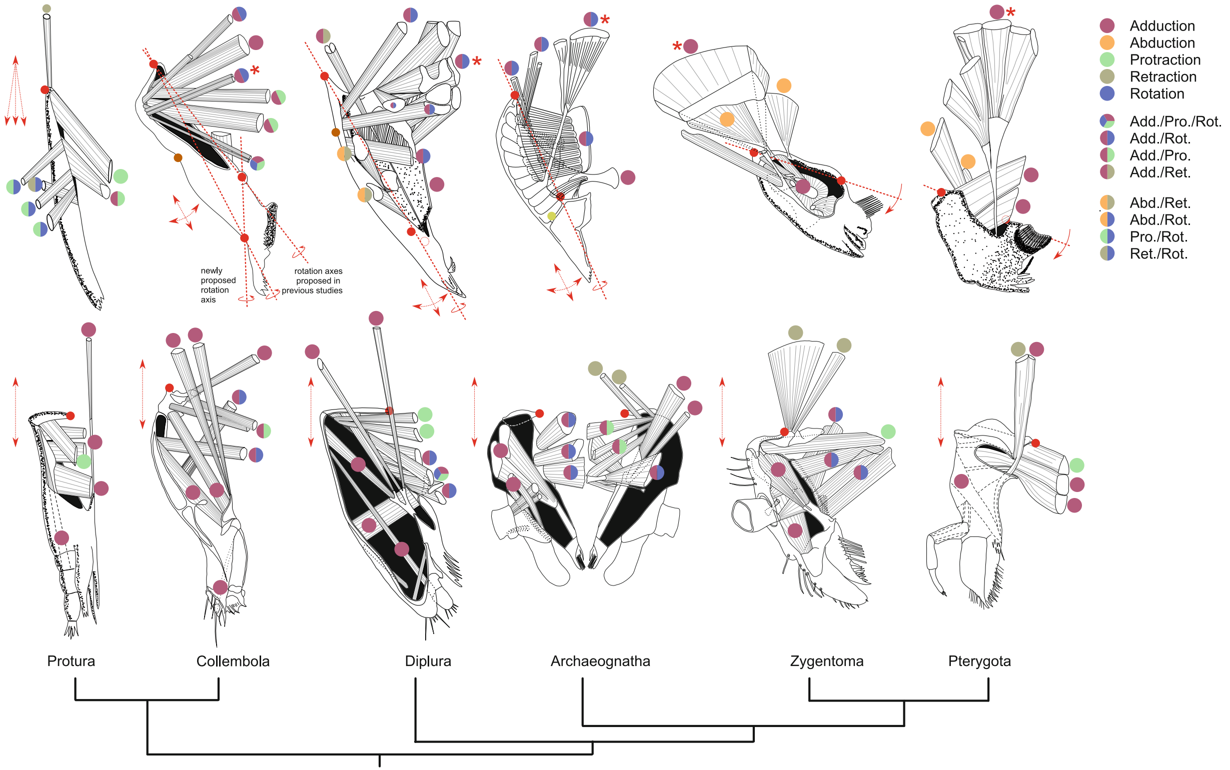

Fig. 6.1 Muscular configuration of the mandibles (upper row) and maxillae (lower row), muscle functions (color coded), and principal mouthpart movement types in early branched Hexapoda together with their phylogenetic relationships (Misof et al. 2014). The red asterisk denotes M. craniomandibularis internus. The red dot denotes points of articulation, the brown dot in Collembola denotes an articulation point of the maxilla with the mandible. Mandibles of Protura and Diplura in dorsal view, all others in cranial view. Drawings based on specimens of *Sinentomon erythranum* (Protura), *Tomocerus catalanus* and *T. plumbeus* (Collembola), *Campodea chardardi* (Diplura), *Thermobia domestica* (Zygentoma), and *Oniscigaster wakefieldi* (Ephemeroptera). Redrawn and modified after François (1970, François et al. 1992), Denis (1928), Hofmann (1908), Bitsch (1963), Chaudonneret (1950), and Staniczek (2001)

them with a double function (Fig. 6.1): protractor-rotators originating at the cephalic wall between the pseudoculus and the pharyngeal muscles, a protractor-adductor muscle originating from the mandibular arm, a protractor originating from the central body of the fulcro-tentorium, and a retractor originating at the dorsal occiput (François et al. 1992). Note that the muscular equipment in Protura seems to be variable concerning the number of protractors and retractors (François 1968; François et al. 1992).

The proturan maxilla is composed of cardo, stipes, galea, lacinia, and maxillary palpus (Fig. 6.1). As in more derived Hexapoda, the proturan maxillary musculature principally allows for protraction/retraction and adduction/abduction of the distal maxilla parts via the lever relations of the cardo with the head and of the cardo with the stipes. The cardo articulates with the posterior arm of the fulcro-tentorium (François et al. 1992) and is connected to the stipes via a syndesmosis. Galea, lacinia, and palpus are broadly connected at their base to the stipes. All parts of the maxilla lie within the gnathal pouch; only the tips of galea, lacinia, and maxillary palpus protrude from it anteriorly together with the mandible tips (Eisenbeis and Wichard 1985). The musculature is composed of a protractor at the cardo which originates at the posterior arm of the endoskeleton and several adductors inserted at the stipes which originate at various parts of the endoskeleton (Fig. 6.1).

6.2.2 Collembola

The majority of Collembola (springtails) show orthognathous biting–chewing mandibles and maxillae. *Anurida sp.* and Pseudarchorutidae (Richards 1979) have stylet-like mouthparts which are supposedly used to penetrate the cell walls of fungi hyphen and roots. These lineages display derived features according to all current phylogenetic estimates based on morphological (D'Haese 2003; Schneider and D'Haese 2013) and molecular datasets (D'Haese 2002; Xiong et al. 2008; Schneider and D'Haese 2013). Therefore, the groundplan condition of collembolan mouthparts is assumed to be of the biting–chewing type and is described in the following. The diet of Collembola may consist of algae, fungi, pollen, and detritus (Paclt 1956; Eisenbeis and Wichard 1985). Mandibles show an elongated distal incisival part which is used for scraping off food particles from the substrate and a proximal molar area which is used for grinding the scraped off particles (Fig. 6.1). The collembolan mandible motion is mainly composed of a rotatory motion and adduction/abduction as well as protraction/retraction (Hofmann 1908; Manton and Harding 1964; Koch 2001).

There are multiple interactions of the mandibles with other head parts and the maxilla, some of which can be interpreted as articulations given the muscular equipment: At the proximal base of the mandible, there is a condyle-like structure which is moveably attached to the gnathal pouch via a ligament (Hofmann 1908; Denis 1928; Koch 2001). Further distal at the caudal side of the mandible, there is an impression into which a stud of the stipes fits. This stud can articulate with the mandible during the simultaneous mouthpart movement of the mandibles and maxillae (Blanke et al. 2015b). Further disto-medial is a mandibular hump which articulates with parts of the endoskeleton (Hofmann 1908; Koch 2001). Even further distal, opposite to the molar area, there is a depression which can articulate with a strongly thickened part of the head capsule in the region of the clypeus. All of the mandible muscles of Collembola insert between the two proximal mandibular "condyles." Several rotator-adductors insert on both sides of the mandibular orifice and several protractor-adductors within the orifice (Fig. 6.1). Due to the small size of Collembola and the entognathous mouthparts, it was not possible so far to generate video footage to visualize mouthpart motion. Statements made here and in the literature are therefore necessarily of qualitative nature and leave room for interpretation. Previous studies suggested that the mandibles mainly rotate around the axis generated by the proximal condyle and more distal articulations with the endoskeleton or the head capsule (Hofmann 1908; Denis 1928; Koch 2001) (Fig. 6.1). However, given the inclination of the molae, this would not allow for a grinding of particles between the molae during all stages of food processing. It appears likely that there exists another principal axis of rotation which is more aligned with the mola (Fig. 6.1). This axis of rotation is generated by the thickened part of the clypeus which articulates with a part of the mandible lateral of the mola and the mandibular hump which articulates with parts of the endoskeleton. Clearly, the mouthpart motions in Collembola deserve further study to understand the interaction of the musculature and the significance of condyle-like structures observed.

