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Mandible Strike Kinematics of the Trap-Jaw Ant Genus *Anochetus* Mayr (Hymenoptera: Formicidae)

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1 **Abstract:** High-speed power-amplification mechanisms are common throughout the animal
2 kingdom. In ants, power-amplified trap-jaw mandibles have evolved independently at least four
3 times, including once in the subfamily Ponerinae which contains the sister genera *Odontomachus*
4 and *Anochetus*. In *Odontomachus*, mandible strikes have been relatively well described and can
5 occur in less than 0.15ms and reach speeds of over 60m/s. In contrast, the kinematics of
6 mandible strikes have not been examined in *Anochetus*, whose species are smaller and
7 morphologically distinct from *Odontomachus*. In this study, we describe the mandible strike
8 kinematics of four species of *Anochetus* representative of the morphological, phylogenetic, and
9 size diversity present within the genus. We also compare their strikes to two representative
10 species of *Odontomachus*. We found that two species, *Anochetus targionii* and *Anochetus*
11 *paripungens*, have mandible strikes that overall closely resemble those found in *Odontomachus*,
12 reaching a mean maximum rotational velocity and acceleration of around 3.7×10^4 rad/s and
13 8.5×10^8 rad/s², respectively. This performance is consistent with predictions based on body size
14 scaling relationships described for *Odontomachus*. In contrast, *Anochetus horridus* and
15 *Anochetus emarginatus* have slower strikes relative to the other species of *Anochetus* and
16 *Odontomachus*, reaching mean maximum rotational velocity and acceleration of around 1.3×10^4
17 rad/s and, 2×10^8 rad/s², respectively. This variation in strike performance among species of
18 *Anochetus* likely reflects differences in evolutionary history, physiology, and natural history
19 among species.

20
21 **Keywords:** Comparative biomechanics, catapult mechanism, functional morphology, power-
22 amplification, mandible strike, Formicidae, kinematics

23 24 **Introduction**

25 Speed is an important trait for the success of many animals. The ability to move quickly to evade
26 predators or capture prey is a significant selection pressure. How fast animals can move depends,
27 in part, on how quickly they can contract muscles to accelerate their limbs. For small animals
28 such as arthropods, the distance they move their limbs is short, requiring higher acceleration
29 values to obtain peak velocities similar to a larger animal (Alexander, 1988). Additionally,
30 muscle fibers are limited by how quickly they can contract (Ellington, 1985; Gronenberg, 1996a;
31 Askew & Marsh, 2002), reducing the ability of organisms to achieve high accelerations via direct

1 muscle contraction. To overcome these constraints, many animals have evolved catapult
2 mechanisms that use a combination of springs, levers, and latches to store and transfer elastic
3 and mechanical energy, allowing them to accelerate their limbs more quickly than possible
4 through muscle contraction alone (Gronenberg, 1996a; Patek *et al.*, 2015). These power
5 amplification or impulse mechanisms have evolved repeatedly in a diverse range of taxa, and
6 result in some of the fastest movements known in the animal kingdom (Gronenberg, 1996a;
7 Patek *et al.*, 2015).

8 In ants, power-amplifying “trap-jaw” mandibles have evolved independently for prey
9 capture at least four times across three subfamilies (Larabee & Suarez, 2014) and possibly
10 repeatedly in a single myrmicine genus (Ward *et al.*, 2014). While each group has different
11 morphological adaptations to store and amplify energy, most have structures that perform similar
12 functions (Gronenberg *et al.*, 1993; Gronenberg & Tautz, 1994; Gronenberg, 1996b; Gronenberg
13 & Ehmer, 1996; Gronenberg *et al.*, 1998; Just & Gronenberg, 1999; Larabee *et al.*, 2017).
14 Elongated mandibles are locked open with a latch mechanism, allowing elastic strain energy to
15 be stored within the head capsule as enlarged mandible closer (adductor) muscles contract. When
16 inter-mandibular mechanosensory trigger hairs are stimulated, the latch is released by the
17 contraction of fast-twitch muscles, allowing the mandibles to close extremely rapidly (Patek. *et*
18 *al.*, 2006; Spagna *et al.*, 2008; Larabee *et al.*, 2017).

19 Most research on the functional morphology and strike kinematics of trap-jaw ants has
20 focused on the genus *Odontomachus* Latreille. In this genus, the mandibles are held open by a
21 latch formed through interactions between the basal condyle of the mandibles and the mandible
22 sockets (Gronenberg *et al.*, 1993). Elastic energy for the mandible strike is likely stored, in part,
23 within enlarged mandibular apodemes, although the exact location of energy storage remains
24 unknown (Gronenberg *et al.*, 1993). Strikes are stimulated by contact with trigger hairs on the
25 mandibles that connect to “giant” sensory neurons (Gronenberg & Tautz, 1994). During a strike,
26 *Odontomachus* mandibles reach peak maximum velocities between 35 and 67 m/s, accelerate
27 tens to hundreds of thousands times faster than gravity, and generate forces over 300 times the
28 mass of an individual ant (Patek *et al.*, 2006; Spagna *et al.*, 2008). Due to the high force-to-body
29 mass ratio of these mechanisms, some *Odontomachus* species use their mandibles to repel small
30 intruders out of their nests (Carlin & Gladstein, 1989), and to perform horizontal or vertical

1 jumps, which can increase survivorship during encounters with predators such as antlions (Patek
2 *et al.*, 2006; Spagna *et al.*, 2009; Larabee & Suarez, 2015).

3 *Anochetus* Mayr is the sister genus to *Odontomachus* and together they represent a single
4 evolutionary transition to power amplified mandibles within the subfamily Ponerinae (Larabee *et*
5 *al.*, 2016). Relative to *Odontomachus*, ants in the genus *Anochetus* are generally smaller, have a
6 distinct head morphology, and frequently ambush and sting their prey when hunting. In contrast,
7 *Odontomachus* species typically rely on the crushing force of their mandibles alone for prey
8 capture (Brown, 1976; Brown, 1978; De la Mora *et al.*, 2008). Performance of mandible strikes
9 is correlated with body size in *Odontomachus* (Spagna *et al.*, 2008), with smaller species
10 generally producing faster but less forceful strikes. While the performance properties of
11 *Anochetus* mandible strikes have never been quantified, they are likely to have similar scaling
12 relationships between performance and body size to species in the genus *Odontomachus*.

