Title: A new avian feeding mechanism: Nectar suction by sunbirds

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Abstract

Nectarivory has independently evolved about 30 times within birds, yet little is known about the nectar-feeding mechanisms used by these very different types of birds. Multiple groups have relatively long bills and tube-like tongues hypothesized to be adaptations for nectar extraction. Sunbirds are the group that exhibits the largest bill and tongue convergence with the well-studied hummingbirds. Using microCT scans we characterize the details of the sunbird feeding apparatus and using high-speed video experiments we describe their nectar-feeding mechanism. Sunbirds collect nectar through their bi-cylindrical tongues reciprocating them around 9 times per second. Multiple lines of kinematic evidence and further fluid dynamics modeling indicate that sunbirds use a unique drinking mechanism not found in any other bird: suction feeding through the tongue. These findings are consistent across a wide sampling of sunbird species from the geographical extremes of their range, implying that these mechanics are shared by the entire Nectariniidae family. Our findings describe a heretofore undescribed

feeding mechanism in vertebrates, suction through the inside of the tongue, and sets the stage for investigating the physical limitations imposed by flowers and fluid dynamical effects of different nectar types in the flowers that sunbirds visit in nature.

Introduction

Suction is one of the most common feeding mechanisms for vertebrates that capture prey underwater (Wainwright et al., 2015). Although most terrestrial vertebrates use lapping or licking to drink, a few groups can suck from pools of liquid by creating a small oral opening connected to an expandable oral cavity (e.g., some mammals; Williams, 2019). The only vertebrate that has been reported to exhibit lingual pumping is a species of bat with lateral tongue grooves, where suction is not possible because these groove edges do not overlap resulting in a lack of seal (Tschapka et al., 2015). For vertebrates without lips or cheeks that allow suction, drinking or surface filter-feeding is a challenge. In birds, suction feeding is restricted to a few groups (e.g., filter feeders) and it is always accomplished by the tongue pushing liquid inside the oral cavity (Rico-Guevara et al., 2019). There are no known examples of vertebrates able to move liquids using active suction along the entire length of the tongue cavities, as in some nectar-feeding insects. Nectarivorous vertebrates would then be prime candidates for such a mechanism to evolve.

Nectarivory allows animals to consume high-caloric and easily digestible meals to fuel their energy-thirsty metabolisms. In return, these nectar-feeders provide pollination services to flowering plants that offer nectar as a reward. Nectar-feeding vertebrates exhibit a variety of sizes, ecologies, and evolutionary histories (Fleming and Muchhala, 2005). Within birds, specialized nectar feeding has evolved independently in approximately 30 clades (Pauw, 2019; Hewes et al. 2022). These groups have separately evolved to fill this specialized ecological

niche and, consequently, exhibit behavioral, functional, and morphological convergence (Stiles, 1981; Fleischer et al., 2008; Janeček et al., 2015; Cuban et al., 2022; Hewes et al. 2022). Some of the most notorious convergent traits evolved in their feeding apparati, such as bill and tongue similarities among taxa in distant geographic regions, for example hummingbirds (Trochilidae) in the Americas, sunbirds (Nectariniidae) in Africa and Asia, honeyeaters (Meliphagidae) in Australia, and honeycreepers (Thraupidae) in Hawaii (Skead, 1967; Paton and Collins, 1989; Downs, 2004; Hewes et al., 2022). Of the many nectar-feeding birds across the world, the feeding mechanisms used to ingest nectar are best known for hummingbirds (Rico-Guevara and Rubega, 2011; Rico-Guevara et al., 2015). Among nectarivorous birds, the taxon most morphologically similar to hummingbirds are sunbirds.

Sunbirds and hummingbirds fill the same ecological niches in different continents, providing pollination services to flowering plants in return for energy-packed rewards (Nicolson and Fleming, 2014; Cheml et al., 2021; Rico-Guevara et al., 2021). These two phylogenetically distinct lineages of birds are visually very similar, with overall small body sizes, relative bill length and shape, and even iridescent coloration converging between them (Stiles, 1981). Given that both sunbirds and hummingbirds have greatly elongated and narrow bills with ample oral cavities, housing equally long and distally bi-cylindrical-hollow-tongues, we expected that these groups would share similar feeding mechanisms, as have been described for hummingbirds and that do not include active suction throughout the entire tongue.

