A novel feeding mechanism: Sunbirds drink nectar via intralingual suction

Authors: David Cuban[1,2], Cynthia Wang-Claypool[3,4], Yohanna Dalimunthe[5], Colleen T. Downs[6], Rauri C. K. Bowie[3,4], Fabian Brau[7], Steven D. Johnson[6], Alejandro Rico-Guevara[1,2]

Affiliations:
[1]*Department of Biology, University of Washington, Life Sciences Building, Box 351800, Seattle, WA 98105, USA*
[2]*The Burke Museum of Natural History and Culture, Ornithology Department, 4300 15th Avenue NE, Seattle, WA 98105, USA*
[3]*Department of Integrative Biology, University of California, Berkeley 3040 Valley Life Sciences, Building, Berkeley, CA 94720*
[4]*The Museum of Vertebrate Zoology, University of California, Berkeley, 3101 Valley Life Sciences Bldg,Berkeley, CA 94720*
[5]*Museum Zoologicum Bogoriense, Research Center for Biosystematics and Evolution, National Research and Innovation Agency of Indonesia (BRIN) | Jalan Raya Jakarta-Bogor KM 46, Cibinong, West Java, Indonesia 16911*
[6]*Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, Pietermaritzburg, 3209, South Africa*
[7]*Nonlinear Physical Chemistry Unit, Université libre de Bruxelles (ULB), CP231, 1050 Brussels, Belgium*

* Corresponding author: David Cuban

Email: david.r.cuban@gmail.com; ORCID: https://orcid.org/0000-0003-4661-7180

Other emails and ORCIDs of others:

Cynthia Wang-Claypool Email: cynthia.yh.wang@berkeley.edu; ORCID: https://orcid.org/0000-0002-7725-5787

Yohanna Dalimunthe Email: yoha008@brin.go.id; ORCID: https://orcid.org/0000-0001-6051-3199

Colleen T. Downs Email: downs@ukzn.ac.za; ORCID: http://orcid.org/0000-0001-8334-1510

Rauri C. K. Bowie Email: bowie@berkeley.edu; ORCID: https://orcid.org/0000-0001-8328-6021

Fabian Brau Email: Fabian.Brau@ulb.be; ORCID: https://orcid.org/0000-0002-8715-5464

Steve Johnson Email: JohnsonSD@ukzn.ac.za; ORCID:https://orcid.org/0000-0002-5114-5862

Alejandro Rico-Guevara Email: colibri@uw.edu; ORCID: https://orcid.org/0000-0003-4067-5312

Abstract

Nectarivory has independently evolved many times among birds, yet little is known about the specialized feeding mechanisms that enable these specialized taxa to efficiently collect this energy-rich resource. Multiple groups have converged on evolving elongated bills and tube-like tongues adapted for nectar extraction. Old World sunbirds (family Nectariniidae) stand out as having the greatest degree of convergence in bill and tongue morphology with the well-studied and highly-specialized New World hummingbirds (family Trochilidae) which drink nectar using elastic filling. However, using museum specimens, high-speed video, and fluid modeling, we show that sunbirds use a previously undescribed and unique drinking mechanism not found in any other vertebrate: intralingual suction through the inside of hollow tubular tongues, a remarkable feat for animals without lips or cheeks.

Introduction

Feeding is a fundamental need of all organisms, and the variety of food acquisition mechanisms have been studied for centuries (Nitzch, 1816; Roth, 1976; Bells and Goosse, 1990; Muller et al., 1982; Schwenk, 2000). Some dietary niches have been created from coevolution between organisms, leading to unique relationships and the mechanics of those interactions. Nectar-feeding animals evolved to drink nectar from plants that offer it as a pollination incentive, but keep it hidden away inside their flowers. Nectar-feeding animals have evolved multiple distinct methods to consume nectar that take advantage of its liquid state. 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), which requires their lips to be in contact with the liquid (or using straws). Only one vertebrate, a species of bat, has been reported to transport liquid along the length of its tongue, using lateral grooves on the surface of their tongues (Tschapka et al., 2015). For these bats, however, suction is not possible because their groove edges do not overlap to form a seal, and their tongues are not hollow but rather muscular (Tschapka et al., 2015). For vertebrates without lips or cheeks, suction is an even greater challenge. In birds, suction feeding is restricted to a few taxa (*e.g.*, filter feeders, pigeons) and it is accomplished with the bill being submerged in water and the tongue acting as a piston (review in Rico-Guevara et al., 2019). There are no known examples of vertebrates able to move liquids through their tongues using active suction by generating their own internal pressure differential - even the nectar-feeding insects that use suction have evolved proboscis and other mouthparts analogous but developmentally distinct from tongues (Kingsolver and Daniel, 1979; Herrel et al., 2006; Kayak et al., 2014).