13 In this study, we describe the mandible strike kinematics of four species of *Anochetus*. In
14 addition to quantifying interspecific variation within *Anochetus*, we compare their strike
15 performance to two species of *Odontomachus*. While *Odontomachus* are generally larger than
16 *Anochetus*, one of our species (*A. emarginatus*) is similar in size to smaller *Odontomachus*
17 (Larabee *et al.*, 2016). We use these data to test the following hypotheses based on the scaling of
18 body size with performance seen in *Odontomachus*: 1) *Anochetus* mandibles will achieve higher
19 accelerations and velocities, and 2) *Anochetus* mandibles will generate less kinetic energy
20 relative to larger species of *Odontomachus*. We also used x-ray micro-tomography (microCT), a
21 method of visualizing three dimensional morphological structures (Friedrich *et al.*, 2014; Wipfler
22 *et al.*, 2016) to characterize the internal morphology of *Anochetus*'s trap-jaw mechanism.

23

24 **Materials and Methods**

25 ***Colony Collection and Maintenance***

26 We selected four species of *Anochetus* representative of the morphological, phylogenetic and
27 size diversity within the genus (Figure 1): two species, *A. horridus* and *A. emarginatus*, from the
28 *emarginatus* species group (Brown, 1976; Brown, 1978; clade F in Larabee *et al.*, 2016); one
29 species, *Anochetus targionii*, from the *mayri* species group (Brown, 1976; Brown, 1978; clade F
30 in Larabee *et al.*, 2016); and one species, *Anochetus paripungens*, from the *rectangularis* species
31 group (Brown, 1976; Brown, 1978; clade G in Larabee *et al.*, 2016). We compared the

1 kinematics of *Anochetus* to two species of *Odontomachus* chosen to represent the large variation
2 in size seen in this genus - *Odontomachus chelifer* (the largest; Figure 1 E) and *O. ruginodis* (one
3 of the smallest; Figure 1 F). The kinematics of *O. ruginodis* mandible strikes were originally
4 described in Spagna *et al.* (2008); videos recorded for that study were reanalyzed using the
5 methods described below.

7 ***Filming and Video Analysis***

8 We filmed mandible strikes with a Phantom V9.1 high speed camera (Vision Research Co.,
9 Wayne, NJ) connected to a Zeiss SteREO Discovery V20 Microscope (Carl Zeiss Inc.,
10 Oberkochen, Germany). Three individuals of *A. horridus* were filmed using a Phantom Miro eX4
11 camera (Vision Research Co., Wayne, NJ) instead of the V9.1. Individual ants were restrained by
12 attaching a size three insect pin (Bioquip, Rancho Dominguez CA) to the vertex of their head
13 with utility wax (Kerr Laboratory Products, Orange, CA). This pin was placed in a custom
14 micromanipulator to position the ant's mandibles into frame prior to striking. Strikes were
15 stimulated by either blowing on the ant or touching the trigger hairs / antennae with an insect pin.
16 Videos were filmed at a rate of 80,000 to 100,000 frames per second (the three *A. horridus*
17 filmed with the Miro eX4 were filmed at 58,823 fps). We recorded between three and five
18 individuals for each species, and between four and twenty strikes per individual (Table 1). After
19 recording, each ant was preserved in a -20°C freezer for at least 24 hours. Within one week of
20 filming, the mass of each ant was measured with a UMX2 ultra microbalance (Mettler Toledo,
21 Columbus, OH). Ants were then imaged using a Leica M205 C stereo microscope (467 nm
22 resolution) attached to a five-megapixel Leica DFC 425 digital microscope camera, and the head
23 width, head length, and mandible lengths measured. The mandibles were then removed and
24 weighed individually using the microbalance.

25 To digitize mandibles strikes, we tracked the tips of each mandible in each video in
26 MATLAB (2014a) using a custom script taken from Spagna *et al.* (2008). The cumulative
27 displacement of the mandibles was then calculated trigonometrically from the x-y coordinates of
28 the mandible tips generated by this script. These values were then exported to R (ver3.3.3) where
29 the cumulative angular displacement was smoothed using a quintic spline via the penalized
30 smoothing splines package (pspline). Instantaneous rotational velocity and rotational acceleration
31 were calculated by taking the first and second derivatives of displacement, respectively, and used

1 to determine the maximum value for each variable. Maximum linear velocity and acceleration
 2 were calculated by multiplying the maximum rotational velocity and acceleration by the length
 3 of the mandible. Rotational kinetic energy (K) was calculated by modeling each mandible as a
 4 thin rod of uniform density rotating about one end, using the equation:

$$K = \frac{1}{6}mr^2w^2$$

5 Where m is the mandible mass, r is the mandible length, and w is the maximum rotational
 6 velocity. Maximum rotational kinetic energy and strike duration were used to estimate maximum
 7 power output (P) for each strike, using the equation:

$$P = \frac{K}{tm_a}$$

8 Where t is the duration of the strike and m_a is the estimated mass of the mandible closer muscle.
 9 This estimate assumes a combined mandible closer muscle mass equal to one fourth that of the
 10 ant's body mass based on the relationship between mandible closer's size and body mass in other
 11 odontomachine species (Larabee unpublished data) and is a conservative estimate of the
 12 maximum power output of the mechanism. Our goal in calculating power output is not to obtain
 13 absolute measurements for each species, but rather estimates that will allow us to determine if
 14 they are using a power amplification mechanism. Time delay between the release of each
 15 mandible during strikes was calculated by subtracting the frame number of the first mandible's
 16 release from the frame number of the second, and dividing the result by the frame rate.

18 **MicroCT**

19 To examine the internal arrangement of head musculature in *Anochetus*, one individual of *A.*
 20 *horridus* was examined using X-ray microtomography (microCT). The ant was fixed in alcoholic
 21 Bouin's solution (Sigma Aldrich Corporation, Steinheim, Germany) for 24 hours, after which it
 22 was washed in 70% ethanol and dehydrated through an ethanol series (at least 20 min each at
 23 70%, 80%, 90%, 95%, and two changes of 100%). The ant was stained overnight in I2E (2%
 24 iodine w/v in 100% ethanol) to increase contrast of muscle tissue and then washed in 100%
 25 ethanol. To preserve microstructure of soft tissue, the specimen was critical point dried
 26 (AutoSamdri-931.GL Supercritical Point Dryer, Tousimis Research Corporation, Rockville,
 27 MD), and stored in a desiccator for approximately 24 hours before scanning. The head of the ant
 28 was placed in an appropriately sized pipette tip which was sealed with cotton and scanned using

1 an Xradia MicroXCT-400 scanner (Carl Zeiss, Oberkochen, Germany) set at 25kV voltage and
2 5W power with an exposure time of three seconds. 1441 images were taken at different rotations
3 spanning 180°. Tomographic reconstruction was performed in Xradia XMReconstructor 8.1.
4 Volume renderings and surface models were produced in Amira 5.6.0 (FEI, Hillsboro, OR) and
5 used to calculate the relative volumes that the mandible abductor, adductor, and trigger muscles
6 occupy in the head capsule.