The drinking mechanics have been explored across a diversity of hummingbird species; we studied sunbirds from the geographical ends of their distribution, different parts of their phylogeny, and with different body and bill sizes. There are 143 species of sunbirds with their ranges spanning Africa, southern Asia, and the Malay Archipelago (Cheke and Mann, 2001; Winkler et al., 2020). Although every species within this family includes nectar in its diet (except *Deleornis fraseri*; Cheke and Mann, 2020), we know nearly nothing about how they drink nectar. Hypotheses were made about their feeding mechanics beginning over a century ago, yet these

ideas haven't been tested (Gadow, 1883; Liversidge, 1967; Downs, 2004; Cuban et al., 2022). Using micro computed tomography (μCT) scans of species from both groups, high-speed videos of sunbirds drinking from transparent artificial flowers, kinematic analyses and fluid dynamics models, we unveil the unique feeding mechanism that sunbirds use to feed on nectar.

Results

Tongue and bill morphology

Sunbird bills are long relative to their body size and generally decurved, and their tongues have approximately the same length as the bill. The sunbird tongue can be described along three distinct sections: (1) distally, the tongue is bifurcated, and made of medially curling, keratinous, and very thin walls that form two hollow cylinders (Fig. S1); (2) in the middle section, the walls are less curled inward with their ends opening up to form a single elliptical cylinder, also hollow across its entire length; (3) in this proximal section, the tongue opens up entirely to form a "V" shaped channel with its edges flared out laterally (Fig 1.

Sunbird and hummingbird tongues are more similar to each other than any of the tongues found among all other nectarivores. Both species' tongues are long, thin, keratinous structures with longitudinal grooves used to transport nectar. At the tip (Fig 1, cross-section 5), both are bifurcated tubes with fringed ends. Although the middle section of the hummingbird tongue has two separate grooves and sunbirds have one, both species can carry nectar in the middle section of their tongue (Fig. 1, cross-section 4). At the proximal portion of the tongue the two groups notably differ. Hummingbird tongues become a solid keratin structure with no internal space to transport nectar within the tongue whereas sunbird tongues unfurl laterally at the base, increasing the volume the tongue could carry (Fig 1, cross-sections 1 and 2). The hummingbird tongue morphology aids in their feeding as they need a strong, rigid structure to

keep the tongue oriented properly when it pushes it between its compressed bill tips. This allows the tongue to store elastic energy before rapidly expanding and filling its hollow portions with nectar, known as elastic-filling. Sunbird tongue morphology consists of a continuous groove, opening the possibility of continuous flow through the entire length of the tongue.

Sunbird and hummingbird bills also show significant convergence. Both are long and narrow, often decurved, and have internal structures that interact with the tongue to aid in nectar-feeding. When closed, hummingbird bills have minimal empty space outside of the tongue grooves, with that volume decreasing towards the distal tip. Protrusions on the inner surfaces of the upper and lower bills guide the tongue while it is protruded and help compress the tongue at the bill tips to wring the tongue of the nectar it held from the previous lick and to elastically load the tongue for the next expansion. Sunbird bills also have some protrusions on the internal surfaces. However, if the bill is closed the tongue is not compressed at any point along its length, indicating that these structures are likely for guiding the tongue only and not for compressing it.

Tongue kinematics and nectar flow

Nectar was offered to birds in this study inside artificial flowers consisting of clear rectangular cross-section corollas and red plastic disks to guide the birds. High-speed videos showed that all sampled sunbirds (15 individuals from 7 species, Table S1) fed in similar ways. First, they protrude their tongue past the slightly open bill tips until the distal portion of the lingual cylinders go into the nectar. Second, they keep their tongue inserted, pausing reciprocation when the tongue is at the point of maximum protrusion, while nectar flows inside the tongue towards the mouth filling the internal tongue capacity. Third, they retract the tongue only partially to swallow, leaving the distal cylinders partly protruded and full of nectar, but not contacting the nectar pool. And fourth, they re-extend the tongue for the next lick cycle stage at which the nectar in the tongue cylinders moves mouthwards (Video S1). The licking cycle period