The collembolan maxilla is composed of cardo, stipes, a fused galea and lacinia, and a short palpus. The principal composition and spatial configuration of the cardo and stipes are the same as in Protura: the cardo articulates with a part of the endoskeleton and is moveably connected to the elongated stipes via a syndesmosis. Considerable disagreement still exists concerning the exact delimitations of galea, lacinia, and palpus to each other since these structures are fused to various degrees in Collembola which is why they were termed "terminal lobe" (Folsom 1900), "maxillar head" (Chen et al. 1997), or "claw" (Hofmann 1908). In any case, the maxilla as a whole is again mainly adapted to protraction/retraction given the muscular equipment so that food particles can be hauled toward the preoral cavity. Protraction is achieved through muscle bundles inserted at the inner side of the cardo; the various muscles inserting at the stipes and the claw allow for adduction and, to a minor degree, rotation of the whole maxilla (Fig. 6.1).

6.2.3 Diplura

Diplura (two-pronged bristletails) have prognathous biting–chewing mouthparts. They are traditionally divided into Projapygoidea + Campodeoidea and Japygoidea based on the shape of the cerci and the presence of a prostheca, a moveable appendage on the mandibular gnathal edge (Bitsch and Jacques 2000; Richter et al. 2002; Koch 2009). While most Campodeoidea are omnivorous with a preference for saprophygy and microphytophagy, Japygoidea are mainly predatory. Despite these differences in general lifestyle, Diplura show a comparably uniform general mouthpart organization: the mandible lacks a distinct molar area; instead the entire gnathal edge is composed of sharp teeth whose left and right sides interlock, just like in neopteran insects (François 1970; Koch 2001). Apart from taxonomically relevant differences in the number of incisivi and similar characters (Allen 2002), more notable differences on the subordinal level concern the origin and insertions of certain muscles such as those responsible for the movement of the cardo or retractors of the mandible (François 1970; Blanke and Machida 2015). The mandibular muscle composition and observations of feeding in Japygidae (*Occasjapyx japonica*, Blanke pers. obs) suggest more forceful adduction capabilities in Diplura compared to Collembola. As in Collembola, the dipluran mandible shows several interactions with parts of the gnathal pouch, endoskeletal elements, or parts of the maxilla which are currently debated regarding their homology (Koch 2000, 2001; Blanke et al. 2015b; Blanke and Machida 2015; Koch 2016). The proximal part of the mandible is formed like a pointed tip and fits into a sclerotized part of the gnathal pouch. Most muscles of the mandible are rotator-adductors, namely those which insert at the dorsal and ventral sides of the thickened mandibular rim. A transverse mandibular tendon connects a large adductor muscle which spans from the left to the right mandible. Two abductor-retractors attach at the dorsal distal rim of the mandible, and further distal, near the end of the mandibular orifice, a retractor-adductor inserts.

The maxilla is composed of cardo, stipes, galea, lacinia, and a very short palpus. According to the muscle equipment, protraction is likely the principal movement of the maxilla so that larger food particles can be hauled toward the mandibles for further processing. The cardo articulates with posterior structures, termed as “lingual stalks” (Koch 2000) or “fulturae” (François 1970), so that activity of the muscles inserting at the cardo or the proximal parts of the stipes results in a protraction of the maxillae. The musculature furthermore consists of several distinct adductors of the lacinia (Fig. 6.1).

6.2.4 Archaeognatha

Archaeognatha (bristletails) have orthognathous biting–chewing mouthparts which are used to consume lichen and detritus (Eisenbeis and Wichard 1985; Dettner and Peters 2011). Although the archaeognathan mandible shows several similarities to collembolan mandibles, such as an elongated incisival area and a pronounced molar area, mandibular articulations are clearly different and the muscle equipment is composed of different functional groups (Bitsch 1963; Koch 2001; Blanke et al. 2015a). Due to the larger size of Archaeognatha, observations of feeding movements were possible (Blanke et al. 2015a). Principal mandible movements consist in large parts of rotation and adduction/abduction. Only a minor portion of rhythmic protraction is realized. Archaeognatha possess three mandibular articulations, two with parts of the head and one with the maxillary palpus (Blanke et al. 2015a). These articulations are all non-permanent. The posterior mandibular articulation is located at the proximal most part of the mandibles. It is a distinct condyle which articulates with the ventral margin of the sclerotized head capsule at height of the gena just ventral of the eyes (Bitsch 1963). As in Diplura, this connection is non-permanent, because the condyle does not touch the infolded genal socket when the mandible is slightly protracted [see supplementary video material in Blanke et al. (2015a)]. The anterior mandibular articulation is located at the base of the molar area. Due to the strong curvature in this part of the mandible, this area serves as a depression which articulates with the region where the anterior tentorial arms connect to the clypeus during rotation of the mandible. Like the posterior articulation, the anterior one is non-permanent. During stronger protraction movements, the base of the mola is not in touch with the tentorio-clypeal area. Due to the striking fine structural similarities of this anterior articulation to the anterior articulation in Zygentoma (see below), it was suggested that these articulations are homologous (Blanke et al. 2015a). The third articulation is composed of a depression at the medio-frontal side of the mandible which serves as a socket for a knob located at the inner side of the first maxillary palpomere (Blanke et al. 2015a). Via this articulating coupling structure and the rest of the base of the maxillary palpus, an anterior and lateral evasion of the mandibles during the rhythmic rotatory movements is prevented. The mandibular musculature consists of a large adductor-rotator which inserts on the posterior mandibular rim near the base of the mola and several additional rotator-adductors which insert at different locations on the anterior side of the mandibular rim (Fig. 6.1). A large muscle bundle inserts within the mandibular orifice and connects to the dorsoventrally oriented parts of the anterior tentorium. In comparison to Diplura and Collembola, fewer muscles move the mandibles although the principal degrees of freedom of the mandibles are the same in all three taxa.

The archaeognathan maxilla is composed of cardo, stipes, galea, lacinia, and a seven-segmented palpus. Again, the principal movement of the maxilla is a protraction so that small food particles can be scraped off the substrate and particles are transported to the mandibles for further processing. There is one articulation of the cardo with the posterior tentorium and another articulation of the base of the palpus with the mandible as mentioned above. In line with its double function as a clamping structure for the mandibles and to reallocate food to the molae, Archaeognatha possess the highest number of distinct maxillary muscle bundles among early evolved Hexapoda (Fig. 6.1). Protractors insert at the cardo and the proximal part of the stipes, and rotator-adductors insert further distal on the ventral wall of the stipes. The lacinia is moved by four distinct adductors and the galea by one adductor and its antagonist, while the palpus is moved by another three muscle bundles (two extensors and one flexor) (Bitsch 1963).