7 8 **Statistics**

9 To compare the kinematic properties of mandible strikes between species, only the fastest of the
10 left and right mandible were used for each strike. Kinematic properties of mandible strikes were
11 compared between species using an ANOVA and post hoc Tukey HSD test with strikes treated
12 as a random effect nested within individuals. All stats were performed in R version 3.3.3 (CRAN
13 Studios) using the package nlme (Pinheiro *et al.*, 2017).

14 15 **Results**

16 The species of *Anochetus* examined in this study exhibit a five-fold difference in body size
17 between the smallest and largest species (Table 1; Figure 1). The mass-specific power of
18 *Anochetus* strikes ranged from 4.3×10^4 to 1.9×10^5 W/kg, with all species producing strikes that
19 have power output values far above those possible through direct muscle contraction alone
20 (Josephson, 1993). The kinematic profiles of *Anochetus targionii* and *A. paripungens* resemble
21 those of *O. ruginodis*, the smaller of the two *Odontomachus* species examined in this study
22 (Figure 2, black curves). *Anochetus horridus* and *A. emarginatus*, in contrast, have different
23 strike kinematic profiles from the other *Anochetus* species examined (Figure 2).

24 Mean strike durations for *A. horridus* (mean \pm SD: 0.251 ± 0.11 ms) and *A. emarginatus*
25 (0.22 ± 0.08 ms) are longer than *A. targionii* (0.101 ± 0.04 ms) and *A. paripungens* ($0.103 \pm$
26 0.04 ms) and are similar to strike durations recorded for the larger *O. ruginodis* (0.19 ± 0.09 ms)
27 and *O. chelifera* (0.24 ± 0.09 ms; Figure 3A). *Anochetus targionii* and *A. paripungens* both have
28 similar maximum rotational velocities ($37,000 \pm 3,000$ rad/s and $36,500 \pm 3,000$ rad/s,
29 respectively, rounded to the nearest five hundred) that are significantly higher than those seen in
30 *Odontomachus* ($31,500 \pm 6,000$ rad/s for *O. ruginodis* and $17,000 \pm 3,500$ rad/s for *O. chelifera*;
31 Figure 3B). *Anochetus horridus* and *A. emarginatus* have maximum rotational velocity values

1 that are similar to each other and are the slowest of all species examined in this study ($14,500 \pm$
 2 $3,000\text{rad/s}$ and $12,500 \pm 2,500\text{rad/s}$, respectively). Maximum rotational velocity is attained at
 3 approximately the same time for all species, but *A. horridus* and *A. emarginatus* accelerate and
 4 decelerate at a slower rate than other *Anochetus* and *O. ruginodis* (Figure 2B, C). Mean linear
 5 velocity was lowest in the mandible strikes of *A. horridus* ($19.9 \pm 4.3\text{m/s}$) and *A. emarginatus*
 6 ($23.6 \pm 4.2\text{m/s}$) and highest in *O. chelififer* ($40.0 \pm 7.5\text{m/s}$), with all other species obtaining
 7 intermediate maximum velocities (*A. targionii*: 29.4 ± 2.4 , *A. paripungens*: $29.0 \pm 2.7\text{m/s}$, *O.*
 8 *ruginodis*: 33.7 ± 6.3 ; Figure 3C).

9 Maximum rotational acceleration was lowest in *A. horridus* ($2.6 \times 10^8 \pm 8.4 \times 10^7\text{rad/s}^2$) and
 10 *A. emarginatus* ($1.8 \times 10^8 \pm 4.5 \times 10^7\text{rad/s}^2$), both of which were similar in value to the larger *O.*
 11 *chelififer* ($2.8 \times 10^8 \pm 8.1 \times 10^7\text{rad/s}^2$). All other species of *Anochetus* and *Odontomachus* examined
 12 obtained peak rotational accelerations two to three times that of *A. horridus* and *A. emarginatus*
 13 (*A. targionii*: $8.8 \times 10^8 \pm 1.1 \times 10^8\text{rad/s}^2$, *A. paripungens*: $8.5 \times 10^8 \pm 9.6 \times 10^7\text{rad/s}^2$, *O. ruginodis*:
 14 $7.0 \times 10^8 \pm 1.7 \times 10^8\text{rad/s}^2$; Figure 3D). Linear acceleration followed the same pattern, with *A.*
 15 *horridus* and *A. emarginatus* reaching the lowest peak linear acceleration ($3.5 \times 10^5 \pm 1.1 \times 10^5\text{m/s}^2$
 16 and $3.5 \times 10^5 \pm 8.3 \times 10^4\text{m/s}^2$, respectively) and all other species reaching peak linear accelerations
 17 approximately two times greater than *A. horridus* and *A. emarginatus* (*A. targionii*: $7.1 \times 10^5 \pm$
 18 $8.9 \times 10^4\text{m/s}^2$, *A. paripungens*: $6.8 \times 10^5 \pm 9.0 \times 10^4\text{m/s}^2$, *O. ruginodis*: $7.5 \times 10^5 \pm 1.9 \times 10^5\text{m/s}^2$, *O.*
 19 *chelififer*: $6.5 \times 10^5 \pm 1.8 \times 10^5\text{m/s}^2$; Figure 3E).

20 Maximum kinetic energy is positively associated with body size (Figure 3F). The
 21 smallest three *Anochetus* species had the lowest kinetic energy values (*A. targionii*: 2.0 ± 0.31
 22 μJ , *A. horridus*: $0.93 \pm 0.35 \mu\text{J}$, *A. paripungens*: $2.4 \pm 0.49 \mu\text{J}$), while *A. emarginatus* and *O.*
 23 *ruginodis*, the two medium sized species, had intermediate kinetic energy values (*A.*
 24 *emarginatus*: $7.1 \pm 2.3 \mu\text{J}$, *O. ruginodis*: $10 \pm 3.4 \mu\text{J}$). *Odontomachus chelififer*, the largest
 25 species, had the most energetic strike of all species examined ($100 \pm 35 \mu\text{J}$).

26 In most strikes examined the mandibles were not released simultaneously (*A. horridus*:
 27 40 of 41 strikes; *A. emarginatus*: 18 of 22 strikes; *A. targionii*: 14 of 17 strikes; *A. paripungens*:
 28 28 of 32 strikes); lag times between each mandible starting its acceleration averaged from 0.03 to
 29 0.12ms among species (Figure 4). This variation was significant (nested ANOVA, $F=6.7$, $df=5$,
 30 $p<0.001$) and paired comparisons revealed that *A. horridus* had longer lag times between
 31 mandibles than *A. targionii* and *A. paripungens* (Tukey HSD, $p<0.001$; other paired comparisons

1 $p > 0.05$). Maximum rotational and linear velocity did not differ significantly between the fastest
2 and slowest mandible within a strike for any species except *A. paripungens* (paired t-test,
3 rotational velocity: $t=6.9$, $df=62$, $p < 0.0001$; linear velocity: $t=4.3$, $df=62$, $p < 0.0001$). In *A.*
4 *targionii*, the first mandible to be released tended to reach a higher maximum rotational velocity
5 than the second (exact binomial test, number of successes =13, number of trials =14, $p=0.001$).
6 This was not the case for *A. paripungens* (exact binomial test, number of successes=9, number of
7 trials=28, $p=0.08$), *A. horridus* (exact binomial test, number of successes=14, number of
8 trials=31, $p=0.72$), or *A. emarginatus* (exact binomial test, number of successes=5, number of
9 trial=13, $p=0.58$). In these species, there is no relationship between which mandible is released
10 first and which obtains a higher velocity. As in *Odontomachus bauri* (Patek *et al.*, 2006),
11 *Anochetus* mandibles begin to decelerate before crossing the midline (Figure 4B, C).

