

Bite force transmission and mandible shape in grasshoppers, crickets, and allies is not driven by dietary niches

Carina Edel¹, Peter T. Rühr¹, Melina Frenzel¹, Thomas van de Kamp², Tomáš Faragó³, Jörg U. Hammel⁴, Fabian Wilde⁴, Alexander Blanke¹

¹Bonn Institute for Organismic Biology, University of Bonn, Bonn, Germany

²Laboratory for Applications of Synchrotron Radiation, Karlsruhe Institute of Technology, Karlsruhe, Germany

³Institute for Photon Science and Synchrotron Radiation, Karlsruhe Institute of Technology, Eggenstein-Lepoldshafen, Germany

⁴Institute of Materials Physics, Helmholtz-Zentrum Hereon, Geesthacht, Germany

Corresponding author: Bonn Institute for Organismic Biology, University of Bonn, An der Immenburg 1, 53121 Bonn, Germany. Email: carina.edel30@gmail.com

Abstract

Although species evolve in response to many intrinsic and extrinsic factors, frequently one factor has a dominating influence on a given organ system. In this context, mouthpart shape and function are thought to correlate strongly with dietary niche and this was advocated for decades, e.g., for insects. Orthoptera (grasshoppers, crickets, and allies) are a prominent case in this respect because mandible shape has been even used to predict feeding preferences. Here, we analyzed mandible shape, force transmission efficiency, and their potential correlation with dietary categories in a phylogenetic framework for 153 extant Orthoptera. The mechanical advantage profile was used as a descriptor of gnathal edge shape and bite force transmission efficiency in order to understand how mandible shape is linked to biting efficiency and diet, and how these traits are influenced by phylogeny and allometry. Results show that mandible shape, in fact, is a poor predictor of feeding ecology and phylogenetic history has a strong influence on gnathal edge shape. Being ancestrally phytophagous, Orthoptera evolved in an environment with food sources being always abundant so that selective pressures leading to more specialized mouthpart shapes and force transmission efficiencies were low.

Keywords: phylogenetic signal, bite efficiency, Orthoptera, mandibles, form–function relationship

Introduction

A conjecture in biology is that form and function vary together in a correlated pattern. This led to the assumption that shape might even predict function and, consequently, aspects of the ecological niche (Feilich & López-Fernández, 2019). In this context, mouthparts are examples of tight adaptations to food sources with remarkable patterns of convergence. Jaw shape and dentition show convergence in mammals in distantly related orders, such as the aye-aye (*Daubentonia madagascariensis*) and squirrels (Berthaume et al., 2019; Evans et al., 2007; Grossnickle, 2020; Morales-García et al., 2021; Morris et al., 2018). A correlation between diet and jaw shape was also found in nonmammal vertebrate orders, such as fishes (Carroll et al., 2004; Wainwright & Richard, 1995), lizards (Metzger & Herrel, 2005), and birds (Olsen, 2017).

In chewing-biting insects, mouthpart shape disparity is extremely high and its relationship to diet is considered to be very tight. This was established by qualitative studies, which investigated Orthoptera and other polyneopterans (Aguirre-Segura et al., 1987; Bennack, 1981; Eilela et al., 2010; Gangwere, 1965; Isely, 1944; Kang et al., 1999; Kaufmann, 1965; Patterson, 1984; Samways et al., 1997; Smith & Capinera, 2005). With ~30,000 species Orthoptera

are the most diverse nonholometabolan biting-chewing insect group. Diet preferences range from phytophage monophagy (e.g., *Boottettix* sp., Otte & Joern, 1976) and obligate carnivory (e.g., *Saga pedo*), to omnivory (Gangwere, 1961; Ingrisch & Köhler, 1998). Feeding mode is equally diverse, including sedentary grazing (most Acrididae), scavenging (e.g., Gryllidae), and active predation (e.g., *Saga pedo*) (Kaltenbach, 1990; Lupu, 2007). More uncommon food sources are found, e.g., within the subfamily Zaprochilinae, which feed on pollen and are a rare example of pollinating Orthoptera (Tan et al., 2017). With different organic materials, nutritional compositions such as protein-to-carbohydrate ratios can vary immensely. A specialization to one food source might limit access to a nutrient-diverse diet. Herbivores and in particular grass feeders, have access to abundant food resources but no easy protein source (Hochuli, 1996; Le Gall & Behmer, 2014). Food toughness also varies, ranging from rather softer animal sources, such as worms and larvae, to tougher plant matter like grasses (Clissold, 2007; Clissold et al., 2009; Schoonhoven et al., 2005). For the majority of herbivorous animals fractionating plant material with their teeth is the key factor affecting nutrient uptake (Sanson, 2006) and its efficiency was associated with mandible morphology (Bennack, 1981).

Received May 8, 2023; revisions received July 26, 2024; accepted September 3, 2024

Associate Editor: Daniel Caetano; Handling Editor: Miriam Zelditch

© The Author(s) 2024. Published by Oxford University Press on behalf of The Society for the Study of Evolution (SSE).

This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial License (<https://creativecommons.org/licenses/by-nc/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited.

For commercial re-use, please contact reprints@oup.com for reprints and translation rights for reprints. All other permissions can be obtained through our RightsLink service via the Permissions link on the article page on our site—for further information please contact journals.permissions@oup.com.

Mandible shape in orthopterans has been categorized into dietary preference types such as graminivorous, forbivorous, carnivorous, detritivorous, and omnivorous, with some in-between forms mentioned (Gangwere, 1966; Isely, 1944). Based on such qualitative descriptions, authors inferred diet preference based on mandible shape (Eiela et al., 2010; Gangwere & Spiller, 1995; Smith & Capinera, 2005). The different mandible types show variation in the geometry of the gnathal edge, the molar region, and in width to length ratio. Similarly to mammals, such shape adaptations are thought to increase nutrient uptake because populations adapt to the evolving hardness and material composition of the food (Bernays et al., 1991; Gangwere, 1965; Patterson, 1983, 1984; Püffel et al., 2021; Weihmann et al., 2015). Shorter stouter mandibles with a clearly defined and ridged molar area were qualitatively linked to tougher plant matters, such as grasses (Gangwere et al., 1998; Kaufmann, 1965). In contrast to this, carnivorous mandibles were described as elongated with a hook-like shape and a flat, nonstructured molar area. Elongation is linked with increased biting speed and is thought to be adapted for prey capturing (Corbin et al., 2015; Stayton, 2006; Westneat, 2004). Between those two disparate forms exists an immense variation of in-between forms with varying degrees of the tooth and molar (Gangwere, 1965; Isely, 1944). Assigning those intermediate shapes to different dietary categories has been attempted (Gangwere, 1965; Ingrisch & Köhler, 1998; Isely, 1944; Kaufmann, 1965; Uvarov, 1966), but a clear and common definition is missing. Here, we use the mechanical advantage (MA) as a bio-mechanical performance metric and shape descriptor for the orthopteran mandible to determine if diet and gnathal edge shape follow the presumed one-to-one mapping in a phylogenetic framework.

Materials and methods

Taxon sampling

We studied 337 species of Orthoptera from 316 different genera, covering all extant families, except Pyrgacrididae, Cylindrachetidae, and Cooloolidae (see online [supplementary material S1](#)). Specimens from the orders Dermaptera, Blattodea, Plecoptera, Zoraptera, Grylloblattodea, and Phasmatodea were used as outgroups. All specimens were dried museum specimens from the National History Museum (London, UK), Zoologisches Forschungsmuseum Koenig (Bonn, Germany), Naturhistorisches Museum (Vienna, Austria), Museum fuer Naturkunde (MfN, Berlin, Germany), and Zoologische Staatssammlung (Munich, Germany).

Ecological data sampling

Eight different diet guilds were defined, based on the most common literature mentions ([Table 1](#)). Using the software “Publish or Perish” (v.7) (Harzing, 2007), a Google Scholar search was conducted for each species. Each of the ~2,000 publications were searched for diet information (using the keywords “diet,” “food,” and “feeding”) and a feeding category was assigned for each species. If no diet information for a species could be found, similar searches were conducted using synonyms, genus, or subfamily status. All diet information from the Orthoptera Species File (Cigliano et al., 2021) (retrieval date 13 April 2021) was extracted and crossreferenced with the literature data. If a mismatch occurred, the literature data got preference. If no literature data was found,

Table 1. Definition of diet guilds based on most common literature mentions.

Diet guilds	Description
Bryovorous	Feeding on algae and moss
Forbivorous	Feeding on herbaceous plants
Graminivorous	Feeding on grasses, sedges and rushes
Mixed-herbivorous	Feeding on both graminoid and herbaceous plants
Carnivorous	Feeding (mostly) in protein sources like other invertebrates
Omnivorous	No discernible food preference
Detritivorous	Feeding on detritus (decomposing organic matter and feces)
Others	Seed-feeding, flower-feeding

the information was supplemented with Orthoptera Species File data (see online supplementary material S2).