6.2.5 Zygentoma

Zygentoma (silverfish) have orthognathous biting–chewing mouthparts which are used to consume algae, lichen, detritus, and cellulose. Zygentoma are the oldest extant lineage displaying a reduction of the degrees of freedom of mandible movement due to the joint configuration (Staniczek 2000; von Lieven 2000). Their bowl-shaped mandibles have an incisival area which reaches proximally the molar area without an intermediate area (Blanke et al. 2014; Koch 2001). Two principal articulations, a posterior and an anterior one, allow for an adduction and, to a minor extent, translation (Blanke pers. obs.). The posterior articulation is composed of a pointed tip which interacts with a pyramidal condylus on the head capsule (von Lieven 2000; Blanke et al. 2014). The anterior articulation is formed as a slight depression at the anterior dorsal margin lateral of the molar area. The head part is a caliper-like structure formed by parts of the anterior tentorial arms and the clypeus. This caliper fits around the dorsal rim of the mandible; its outer part interacts with the depression on the mandible during adduction/abduction (von Lieven 2000; Blanke et al. 2014, 2015a). The caliper furthermore allows translation of the mandible along the main axis of the caliper opening. The mandibular muscles in Zygentoma are characterized by a reduction in their double functions compared to non-dicondylic hexapods. Mandible adduction is accomplished by a cranial main adductor inserting at the posterior medial rim and a group of smaller tentorial muscles inserting within the mandibular orifice. Abduction is realized by two cranial muscles inserting at the lateral parts of the anterior mandibular rim.

The zygentoman maxilla shows the typical orthopteroid configuration. Unlike in Archaeognatha and entognathous Hexapoda, the bowl-shaped cardo articulates with the head capsule near the confluence of the posterior tentorial arms with the head. Cardo and stipes are connected via a broad syndesmosis. The stipes bears a five-segmented palpus, a pointed and sclerotized lacinia, and sickle-shaped galea. Compared to the mandibular musculature, protraction and adduction movements of the maxillae are still achieved by several muscles with double functions. Three protractors/retractors insert at the cardo, and several adductor-rotators insert at the ventral stipital wall or inside the stipes, while lacinia and galea are moved by a stipital adductor each (Fig. 6.1).

More detailed biomechanical information concerning the functional properties of the mouthparts, their piercing or biting strength, or the incurred strains on the head capsule is currently not available for the taxa mentioned above. The author is also not aware of any biomechanical studies using modern engineering methods which would cover the head mechanics of Protura, Collembola, Diplura, Archaeognatha, or Zygentoma in a quantitative framework.

6.2.6 Pterygota

Winged insects (Pterygota) show a reduction in mandibular degrees of freedom (DOFs) and mouthpart musculature (von Lieven 2000; Staniczek 2000, 2001). The mandibles of most pterygotes display a roughly quadratic dorsal opening toward the head lumen. Usually the tendon of the main mandibular adductor attaches at the medial corner, whereas the abductor attaches at the lateral side. The anterior and posterior mandibular articulations with the head are located at the remaining corners. The number of incisivi, shape, and presence of a mola, however, vary strongly among biting–chewing winged insect lineages, as do the areas between these regions (Chapman 1998; Grimaldi and Engel 2005; Beutel et al. 2014). The most severe deviation from the general setup of the mandibular articulations and muscle insertions is shown by mayflies (= Ephemeroptera), which have a posterior cylinder-like joint and an anterior articulation complex largely similar to the one of Zygentoma (Staniczek 2000, 2001), whereas Odonata and Neoptera uniformly show ball-and-socket joint configurations. These two fixed ball-and-socket joints generate a fixed rotation axis, restricting the DOFs of the mandible to a single plane. Note that although Zygentoma and Ephemeroptera also possess an anterior mandibular articulation, their joint configuration is not permanent, so that movement is not restricted to a single plane; this morphology was termed “facultative dicondyly” by Staniczek (2000, 2001). The ball-and-socket joint system of Odonata and Neoptera is maintained stable irrespective of the particular food preference of a given lineage although the rest of the mandible shape can be remarkably variable. Despite the reduced DOFs, the muscular equipment in Ephemeroptera and Odonata is the same compared to Zygentoma, with the exception of the absence of one abductor muscle (Blanke et al. 2012). In Neoptera, a further reduction of the mandibular musculature took place. The muscles inserting at the anterior and posterior mandibular rim are absent in most lineages; the tentorial muscles inserting within the mandibular orifice are strongly reduced and in many cases absent (Wipfler et al. 2011; Blanke et al. 2012). The maxilla of winged insects also shows a further reduction in musculature although the DOFs of the craniocardinal articulation are the same as for primary wingless insects. The cardo is moved by one retractor and one protractor, the stipes is adducted by two muscles which originate from the tentorium, and lacinia and galea are adducted by one muscle each (Fig. 6.1). Again, this muscle equipment can vary considerably in more derived lineages, a detailed account for each order is, however, out of scope of this contribution.

6.2.7 Trends in Biting–Chewing Mouthpart Evolution

The above-presented brief outline of the functional morphology of the mouthparts and their muscle configuration can be summarized as follows:

- The rotation axis of the mandible is nearly aligned with the distal incisivi in entognathous Hexapoda and is "lifted" anteriorly toward the cephalo-caudal axis in silverfish and winged insects (Fig. 6.1, red dotted line).
- The mandible muscle equipment becomes reduced from Protura to winged insects although exceptions exist for the maxillae (see Archaeognatha).
- The DOFs of the mandible become reduced. Adduction/abduction becomes the only movement type in winged insects.
- Articulation types with the head and endoskeletal elements range from multicondylic (Collembola, Diplura) to facultative dicondylic (Archaeognatha, Zygentoma, and Ephemeroptera) to an obligate dicondyly (Odonata, Neoptera). The mouthpart articulations in Protura need to be reinvestigated.

6.3 Comparative Biomechanics of Biting–Chewing Mouthparts

6.3.1 Experimental Assessments

Due to the small size of most insect species (Chown and Gaston 2010), even simple biomechanical assessments such as bite force measurements involve complex experimental setups which are currently limited by the size of the force-sensing element which can be introduced between the mandibles. Weihmann et al. (2015a) used a bespoke strain gauge-based 2D force transducer with a tip element of 0.8 mm diameter; David et al. (2016a) used a piezoelectric 1D force sensor with 0.63 mm diameter. Therefore, insects with a gape no less than approximately 5 mm should be measured with currently available setups in order to ensure that the adductor muscles operate near their maximum force outputs (Blümel et al. 2012b, c). Due to the size/gape problematic, the bite forces of only 21 species from three insect "orders" (Odonata, Blattodea, Coleoptera) were measured so far. Head width (Fig. 6.2) and muscle size (Wheater and Evans 1989) were found to be reliable predictors of bite force, while other morphometric data such as body length or body weight are poor predictors of bite force (Wheater and Evans 1989). Note that head width is by far not a universal predictor of bite force (Senawi et al. 2015). Rather, this metric likely depends on the particular arrangement of the head muscles for which head width can be one proxy among many. Due to the abovementioned difficulties with regard to insect size, and the size of their mouthparts in particular, modeling approaches came into focus recently.

6.3.2 Functional Morphology of Biting–Chewing Mouthparts using Musculoskeletal Modeling

An emerging technique to study aspects of the biomechanics, such as the kinematics and kinetics, of an arbitrarily sized organism is musculoskeletal modeling of the particular movement system (Curtis et al. 2008; Shi et al. 2012; Watson et al. 2014). Such simulations are subsumed under the umbrella term multibody dynamics analysis (MDA), placing an emphasis on the investigation of moving structures which are connected to each other by joints and/or muscles. Given accurate information about skeletal geometries and muscle characteristics, MDA allows to predict the resulting forces in a movement system, such as bite forces or joint reaction forces with acceptable accuracy (Fig. 6.2) (Curtis et al. 2008, 2010; Gröning et al. 2013; Blanke et al. 2017b) so that even fossils can be studied (Bates and Falkingham 2012; Snively et al. 2013). MDAs for insects so far used simple non-Hill-type muscle models in conjunction with experimentally measured bite forces. These studies showed that the measured bite forces can be simulated with MDA when approximately 80% of muscle activation are assumed (David et al. 2016a, b). This seems to be in accordance with measured muscle activation levels in relation to maximum force outputs in insect locomotion systems (Blümel et al. 2012a, b). However, a further refinement of the muscle models used for MDAs of insects, i.e., an investigation of mouthpart muscle properties, should have high priority to increase the accuracy of the predictions made.