Vertebrates are responsible for 3-25% of plant pollination across habitats, and amongst them birds are the most diverse pollinators, with over 920 pollinating species (Ratto et al., 2018; Fleming and Muchhala, 2008). Within birds, specialized nectar feeding has evolved independently in approximately 30 clades (Pauw, 2019; Hewes et al. 2022), which exhibit varying degrees of morphological, functional, and behavioral convergence (Stiles, 1981; Fleischer et al., 2008; Janeček et al., 2015; Cuban et al., 2022; Hewes et al. 2022). Some of the

most identifiable convergent traits to this specialized dietary niche occur in the feeding apparatus. Bill and tongue similarities are evident among taxa in distant geographic regions; for example, hummingbirds (Trochilidae) in the Americas, sunbirds (Nectariniidae) in Africa and Asia, honeyeaters (Meliphagidae) in Australia, asities (Philepittidae) in Madagascar, 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 nectar drinking mechanisms are best known for hummingbirds (Rico-Guevara et al. 2015; Rico-Guevara and Rubega, 2017; Rico-Guevara et al., 2023). A taxon morphologically similar to hummingbirds, yet phylogenetically distinct, are the sunbirds whose feeding mechanism has not been previously elucidated (Paton and Collins, 1989).

There are 142 species of nectarivorous sunbirds, and their ranges span Africa, southern Asia, and the Malay Archipelago (Cheke and Mann, 2001; Winkler et al., 2020). For over a century, hypotheses about their feeding mechanics have been proposed (Gadow, 1883; Liversidge, 1967; Cheke and Mann, 2001; Downs, 2004), with capillarity as the most recently noted (Kohler et al., 2010; Kim et al., 2011), yet these ideas have not been tested (Cuban et al., 2022). The mechanics of drinking nectar have been explored across a diversity of hummingbird species, and given that both sunbirds and hummingbirds have elongated and narrow bills, housing equally long and distally bi-cylindrical-hollow tongues (Downs, 2004; Rico-Guevara, 2017), we expected that these groups would employ similar feeding mechanisms. We studied sunbirds from both Africa and Asia, sampling seven species from multiple clades across the phylogeny, as well as species across a wide range of body and bill sizes. To comprehensively study how sunbirds feed, we used micro-computed tomography (µCT) scans and microscope image analysis, high-speed videos of sunbirds drinking from transparent artificial flowers, kinematic analyses, and fluid dynamics models. We discovered a unique feeding mechanism among vertebrates, intralingual suction, that sunbirds use to feed on nectar.

Results

Tongue morphology, kinematics, and nectar flow

We used microscopes and µCT scans of dissected sunbird tongues to detail their morphology (Fig 1A and 1B). 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 1C XS6); (2) in the middle section the tongue is no longer bifurcated, the walls are less curled inward with their edges opening toward each other, forming a single elliptical cylinder, hollow across its entire length (Fig 1C XS4-5); (3) in the proximal section the walls of the lingual cylindrical groove are much thicker, and the tongue opens to form a “U”-shaped channel with its edges flared out laterally (Fig 1C XS1-3).

To visualize the nectar flow and tongue movement of sunbirds feeding on artificial nectar, we fed birds *ad libitum* with red dyed (to enhance flow visualization) sucrose solutions of 20% w/w. Dorsal and lateral view videos, captured using synchronized high-speed cameras, showed that all sampled sunbirds (9 individuals across seven species, Table S1) fed in similar ways. 1) They protruded their tongue past the open bill tips until the distal portion of the lingual cylinders entered the nectar. 2) They kept their tongue inserted while nectar flowed towards the

mouth, filling the internal tongue capacity. 3) They retracted the tongue only partially to swallow, leaving the distal cylinders partly protruded from the bill and full of nectar. 4) Then, without squeezing the tongue with the bill tips, they re-extended it for the next lick cycle (*e.g.*, Video S1). Using the dorsal videos of the transparent nectar chamber, we tracked the tongue motion and fluid flow during the lick cycle for all individuals (e.g., Fig. 2A). Figure 2 shows the data for a malachite sunbird *Nectarinia famosa*. The position of the tongue tip, nectar meniscus in the reservoir, and nectar meniscus in the tongue are measured relative to a fixed point at the base of the artificial flower (Fig. 2A) over multiple tongue extensions and retractions per feeding bout (*e.g.*,Fig. 2B). After initial videography experiments, we did not focus on recording or tracking the bill tips as they remained open and relatively stationary during feeding so we determined that, surprisingly, they were not actively involved in the sunbird nectar collection biomechanics (*e.g.*, Video S1). By subtracting the position of the reservoir meniscus from the tongue tip position, we found the immersion depth to vary between 1.3 and 2.1 mm and an average lick period of ~0.11 s (Fig. 2C). Notably, sunbirds did not immerse their tongues in the expected way relative to other nectar-feeding birds. They kept their tongues stationary for long “pauses” similar in length to the time they were moving their tongues instead of immediately retracting them like other birds. We subtracted the reservoir meniscus position from the tongue meniscus position to calculate the nectar column position in the tongue relative to the nectar reservoir, h. (Fig. 2C and 2D). Each of the licks were 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 provided strong evidence for a linear relationship between meniscus position and time (Fig. 2F).