12 The microCT scan of *A. horridus* revealed the mandible closer (adductor) muscles (AdM)
13 occupy most of the ventral and posterior sections of the head capsule and account for 20% of the
14 total head capsule volume (Figure 5). Contraction of these muscle when the mandibles are
15 locked open likely deforms the mandible apodemes, allowing elastic energy to be stored prior to
16 a strike. The trigger muscles (fAdM) are specialized sections of the mandible closer muscle that
17 consist of a small group of muscle fibers inserting on the mandible adductor apodeme
18 ventrolaterally and originating at the ventrolateral side of the postgenal section of the head
19 capsule. They occupy 0.17% of the head capsule volume and account for 0.9% of the volume of
20 the mandible adductor muscle. These fibers are likely fast twitch muscle fibers based on previous
21 studies of this muscle in other species of trap-jaw ants, and their contraction rotates the
22 mandibles out of their locked position and allows the mandibles to swing shut when the elastic
23 energy stored in the apodemes is released. The mandible opener (abductor) muscles (AbM) are
24 much smaller than their closer counterparts, occupying 2.5% of the total head capsule volume.
25 The mandible abductor muscles insert near the base of the mandible and attach to the medial
26 portion of the postgena in between the closer muscles. Contraction of these muscles opens the
27 mandibles and, if contracted far enough, locks the mandibles into the open position.

28 **Discussion**

29 ***Influence of body size and morphology on strike performance***

1 Our estimates of mass specific power output for each species exceed those possible through
2 muscle contraction alone (Josephson, 1993), confirming that *Anochetus* mandible strikes are
3 indeed power amplified. All species followed a pattern of increasingly energetic strikes with
4 larger body mass. This relationship is likely driven primarily by the increase in mandible mass as
5 body size increases. *Anochetus targionii* and *A. paripungens* mandible strikes closely resemble
6 those of *Odontomachus ruginodis*, although they consistently outperform *O. ruginodis* in many
7 aspects of their strike kinematics, on average obtaining higher peak rotational velocities and
8 accelerations. As both species are considerably smaller than *O. ruginodis*, these results are
9 consistent with the relationship between strike performance and body size found in
10 *Odontomachus* (Spagna *et al.*, 2008). In contrast, *A. horridus* and *A. emarginatus* (both from the
11 *emarginatus* species group) have similar mandible strikes that consistently underperform other
12 *Anochetus* and *Odontomachus* species, on average obtaining lower peak velocities and
13 accelerations. This relationship cannot be explained by relative differences in body size, as the
14 body mass of *A. horridus* is intermediate between *A. targionii* and *A. paripungens*, and one fifth
15 that of *A. emarginatus*. Other factors, such as similar head and mandible morphology, differing
16 life history strategies, or evolutionary constraints (Larabee *et al.*, 2016) may partially explain
17 differences in strike performance of *A. horridus* and *A. emarginatus* relative to other *Anochetus*
18 species.

19 Both *A. horridus* and *A. emarginatus* have relatively long, thin mandibles with respect to
20 their head width compared to the other *Anochetus* species. The average mandible length to head
21 width ratio is 1.32 and 1.12 for *A. horridus* and *A. emarginatus*, respectively, compared to 0.74
22 and 0.69 for *A. targionii* and *A. paripungens*. These differences in relative mandible length,
23 however, do not translate to differences in relative mass; the average mandible mass to body
24 mass ratio is 0.011 and 0.012 for *A. horridus* and *A. emarginatus* compared to 0.011 and 0.010
25 for *A. targionii* and *A. paripungens*. Having more elongate mandibles increases the minimum
26 distance needed between the ant and its prey for a strike to be successful, possibly increasing the
27 chances of successfully capturing prey. The reduced strike performance seen in *A. horridus* and
28 *A. emarginatus* may be an adaptation to prevent their mandibles from fracturing under the
29 increased stresses of a more forceful strike. The reduced strike performance in this species group
30 could therefore be the result of a trade-off between the probability of successfully capturing prey

1 and the amount of internal stress the mandible experiences when biting, an idea that warrants
2 future study.

3 ***Influence of physiology on strike performance***

4 Differences in muscle geometry and composition might explain differences in *A. horridus*
5 and *A. emarginatus* strike performance (see for example David *et al.*, 2016). However, the
6 muscle arrangement within the head capsule of *A. horridus* we report here is similar to that of *A.*
7 *graeffei* as described by Gronenberg & Ehmer (1996). In ants, muscle attachment angle and the
8 proportion of mandible closer muscle consisting of fast and slow twitch muscle fibers both
9 influence bite performance (Gronenberg *et al.*, 1997; Paul & Gronenberg, 1999). *Anochetus*
10 species do not possess fast twitch fibers in their mandible closer muscle and rely on stored elastic
11 energy (likely in the muscle apodeme or cuticle of the head) to provide the speed needed for their
12 strikes (Gronenberg & Ehmer, 1996). Differences in strike kinematics are thus likely not due to
13 underlying physiological differences in mandible closer muscle fibers between species, and
14 likely reflect differences in the material properties of the elastic energy storing component of the
15 mechanism. Determining the specific structures responsible for elastic energy storage within the
16 head capsule of *Odontomachus* and *Anochetus* prior to mandible release and examining species
17 level differences in the material properties of those structures may help to explain performance
18 differences in future studies.

19 The venom potency of trap-jaw ants is another aspect that may influence the mandible
20 strike performance. Both mandibles and venom are important features for prey capture and one
21 may be negatively correlated to the other. This is well illustrated in scorpions where scorpions
22 with more potent venom possess relatively slender claws (Van der Meijden *et al.*, 2010).
23 Although little data on the potency and the toxicity of ant venoms are available, both *A. horridus*
24 and *A. emarginatus* have unusual venom compositions that vastly contrast with venoms of
25 *Odontomachus* and other ponerine ants (Touchard *et al.*, 2015). Furthermore, the investigation of
26 the *A. emarginatus* venom resulted in the discovery of a novel family of neurotoxins that
27 reversibly paralyzes insects (Touchard *et al.*, 2016). Nevertheless, further venom investigations
28 extended to other *Anochetus* species are needed to support this hypothesis.