is approximately 0.11 seconds from one tongue extension to the next with variable tongue protrusion lengths between individual feeding bouts. An example of tongue kinematics and nectar flow during feeding are plotted in Figure 2. To visualize the nectar flow and tongue movement of sunbirds feeding on artificial nectar we fed birds *ad libitum* with red dyed sucrose solutions of 20% w/w. The tongue, nectar reservoir meniscus, and nectar meniscus seen in the tongue are measured relative to an arbitrary point at the edge of the video (Fig. 2A). As the bird fed, it extended its tongue into the nectar reservoir and pause, while nectar could be observed flowing inside the tongue towards the mouth before the tongue retracted partially and began the cycle over again at a frequency of ~9 s^{-1} (Fig. 2B). By subtracting the position of the reservoir meniscus from the tongue position we find the immersion depth to vary between 1.3 and 2.1 mm (Fig. 2C). We subtract the reservoir nectar meniscus position from the tongue nectar meniscus position and find that the average licking period is ~ 0.11 s (Fig. 2D). Each of the licks are overlaid with each other relative to the tongue insertion time comparing the position, h, of the nectar meniscus in the tongue (Fig. 2E). Averaging all the tongue meniscus positions for each lick at the same relative time in the lick cycle shows strong evidence for a linear relationship between meniscus position and time (Fig. 2F). The first lick was not included in the average as in each trial it differs from the subsequent licks.

Fluid dynamic modeling

Figure 3 shows the nectar meniscus rise in the tongue averaged across multiple licks of a *Nectarinia famosa* (linear fit) in comparison with three feeding mechanics fluid models of increasing complexity. The capillarity model has been proposed before as the mechanism used by nectar-feeding birds. The model accounts for the surface tension of the sucrose solution at the tongue-air-nectar interface and the viscosity of the nectar. As the model shows significant error relative to the measured meniscus position capillarity on its own does not explain our observations. Including the inertial effects of accelerating the fluid from a static position brings

the initial meniscus position closer to that of the observed values. However, when we include a time-varying pressure differential in the model the predicted values almost perfectly match our experimental data. The pressure differential itself is found to increase linearly with time, implying that whatever internal motion the bird is doing to generate suction must be happening continuously during the tongue's immersion period in the nectar. Derivations of the fluid models are available in the supplementary materials.

Additional mechanistic observations

In many videos bubbles can be seen moving in the tongue when a bird does not make complete contact between its tongue tips and the nectar reservoir (Video S2). If capillarity was the sole mechanism used by sunbirds then no bubbles could be present as the surface tension at the distal end of the tongue would not allow for bubbles to pass into the tongue. Moreover, the nectar columns inside the tongue cylinders from the previous lick move mouthwards before the tongue tips contact the nectar reservoir (see trailing menisci in Video S1, S3). When the tongue is being extended the distal end is not in contact with a nectar reservoir, therefore there is a surface tension force applied pulling the nectar in the tongue towards the tongue tip, opposing any surface tension forces applied at the unseen proximal end of the tongue cavity. Since the nectar does, in fact, move toward the mouth at this time, an additional force, must be applied to affect this motion. Additionally, a *Chalcomitra amethystina* was recorded while its tongue suddenly dropped down from contact with its upper bill resulting in nectar flowing out of its mouth. We hypothesize this results from the failure of a hermetic seal between the tongue and upper bill as the bird moved its tongue too far down while feeding (Video S4). In all feeding events, synchronized side views evidence a downward motion of the throat while nectar is flowing inside the tongue cylinders, as observed in the top view (e.g., Videos S1). This downward motion of the throat corresponds to the area where the hyoid bones that support the tongue base move through, thus consequently corresponding to the V section of the tongue

being depressed within the oral cavity. Lastly, at the end of each lick cycle a stereotypic swallowing motion was observed in the throat when the tongue is partially retracted before re-extension.

Discussion

For hundreds of years it was believed that capillarity was the main mechanism for nectar feeding in birds. Using fluid dynamic models, Kim et al (2011) showed correspondence between the optimal concentration for caloric ingestion, from previous studies, and the predicted energy intake peak based on the feeding mechanism. In such study, three bird groups were assumed to use capillarity, called by them capillary suction, as their drinking mechanism: hummingbirds, honeyeaters, and sunbirds (Fig. 1, Kim et al. 2011). Since then, for hummingbirds, the capillary filling mechanism has been disproved (Rico-Guevara and Rubega, 2011), for honeyeaters, only one out of five species exhibited tongue kinematics consistent with capillarity (Hewes et al., 2023), and here we tested if capillary rise alone could explain the recorded flow patterns. Hummingbirds and most honeyeaters employ an expansive filling mechanism (Rico-Guevara et al., 2015; Cuban et al., 2022; Hewes et al., 2023)., so our initial hypothesis was that sunbirds – with convergent traits in their feeding apparatus morphology– would also use a similar technique. However, our study shows that for sunbirds, the main nectar intake mechanism is neither capillarity nor expansive filling. Instead, we found that sunbirds move nectar through their tongues over relatively longer immersion times in the floral nectar reservoirs and do not use of their bill tips to compress their tongues to squeeze the nectar and move it inside the bill, which also stores the elastic energy needed for the expansive filling mechanism to work (Rico-Guevara et al., 2015; Cuban et al., 2022; Hewes et al., 2023). In fact, sunbirds keep their bills slightly open during the entire feeding process with multiple licks occurring before the bill and