Fluid dynamic modeling

Figure 3 shows the nectar meniscus rise in the tongue averaged across multiple licks of individuals from each species of sunbird in the study in comparison with three feeding mechanics fluid models of increasing complexity. First, the capillarity model, accounted for the surface tension of the sucrose solution at the air-nectar interface inside the tongue and the viscosity of the nectar. As the model shows significant deviation relative to the measured meniscus position, especially after a few initial milliseconds, capillarity on its own does not explain our observations. Second, also modeling capillarity, but including the inertial effects of accelerating the fluid from a static position brought the initial meniscus position closer to that of the observed values, especially during the initial fluid climb (first few milliseconds), after which the empirical data still mismatch. Third we included a time-varying applied difference of pressure in the model, which resulted in a satisfactory fit of the output with our empirical measurements, and provided support for suction being the primary mechanism at play (Fig 3). The slope, or velocity, of the nectar meniscus in the birds’ tongues matched the predicted slope of a pressure-dominated (linear) flow. The applied difference of pressure 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. One individual, the brown-throated sunbird *Anthreptes malacensis*, showed evidence of using suction during one of its feeding bouts and a second mechanism (capillary filling only) when its tongue was extended near its maximum during a separate feeding bout (data shown in Fig. 3).

See “Derivation of fluid models” in the Supplementary Materials for detailed derivations of the fluid models.

Mechanistic hypothesis testing of the tongue filling process

In addition to the fluid dynamics modeling, other lines of evidence also support the intralingual suction hypothesis. In several videos, bubbles can be seen moving inside the tongue when a bird does not make complete contact between its tongue tips and the nectar reservoir (e.g., Video S2). If capillarity was the sole mechanism used by sunbirds then no bubbles would be present inside the cylinders, as the surface tension at the distal end of the tongue would not allow bubbles to pass into the tongue. Moreover, in several instances, we observed that the nectar columns inside the tongue cylinders from the previous lick moved mouthwards before the tongue tips contacted the nectar reservoir (see trailing menisci in Videos S1, S3). This occurs whenever there is sufficient distance between the bill tip and the nectar reservoir, as the suction mechanism seems to begin while the tongue is being extended, regardless of its position relative to the nectar reservoir. In these instances, when the tongue is being extended, and its tips are not in contact with the nectar yet, there is a nectar-air interface at both the distal and proximal end of the tongue tubes. The distal interface creates a surface tension force pulling the nectar in the tongue towards the tip of the tongue which opposes surface tension forces applied at the unseen proximal end of the tongue cavity. The cancellation of surface tension forces means that by capillarity alone (in the absence of any external shape change) the nectar column would not rise (Jian-Lin et al., 2007). Since the nectar does, in fact, move toward the mouth at this time, an additional force must be applied to result in the observed motion. Additionally, an amethyst sunbird *Chalcomitra amethystina* was recorded while its tongue suddenly dropped down from contact with its upper bill resulting in nectar flowing out of its oral cavity (Video S4). We hypothesize this results from the failure of a hermetic seal between the tongue and upper bill (see Discussion) as the bird moved its tongue too far out/down while feeding. Lastly, in all feeding events, we observed throat motions that could be the tongue moving inside the mouth to generate suction. Using synchronized side views, we observed a downward motion of the throat while nectar was simultaneously flowing inside the tongue cylinders, as observed in the top view (e.g., Video S1). This downward motion of the throat corresponded to the area where the hyoid bones that support the tongue base move through, thus consequently corresponding with the “U”-shaped cross-section of the tongue (Fig 1C XS1-2) being depressed within the oral cavity.