29 All four *Anochetus* exhibited a lag between the release of the first and second mandibles
30 during a strike. These lag times were similar to those observed in both *Odontomachus* species,
31 and there was no difference in performance between the first and second mandible to be released

1 with the exception of *A. targionii*, in which the first mandible to be released consistently reached
2 a higher maximum rotational velocity compared to the second. This contrasts with the findings
3 of Patek *et al.* (2006), who found that in *O. bauri* the second mandible to be released usually
4 reached a higher maximum velocity. A delay between mandibles in their release may be the
5 result of the time it takes to transmit a signal from sensory neurons to the corresponding motor
6 neurons (Patek *et al.*, 2006). In *A. graeffei*, the sensory neurons attached to trigger hairs do not
7 cross over to the opposing side of the subesophageal ganglion like they do in *Odontomachus*
8 (Gronenberg & Tautz, 1994; Gronenberg & Ehmer, 1996), suggesting that *Anochetus* should
9 have longer lag times compared to its sister genus. Our results are not consistent with this
10 pattern, possibly because the difference in lag time is so minute that we were not able to detect it
11 at the frame rates used in this study. It is also possible that this neuronal configuration is
12 restricted to certain species like *A. graeffei*, and in the species examined in this study crossing
13 over of the sensory trigger neurons does occur in a similar manner to *Odontomachus*. Future
14 studies using histological methods to examine how neurophysiology varies between species and
15 examining the performance of *A. graeffei* mandible strikes will be able to answer this question.
16 Lag time between mandible release is likely restricted to ponerine trap-jaw ants; in many
17 myrmicine trap-jaw ants (*Daceton*, *Orectognathus*, *Epopostruma*, and *Strumigenys*) the labrum
18 is modified to act as the latch, allowing the mandibles to be released simultaneously
19 (Gronenberg, 1996b).

20 In all species examined, both mandibles begin to decelerate before crossing the midline,
21 similar to *Odontomachus* mandible strikes (Patek *et al.*, 2006). This premature deceleration is
22 thought to be adaptive as it would prevent the mandibles from crashing into each other at full
23 force if the ant misses its target. Examining the kinematics of more phylogenetically independent
24 trap-jaw mechanisms (e.g. in other ant genera) will determine if this deceleration is a universal
25 characteristic of trap-jaw mandibles to reduce mandible wear or if it is restricted to certain taxa.
26 Most myrmicine trap-jaw ant genera, for example, are smaller bodied and likely generate less
27 force than ponerine trap-jaw ants which have more massive mandibles. Preventing mandibles
28 from colliding at full force may be less of an issue in smaller species.

29 Gronenberg & Ehmer (1996) described the trap-jaw mechanism in *A. graeffei*, noting that
30 the morphology, musculature, and neurophysiology of the mechanism are generally similar to
31 *Odontomachus* but differ in a few key characteristics. *Anochetus graeffei* has a trigger muscle

1 composed of fibers that attached indirectly to the mandible apodeme via short, thin filaments,
2 while in *Odontomachus* the trigger muscle fibers all attach to the apodeme directly (Gronenberg
3 & Ehmer, 1996). The mandible closer muscle of *A. graeffei* also contains more filament-attached
4 muscle fibers compared to the closer muscle in *Odontomachus* (Gronenberg & Ehmer, 1996).
5 This interspecific variation in physiology may account for some of the differences we see in
6 kinematics between *Anochetus* and *Odontomachus*. The microCT scan of *A. horridus* suggests
7 that muscle arrangement is likely consistent across species of *Anochetus* as muscle arrangement
8 in *A. horridus* closely resembles that of *A. graeffei* at the level of detail discernable via MicroCT
9 scans. More detailed studies comparing head capsule musculature and innervation at the cellular
10 level are needed to confirm this.

11 ***Influence of phylogeny on strike performance***

12 The confounding effect of shared evolutionary relatedness may also partially explain the
13 strike performance patterns we observed. *Anochetus horridus* and *A. emarginatus* are closely
14 related, both being members of the *emarginatus* species group (Larabee *et al.*, 2016). In contrast,
15 *A. targionii* and *A. paripungens* originate from the phylogenetically and geographically distinct
16 *mayri* and *rectangularis* species groups (distributed throughout the new and old world tropics
17 respectively; Larabee *et al.*, 2016). The strong similarities in their strike performance suggests
18 that morphology and body size are a large component of what determines strike performance in
19 this genus. However, the scope of this study does not allow for large scale comparisons of the
20 relative roles of phylogeny and morphology on strike performance.

21 ***Conclusion***

22 Our results suggest that phylogeny, physiology, morphology and natural history of trap-
23 jaw ant species may each play an important role in determining strike performance, although
24 understanding the relative role of each will require describing the kinematics of a larger number
25 of species in an explicit phylogenetic context. The repeated evolution of power amplified
26 mandibles in “trap-jaw” ants has been implicated in increased diversification rates and lineage
27 persistence (Pie & Tscha, 2009; Moreau & Bell, 2013; Larabee & Suarez, 2014), although this
28 idea has not yet been tested empirically. Future work should focus on describing the strike
29 performance of additional *Odontomachus* and *Anochetus* species, and combine this data with
30 phylogenetic (Larabee *et al.*, 2016), natural history (Brown, 1976; Brown, 1978), and
31 morphological information to examine the relative importance of these factors on strike

1 performance. Future studies that study the performance of other independent evolutions of trap-
2 jaw mechanisms, such as those in the subfamily Myrmecinae, will also shed light on which
3 kinematic properties of mandible strikes, if any, are universal to all trap-jaw ants.

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13 **Tables and Figures**

14 **Table 1.** Summary of *Anochetus* and *Odontomachus* measurements. Values in each column are
15 species means for a given trait \pm standard deviation. Species are listed by genus top to bottom by
16 increasing body mass. Mandible closer muscle mass is estimated by multiplying the total body
17 mass by 0.25. n, number of strikes; i, number of individuals. *Anochetus targionii* was collected
18 from leaf litter at the Villa Carmon Biological Research station in Peru (12.89474°S
19 71.403850°W) in August of 2013; *A. horridus* was collected from under a log and a colony of *A.*
20 *emarginatus* was collected from the roots of epiphytes at the Nouragues National Nature
21 Reserve, French Guiana (3.982411°S 52.563872°W) in March of 2016; *A. paripungens* was
22 collected from the soil in Humpty Doo, NT, Australia (12°34'21.37"S 131° 5'2.43"E) in April of
23 2010; *O. chelifer* was collected from Viçosa, Minas Gerais, Brazil (20°45'28"S 42°51'46"W) in
24 October of 2014; *O. ruginodis* was collected in October of 2005 from Archbold Biological
25 Station in Florida (27°11'5.61"N 81°20'19.64"W).