μCT-scanning and 3D reconstruction

The heads of all specimens were scanned with synchrotron radiation microcomputed tomography at different imaging facilities. In total, 98 scans were done at KIT Light Source (Karlsruhe Institute of Technology, Karlsruhe, Germany), 44 at TOMCAT (Stampanoni et al., 2006) (Swiss Light Source, Paul-Scherrer-Institute, Villigen, Switzerland), and 21 at the Center for Biohybrid Medical Systems (Aachen, Germany). A further 190 specimens were scanned at Deutsches Elektronen Synchrotron (Hamburg, Germany) of which 106 were processed at the IBL-P05 imaging beamline (Khokhriakov et al., 2017; Moosmann et al., 2014; Wilde et al., 2016) (operated by the Helmholtz-Zentrum Hereon at PETRA III) and 74 larger specimens at the Phoenix Nanotom M, General Electric (Boston, MA) housed at Deutsches Elektronen Synchrotron. Each scan was downsampled to ~300 MB with Fiji (Schindelin et al., 2012) using a stack-cropping macro script of Rühr et al. (2021), which also generates “HDR5-Analyse” files with a corresponding.hdr file for import into ITK-Snap (v. 3.8) (Yushkevich et al., 2006). 3D reconstruction was done in ITK-Snap with a presegmentation by hand and completed using a semiautomatic segmentation algorithm. Mis-assigned voxels were afterwards corrected by hand and a smooth.stl surface was exported for import into Blender (v. 3.8) (Hess, 2010).

MA and the bite efficiency profile

Orthoptera have a dicondylic mandible that articulates with the head capsule via two ball-and-socket joints. The mandibles, therefore, rotate around only one axis going through the centers of those two joints creating a virtual hinge joint. The mandibles are mainly moved by two muscles, a closer muscle that occupies most of the head volume and a much smaller opener muscle (Chapman, 1995; Snodgrass, 1935). The mandibles are slightly asymmetrical with the left mandible overlapping the right mandible and both mandible's biting areas fitting together in a lock-and-key mechanism (Chapman, 1995; Snodgrass, 1935). Because of this, only the left mandible is used in all analyses. The biting area of the mandibles differentiates into a distal incisor lobe (pars incisivus) and a proximal molar lobe (pars molaris) (Chapman, 1995; Richter

et al., 2002). Together the lobes form the gnathal edge of the mandible (Edgecombe et al., 2003).

The effectivity of the force transmission from the muscles via the mandibles to the biting area can be described with the MA, which is the ratio of in-lever to out-lever length (Clissold, 2007; Westneat, 2004). For insect mandibles, the in-lever is the perpendicular distance between the fulcrum and muscle insertion point, whereas the out-lever is the distance between the fulcrum and the biting point (Figure 1A, B).

3D reconstructed mandibles were used for MA measurements with Blender (v. 2.81) (see online supplementary material S3) and R (v. 4.2). After import in Blender a right triangle plane was defined between the rotation axis and the closer muscle insertion point which was then rotated so that the planes of all mandibles were aligned on the same level. The start and endpoint 3D coordinates for the in-levers were then exported. The mandibles were flattened along the sagittal midline and a line with 400–800 vertices wrapped around the gnathal edge (Figure 1B). 3D coordinates were exported from Blender into R (v. 4.2.1) (R Core Team, 2022) and the in-lever and out-lever lengths were calculated for both mandible muscles. Because a clear definition of the start of the molar area was often impossible, the biting area was measured from the closer muscle insertion point to the most distal incisivi and normalized. The mechanical advantage was then calculated for each point along the gnathal edge resulting in a mechanical advantage profile (MAP). The nonlogged regression of inlever versus outlever passes through the origin (see online supplementary material S4), which is why we continued to use the ratio of both lever measurements for all further analyses (Curran-Everett, 2013). A polynomial function was fitted on the MAP for each specimen. The best polynomial function fit for all mandibles was determined based on the Akaike (AIC) and Bayes (BIC) information criteria (Bozdogan, 1987). Polynomial models from 1st to 20th degree were tested with the function `best_fit()` in `forceR` (v1.0.20) (Rühr & Blanke, 2022) to determine the AIC value that changes less than 5% from one value to the next. Further statistical tests were then conducted with the coefficients of the polynomial curve with the best fit according to the AIC.

Phylogenetic comparative methods

Phylogenetic signal was determined using the most recent and comprehensive time-calibrated Orthoptera phylogeny available (Song et al., 2020). First, an evaluation of taxon overlap between the Song et al. (2020) phylogeny and the used taxon sampling was conducted and a tip substitution based on the most-restrictive taxonomic rank was implemented. Species that had no match in the taxon sampling were pruned from the tree using `drop.tip` in `ape` (v 5.7.1) (Paradis & Schliep, 2019). Twelve species that had an unequivocal sister group (the same genus or family/subfamily branch only had one tip) were manually added with `addTip` in `TreeTools` (v 1.10.0) (Smith, 2019). This function has the advantage that not only the new edge length could be defined but also the edge length of the already present sister group. To keep the tree ultrametric the edge length of the new tip was randomized between 0 and the edge length of the sister group. These procedures led to a subset of 153 taxa (out of 343 taxa) which were used for phylogenetic comparative statistics reported in the main text.

To check if the phylogenetic signal was influenced by adding taxa manually to the tree, 1,000 trees with random new edge lengths for the added 12 taxa were calculated. Phylogenetic signal, in the form of K_{mult} (the multivariate version of Blomberg's K ; Blomberg et al., 2003) for the polynomial coefficients of all 1,000 randomized trees was calculated with `physignal()` in `geomorph` (v 4.0.6) with 999 iterations (Adams & Otárola-Castillo, 2013). The tree with a phylogenetic signal closest to the mean K_{mult} of all randomized trees was used in all further statistical analyses.

A potential correlation between the mechanical advantage profiles and log mandible length was tested jointly with estimating phylogenetic effects using a phylogenetically informed (phylogenetic generalized least squares [PGLS]) regression (`procD.lm.pgls` in `geomorph` v 4.0.6) (Adams & Otárola-Castillo, 2013) with 10,000 permutations (See online supplementary material S5). This PGLS regression implementation assumes a Brownian Motion evolutionary model. For further analysis of the phylogenetic and allometric corrected data, the residuals of the PGLS function were used.

To ascertain which evolutionary model fits the data best, the package `mvMorph` (Clavel et al., 2015, v. 1.1.6) was used.

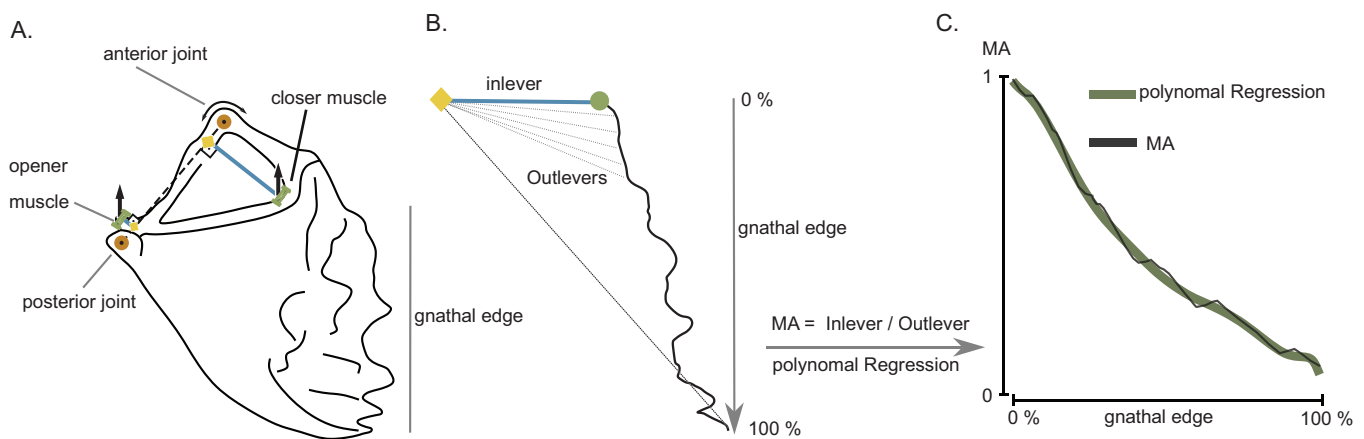


Figure 1. Methodological overview for mechanical advantage measurements and their translation into bite efficiency profiles. (A) A schematic of a typical mandible with the rotation axis point (yellow) between the joints (orange) and the in-lever (blue). (B) Gnathal edge measurements and calculation of mechanical advantage for a rotated mandible so that the rotation axis is perpendicular to the plane of projection. In-lever with the point of rotation (yellow) and closer muscle insertion point (green). (C) Example of the mechanical advantage (MA) progression along the gnathal edge (black) and the resulting polynomial curve (green).

The function `mvglS()` uses a maximum likelihood approach (method = "LL" in function) to fit multivariate linear models to multivariate data. The data fit was tested for Brownian Motion, Ornstein-Uhlenbeck, and Early Burst models against dietary category using the AIC criterion (see online [supplementary material S6](#)).