tongue are removed from the flower corolla. The kinematic measurements of the tongue and nectar movements demonstrate that a simple capillary filling mechanism is unable to explain the nectar uptake patterns reported here. In the end, the only mechanistic model that matches the collected data is the one that includes a pressure differential within the tongue cylinders, strong evidence for the use of active suction.

Coupling the inferences from the top view videos of the flower corolla and the side view videos of the birds bill and upper body, we propound the mechanism used by sunbirds to generate an increasing pressure gradient when drinking nectar. Figure 4 shows a cut-away diagram of the feeding cycle with the tongue motions that can generate the pressure differential. The tongue lies centered inside the slightly open bill; a ridge in the roof of the oral cavity matches the dorsal tongue shape (cross-section 1 in Fig. 4A) and would help to maintain the tongue centered as it slides along the upper bill. When the tongue is protruded to reach the nectar reservoir, the proximal and middle sections are pressed against the maxilla's ventral surface (Fig. 4B). The "U" shape and flexion of the proximal tongue section allows for a hermetic seal against the maxilla (cross-sections 2-3 in Fig. 4B), which allows for the combined action of capillary forces and active suction that explain the intralingual menisci advance rate (Fig. 3). The tongue is then depressed in the oral cavity resulting in the slight visible movement of the throat. The increased volume between the tongue and maxilla creates a region of lower pressure relative to the atmosphere which draws nectar through the tubular shaped distal and middle sections of the tongue (cross-sections 3-4 in Fig. 4C). Finally, the tongue is pulled proximally towards the throat and unseals from the maxilla, allowing for the bird to swallow the nectar now in the oral cavity (Fig. 4D) before re-extending the tongue for the next lick cycle (Fig. 4E and 4F).

The mechanistically unique feeding style of sunbirds adds another interesting physical solution to the evolutionary challenge of feeding on small quantities of liquid food concealed in hard-to-reach spaces. The flowers that sunbirds and hummingbirds feed from often have

relatively long, narrow, and tubular corollas with nectar located at the base. However, the two bird lineages must have had slightly different morphological traits or environmental pressures that led to the different adaptations of their feeding apparatus to be able to extract energy efficiently enough from the local flowers they co-evolved with. As natural selection trends towards relatively advantageous traits even a small difference between each sunbird and hummingbird ancestors could result in evolutionary patterns that separately selected for different behaviors and morphologies that improved their nectar extraction rates. Further studies of how efficient nectar-feeding birds are at drinking nectar of different sugar concentrations would allow for deeper understanding of the plant-pollinator evolution as well as the interspecies dependencies of birds and flowers in the world today.

In our work, we unveil a previously unknown method to generate suction through a straw-like tongue in vertebrates without cheeks or lips. Additionally, the tongue itself is not a closed tube and is not made of soft tissue that typically would be seen in pressure-generating organs. This discovery raises new mechanistic questions for other vertebrate and invertebrate groups that achieve similarly unique results with the many diverse materials, structures, and physics phenomena of which the biological world is comprised.

Materials and Methods

Morphological analysis of bill and tongue

We used micro computed tomography (microCT) scans of the sunbird *Cyanomitra olivacea* and the hummingbird *Calypte anna* at ~20 micron resolution to compare morphology and measured internal tongue and oral cavity volumes. The CT scanner x-ray source voltage and current was 42 kV and 560 microAmps, respectively. We analyzed the scans using the 3D Slicer software and the SlicerMorph package (Rolfe et al., 2021). Transverse section images were taken along

the bill and tongue at 5 points that showed relevant anatomical features of interest. We measured the tongue structure dimensions and internal volume by adding landmark points and segmenting out the internal volume of the tongue.