Despite the obvious relevance of MDA to study forces and moments in arbitrarily sized biological systems, MDA requires a lot of raw data from different sources such as precise geometric data, movement data, muscle properties, and bite forces. Therefore, the study of biomechanical systems using MDA on an

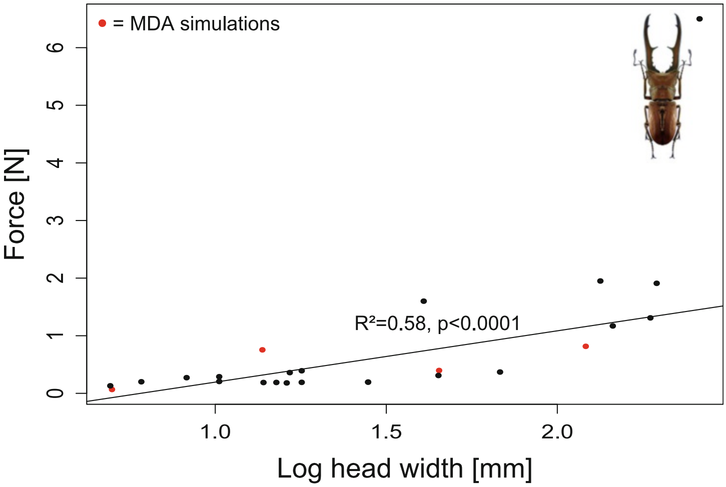

Fig. 6.2 Relationship between bite force and head width in selected insects for which bite force measurements are currently available. Data points in red are results from multibody dynamics analyses (MDA), i.e., simulations of mandible biting. So far male stag beetles were shown to have unusually high bite forces given their head width (Goyens et al. 2014). The regression was calculated without the data for the male stag beetle. Image of *C. metallifer* courtesy of Udo Schmidt. Data based on Wheater and Evans (1989), Goyens et al. (2014), Weihmann et al. (2015b), and David et al. (2016a, b)

evolutionary scale including many taxa is currently not feasible. On a broader scale, biomechanical determinants such as the mechanical advantage (MA), which are directly measureable on a given specimen, could yield initial insights into the performance transitions in evolving movement systems such as insect mouthparts.

6.3.3 The Mechanical Advantage (MA) as a Performance Metric for Insect Mouthparts

The MA is a straightforward biomechanical metric which in a biological context was first introduced for vertebrates (Westneat 1995, 2004) and was used since in many studies on vertebrate and arthropod jaw mechanics (Cooper and Westneat 2009; Sakamoto 2010; Habegger et al. 2011; Dumont et al. 2014; Senawi et al. 2015; Cox and Baverstock 2015; Weihmann et al. 2015b; Fujiwara and Kawai 2016; Blanke et al. 2017a; Fabre et al. 2017; Olsen 2017). The MA is defined as the inlever to outlever ratio. For dicondylic insect mandibles, the inlever is the distance between the application of the input force and the joint axis, while the outlever arm is the distance from the biting point to the joint axis (Fig. 6.3).

The MA thus indicates the percentage of force transmitted to the food item (i.e., the effectivity of the lever system). Although more detailed investigations concerning muscular insertion angles, muscle volumes, spatial arrangements, and muscle characteristics would be needed to quantify the forces applied to the food, the MA constitutes a useful mechanical performance index: it allows a size independent comparison of the relative efficiencies of force transmission within the mandibular lever system and it can be readily measured in a wide array of dried museum specimens as well as freshly collected ones.

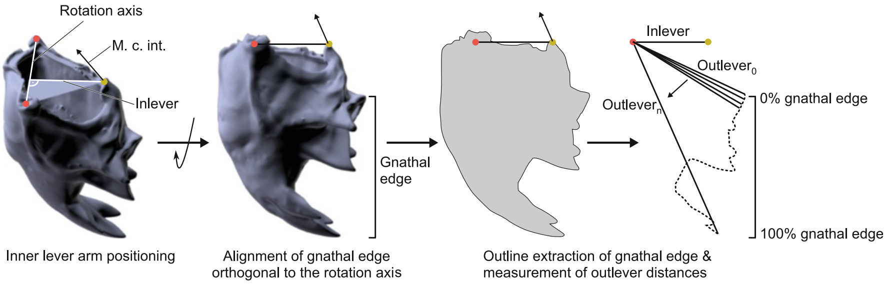

Fig. 6.3 Workflow for extraction of the mandibular mechanical advantage illustrated on the mandible of *Neopetalia punctata* (Odonata: Anisoptera). Note that for a comparison across different insect lineages only the inlever component of the main mandibular adductor M. craniomandibularis internus (M. c. int.) was calculated (Inlever distance between red and yellow dot). This muscle solely has an adductive function in Dicondylia and a mixed adductive-rotatory function in entognathous Hexapoda. Dotted line = gnathal edge; Red = articulation points; Yellow = tendon insertion of M. craniomandibularis internus

The MA here is used on a phylogenetically diverse sample of Hexapoda ranging from Collembola to Psocodea. Given the morphologies and functional changes across early evolved Hexapoda summarized in the introduction, the extent to which such a simple lever measurement might serve as a proxy for the more complex changes observed with respect to joint configuration, main axes of rotation, DOFs, and musculoskeletal configurations was studied. Furthermore, the size and relative location of the performance space of each lineage expressed as the relative efficiency of force transmission of the mandibular lever system was investigated.

6.4 Studying the Mechanical Advantage in Early Evolved Hexapoda

Seventy-seven taxa ranging from Collembola to Psocodea were studied for the mechanical advantage (MA) of their mandibles. Species were investigated using micro-computed tomography (µCT) carried out at several synchrotron facilities: Beamline BW2 and IBL P05 of the outstation of the Helmholtz Zentrum Geesthacht at the Deutsches Elektronen Synchrotron (DESY), the beamline TOMCAT at the Paul Scherrer institute (PSI), the TOPO-TOMO beamline of the Karlsruhe Institute of Technology (KIT), and beamline BL47XU of the Super Photon Ring 8GeV (SPring-8, Table 6.1).

MA measurements were carried out on the segmentations of the left mandible for each specimen. Automatic segmentations were performed using the software ITK-snap (Yushkevich et al. 2006) after which STL files were imported into the software Blender (www.blender.org) for further processing (Fig. 6.3). The gnathal edge was defined *sensu* Richter et al. (2002) as the area from the *pars molaris* (proximal to the mouth opening) to the *pars incisivus* (distalmost tooth). Since the homology of subparts of the gnathal area is debated (Staniczek 2000; Richter et al. 2002; Fleck 2011), the gnathal outline, as seen when orienting the mandible in line with the rotation axis (Fig. 6.3), was scaled as a percentage of tooth row length. For this, ~800 points for each specimen were wrapped against the gnathal outline in Blender and the distance between each point orthogonal to the mandibular rotation axis (= outlever) was measured. Similarly, one point was placed at the insertion point of M. craniomandibularis internus on the mandible and the distance from this point orthogonal to the rotation axis was measured (= inlever). All measurements and calculations were carried out in the R software environment (v. 1.1.383) using custom scripting. The MAs for each specimen were computed and polynomial functions of the first–sixth order were fitted against each MA profile. The Akaike and Bayes information criteria (AIC and BIC) were used to determine the polynomial function with the best relative fit which was then used for further analysis.