To explore the patterns of variation within the bite efficiency on the gnathal edge, a phylogenetic Principal Component Analysis (pPCA) on the polynomial coefficients was calculated using `mvglS.pca` in `mvMorph` (v. 1.1.6) (see online [supplementary materials S7](#) and [S8](#)). Disparity patterns within dietary and superfamily groups were tested with the function `morphol.disparity` in `geomorph` (v 4.0.6) (see online [supplementary materials S9](#) and [S10](#)). All analyses were conducted for both, the opener and the closer muscles.

Results

Bite efficiency profile patterns

A polynomial curve of the ninth order had the best fit based on the AIC scores. The mechanical advantage profile (MAP) of Orthoptera had the highest MA at the proximal end, which varied between 0.94 and 0.63 at the closer muscle and 0.35 and 0.09 at the opener muscle ([Figure 2](#), right). It then decreased by ~70% along the gnathal edge until it reached its lowest value at the most distal end. The outgroups, in contrast, showed a lower proximal MA which ranged from 0.65 to 0.48 at the closer and 0.4 to 0.16 at the opener muscle. The progression of the MA was visually similar between most orthopteran superfamilies ([Figure 2](#), right) with some showing areas of decreased negative slope. The Gryllotalpoidea (mole and ant crickets), Grylloidea (crickets), Hagloidea (grigs), and Tanaoceroidea (desert long-horned grasshoppers) had this slope around the 25% position and the Tetrigoidea (pygmy grasshoppers) at the 50% position. Superfamilies with a more uniform MAP were the Schizodactyloidea (dune crickets), Stenopelmatoidea, Rhaphidophoroidea (cave crickets), and Tettigonioida.

MAP allometry, phylogenetic signal, and relation to diet

The relationship of log inlever versus log outlever of the distal incisivus was a linear one with a slope of 0.97 ($R^2 = 0.96$) for the opener muscle and a slope of 0.94 ($R^2 = 0.83$) for the closer muscle ([Figure 3A, B](#)) with the slopes for the dietary categories not being significantly different from each other. Analysis of the distal MA values ([Figure 3C, D](#)) showed that detritivorous and carnivorous Orthoptera showed the lowest distal MA for the closer muscle and graminivorous the highest, whereas carnivorous species have the lowest distal MAs for the opener muscle and bryovorous the highest.

Mandible length, i.e., the distance from the articulation axis to the distalmost incisivus, had a 62-fold size variation from 0.18 to 9.29 mm ([Figure 2](#)). PGLS regression of the MAPs against log mandible length had a significant but very low explanatory value for the closer muscle MAP ($R^2 = 0.15$; $p = 0.001$) and was non-significant for the opener muscle MAP ($R^2 = 0.02$; $p = 0.05$). The homogeneity of slopes of unique versus common allometry could not be rejected meaning that families and superfamilies within Orthoptera do not show significantly different allometric slopes ([Supplementary material S5](#)).

There was significant ($p < 0.05$) phylogenetic signal in the MAPs for the whole taxon set, as well as a larger subset, the

Acridoidea, with K_{mult} values below 1. For another larger subclade, Tettigonioida, phylogenetic signal was not significant ([Table 2](#)). The comparison of evolutionary models for the polynomial coefficients of the MAPs in relation to diet (for the whole taxon set) showed that a Brownian motion evolutionary model was equally likely to an early burst model (see online [supplementary material S6](#)), but the rate decay parameter r was zero which indicates a BM-like trait evolution. Phylogenetic MANOVAs coupled to phylogenetic ANOVAs resulted in significant relations of the MAPs with dietary categories albeit with comparably low f -values (Closer muscle: F -value: 1.63; $p = 0.0012$; Opener muscle: F -value: 1.64; $p = 0.0011$).

The morphospace of MAPs

A pPCA of the polynomial coefficients showed that PCs 1 and 2 described 78% of the variation in the data set ([Figure 4A, C](#)). No distinct functional, ecological, or taxonomical groups, except the outgroups, could be determined based on visual inspection ([Figure 4](#)). PC loadings (see online [supplementary material S8](#)) indicate that PCs 1 and 2 mainly code for the first two polynomial coefficients while PCs 3 and 4 mainly code for the third and fourth polynomial coefficients as well as the intercept (see online [supplementary material S8](#), for data for the opener muscle). Feeding guilds ([Figure 4A, B](#)) did not show marked differences for the closer muscle while for the opener muscle the omnivorous group showed the largest morphospace occupation. The morphospace of taxonomic groups also showed no visually discernible groupings for the closer muscle ([Figure 4C, D](#)), whereas for the opener muscle the outgroup and Gryllotalpoidea deviated from all other lineages with Gryllotalpoidea showing a higher disparity within the PCA than all other Orthoptera and with a recognizable distinction between the families Gryllotalpidae (mole crickets) and Myrmecophilidae (ant-crickets). The ant crickets clustered around the central point of the dataset whereas the Gryllotalpidae separated into the lower right quadrant. Gryllotalpidae also showed the highest disparity among the superfamilies and they were, besides the outgroups, the only superfamily with a significant difference in disparity compared to all other superfamilies (see online [supplementary material S9](#)). For the opener muscle MAPs, disparity signal was more mixed with the outgroup and Tanaoceroidea showing significant differences, whereas Gryllotalpoidea did not show significant differences in disparity to other superfamilies (see online [supplementary material S9](#)). Disparity signal between dietary groups was only significant for omnivorous compared with mixed-herbivorous and graminivorous for the closer muscle, whereas for the opener muscle the forbivorous group was significantly different in disparity to carnivorous, graminivorous, mixed-herbivorous, and omnivorous groups (see online [supplementary material S10](#)).

Discussion

For many taxa, it was shown that mouthpart phenotypes correlate with aspects of the feeding ecology ([Blomberg et al., 2003](#); [Evans et al., 2007](#); [Kienle & Berta, 2016](#); [Meyers et al., 2006](#); [Montaña & Winemiller, 2013](#); [Nogueira et al., 2009](#); [Prevosti et al., 2012](#); [Santana et al., 2022](#)), which even lead to predictions of feeding preferences ([Firmat et al., 2010](#)). Due to the involvement of mouthparts in the cutting and mastication of food, an adaptation to increase food consumption

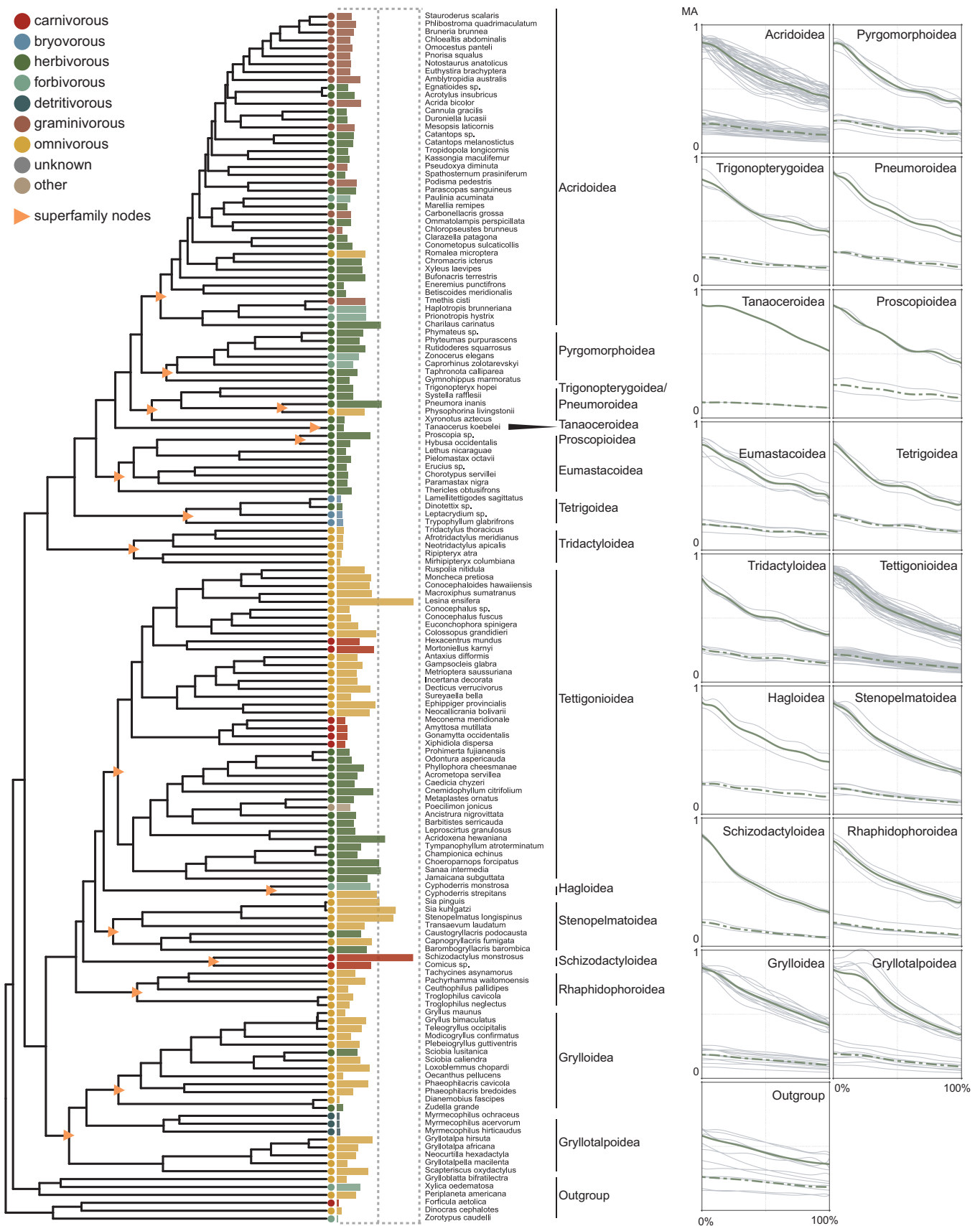


Figure 2. The evolution of dietary categories, mandible size and mechanical advantage in Orthoptera. Left: Phylogenetic relationships (adapted from Song et al., 2020) with colored bars indicating dietary category and absolute mandible length in mm. Right: Mechanical advantage profiles and its variation among species of each superfamily (gray lines; dataset with phylogenetic and allometric correction; $N = 153$) for the closer muscle (solid line) and the opener muscle (dotted line). X-axis = Percentage of gnathal edge with 0% as the most proximal and 100% as the most distal point of the gnathal edge.