26
27 **Figure 1.** Representative images of study species displaying the morphological and size
28 variation present within *Anochetus* and *Odontomachus*. Images are to scale. A: *Anochetus*
29 *targionii*. B: *Anochetus horridus*. C: *Anochetus paripungens*. D: *Anochetus emarginatus*. E:
30 *Odontomachus chelifer*. F: *Odontomachus ruginodis*. All images are from Antweb.org.

1 **Figure 2.** Representative kinematic profiles of *Anochetus* mandible strikes. A: Angular
 2 displacement versus time. Points represent raw cumulative displacement data, curves are the
 3 spline fitted to those points. B: Angular velocity versus time. C: Angular acceleration versus
 4 time. D: representative frames of the *A. targionii* mandible strike described in A-C. E:
 5 representative frames from the video of the *A. emarginatus* mandible strike described in A-C.
 6 For panels A-C, species are indicated by color: Blue: *A. targionii*. Red: *A. horridus*. Purple: *A.*
 7 *emarginatus*. Black: *Odontomachus ruginodis*. *Odontomachus chelifer* closely resembles *O.*
 8 *ruginodis* and was not included in these graphs. Numbers between D and E indicate the time in
 9 milliseconds relative to the start of the mandible strike. Strikes depicted here are shown in
 10 Supplemental Videos 1-4.

11 **Figure 3.** Comparative mandible strike kinematics for *Anochetus* and *Odontomachus* species
 12 included in this study. Values shown are means of the maximum values for the left and right
 13 mandibles of each strike. Species are arranged by body mass, with the smallest species on the left
 14 and the largest species on the right. Error bars denote one standard deviation from the mean. All
 15 variables examined differed significantly between species (Nested ANOVA, $df=5$, $p<0.05$). Bars
 16 that share letters at their bases are not statistically distinguishable from one another based on a
 17 Tukey HSD test at the $p=0.05$ level. A: strike duration; B: maximum rotational velocity; C:
 18 maximum linear velocity; D: maximum rotational acceleration; E: maximum linear acceleration,
 19 F: maximum kinetic energy (*O. chelifer* excluded from graph due to large difference from other
 20 species).

21 **Figure 4.** Delay in mandible release (the time difference between when the first and second
 22 mandible begin to move) is present in all *Anochetus* spp. examined. A-C: graphs displaying
 23 kinematic profiles of the left and right mandibles during a representative *A. targionii* strike (the
 24 same strike depicted in Figure 2). Points represent the raw displacement data used to calculate
 25 the spline. Solid lines represent the left mandible, dotted lines represent the right mandible. A:
 26 angular displacement vs time; B: angular velocity vs time; C: angular acceleration vs time. D:
 27 Box and whisker plot depicting the time delay in mandible release between the left and right
 28 mandibles for all mandible strikes examined.

29 **Figure 5.** Reconstructed model of *Anochetus horridus* head capsule from a micro-CT scan. A:
 30 2D coronal section of head capsule. B: dorsal view, with the left side of the head capsule
 31 removed to show the arrangement of muscles relevant to the trap-jaw mechanism and the right

1 side showing the external features of the head. C: Lateral view cut away to display the same
2 structures labeled in A. AdM: mandible adductor muscle, AbM: mandible abductor muscle,
3 fAdM: fast twitch adductor muscle (trigger muscle), M: mandible and mandible apodeme. Voxel
4 size: $2.0 \mu\text{m}^3$.

5 **Supporting Information**

6 **Supplemental Video 1:** representative mandible strike of *Anochetus targionii*. The strike is the
7 same one depicted in figures 2A-D and 4A-C. The video was filmed at 80,000 frames per
8 second.

9
10 **Supplemental Video 2:** Representative mandible strike of *Anochetus horridus*. The strike is the
11 same one depicted in figure 2A-C. The video was filmed at 100,000 frames per second.

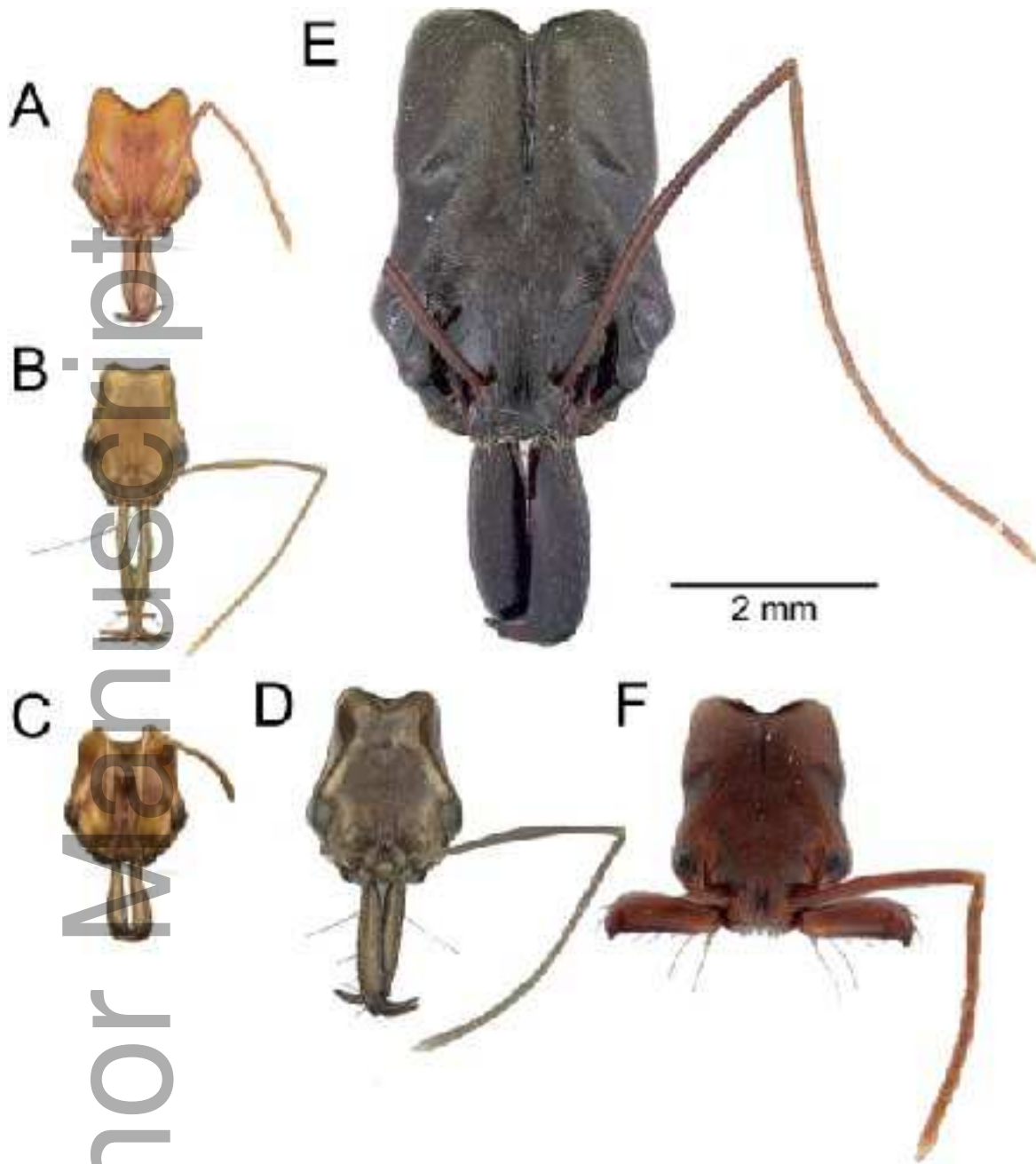
12
13 **Supplemental Video 3:** Representative mandible strike of *Anochetus paripungens*. The strike is
14 the same one depicted in figure 2A-C. The video was filmed at 88,888 frames per second.