In order to be able to compare MA values between taxa with different joint configurations (mainly entognathous vs. ectognathous lineages), and to prevent a violation of the homology hypotheses for muscles across Hexapoda (Rühr et al.

Table 6.1 Taxon sampling studied (in alphabetical order) and coding of discrete character traits

Order	Species	Coll.	Food	Cond. type	DOF	DTA	CT
Archaeognatha	*Machilis germanica*	BL	H	fac. dic	3	L	A
Archaeognatha	*Meinertellus cundinamarcensis*	BL	H	fac. dic	3	L	A
Archaeognatha	*Pedetontus unimaculatus*	BL	H	fac. dic	3	L	A
Archaeognatha	*Trigoniophthalmus alternatus*	BL	H	fac. dic	3	L	A
Collembola	*Pogonognathellus flavescens*	BL	O	multic.	4	L	A
Dermaptera	*Diplatys flavicollis*	MFN	O	dic.	1	F	P
Dermaptera	*Forficula auricularia*	BL	O	dic.	1	F	P
Dermaptera	*Labidura riparia*	MFN	C	dic.	1	F	P
Diplura	*Atlasjapyx cf atlas*	ZFMK	C	multic.	3	L	A
Diplura	*Campodea sp.*	BL	H	multic.	3	L	A
Diplura	*Catajapyx aquilionaris*	BL	C	multic.	3	L	A
Diplura	*Lepidocampa weberi*	BL	H	multic.	3	L	A
Diplura	*Metriocampa sp.*	BL	H	multic.	3	L	A
Diplura	*Occasjapyx japonicus*	BL	C	multic.	3	L	A
Embioptera	*Antipaluria urichi*	BÜ	H	dic.	1	L	P
Embioptera	*Aposthonia japonica*	SU	H	dic.	1	L	P
Embioptera	*Embia ramburi*	BL	H	dic.	1	L	P
Embioptera	*Metoligotoma* sp.	MFN	H	dic.	1	L	P
Ephemeroptera	*Ephemera danica*	BL	D	fac. dic	2	L	P
Ephemeroptera	*Epeorus* sp.	BL	H	fac. dic	2	L	P
Ephemeroptera	*Siphlonurus lacustris*	STAN	H	fac. dic	2	L	P
Grylloblattodea	*Grylloblatta bifratrilecta*	BL	O	dic.	1	L	P
Odonata	*Aeshna cyanea*	BL	C	dic.	1	F	P
Odonata	*Aeschnophlebia longistigma*	ZFMK	C	dic.	1	F	P
Odonata	*Anaciaeshna isoceles*	ZFMK	C	dic.	1	F	P
Odonata	*Anotogaster sieboldii*	ZFMK	C	dic.	1	F	P
Odonata	*Calopteryx virgo*	BL	C	dic.	1	F	P
Odonata	*Coenagrion puella*	BL	C	dic.	1	F	P
Odonata	*Cordulegaster bidentata*	BL	C	dic.	1	F	P
Odonata	*Cordulia aenea*	BL	C	dic.	1	F	P
Odonata	*Crocothemis erythraea*	BL	C	dic.	1	F	P
Odonata	*Epiophlebia superstes*	BL	C	dic.	1	F	P
Odonata	*Epophthalmia elegans*	ZFMK	C	dic.	1	F	P
Odonata	*Hagenius brevistylus*	ZFMK	C	dic.	1	F	P
Odonata	*Libellula depressa*	BL	C	dic.	1	F	P
Odonata	*Lestes virens*	BL	C	dic.	1	F	P
Odonata	*Macromia taeniolata*	ZFMK	C	dic.	1	F	P
Odonata	*Mecistogaster linearis*	ZFMK	C	dic.	1	F	P
Odonata	*Mnais* sp.	ZFMK	C	dic.	1	F	P
Odonata	*Neopetalia punctata*	ZFMK	C	dic.	1	F	P

(continued)

Table 6.1 (continued)

Order	Species	Coll.	Food	Cond. type	DOF	DTA	CT
Odonata	*Oligoaeshna pryeri*	ZFMK	C	dic.	1	F	P
Odonata	*Onychogomphus forcipatus*	ZFMK	C	dic.	1	F	P
Odonata	*Phenes raptor*	ZFMK	C	dic.	1	F	P
Odonata	*Phyllopetalia apicalis*	ZFMK	C	dic.	1	F	P
Odonata	*Platycnemis pennipes*	BL	C	dic.	1	F	P
Odonata	*Pyrrhosoma nymphula*	BL	C	dic.	1	F	P
Odonata	*Sympetrum vulgatum*	BL	C	dic.	1	F	P
Odonata	*Tachopteryx thoreyi*	ZFMK	C	dic.	1	F	P
Odonata	*Zonophora baetesi*	ZFMK	C	dic.	1	F	P
Orthoptera	*Acheta domesticus*	BL	O	dic.	1	F	P
Orthoptera	*Comicus calcaris*	ZSM	O	dic.	1	F	P
Orthoptera	*Conocephalus dorsalis*	GÖ	O	dic.	1	F	P
Orthoptera	*Diaphanogryllacris laeta*	ZFMK	O	dic.	1	F	P
Orthoptera	*Gryllus bimaculatus*	BL	O	dic.	1	F	P
Orthoptera	*Hemideina crassidens*	GÖ	O	dic.	1	F	P
Orthoptera	*Meconema meridionale*	GÖ	C	dic.	1	F	P
Orthoptera	*Papuaistus* sp.	GÖ	O	dic.	1	F	P
Orthoptera	*Prosopogryllacris* sp.	MFN	O	dic.	1	F	P
Orthoptera	*Stenobothrus lineatus*	GÖ	H	dic.	1	F	P
Orthoptera	*Stenopelmatus* sp.	ZSM	O	dic.	1	F	P
Orthoptera	*Pholidoptera griseoaptera*	GÖ	O	dic.	1	F	P
Orthoptera	*Tettigonia viridissima*	GÖ	O	dic.	1	F	P
Orthoptera	*Tridactylus* sp.	ZSM	H	dic.	1	F	P
Orthoptera	*Troglophilus neglectus*	ZSM	O	dic.	1	F	P
Orthoptera	*Xya variegata*	NHM	D	dic.	1	F	P
Phasmatodea	*Agathemera crassa*	ZSM	H	dic.	1	F	P
Phasmatodea	*Peruphasma schultei*	BL	H	dic.	1	L	P
Plecoptera	*Oemopteryx* sp.	MFN	C	dic.	1	L	P
Plecoptera	*Perla marginata*	BL	C	dic.	1	L	P
Psocodea	*Caecilius* sp.	FF	H	dic.	1	F	P
Zoraptera	*Zorotypus caudelli*	BL	H	fac. dic	2	L	A
Zygentoma	*Atelura formicaria*	BL	H	dic.	1	L	P
Zygentoma	*Lepisma saccharina*	BL	H	fac. dic	2	L	A
Zygentoma	*Maindronia neotropicalis*	BL	C	fac. dic	2	L	A
Zygentoma	*Thermobia domestica*	BL	H	fac. dic	2	L	A
Zygentoma	*Tricholepidion gertschi*	BL	H	fac. dic	2	L	A