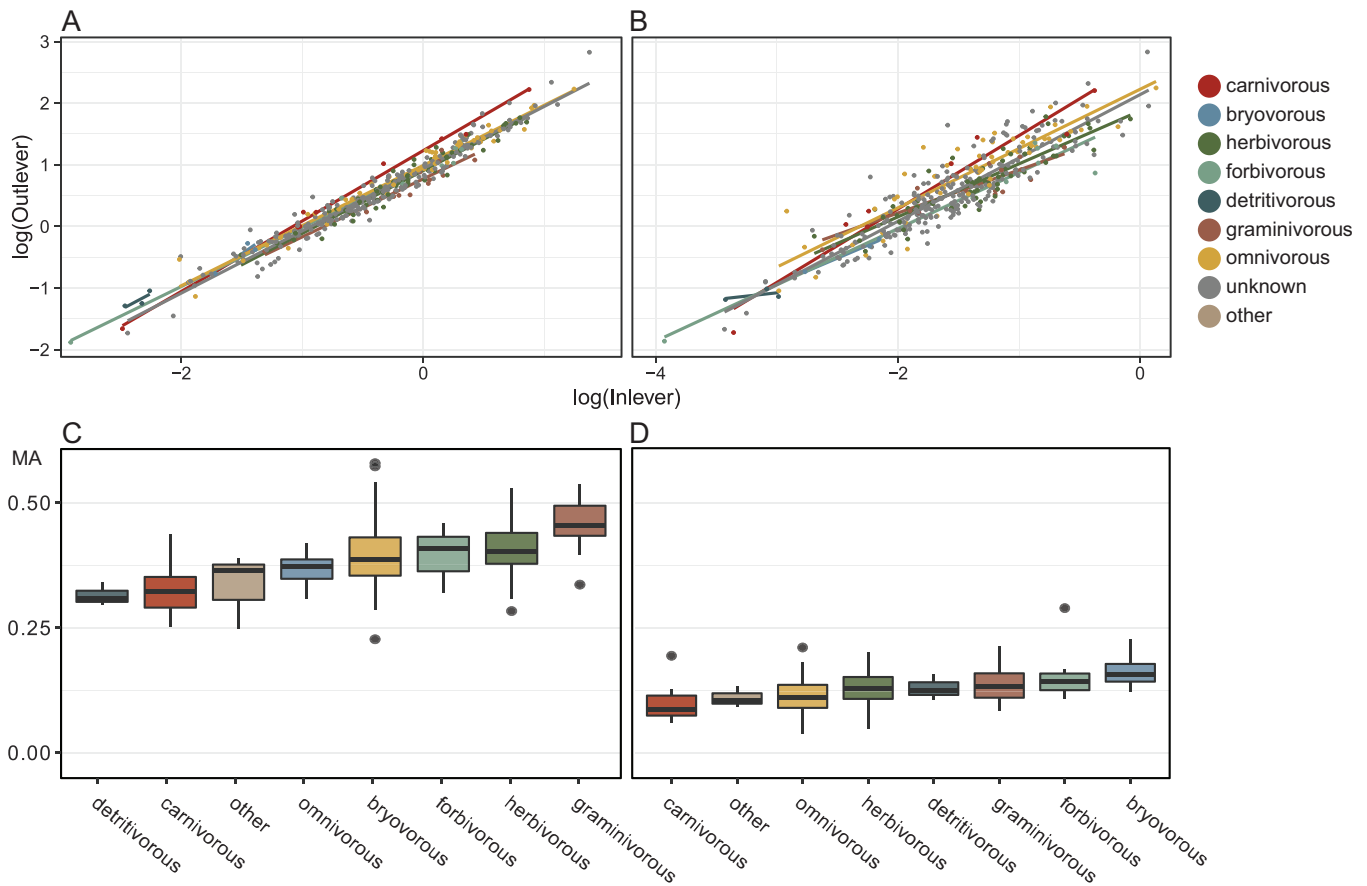


Figure 3. The relationship between inlever and outlever for the closer (A) and opener (B) muscles of the mandibles for the full dataset ($N = 343$) together with dietary categories. Lines are regressions for each dietary category. The overall R^2 is 0.96 for the closer and 0.83 for the opener muscle lever relationships and the overall slopes are 0.97 and 0.94, respectively. Note that slopes for dietary categories are not significantly different from each other. (C) shows the distalmost mechanical advantage (MA) for the closer muscle, whereas (D) shows the distal mechanical advantage for the opener.

Table 2. Results of phylogenetic signal testing.

Data	Muscle	K_{mult}	P
Polynomial coefficients (all taxa)	Closer	0.97	0.001
Polynomial coefficients (all taxa)	Opener	0.35	0.001
Poly. coeff. Tettigoniodea	Closer	0.38	0.77
Poly. coeff. Tettigoniodea	Opener	0.49	0.21
Poly. coeff. Acarioidea	Closer	0.61	0.013
Poly. coeff. Acarioidea	Opener	0.61	0.005

Larger subclades with species numbers >15 were also tested for phylogenetic signal (Acarioidea $n = 40$; Tettigoniodea $n = 40$).

efficiency generally is expected (Stephens & Krebs, 2019). Although it was shown that mouthparts are in no way strictly a function of bite force transmission efficiency but instead also have to withstand the reaction forces imposed by the food items (Soons et al., 2010, 2015), several arguments support the view that, in theory, mechanical advantage profiles are an important trait in dietary niche adaptation: First, in insects, an increased intake rate determines survival not only by the acquisition of nutrients because feeding also can increase the risk of predation (Bernays, 1997). Also, grasshoppers consume the equivalent of their body mass per day during growth and continue to consume comparably large quantities of food as adults (Davey, 1954), which puts the mandibles

and their muscles under constant strain. One would expect that an adaptation of the force transmission to diet is observable in such a scenario and indeed our results for the distal MA in relation to diet (Figure 3C) point into this direction. However, contrary to the established notion of a tight correlation of mandible shape with feeding ecology, our results show that diet is not the main determinant behind the diversification of bite force transmission profiles and, consequently, mandible shape in Orthoptera. We found phylogenetic signal with closely related species being less similar than expected under a Brownian motion model of evolution and, although there was no difference in AIC between a BM and an early burst model (see online supplementary material S6), a preference for BM-like trait evolution is likely given the decay rate of zero. However, preference for a Brownian motion model of trait evolution does not mean per se that the trait evolves in a nonadaptive manner: One has to take into account that we present here a rather large phylogenetic scope that might blur heterogeneity among single clades in which the evolution of mandible shape and mechanical advantage might still be adaptive (see results for Acarioidea, Table 2).