15
16 **Supplemental Video 4:** Representative mandible strike of *Anochetus emarginatus*. The strike is
17 the same one depicted in figure 2A-C, E. The video was filmed at 80,000 frames per second.

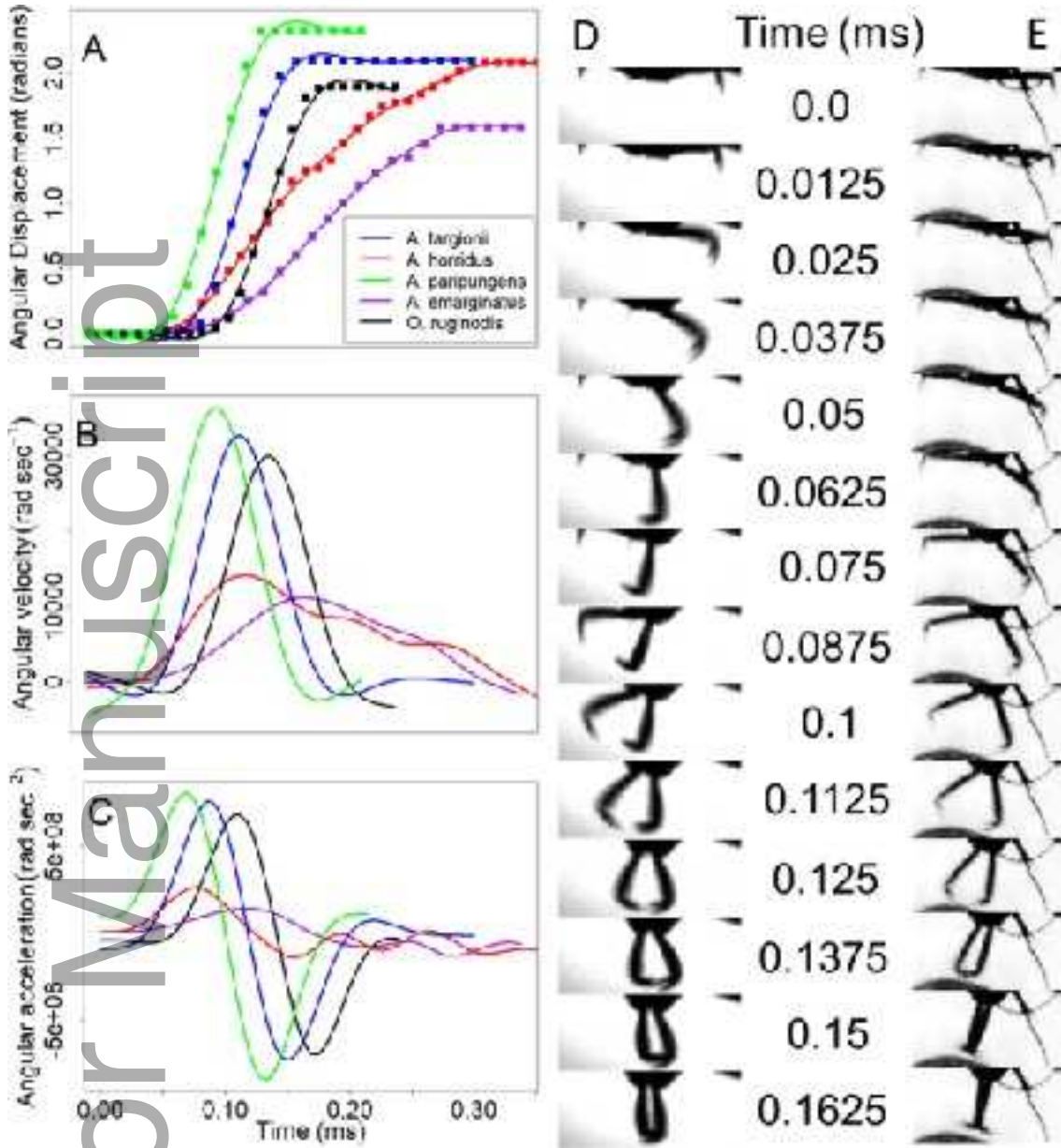
Table 1. Summary of *Anochetus* and *Odontomachus* measurements

Species	Locality	n	i	Head width (mm)	Body mass (mg)	Mandible length (mm)	Mandible mass (μ g)	Estimated closer muscle mass (mg)
<i>A. targionii</i>	Peru	17	4	1.07 \pm 0.013	1.17 \pm 0.001	0.80 \pm 0.01	13.65 \pm 0.64	0.29 \pm 0.02
<i>A. horridus</i>	French Guiana	41	5	1.03 \pm 0.015	1.39 \pm 0.09	1.33 \pm 0.03	12.99 \pm 6.3	0.35 \pm 0.02
<i>A. paripungens</i>	Australia	32	5	1.17 \pm 0.013	1.62 \pm 0.1	0.81 \pm 0.04	16.69 \pm 1.9	0.41 \pm 0.03
<i>A. emarginatus</i>	French Guiana	22	3	1.72 \pm 0.03	5.85 \pm 0.31	1.93 \pm 0.1	72.72 \pm 5.7	1.46 \pm 0.08
<i>O. ruginodis</i>	Florida, USA	15	5	1.62 \pm 0.1	5.66 \pm 0.05	1.08 \pm 0.03	52.33 \pm 6.9	1.42 \pm 0.13
<i>O. chelififer</i>	Brazil	15	3	2.68 \pm 0.17	30.1 \pm 5.6	2.34 \pm 0.13	366.33 \pm 93	7.53 \pm 1.4