Coll. collection, *cond. type* articulation type, *DOF* degrees of freedom, *DTA* connection of dorsal tentorial arms to head, *CT* corpotentorium, *BL* collection by the author, *BÜ* collection by Dr. Sebastian Büsse, *SU* collection of the Sugadaira Montane Research Center, Japan, *STAN* material provided by Dr. Arnold Staniczek, *GÖ* material provided by Dr. Fanny Leubner and Dr. Sven Bradler, Göttingen, *FF* material provided by Dr. Frank Friedrich, Hamburg; H, herbivore, *O* omnivore, *C* carnivore, *D* detrivore, *fac. dic.* facultative dicondyly, *multic.* multicondyly, *dic.* obligate dicondyly, *L* muscular/fibrillous connection, *F* fixed/sclerotized connection, *A* absent, *P* present, *MFN* Museum für Naturkunde Berlin, *ZFMK* Zoological Research Museum Alexander Koenig, *ZSM* Bavarian State Collection of Zoology, *NHM* Natural History Museum Vienna in preparation; Wipfler et al. 2011; Blanke et al. 2012; Blanke and Machida 2015), several simplifications had to be made. Firstly, only the MA with respect to the main mandibular adductor (M. craniomandibularis internus fide Wipfler et al. 2011) was calculated. This adductor muscle delivers the main part of the bite force in dicondylic insects (David et al. 2016a, b), but it is acting mainly as a rotator in Collembola, and as a rotator-adductor in Diplura and Archaeognatha as explained in the introduction. As such, the MA in Collembola, Diplura, and Archaeognatha also is an index for the effectiveness of performing a rotatory motion rather than solely an adduction. Since rotatory mandible movements are mainly used by these lineages for food uptake, the biological meaning of the MA—the effectivity of the force transmission to the food item—is maintained in these cases. A further simplification had to be made with regard to the anterior points of contact between the mandible and the various head structures across Hexapoda. For Collembola and Diplura, the dorso-anterior interaction points of the mandibles with other head structures were interpreted as anterior articulation points. It has to be emphasized that this does not imply homology of these interaction points with the anterior mandibular articulations of Ectognatha although evidence exists in favor of such an interpretation (Koch 2001).

Phylognetic signal was assessed using the most recent phylogenetic estimate of the 1kite consortium (www.1kite.org) as a basis (pers. comm. B. Misof on behalf of 1kite). The phylogeny was pruned in order to contain only the taxa analyzed here. Phylogenetic signal was assessed using the K statistic as implemented in geomorph v.3.0.5 (Adams 2014a) with 10,000 random permutations. This test statistic was found to be the most efficient approach to test for phylogenetic signal (Pavoine and Ricotta 2013). Since significant phylogenetic signal was detected, a principal component analysis (PCA) as well as phylogenetic PCA as implemented in the phytools package v.0.6–44 (Revell 2009) was carried out. Tests for phylogenetic signal were also conducted for alternative (and debated) deep level relationships within Hexapoda, namely the potential sister-group relationship of Diplura with Ellipura [Protura + Collembola; (Dell'Ampio et al. 2009, 2014)] and the Metapterygota (Odonata + Neoptera) and Chiastomyaria (Ephemeroptera + Neoptera) hypotheses (Simon et al. 2018). Because the statistical significance of the phylogenetic signal was not influenced by these alternative topologies, only the results for the topology with Diplura as sister group to Ectognatha and Odonata + Ephemeroptera (= Palaeoptera), which represents the most recent phylogenetic estimate of the deep level relationships within Hexapoda, are presented in the following. The tempo of the MA variation was tested using the evolutionary rate parameter under a Brownian motion model of evolution as implemented in geomorph (Adams 2014b). It was tested whether the rates of evolution varied significantly depending on several group designations: the taxonomic rank of orders, the joint configuration (multicondylic, facultative dicondylic, obligate dicondylic), the connection type of the dorsal tentorial arms with the head (sclerotized or ligamentous), fusion of the anterior and posterior tentoria (corpotentorium absent/present), the degrees of freedom of the mandible (DOF), and the food preference (herbivorous, omnivorous, carnivorous, detrivorous). See Table 6.1 for group designations to each species.

6.5 Characteristics of Mechanical Advantage (MA) Evolution of Mouthparts and Correlation with Food Preference

Calculation of the MA along the entire gnathal edge revealed characteristic MA curve progressions for several systematic groups within Hexapoda (Fig. 6.4). The collembolan showed an exponential increase in the MA until approximately 80% of the tooth row followed by an almost linear decline. Diplura all showed a strongly parabolic decline from high MA values approximately 1.2–1.8 down to 0.05–0.8. Archaeognatha showed an almost linear increase in their MA; in Zygentoma curve progression is vice versa with an almost linear decrease toward the 100% tooth row position. In Ephemeroptera and Odonata, the otherwise linear decline in MA from 0 to 100% tooth row length is characterized by a peak in MA at the 40% and 70% tooth row position, respectively. All other investigated taxa show an almost linear decrease in MA from the 0 to 100% tooth row position.

A polynomial function of the fifth order resulted in the best relative fit on the MA curves according to the AIC value (−765.4). The first four principal components (PCs) accounted for 98.3% of the variation in MA (Table 6.2). Visual representation of the PCs of the polynomial coefficients showed a lineage-specific distinction between the above-described curve progressions (Fig. 6.5).

Taxa such as Collembola, Diplura, and Archaeognatha with mandible motions composed of rotatory and adduction-abduction movements (and corresponding MAs which reflect this diversity in mandible motion types) mostly scored at the extremes of the PCs. For example, the springtail scores at the positive extreme of PC1, while Diplura, although they occupy a comparably wide variance space, mostly cluster near the negative extreme of PC1. Archaeognatha mostly score at the positive extreme of PCs 1, 3, and 4; by comparison, Zygentoma (with the exception of *Maindronia neotropicalis*) score near the center of each PC, while Ephemeroptera occupy a comparably wide performance space along PC2. All other taxa cluster near the center of each PC.

Since significant phylogenetic signal ($K = 1.19$, $p = 0.0001$) was detected in the data, a phylogenetic PCA as implemented in the phytools package (Revell 2012) was carried out. This resulted in a similar lineage-dependent distribution of the data with most of the variance associated with PC1 (Fig. 6.5).

In both PCAs PC1 mainly codes for the inclination of the MA curve and its slope, the curve progression from high to low values, and the vertical position of the curve. PC2 mainly codes for whether there is a local maximum with sharp fall-offs on both sides. PC3 likely codes whether the curve progression goes from higher MA values to lower ones or vice versa, and PC4 likely codes for the slope of the MA curve and the general progression from high to lower MA values. However, due to the low variance associated with PCs3 + 4 further observations are necessary to elucidate whether the association of MA progressions remains stable for these PCs.

Analysis of the evolutionary rates of MA variation resulted in nonsignificant rate ratios when partitioning the data at the taxonomic rank of orders (observed rate ratio