Our results are in contrast to qualitative studies based on the visual sorting of mandible types into different dietary categories (Gangwere, 1965, 1966; Isely, 1944; Patterson, 1984; Wheater & Evans, 1989) and studies for other animal groups. In Mesozoic mammals, shorter jaws and increased MAs are associated with herbivory, whereas intermediate and

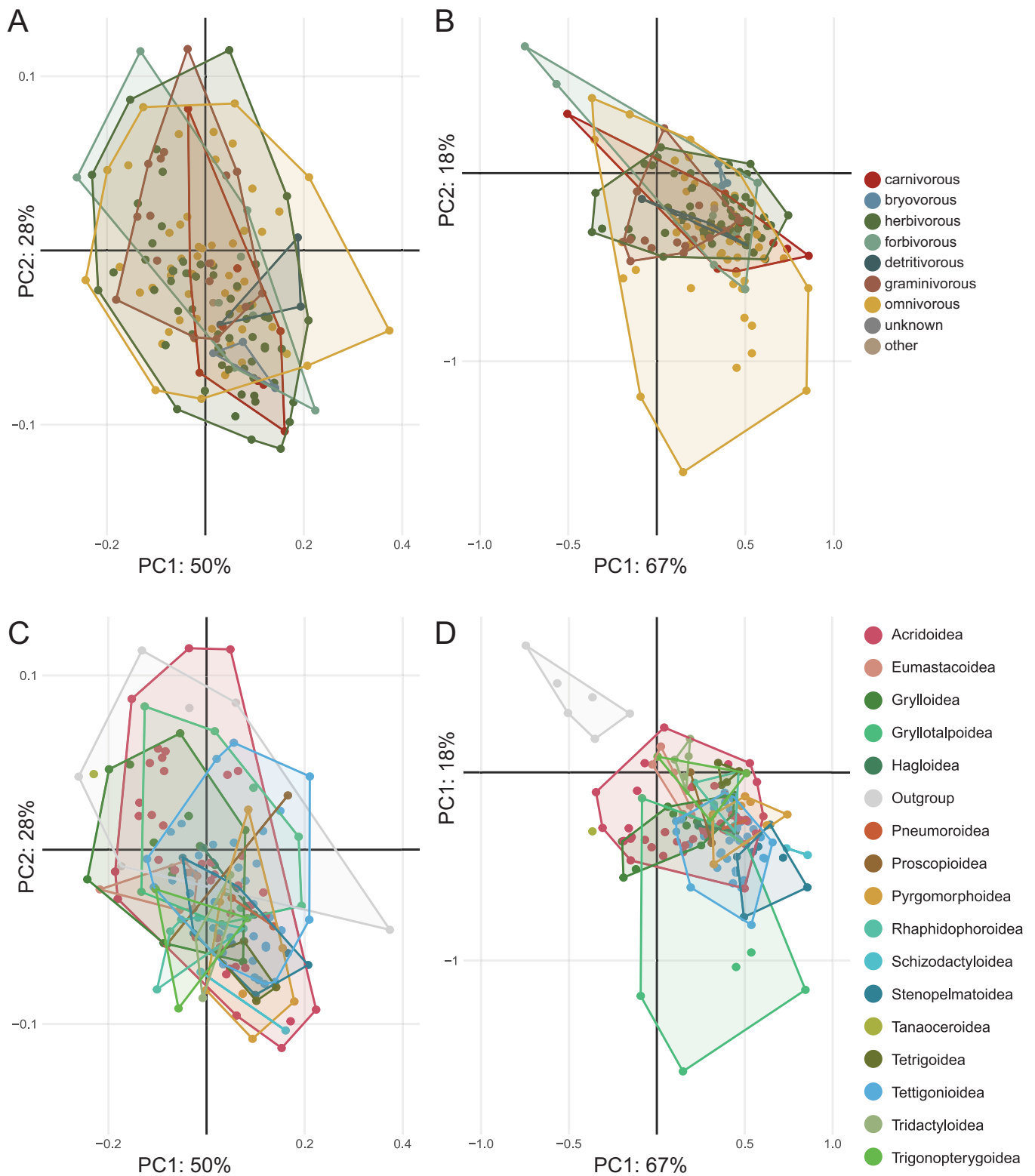


Figure 4. The morphospace of the mechanical advantage profiles along the whole gnathal edge in Orthoptera. Principal components (PCs) 1 and 2 for the closer (A + C) and the opener muscles (B + D). Datapoints in A + B colored according to dietary categories and in C + D according to families. For both, closer and opener muscles, PC1 codes mainly for the first coefficient of the polynomial curve describing the mechanical advantage profile (the general shape of the function) while PC2 codes mainly for the second coefficient (the symmetry and turning points of the function).

longer jaws and lower MAs are associated with insectivory and carnivory (Morales-García et al., 2021). Similar results were found for rodents (Anderson et al., 2014; Missagia et al., 2021), birds (Olsen, 2017), and reptiles (Bestwick et al., 2021).

In Orthoptera, despite a 62-fold mandible size variation, correlation to MA variation along the gnathal edge held very low explanatory power. Apparently, as long as the ratio between the in-lever and out-lever stays within the observed

range, no strong shape adaptations to diet or size evolved. A comparable effect was observed for suction-feeding teleost fishes where size differences in multiple traits (gape width, buccal length, cross-sectional area of the epaxial muscle, lengths of the epaxialis, and buccal cavity moment arms) evolved toward similar performance (Wainwright et al., 2007).

Another possibility is that muscle volume and angle, as well as muscle physiology, compensate for a less-than-optimal mandible shape that might render shape adaptations redundant. Bernays (1986) showed that grass-feeding grasshoppers have an increased head mass due to an increase in mandible musculature that might be enough to increase food throughput to meet nutritional needs. Muscle physiology was linked to foraging habits in ants (Gronenberg et al., 1997) where the composition of muscle fiber types determined mandible speed. Although we did not quantify muscle mass in our study, such changes are one option to account for different dietary niches although, in evolutionary terms, a change in mandible shape, e.g., along the molar region, appears to be a more simple adaptation than larger changes in muscle angles, masses, and, consequently, associated changes of other head parts to accommodate such different muscle configurations.

Gnathal edge disparity in Orthoptera

Despite the overall low explanatory power of diet for mandible shape, we also found that the closer muscle had the highest distal MA within grass feeders and the lowest in detritivores and carnivorous Orthoptera (Figure 3). This followed the expectation that tougher plant matter like grasses necessitates a higher force transmission and a lower MA is more advantageous in carnivory, due to an increase in biting speed. Despite this, the explanatory power of diet for the MA was low and no distinct dietary functional groups for the mechanical advantage profile along the gnathal edge could be found. What little correlation could be found was mostly due to differences between graminivorous and omnivorous Orthoptera to the other dietary guilds (see online [supplementary material S10](#)).

Despite the generally low explanatory power of feeding categories for mandible shape and efficiency, there are some notable examples of specialization in our dataset. The superfamily group with the highest disparity are the Gryllotalpoidae, which includes the mole-crickets and ant-crickets. They are two families with very specialized and different living environments: The ant crickets live inquiline with the ants and obtain food by either grooming or trophallaxis for which they have modified mouthparts (Komatsu & Maruyama, 2016; Wetterer & Hugel, 2008). Mole crickets are adapted for digging and live mostly underground. They have a nearly prognathic head orientation with a shortened-out lever distance and an increase in the MA in the proximal part of the mandible. The genus *Oecanthus* similarly shows a more prognathic head orientation (Hudson, 1945) and shows similar angling of the mandible and a slight increase in mechanical advantage. A case of dietary conservatism on a family level can be found in the Tetrigidae (Kuřavová et al., 2017), which prefer algae, mosses, and lichens. Their mandible shows a specialized scraping ridge at their molar area (Kuravova & Kocarek, 2016; Kuřavová et al., 2014), which was theorized to follow convergent adaptation in algae grazers (Arens, 1994; Kuřavová et al., 2017).

In summary, although there are many shape differences observable for orthopteran mandibles, our results show that there are also many *intermediate* mandible forms that probably lead to the observed very low explanatory values. For example, the mandibles of the forb-feeding Acrididae *Paulinia acuminata* look fundamentally different to the forb-feeding Prophalangopsidae *Cyphoderris monstrosa*, whereas the predatory *Phisis* sp. looks similar to the omnivore *Capnogryllacris*.

Omnivory as a stable evolutionary plateau

While Orthoptera are generally perceived as phytophagous animals that mostly feed on plant matter, most orthopterans cannot be categorized into only one dietary group. Many species feed indiscriminately on plant matter but do not refuse protein sources like dead arthropods when provided (Bernays & Chapman, 1970; Ingrisich & Köhler, 1998). Even strictly defined grass feeders such as the Gomphocerinae or *Romalea microptera* can be observed to feed on other arthropods (Clark, 1948; Richardson et al., 2012). The advantage of such omnivory is that animals always have access to resources in the form of abundant plant matter as well as highly nutritious protein-rich food sources such as animal matter.

Our results are in line with this facultative omnivory of many species. Orthopteran mandibles operate at a performance plateau rather than separated peaks. This is a characteristic of morphological stasis in which environments may change dramatically but morphology does not follow (Wake et al., 1983). For example, Zelditch, (2020) found that while tree squirrels are morphologically specialized, they are ecological generalists, which lead to a performance plateau. The beaks of Darwin finches were equally found to lack diet specialization in preference for versatility when studied on phylogenetic levels similar to our study (Navalón et al., 2019). However, many other studies found clear and strong correlations of beak shape (and head widths) in Darwin's finches (Herrel et al., 2005a, b, 2009; Soons et al., 2010, 2015). This might point to the well-known general problem of macroevolutionary perspective and phylogenetic scale in ecology and evolution with studies on a wide macroevolutionary levels showing less signal of adaptation as compared with studies on smaller subsets of clades (Graham et al., 2018; Jablonski, 2007).

Orthoptera originated ~355 million years ago (Song et al., 2020) and persisted despite massive environmental and climatic changes as well as mass extinctions. One major factor of their microhabitat, plants, remained relatively stable in the sense that food was always highly abundant. Radiations took place mostly in the Mesozoic within Ensifera in correlation with the angiosperm radiation and for the Caelifera during the Cenozoic coinciding with the spreading of grasslands (Song et al., 2020), but the principle food source always remained in high abundance. Such stable feeding environments with abundant nutritional access possibly did not result in a clear-cut specialization of mouthpart configuration.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

All data to conduct the analyses including the R scripts were made available under <https://doi.org/10.5281/zenodo.12820631> via Zenodo.org.