Experimental Design

We used high-speed cameras to capture the nectar, tongue, and bill movement XX individuals from 7 sunbird species (*Nectarinia famosa* [n = 3], *Cinnyris afer* [n = 2], *C. talatala* [n = 1], *C. jugularis* [n = 1], *Chalcomitra amethystina* [n = 3], *Cyanomitra olivacea* [n = 2], *and Anthreptes malacensis* [n = 1])(Table S1) while they fed on nectar from artificial flowers (described below). South African sunbird species (5, Table S1) were captured in Umgungundlovu district of KwaZulu Natal in grassland areas with aloes and foothill areas with proteas between June and August of 2022 and 2023. Experiments with these species were conducted at the University of KwaZulu-Natal Pietermaritzburg in the outdoor Animal House aviaries. The Indonesian sunbird species (2, Table S1) were captured on Gunung Ambang and Gunung Klabat in North Sulawesi, Indonesia in July 2023. Experiments with these species were conducted in field camps established at each site. The artificial flower (Fig. S2) consisted of a red plastic ring attached to the end of a clear rectangular prism made of thin glass (5.9 mm width x 1 mm height) oriented horizontally that was filled with artificial nectar (20% w/w sugar concentration). When birds fed from the artificial flower, they partially inserted their bills through the red disk into the tube and extended their tongues to feed. Three high-speed cameras (Chronos 1.4, Krontech) were used to film, one oriented to film the clear tube from above, and a second filming the side of the bird's bill and head. Experiments with the Indonesian species used two cameras (Chronos 1.4, Krontech) filming the clear tube from above and the side of the bill and head. The cameras used Nikkor 105mm macro lenses (Nikon) and a film rate of 1000 to 4000 frames/second.

Video Analysis

We analyzed the video data using dltdv8a (Hedrick, 2008), tracking the tongue tip, bill tip, corolla nectar meniscus in the prismatic corolla of the artificial flower, and nectar menisci inside the tongue for multiple licks across multiple feeding bouts for each individual sunbird recorded in the experiment. Corolla nectar meniscus is defined as the edge of the nectar in the clear prismatic chamber at roughly the midpoint of the tube's width. The tongue nectar menisci are defined as the leading surface of nectar as it is drawn into the tongue and the trailing surface of the column of nectar as it moves through the tongue (these are found at different times in the feeding process, Video S1, S2, S3). The video data was calibrated using the known width of the nectar reservoir (5.9 mm) and the recording frame rate. The volume and volumetric rate of nectar consumption was calculated by measuring the position change of the corolla nectar meniscus multiplied by the nectar reservoir's cross-sectional area and the duration of time passed between the beginning and end of the time that the tongue was in contact with the nectar. Detailed derivations of the fluid models are available in the supplementary materials.