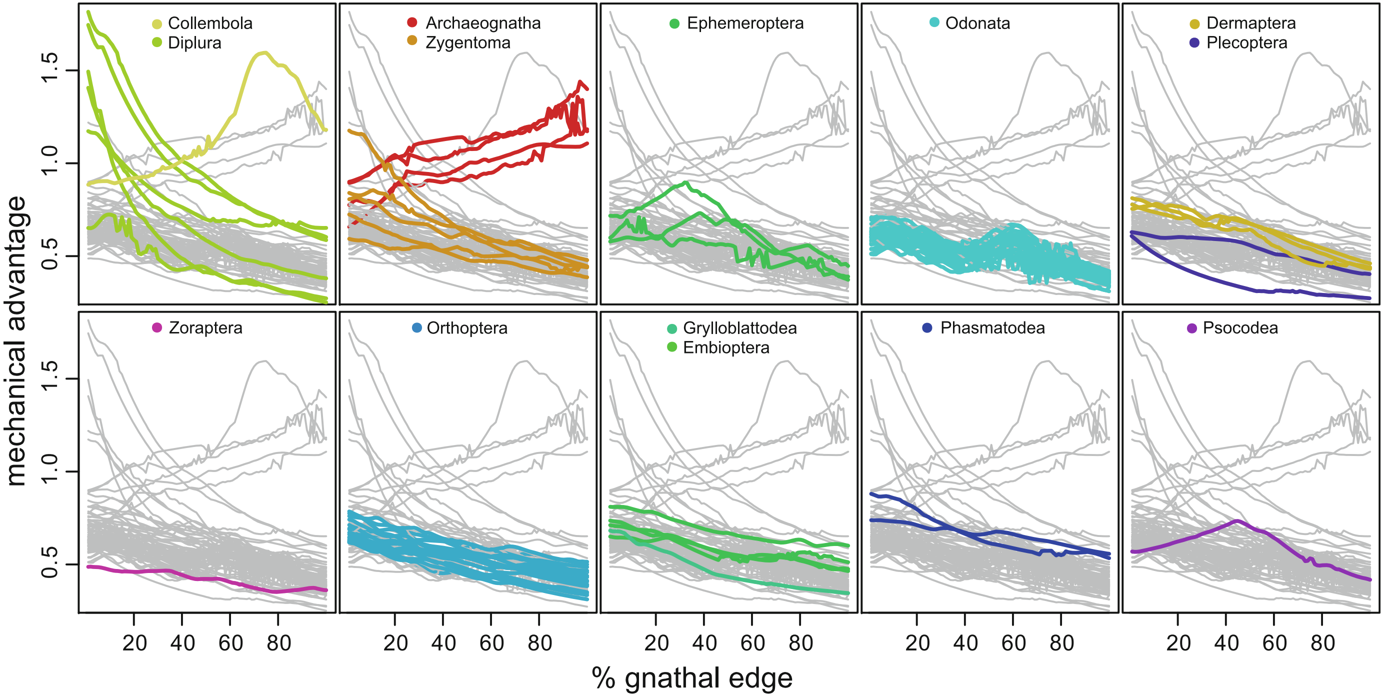

Fig. 6.4 Progression of biting efficiency as expressed by the mechanical advantage against percent gnathal edge position (see Fig. 6.3 right) in selected non-holometabolous biting–chewing insects. For clarity biting efficiency of each lineage (colored) is shown with respect to the rest of the taxon sampling (gray)

Table 6.2 Summary of the principal components of the mandibular mechanical advantage progression for the uncorrected (upper rows) and the phylogeny corrected data (lower rows)

	PC1	PC2	PC3	PC4	PC5	PC6
Uncorrected data						
Standard deviation	0.80	0.27	0.20	0.12	0.09	0.07
Proportion of variance	0.82	0.09	0.05	0.02	0.01	0.01
Cumulative proportion	0.82	0.91	0.96	0.98	0.99	1.00
Phylogeny taken into account						
Standard deviation	1.30	0.55	0.39	0.27	0.25	0.21
Proportion of variance	0.73	0.13	0.07	0.03	0.03	0.02
Cumulative proportion	0.73	0.86	0.92	0.95	0.98	1.00

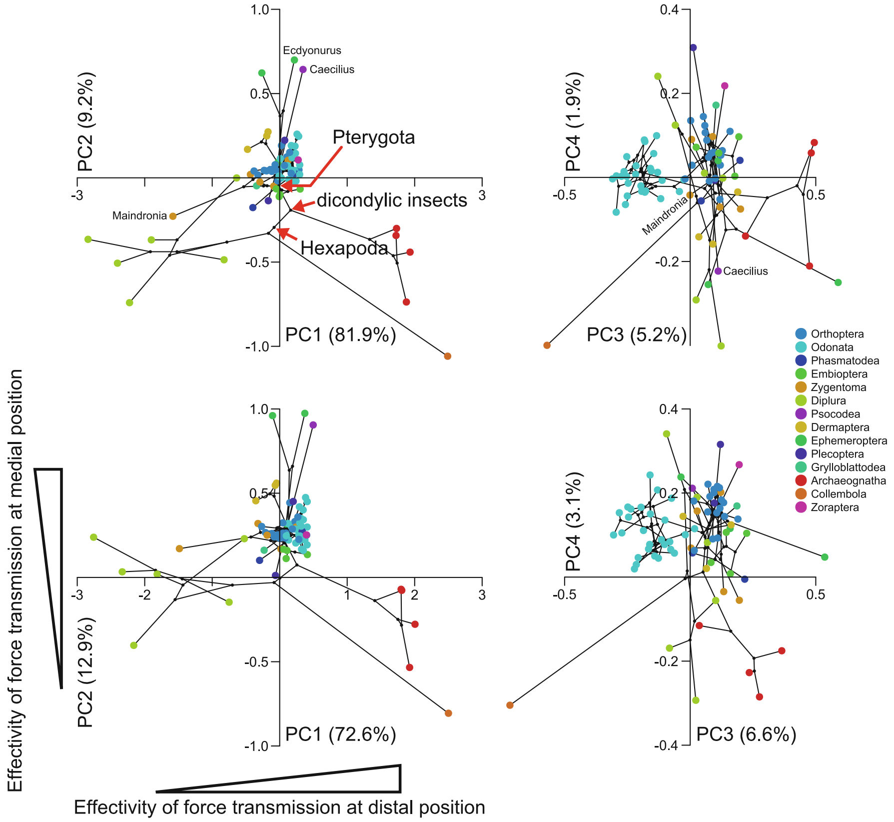

Fig. 6.5 Principal component analysis (PCA) of MA progression with the first four PCs shown. 2D plots of the first four uncorrected (upper row) and phylogeny-corrected PCs (lower row). Same lineage-specific color code as in Fig. 6.4. Note that the indication of the functional interpretation of the PCs in the lower left plot is also applicable to the upper left plot. Functional interpretations for PCs3+4 are not shown due to the low variance associated with these PCs

Table 6.3 Correlations of discrete morphological character states related to joint and endoskeleton morphology with MA variation across the taxon sampling for the uncorrected (upper rows) and the phylogeny corrected data (lower rows)

	SS	MS	R^2	F	Z	p
Uncorrected data						
DOF	29.14	14.57	0.49	107.29	5.16	0.0001
Joint config.	13.49	6.75	0.23	49.67	4.48	0.0001
CT present	3.59	3.59	0.06	26.40	3.45	0.0001
dicondyly:food	2.48	0.83	0.04	6.10	5.08	0.0001
Food pref.	1.21	0.40	0.02	2.96	2.08	0.0199
DTA connection	0.48	0.48	0.01	3.54	1.62	0.0428
Phylogeny taken into account						
DOF	45.21	22.61	0.26	15.06	5.39	0.0001
Joint config.	8.83	4.41	0.05	2.94	3.88	0.0001
dicondyly:food	17.09	5.70	0.10	3.80	5.38	0.0001
Food pref.	5.60	1.87	0.03	1.24	1.85	0.0420
CT present	1.55	1.55	0.01	1.03	2.77	0.0014
DTA connection	1.97	1.97	0.01	1.31	1.43	0.1103

(ORR): 26.4, $p = 0.661$) or according to food preference (ORR: 7.01, $p = 0.25$). Evolutionary rates were significantly different when partitioning the data according to the general type of articulation (ORR: 11.4, $p = 0.012$) with multicondylic taxa having the fastest rates (1.70), followed by facultative dicondylic taxa (0.74) and obligate dicondylic taxa (0.15). Evolutionary rates were also significantly different between taxa with different connection types of the dorsal tentorial arms and fused anterior and posterior tentoria (ORRs: 5.21/7.64, $p = 0.008/0.0001$).