Author contributions

C.E.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, visualization, writing-original draft, writing-review, and editing. T.v.d.K.: investigation, methodology, resources, software, writing review, and editing. T.F.: investigation, methodology, resources, software, writing review, and editing. J.U.H.: investigation, methodology, resources, software, writing review, and editing. F.W.: investigation, methodology, resources, software, writing review, and editing. P.T.R.: investigation, writing review, and editing. M.F.: investigation, writing-review, and editing. A.B.: conceptualization, formal analysis, funding acquisition, investigation, project administration, resources, supervision, writing-review, and editing.

Funding

A.B. and C.E. were supported by the Deutsche Forschungsgemeinschaft under the Individual Research Grants program (grant agreement No. BL 1355/4-1) awarded to A.B. A.B. was further supported by the European Research Council under the European Union's Horizon 2020 research and innovation program (grant agreement No. 754290, "Mech-Evo-Insect"). Microcomputed tomography-scanning was funded by the following, facility-specific grants awarded to A.B.: HZG at Deutsches Elektronen Synchrotron: I-20170190, I-20170896, I-20190019; Swiss Light Source: 20171469.

Conflict of interest: The authors declare no competing interests.

Acknowledgments

Loan of museum specimens were kindly organized by B. Price (National History Museum), H. Zettel (Naturhistorisches Museum), D. Zimmermann (Naturhistorisches Museum), J. Deckert (Museum fuer Naturkunde), R. Peters (ZFMK) and L. Hendrich (Zoologische Staatssammlung). We also thank the members of the Karlsruhe Institute of Technology the Deutsches Elektronen Synchrotron, and the Helmholtz Zentrum Hereon for access to their facilities and their assistance.

References

- Adams, D. C., & Otárola-Castillo, E. (2013). Geomorph: An R package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution*, 4, 393–399.
- Aguirre-Segura, A., Arcos, M., Moyano, F., & Pascual, F. (1987). Tipos adaptivos de morfología mandibular en algunas especies de ortópteros ibéricos. *Graellsia*, XLIII, 225–235.
- Anderson, P. S., Renaud, S., & Rayfield, E. J. (2014). Adaptive plasticity in the mouse mandible. *BMC Evolutionary Biology*, 14, 85. <https://doi.org/10.1186/1471-2148-14-85>
- Arens, W. (1994). Striking convergence in the mouthpart evolution of stream-living algae grazers. *Journal of Zoological Systematics and Evolutionary Research*, 32(4), 319–343. <https://doi.org/10.1111/j.1439-0469.1994.tb00490.x>
- Bennack, D. E. (1981). The effects of mandible morphology and photosynthetic pathway on selective herbivory in grasshoppers. *Oecologia*, 51(2), 281–283. <https://doi.org/10.1007/BF00540615>
- Bernays, E. A. (1986). Diet-induced head allometry among foliage-chewing insects and its importance to Graminivores. *Science (New York, N.Y.)*, 231(4737), 495–497. <https://doi.org/10.1126/science.231.4737.495>
- Bernays, E. A. (1997). Feeding by lepidopteran larvae is dangerous. *Ecological Entomology*, 22(1), 121–123. <https://doi.org/10.1046/j.1365-2311.1997.00042.x>
- Bernays, E. A., & Chapman, R. F. (1970). Food selection by *Chorthippus parallelus* (Zetterstedt) (Orthoptera: Acrididae) in the field. *Journal of Animal Ecology*, 39(2), 383–394. <https://doi.org/10.2307/2977>
- Bernays, E. A., Jarzembowski, E. A., & Malcolm, S. B. (1991). Evolution of insect morphology in relation to plants [and discussion]. *Philosophical Transactions of the Royal Society*, 333, 257–264.
- Berthaume, M. A., Winchester, J., & Kupczik, K. (2019). Ambient occlusion and PCV (portion de ciel visible): A new dental topographic metric and proxy of morphological wear resistance. *PLoS ONE*, 14(5), e0215436. <https://doi.org/10.1371/journal.pone.0215436>
- Bestwick, J., Unwin, D. M., Henderson, D. M., & Purnell, M. A. (2021). Dental microwear texture analysis along reptile tooth rows: Complex variation with non-dietary variables. *Royal Society Open Science*, 8(2), 201754. <https://doi.org/10.1098/rsos.201754>
- Blomberg, S. P., Garland T., Jr, & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, 57, 717–745.
- Bozdogan, H. (1987). Model selection and Akaike's Information Criterion (AIC): The general theory and its analytical extensions. *Psychometrika*, 52(3), 345–370. <https://doi.org/10.1007/bf02294361>
- Carroll, A. M., Wainwright, P. C., Huskey, S. H., Collar, D. C., & Turingan, R. G. (2004). Morphology predicts suction feeding performance in centrarchid fishes. *Journal of Experimental Biology*, 207(Pt 22), 3873–3881. <https://doi.org/10.1242/jeb.01227>
- Chapman, R. F. (1995). Mechanics of food handling by chewing insects. In R. F. Chapman & G. de Boer, eds. *Regulatory mechanisms in insect feeding* (pp. 3–31). Springer US.
- Cigliano, M. M., Braun, H., Eades, D. C., & Otte, D. (2021). Orthoptera Species File. Date accessed September 11, 2022. <http://orthoptera.speciesfile.org/>
- Clark, E. J. (1948). Studies in the ecology of British Grasshoppers. *Transactions of the Royal Entomological Society of London*, 99, 173–222.
- Clavel, J., Escarguel, G., & Merceron, G. (2015). MvMorph: An R package for fitting multivariate evolutionary models to morphometric data. *Methods in Ecology and Evolution*, 6(11), 1311–1319. <https://doi.org/10.1111/2041-210x.12420>
- Clissold, F. (2007). The Biomechanics of chewing and plant fracture: Mechanisms and implications. *Advances in Insect Physiology*, 34, 317–372.
- Clissold, F. J., Sanson, G. D., Read, J., & Simpson, S. J. (2009). Gross vs. net income: How plant toughness affects performance of an insect herbivore. *Ecology*, 90(12), 3393–3405. <https://doi.org/10.1890/09-0130.1>
- Corbin, C. E., Lowenberger, L. K., & Gray, B. L. (2015). Linkage and trade-off in trophic morphology and behavioural performance of birds. *Functional Ecology*, 29, 808–815.
- Curran-Everett, D. (2013). Explorations in statistics: The analysis of ratios and normalized data. *Advances in Physiology Education*, 37(3), 213–219. <https://doi.org/10.1152/advan.00053.2013>
- Davey, P. M. (1954). Quantities of Food eaten by the Desert Locust, *Schistocerca gregaria* (Forsk.), in Relation to Growth. *Bulletin of Entomological Research*, 45(3), 539–551. <https://doi.org/10.1017/s0007485300029618>
- Edgecombe, G., Richter, S., & Wilson, G. (2003). The mandibular gnathal edges: Homologous structures across Mandibulata? *African Invertebrates*, 44, 115–135.
- EIela, S. A., ElSayed, W., & Nakamura, K. (2010). Mandibular structure, gut contents analysis and feeding group of orthopteran species collected from different habitats of Satoyama area within Kanazawa City, Japan. *The Journal of Threatened Taxa*, 02(05), 849–857. <https://doi.org/10.11609/jott.02346.849-57>
- Evans, A. R., Wilson, G. P., Fortelius, M., & Jernvall, J. (2007). High-level similarity of dentitions in carnivorans and rodents. *Nature*, 445(7123), 78–81. <https://doi.org/10.1038/nature05433>
- Feilich, K. L., & López-Fernández, H. (2019). When does form reflect function? Acknowledging and supporting ecomorphological assumptions. *Integrative and Comparative Biology*, 59(2), 358–370. <https://doi.org/10.1093/icb/icz070>