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447 **Figures:**

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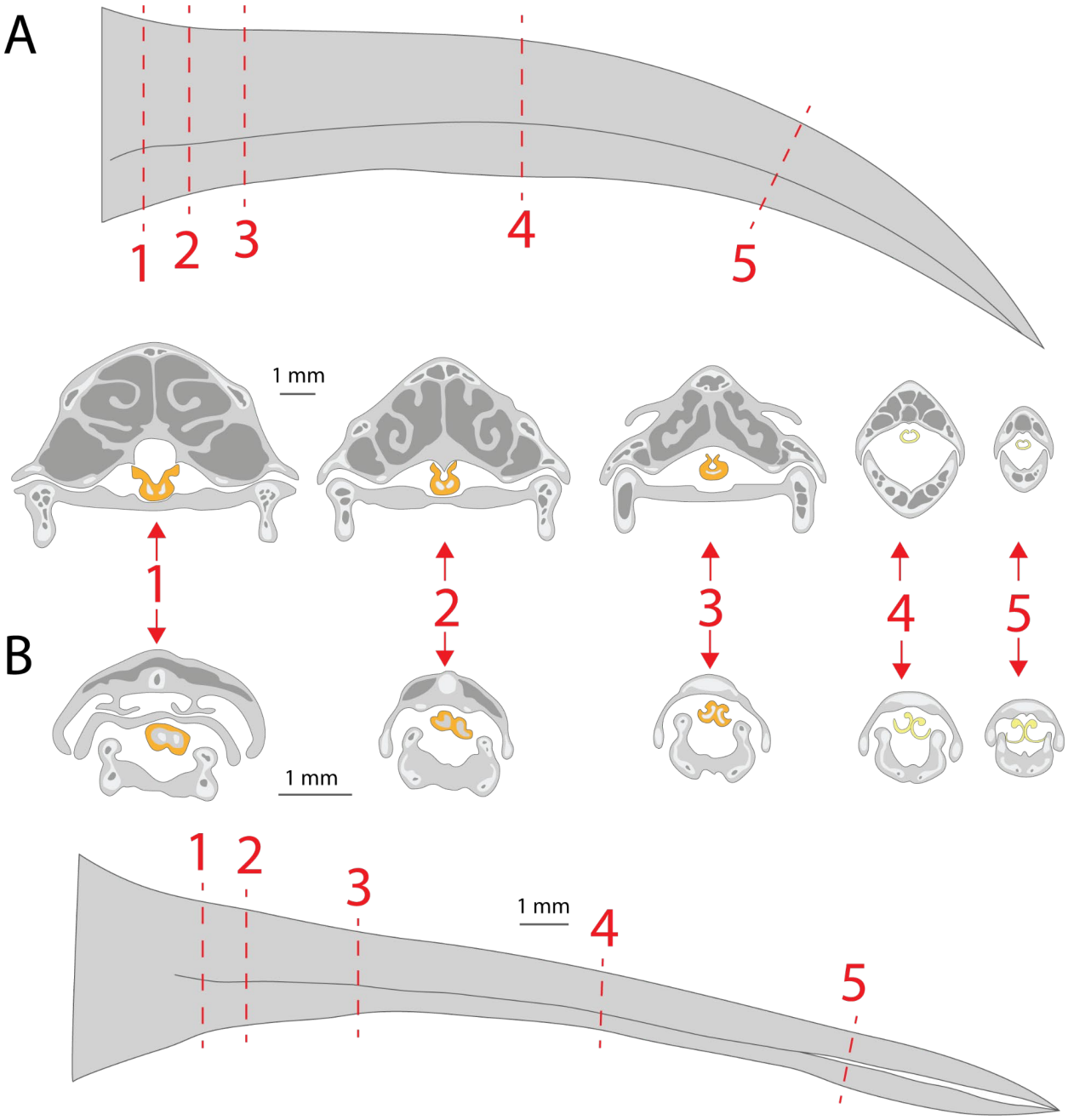

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452 **Figure 1: Cross-sections of a sunbird (above, *Cyanomitra olivacea*) and hummingbird**

453 **(below, *Calypte anna*) from microCT images.** The gray structures at the top and bottom are

lateral views of the bills. Dashed red lines crossing them correspond to the numbered cross-sections. Cross-sections were taken at proportionally similar points along the longitudinal axis of the bills, showing structures of the bill and tongue relevant to the feeding mechanics of each. The cross-sections show the keratin structure (gray), the underlying bone (light-gray), and the tongues (orange and yellow) of each bird. Both species have internal morphology of the bill that guides the tongue along the longitudinal axis when it is extended. The sunbird has notably more empty volume in the bill outside of the tongue grooves at the dorsal tip.