Analyses of the correlation of the MA progressions with several morphological characters such as the degrees of freedom of the mandibles (DOFs), the joint configuration (multicondylic, facultatively dicondylic, obligate dicondylic), food preferences (herbivorous, omnivorous, carnivorous, detrivorous), and the general configuration of the endoskeleton resulted in significant correlations of almost all of these characters with the MA progressions of the mandibles (Table 6.3). DOFs and joint configurations explained 0.49 and 0.23% of the variance observed, while all other factors explained only a very minor proportion of the variance. Corrected for shared ancestry, coefficients of determination dropped considerably to 0.26 and 0.05 for the DOFs and the joint configuration, respectively.

6.6 Interpretation of the Mandibular Performance Space Occupation

Overall, the PCA of the MA progression reflects the principal lever arm differences resulting from the diverse set of mandible types analyzed here: taxa without obligate dicondylic mandibles such as Collembola, Diplura, Archaeognatha, Zygentoma, and

Ephemeroptera have the tendency to score at the extremes of the PCs due to their different MA progressions (Fig. 6.4). Closer inspection of the PCs reveals interesting functional associations between the different lineages. Collembola and Archaeognatha both scored at the positive extreme of PC1. Both lineages possess biting–chewing mandibles which perform a rolling motion around the dorsoventral axis with the rotation axis nearly aligned with the position of the distal incisivi (Fig. 6.1). Both taxa also possess a pronounced molar area to grind particles which is at a near orthogonal inclination to the rotation axis and therefore is advantageous regarding the effectiveness of the force transmission to the food item.

In contrast, Diplura scored at the negative extreme of PC1 and occupy a comparably wide lever arm performance space with no clear separation between Projapygoidea + Campodeoidea and the predatory Japygoidea. Diplura are characterized by prognathous mandibles whose main axis of rotation is not aligned with the distal row of incisivi and which are also capable of limited protraction and retraction movements of their mandibles. This is likely advantageous to rip off food particles from the substrate or prey. The comparably wide performance space occupation is mainly related to the vertical positioning of the slopes which shows that the distance of the gnathal edge to the rotation axis is more variable in Diplura compared to the other studied lineages.

In Zygentoma, the shift of the axis of rotation between the anterior and posterior joints leads to a shift of the biomechanical role of the M. craniomandibularis internus toward a purely adductive motion. This functional shift is also reflected in the PCs of the MA due to the clustering with the rest of Dicondylia. The silverfish *Maindronia neotropicalis* occupies a remarkable position within the dipluran performance space. The position of this species in PC space indicates that a considerable proportion of protraction and adduction might characterize the mandible motion. Living specimens should be investigated for their feeding habits, especially the amount of protraction/retraction, to corroborate this data. The rest of Zygentoma and winged insects agglomerated near the center of the first two PCs which account already for >90% of the variance associated with the mandibular mechanical advantage (Fig. 6.5). This clearly reflects the increased restriction of mandibular motion to adduction and abduction and the shift of the rotation axis toward the cephalocaudal axis.

6.7 Phylogenetic Signal in the Mechanical Advantage (MA)

Significant phylogenetic signal in the MA data with a K value greater than 1 means that there is a constraining phylogenetic effect on the variation in the effectivity of mandibular force transmissions: measured MAs are more similar than would be expected under a Brownian motion model of evolution, i.e., by a random unrestricted evolution of MA values (Adams 2014a; Blomberg et al. 2003).

However, this general pattern of phylogenetic signal in the MA data is not uniformly distributed. Analysis of the evolutionary rates (Adams 2014b) revealed that MAs associated with multicondyly and facultative dicondyly evolved at the fastest rates compared to the relative evolutionary stasis of obligate dicondylic taxa (Odonata + Neoptera). Associated with these significant rate changes in joint configuration are the connection types of the dorsal tentorial arms and the fusion of the anterior and posterior elements of the endoskeleton. Together with the phylogenetic signal in MAs, these data in summary suggest that the type of mandibular articulation (with its implications for rotation axis shifts) and the configuration of the endoskeleton lead to the comparatively static MA values in Odonata and Neoptera.

The detection of phylogenetic signal in this functional metric contrasts the common notion that specific functional selection pressures such as optimization toward more effective force transmission or, alternatively, toward faster biting movements (Westneat 1994, 2004; Sakamoto 2010) are the main drivers of the biomechanical performance space of food processing in the studied lineages at this taxonomic level. Phylogenetic signal in the MA with a *K*-value higher than 1 has also been detected for the mandibles of theropod dinosaurs (Sakamoto 2010), but it remained unclear whether this signal shows a uniform distribution or is dependent on certain lineages or functional types as is the case for the present data. Generally, a *K*-value higher than one is unusual for morphology-related data such as the MA (Blomberg et al. 2003). Based on a meta-analysis of literature data it appears that in most cases, *K* is lower than one (Blomberg et al. 2003) which would mean that morphological traits are less similar among species than expected from a Brownian motion model. This is intuitive, as these traits should be more malleable as a reaction to environmental effects rather than being constrained by shared ancestry as indicated here.

6.8 Mouthpart Performance in Dicondylic and Winged Insects

According to the phylomorphospace reconstruction of the principal components of MA progression variation, the most recent common ancestors (MRCA) of dicondylic insects, Pterygota and Hexapoda, respectively, score near the center of the first PC (Fig. 6.5, red arrows). This suggests that all three MRCAs probably possessed mouthpart configurations which showed MA progressions similar to the ones of recent obligate dicondylic insects. Regarding PC2, the three MRCAs are located on the negative side with a gradual transition toward the center of PCs1 + 2 from Hexapoda to Pterygota. The investigated Phasmatodea show a comparable location, and, interestingly, they are the ones with the highest MA values at the distal incisivi among the studied Dicondylia (Fig. 6.4). Given the phylomorphospace reconstruction, it appears that higher mandibular force transmission effectivities can be postulated for the MRCA of Hexapoda with a decrease toward the MRCA of winged insects. The type of mandibular articulation which realized this higher mandibular effectivity in force transmission to the food items, however, remains unclear.

Early branched Hexapoda show a high disparity in mouthpart shapes and biomechanics. It is clear that these changes cannot be attributed to a single effect, e.g., miniaturization in Protura, Collembola, and Diplura as these taxa again show different modes of food uptake. The results from this study indicate that primary wingless taxa have mandible configurations which are partly, e.g., in the molar area, advantageous and effective with regard to the lever system. In a timeframe of ~twenty million years [MRCA Zygentoma → MRCA Pterygota (Misof et al. 2014)], a rather ineffective dicondylic mandible system with regard to the distal incisivi evolved. This dicondylic mandible system remains a stable configuration across all insects with biting–chewing mouthparts even beyond the ones studied here (such as beetles, bees, and ants). The fact that this type of "ineffective" mandible setup is an evolutionary stable solution might be related to several other factors besides phylogenetic inheritance. For example, with dicondylic mandibles wider gape angles can be realized compared to the other observed solutions and a fixed axis of rotation requires fewer muscles within the system to control mandible movement. Therefore, the larger gape angles of dicondylic mandibles principally should allow to take up more energy per time interval. Flight imposes high energetic costs, and this might have positively selected the intake of large food volumes in a rapid manner rather than a time-consuming preprocessing of the food through chewing–grinding motions seen in entognathous Hexapoda, bristletails, and silverfish. The fact that a dicondylic food uptake system occurred almost concomitantly with wings and other aerial locomotion types (Hasenfuss 2002; Yanoviak et al. 2009) is certainly worth considering in future studies regarding the evolutionary linkage of different body parts.

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