- Firmat, C., Rodrigues, H. G., Renaud, S., Hutterer, R., Garcia-Talavera, F., & Michaux, J. (2010). Mandible morphology, dental microwear, and diet of the extinct giant rats *Canariomys* (Rodentia: Murinae) of the Canary Islands (Spain). *Biological Journal of the Linnean Society*, 101, 28–40.
- Gangwere, S. K. (1961). A monograph on food selection in Orthoptera. *Transactions of the American Entomological Society*, 1890–87, 67–230.
- Gangwere, S. K. (1965). The structural adaptations of mouthparts in Orthoptera and Allis. *Revista española de entomología*, 41(1), 67–85.
- Gangwere, S. K. (1966). Relationships between the mandibles, feeding behavior, and damage inflicted on plants by the feeding of certain Acridids (Orthoptera). *Michigan Entomology*, 1, 13–16.
- Gangwere, S. K., McKinney, J. C., Ernemann, M. A., & Bland, R. G. (1998). Food selection and feeding behavior in selected Acridoidea (Insecta: Orthoptera) of the Canary Islands, Spain. *Journal of Orthoptera Research*, 7, 1–21. <https://doi.org/10.2307/3503485>
- Gangwere, S. K., & Spiller, D. O. (1995). Food Selection and feeding behavior in selected orthoptera sen. lat. of the Balearic Islands, Spain. *Journal of Orthoptera Research*, 4, 147–160. <https://doi.org/10.2307/3503470>
- Graham, C. H., Storch, D., & Machac, A. (2018). Phylogenetic scale in ecology and evolution. *Global Ecology and Biogeography*, 27(2), 175–187. <https://doi.org/10.1111/geb.12686>
- Gronenberg, W., Paul, J., Just, S., & Hölldobler, B. (1997). Mandible muscle fibers in ants: Fast or powerful? *Cell and Tissue Research*, 289(2), 347–361. <https://doi.org/10.1007/s004410050882>
- Grossnickle, D. M. (2020). Feeding ecology has a stronger evolutionary influence on functional morphology than on body mass in mammals. *Evolution*, 74(3), 610–628. <https://doi.org/10.1111/evo.13929>
- Harzing, A. W. (2007). Publish or Perish.
- Herrel, A., Podos, J., Huber, S. K., & Hendry, A. P. (2005a). Bite performance and morphology in a population of Darwin's finches: Implications for the evolution of beak shape. *Functional Ecology*, 19(1), 43–48. <https://doi.org/10.1111/j.0269-8463.2005.00923.x>
- Herrel, A., Podos, J., Huber, S. K., & Hendry, A. P. (2005b). Evolution of bite force in Darwin's finches: A key role for head width. *Journal of Evolutionary Biology*, 18(3), 669–675. <https://doi.org/10.1111/j.1420-9101.2004.00857.x>
- Herrel, A., Podos, J., Vanhooydonck, B., & Hendry, A. P. (2009). Force-velocity trade-off in Darwin's finch jaw function: A biomechanical basis for ecological speciation? *Functional Ecology*, 23(1), 119–125. <https://doi.org/10.1111/j.1365-2435.2008.01494.x>
- Hess, R. 2010. *Blender foundations: The essential guide to learning blender 2.6*. Focal Press.
- Hochuli, D. F. (1996). The ecology of plant/insect interactions: Implications of digestive strategy for feeding by phytophagous insects. *Oikos*, 75(1), 133. <https://doi.org/10.2307/3546331>
- Hudson, G. B. (1945). A study of the tentorium in some orthopteroid Hexapoda. *Journal of the Entomological Society of Southern Africa*, 8, 71–90.
- Ingrisch, S., & Köhler, G. (1998). Die Heuschrecken Mitteleuropas. *Westarp Wissenschaften* (pp. 472).
- Isely, F. B. (1944). Correlation between mandibular morphology and food specificity in Grasshoppers I. *Annals of the Entomological Society of America*, 37(1), 47–67. <https://doi.org/10.1093/aesa/37.1.47>
- Jablonski, D. (2007). Scale and hierarchy in Macroevolution. *Palaeontology*, 50(1), 87–109. <https://doi.org/10.1111/j.1475-4983.2006.00615.x>
- Kaltenbach, A. (1990). The predatory Saginae. *The Tettigoniidae Biology, Systematics and Evolution*, 1, 280–320.
- Kang, L., Gan, Y., & Li, S. (1999). The structural adaptation of mandibles and food specificity in Grasshoppers on Inner Mongolian Grasslands. *Journal of Orthoptera Research*, 257(8), 257. <https://doi.org/10.2307/3503442>
- Kaufmann, T. (1965). Biological Studies on Some Bavarian Acridoidea (Orthoptera), with Special Reference to Their Feeding Habits. *Annals of the Entomological Society of America*, 58(6), 791–801. <https://doi.org/10.1093/aesa/58.6.791>
- Khokhriakov, I., Beckmann, F., & Lottermoser, L. (2017). *Integrated control system environment for high-throughput tomography*. SPIE.
- Kienle, S. S., & Berta, A. (2016). The better to eat you with: The comparative feeding morphology of phocid seals (Pinnipedia, Phocidae). *Journal of Anatomy*, 228(3), 396–413. <https://doi.org/10.1111/joa.12410>
- Komatsu, T., & Maruyama, M. (2016). Taxonomic recovery of the ant cricket *Myrmecophilus albicinctus* from *M. americanus* (Orthoptera, Myrmecophilidae). *ZooKeys*, 589, 97–106. <https://doi.org/10.3897/zookeys.589.7739>
- Kuřavová, K., Hajduková, L., & Kočárek, P. (2014). Age-related mandible abrasion in the groundhopper *Tetrix tenuicornis* (Tetrigidae, Orthoptera). *Arthropod Structure*, 43(3), 187–192. <https://doi.org/10.1016/j.asd.2014.02.002>
- Kuravova, K., & Kocarek, P. (2016). Mandibular morphology and dietary preferences in two pygmy molecrickets of the genus *Xya* (Orthoptera: Tridactylidae). *Turkish Journal of Zoology*, 40, 720–728.
- Kuřavová, K., Šipoš, J., Rodzaj, A. W., Kahar, R. S., & Kočárek, P. (2017). Feeding patterns in tropical groundhoppers (Tetrigidae): A case of phylogenetic dietary conservatism in a basal group of Caelifera. *Zoological Journal of the Linnean Society*, 179, 291–302.
- Le Gall, M., & Behmer, S. T. (2014). Effects of protein and carbohydrate on an insect Herbivore: The vista from a fitness landscape. *Integrative and Comparative Biology*, 54(5), 942–954. <https://doi.org/10.1093/icb/ucu102>
- Lupu, G. (2007). Carnivorous and omnivorous species of Orthoptera order recorded in the Danube Delta Biosphere Reserve. *Scientific Annals of the Danube Delta Institute*, 13, 55–58.
- Metzger, K. A., & Herrel, A. (2005). Correlations between lizard cranial shape and diet: A quantitative, phylogenetically informed analysis. *Biological Journal of the Linnean Society*, 86(4), 433–466. <https://doi.org/10.1111/j.1095-8312.2005.00546.x>
- Meyers, J. J., Herrel, A., & Nishikawa, K. C. (2006). Morphological correlates of ant eating in horned lizards (Phrynosoma). *Biological Journal of the Linnean Society*, 89(1), 13–24. <https://doi.org/10.1111/j.1095-8312.2006.00654.x>
- Missagia, R. V., Patterson, B. D., Krentzel, D., & Perini, F. A. (2021). Insectivory leads to functional convergence in a group of Neotropical rodents. *Journal of Evolutionary Biology*, 34(2), 391–402. <https://doi.org/10.1111/jeb.13748>
- Montaña, C. G., & Winemiller, K. O. (2013). Evolutionary convergence in Neotropical cichlids and Nearctic centrarchids: Evidence from morphology, diet, and stable isotope analysis. *Biological Journal of the Linnean Society*, 109(1), 146–164. <https://doi.org/10.1111/bij.12021>
- Moosmann, J., Ershov, A., Weinhardt, V., Baumbach, T., Prasad, M. S., LaBonne, C., Xiao, X., Kashef, J., & Hofmann, R. (2014). Time-lapse X-ray phase-contrast microtomography for in vivo imaging and analysis of morphogenesis. *Nature Protocols*, 9(2), 294–304. <https://doi.org/10.1038/nprot.2014.033>
- Morales-García, N. M., Gill, P. G., Janis, C. M., & Rayfield, E. J. 2021. Jaw shape and mechanical advantage are indicative of diet in Mesozoic mammals. *Commun. Biol.* 4, 1–14.
- Morris, P. J. R., Cobb, S. N. F., & Cox, P. G. (2018). Convergent evolution in the Euarchontoglires. *Biology Letters*, 14(8), 20180366. <https://doi.org/10.1098/rsbl.2018.0366>
- Navalón, G., Bright, J. A., Marugán-Lobón, J., & Rayfield, E. J. (2019). The evolutionary relationship among beak shape, mechanical advantage, and feeding ecology in modern birds. *Evolution*, 73(3), 422–435. <https://doi.org/10.1111/evo.13655>
- Nogueira, M. R., Peracchi, A. L., & Monteiro, L. R. (2009). Morphological correlates of bite force and diet in the skull and mandible