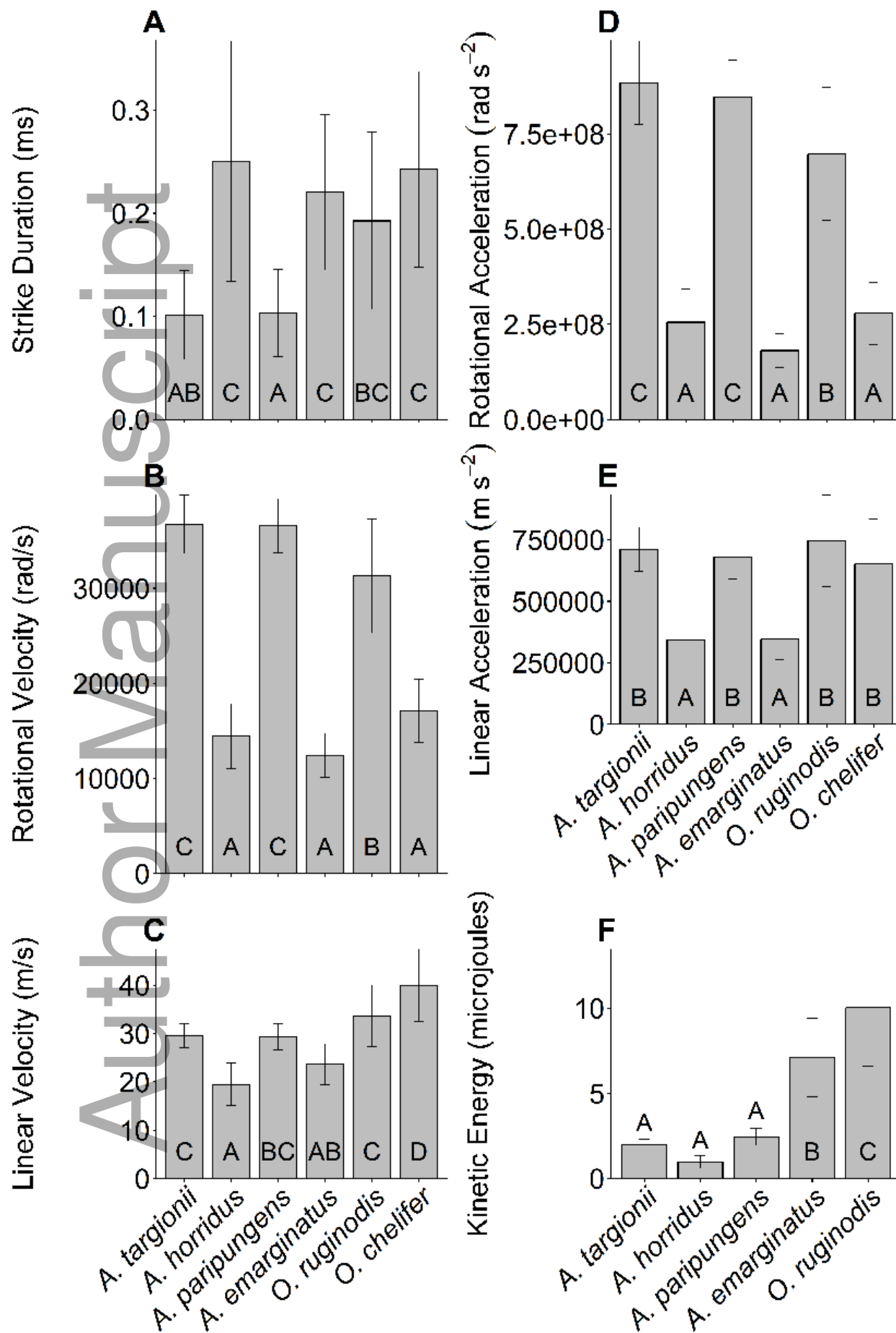
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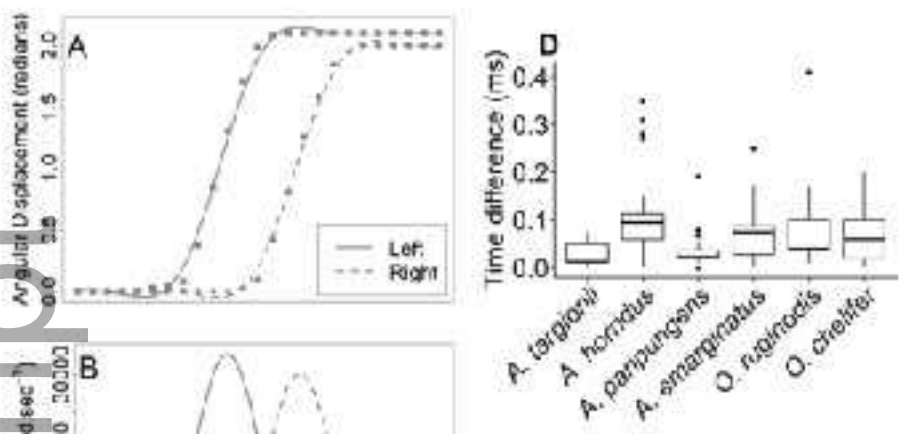
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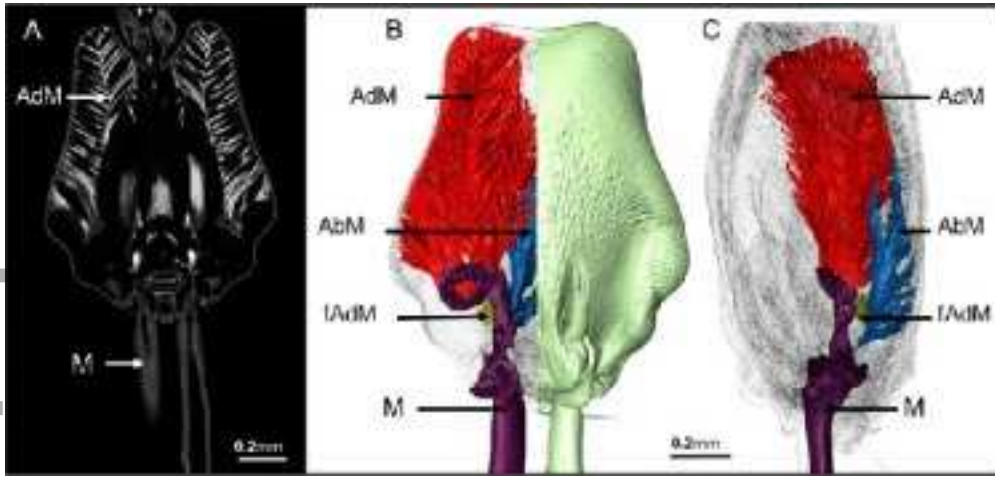
jzo_12580_f2.tif



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jzo_12580_f4.tif



jzo_12580_f5.tif