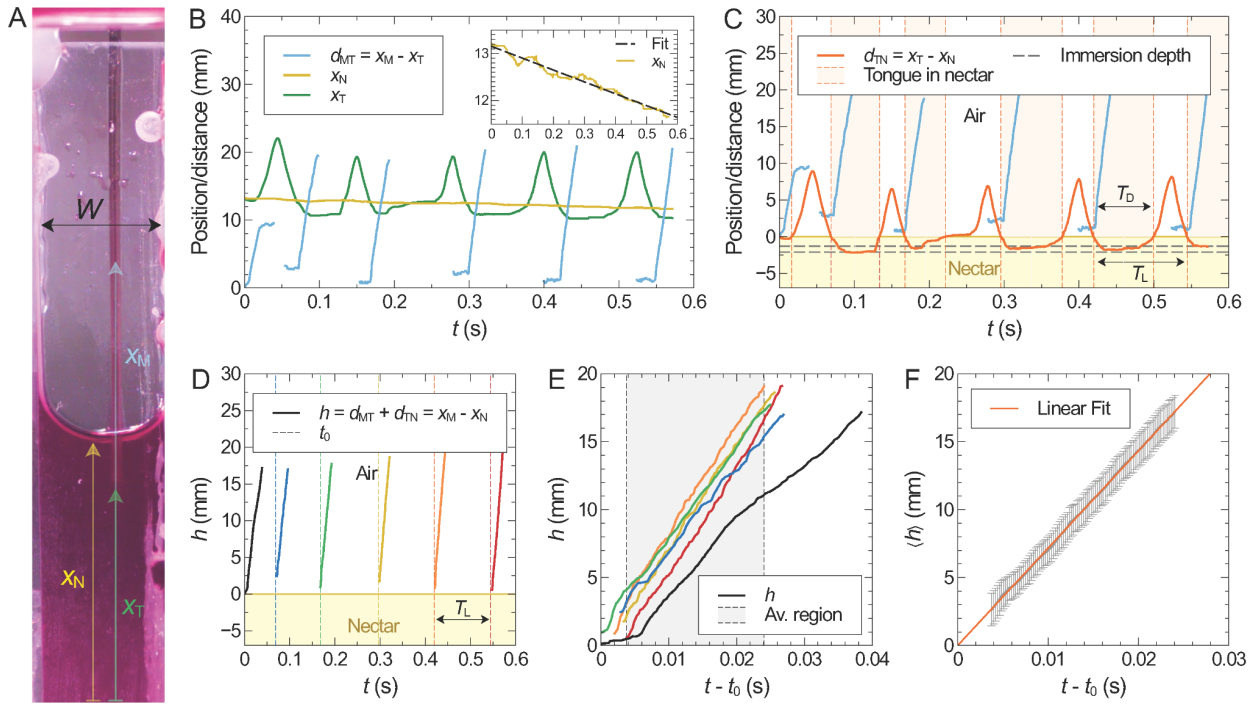

Figure 2: Kinematic measurements of a *Nectarinia famosa* tongue and red colored nectar during multiple lick cycles. (A) Frame of a video showing the nectar reservoir (W = 5.9 mm) and the bi-cylindrical distal portion of the tongue where only the tips are immersed in the nectar (dyed magenta to improve visualization). Arrows indicate the position of the nectar, xN, of the tongue tip, xT, and of the meniscus inside the tongue, xM, with respect to an arbitrary fixed

point. Bill tip (not visible) towards the top of the frame. **(B)** Evolution of xN, xT and dMT = xM − xT as a function of time. **Inset**: Evolution of xN as a function of time together with a linear fit. **(C)** Evolution of the position of the tip of the tongue relative to the position of the nectar, dTN = xT − xN, as a function of time. The shaded area corresponds to the intervals of time where the tongue is in the nectar. Average tongue dipping time, TD ≃ 0.07 s. The maximal immersion depth of the tongue in the nectar varies between 1.3 and 2.1 mm. **(D)** Evolution of the distance h between the liquid meniscus inside the tongue and the nectar reservoir as a function of time. t0 corresponds to the time at which the tip of the tongue touches the nectar in the extension phase for each capture process. Average licking period, TL ≃ 0.11 s. **(E)** Evolution of h as a function of t − t0. **(F)** Average of the data shown in panel E (without the first lick). The region where the average is performed is shown in panel E and corresponds to the time interval where there is data for all the licks averaged.

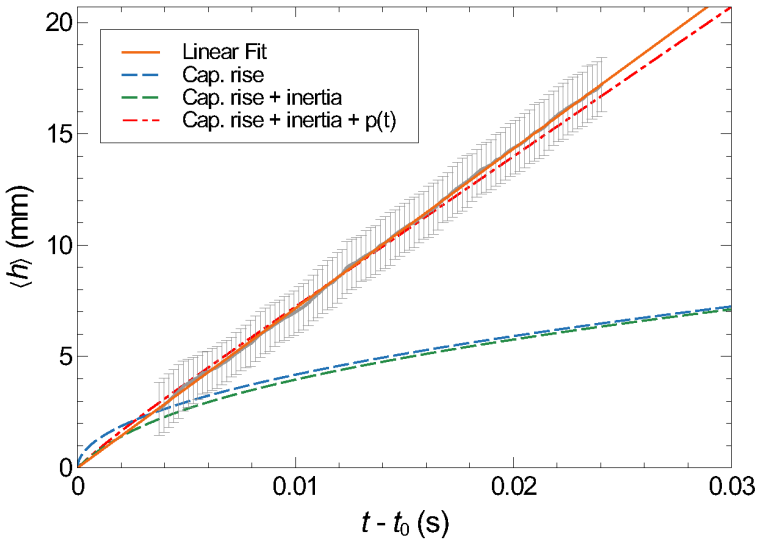

Figure 3: Evolution of ⟨h⟩ as a function of time (see Fig. Yf) together with the evolution predicted by capillary rise only (blue dashed curve), by capillary rise and inertial effects (green dashed curve) and by capillary rise, inertial, effects, and a difference of pressure across tongue's length varying linearly in time (red dashed dotted curve).