- of phyllostomid bats. *Functional Ecology*, 23(4), 715–723. <https://doi.org/10.1111/j.1365-2435.2009.01549.x>
- Olsen, A. M. (2017). Feeding ecology is the primary driver of beak shape diversification in waterfowl. *Functional Ecology*, 31(10), 1985–1995. <https://doi.org/10.1111/1365-2435.12890>
- Otte, D., & Joern, A. (1976). On feeding patterns in desert grasshoppers and the evolution of specialized diets. *Journal of the Academy of Natural Sciences of Philadelphia*, 128, 89–126.
- Paradis, E., & Schliep, K. (2019). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35(3), 526–528. <https://doi.org/10.1093/bioinformatics/bty633>
- Patterson, B. D. (1983). Grasshopper mandibles and the niche variation hypothesis. *Evolution*, 37(2), 375–388. <https://doi.org/10.1111/j.1558-5646.1983.tb05546.x>
- Patterson, B. D. (1984). Correlation between mandibular morphology and specific diet of some desert Grassland Acrididae (Orthoptera). *American Midland Naturalist*, 111(2), 296–303. <https://doi.org/10.2307/2425324>
- Prevosti, F. J., Turazzini, G. F., Ercoli, M. D., & Hingst-Zaher, E. (2012). Mandible shape in marsupial and placental carnivorous mammals: A morphological comparative study using geometric morphometrics. *Zoological Journal of the Linnean Society*, 164(4), 836–855. <https://doi.org/10.1111/j.1096-3642.2011.00785.x>
- Püffel, F., Pouget, A., Liu, X., Zuber, M., Kamp, T. van de, Roces, F., & Labonte, D. (2021). Morphological determinants of bite force capacity in insects: A biomechanical analysis of polymorphic leaf-cutter ants. *Journal of the Royal Society Interface*, 18, 20210424.
- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Richardson, M. L., Reagel, P. F., Mitchell, R. F., & Whitman, D. W. (2012). Opportunistic Carnivory by Romalea microptera (Orthoptera: Acrididae). *Annals of the Entomological Society of America*, 105(1), 28–35. <https://doi.org/10.1603/an11057>
- Richter, S., Edgecombe, G. D., & Wilson, G. D. F. (2002). The lacinia mobilis and Similar Structures: A valuable character in arthropod phylogenetics? *Journal of Comparative Zoology*, 241, 339–361.
- Rühr, P. T., & Blanke, A. (2022). forceX and forceR: A mobile setup and r package to measure and analyse a wide range of animal closing forces. *Methods in Ecology and Evolution*, 13(9), 1938–1948. <https://doi.org/10.1111/2041-210x.13909>
- Rühr, P. T., van de Kamp, T., Faragó, T., Hammel, J. U., Wilde, F., Borissova, E., Edel, C., Frenzel, M., Baumbach, T., & Blanke, A. (2021). Juvenile ecology drives adult morphology in two insect orders. *Proceedings of the Royal Society B: Biological Sciences*, 288, 20210616.
- Samways, M. J., Osborn, R., & Saunders, T. L. (1997). Mandible form relative to the main food type in Ladybirds (Coleoptera: Coccinellidae). *Biocontrol Science and Technology*, 7(2), 275–286. <https://doi.org/10.1080/09583159730974>
- Sanson, G. (2006). The biomechanics of browsing and grazing. *American Journal of Botany*, 93(10), 1531–1545. <https://doi.org/10.3732/ajb.93.10.1531>
- Santana, S. E., Grossnickle, D. M., Sadier, A., Patterson, E., & Sears, K. E. (2022). Bar dentitions: A model system for studies at the interface of development, biomechanics, and evolution. *Integrative and Comparative Biology*, 62(3), 762–773. <https://doi.org/10.1093/icb/icac042>
- Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B., Tinevez, J.-Y., White, D. J., Hartenstein, V., Eliceiri, K., Tomancak P., & Cardona, A. 2012. Fiji: An open-source platform for biological-image analysis. *Nat. Methods*, 9, 676–682.
- Schoonhoven, L. M., Van Loon J. J., & Dicke M. (2005). *Insect-plant biology*. Oxford University Press on Demand.
- Smith, M. R. (2019). *TreeTools: Create, modify and analyse phylogenetic trees*. Comprehensive R Archive Network.
- Smith, T.R., & Capinera, J.L. (2005). Mandibular morphology of some floridian grasshoppers (Orthoptera: Acrididae). *Florida Entomologist*, 88(2), 204–207. [https://doi.org/10.1653/0015-4040\(2005\)088\[0204:mmosfg\]2.0.co;2](https://doi.org/10.1653/0015-4040(2005)088[0204:mmosfg]2.0.co;2)
- Snodgrass, R. (1935). *Principles of insect morphology*. McGraw-Hill Publishing Co.
- Song, H., Béthoux, O., Shin, S., Donath, A., Letsch, H., Liu, S., McKenna, D. D., Meng, G., Misof, B., Podsiadlowski, L., Zhou, X., Wipfler, B., & Simon, S. (2020). Phylogenomic analysis sheds light on the evolutionary pathways towards acoustic communication in Orthoptera. *Nature Communications*, 11(1), 4939. <https://doi.org/10.1038/s41467-020-18739-4>
- Soons, J., Genbrugge, A., Podos, J., Adriaens, D., Aerts, P., Dirckx, J., & Herrel, A. (2015). Is beak morphology in Darwin's finches tuned to loading demands? *PLoS ONE*, 10(6), e0129479. <https://doi.org/10.1371/journal.pone.0129479>
- Soons, J., Herrel, A., Genbrugge, A., Aerts, P., Podos, J., Adriaens, D., Witte, Y. de, Jacobs, P., & Dirckx, J. (2010). Mechanical stress, fracture risk and beak evolution in Darwin's ground finches (Geospiza). *Philosophical Transactions of the Royal Society B - Journals*, 365(1543), 1093–1098. <https://doi.org/10.1098/rstb.2009.0280>
- Stampanoni, M., Grosio A., Isenegger, A., Mikuljan, G., Chen, Q., Bertrand, A., Henein, S., Betemps, R., Frommherz, U., Böhrer, P., Meister, D., Lange, M., & Abela, R. 2006. Trends in synchrotron-based tomographic imaging: The SLS experience. In *Bonse* (Eds.), *Developments in X-Ray tomography V* (pp. 193–206). Ulrich Proceedings of the SPIE. <https://doi.org/10.1117/12.679497>
- Stayton, C. T. (2006). Testing hypotheses of convergence with multivariate data: Morphological and functional convergence among herbivorous lizards. *Evolution*, 60(4), 824–841.
- Stephens, D. W., & Krebs, J. R. (2019). *Foraging theory*. Princeton University Press.
- Tan, M. K., Artchwakom, T., Wahab, R. A., Lee, C. -Y., Belabut, D. M., & Tan, H. T. W. (2017). Overlooked flower-visiting Orthoptera in Southeast Asia. *Journal of Orthoptera Research*, 26, 143–153.
- Uvarov, S. B. 1966. *Grasshoppers and locusts. A handbook of general acridology. Volume I. Anatomy, physiology, development, phase polymorphism, introduction to taxonomy*. Cambridge University Press.
- Wainwright, P., Carroll, A. M., Collar, D. C., Day, S. W., Higham, T. E., & Holzman, R. A. (2007). Suction feeding mechanics, performance, and diversity in fishes. *Integrative and Comparative Biology*, 47(1), 96–106. <https://doi.org/10.1093/icb/icm032>
- Wainwright, P. C., & Richard, B. A. (1995). Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes*, 44, 97–113.
- Wake, D. B., Roth, G., & Wake, M. H. (1983). On the problem of stasis in organismal evolution. *Journal of Theoretical Biology*, 101(2), 211–224. [https://doi.org/10.1016/0022-5193\(83\)90335-1](https://doi.org/10.1016/0022-5193(83)90335-1)
- Weihmann, T., Reinhardt, L., Weißing, K., Siebert, T., & Wipfler, B. (2015). Fast and powerful: Biomechanics and bite forces of the mandibles in the American Cockroach *Periplaneta Americana*. *PLoS ONE*, 10(11), e0141226. <https://doi.org/10.1371/journal.pone.0141226>
- Westneat, M. W. (2004). Evolution of levers and linkages in the feeding mechanisms of fishes I. *Integrative and Comparative Biology*, 44(5), 378–389. <https://doi.org/10.1093/icb/44.5.378>
- Wetterer, J., & Hugel, S. (2008). Worldwide spread of the ant cricket *Myrmecophilus americanus*, a symbiont of the longhorn crazy ant, *Paratrechina longicornis*. *Sociobiology*, 52, 157–165.
- Wheater, C. P., & Evans, M. E. G. (1989). The mandibular forces and pressures of some predacious Coleoptera. *Journal of Insect Physiology*, 35(11), 815–820. [https://doi.org/10.1016/0022-1910\(89\)90096-6](https://doi.org/10.1016/0022-1910(89)90096-6)
- Wilde, F., Ogurreck, M., Greving, I., Hammel, J. U., Beckmann, F., Hipp, A., Lottermoser, L., Khokhriakov, I., Lytaev, P., Dose, T., Burmester, H., Müller, M., & Schreyer, A. (2016). Micro-CT at the imaging beamline P05 at PETRA III. *AIP Conference Proceedings*, 1741, 030035.
- Yushkevich, P. A., Piven, J., Hazlett, H. C., Smith, R. G., Ho, S., Gee, J. C., & Gerig, G. (2006). User-guided 3D active contour segmentation of anatomical structures: Significantly improved efficiency and reliability. *Neuroimage*, 31(3), 1116–1128. <https://doi.org/10.1016/j.neuroimage.2006.01.015>
- Zelditch, M. L., Li, J., & Swiderski, D. L. (2020). Stasis of functionally versatile specialists. *Evolution*, 74(7), 1356–1377. <https://doi.org/10.1111/evo.13956>