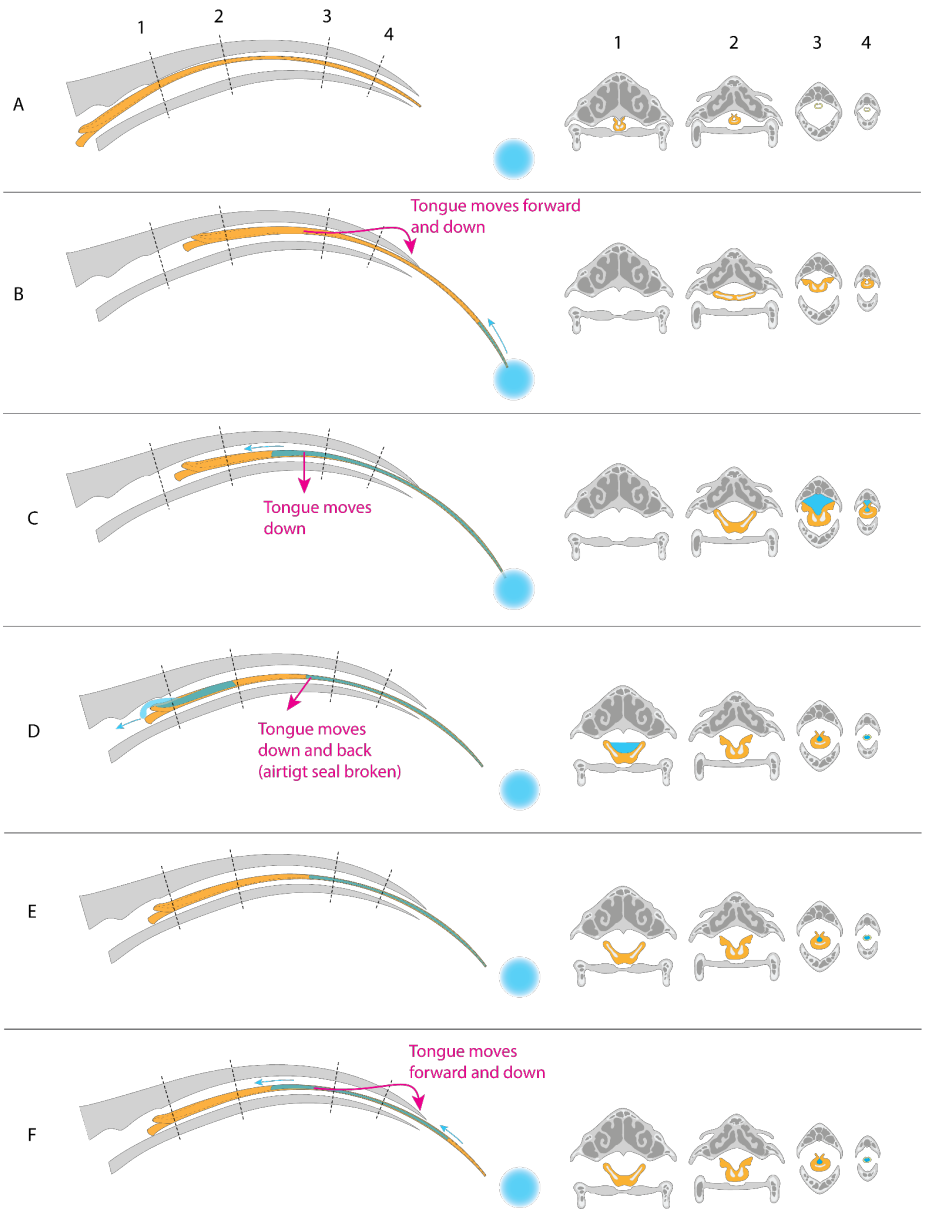

Figure 4: Biomechanical method of sunbird suction feeding. Sagittal cross sections of the bill and tongue of a sunbird while feeding **(left)**. Transverse cross sections of the bill and tongue while feeding **(right)**. (A) Initial position, (B) Tongue extension and pressing into upper palate, (C) Tongue depression while tongue edges sealed against upper bill, (D) Partial retraction and swallowing to remove nectar from proximal trough of tongue, (E) Re-extension for next lick, some nectar often remains in the tubular portion of the tongue from the previous lick cycle, (F)

During re-extension, nectar left over from the previous lick will be drawn back in the tongue via suction as the bird begins to generate a pressure differential across the length of the tongue before the tongue tips make contact with the nectar reservoir.