Discussion

For over two centuries, it was believed that the passive capillary force was the main mechanism for nectar feeding in birds (Kim et al., 2012; Nitzch, 1816; Kim and Bush, 2012; Paton and Collins, 1989). Using fluid dynamic models, Kim et al. (2011) showed correspondence between the optimal concentration for caloric ingestion, using published data, and the predicted energy intake peak based on the feeding mechanism. In their study, three bird groups – hummingbirds, honeyeaters, and sunbirds – were assumed to use capillarity, which they termed “capillary suction”, as their drinking mechanism (Fig. 1 from Kim et al. 2011). Since

then, the capillary filling mechanism has been disproved for hummingbirds (Rico-Guevara and Rubega, 2011; Rico-Guevara and Rubega, 2012; Rico-Guevara et al., 2015; Rico-Guevara et al., 2019b), and for most honeyeaters—only one out of five species exhibited tongue kinematics consistent with capillarity (Hewes et al., 2023). Hummingbirds and most honeyeaters employ fluid trapping with their fimbriated tips and an expansive filling mechanism to load up the tongue grooves with nectar by compressing their tongues dorso-ventrally such that once in contact with the nectar reservoir, the elastic energy restores their shape and draws in nectar. (Rico-Guevara and Rubega, 2011; Rico-Guevara et al., 2015; Hewes et al., 2023). To offload the nectar inside the bill and swallow it, they wring their tongues with their bill tips at the beginning of the subsequent lick (Rico-Guevara et al., 2023; Rico-Guevara et al., 2024; Hewes et al., 2023). Our initial hypothesis was that sunbirds - with convergent traits in their feeding apparatus morphology - would also use similar techniques. However, our results were not consistent with this initial hypothesis. Unexpectedly, sunbirds do not use their bill tips to compress their tongues while feeding. In contrast, sunbirds keep their bills slightly open during the entire feeding process, with the tongue reciprocating along the maxilla, keeping the mandible apparently disengaged from the drinking mechanism. Tongue kinematics, nectar flow, and fluid dynamics models demonstrated that a simple capillary filling mechanism cannot explain the nectar uptake patterns reported here for sunbirds. Instead, sunbirds move nectar through their tongues over relatively longer immersion times, with shallower licks, and at a slower licking rate than hummingbirds and honeyeaters (Table S1, Hewes et al., 2023; Rico-Guevara et al., 2023). The only mechanistic model that matched the collected data was the one that included a difference of pressure within the tongue cylinders.

We propose that sunbirds use active suction to generate a pressure gradient when drinking nectar. Figure 4 shows cross-section diagrams of the feeding apparatus across the lick cycle, depicting the tongue motions that could generate such a pressure differential. Initially, 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 [XS1] in Fig. 4A) and would help to maintain the tongue centered as it slides along the upper bill. When the tongue is extended to reach the nectar reservoir, its base is lifted, pressing against the mouth's roof (Fig. 4B). We hypothesize that pressing the base upwards results in a partial flattening of the "U"-shaped (in cross section) proximal tongue region that pushes out the air trapped between the tongue dorsal surface and the oral roof. The flexible tongue edges would create a hermetic seal against the maxilla producing a "suction cup" effect (XS2-3 in Fig. 4B). Meanwhile, when the tongue tips make contact with the nectar reservoir, capillary forces initiate the wetting of the inner tongue spaces at the fringed tip and a rising meniscus can form via capillarity inside the tongue cylinders (which have a ventrolateral longitudinal slit). The intralingual meniscus advancement rate can be explained by the addition of active suction (Fig. 3). Suction begins when the tongue base is depressed in the oral cavity, evidenced by the slight visible movement of the throat (Video S1). The increasing space between the tongue and oral roof (sealed at the back by the proximal tongue edge) creates a region of lower pressure relative to the atmosphere which draws nectar through the tubular-shaped distal and middle regions of the tongue (XS 3-4 in Fig. 4C). It is important to note that although there are narrow gaps formed by the longitudinal slits along the tongue, the tightly curled and sometimes overlapping tongue edges could allow the tongue to work as a straw in the presence of a strong suction action. Next, the tongue is pulled proximally

towards the throat and as it is retracted, it unseals from the maxilla, allowing the bird to swallow the nectar now in the proximal end of the oral cavity (Fig. 4D). The nectar column breaks near the proximal end of the semi-cylindrical section of the tongue, leaving some nectar trapped in the middle and distal portions where the internal lingual cylinders are thin enough for surface tension forces to prevent dislodging of the liquid inside (Fig. 4D). The tongue is now back at its approximate initial position but still contains some nectar within the lingual cylinders (Fig. 4E). To complete the ingestion of the entire nectar aliquot, as the lick cycle begins again, the tongue is extended while its proximal portion is pressed into the roof of the mouth before being pulled down to generate negative pressure. The nectar already in the lingual cylinders flows towards the back of the tongue because of the pressure differential at the tongue base (Fig. 4F). In some cases, this occurs even before the tongue tip makes contact with the nectar reservoir if the tongue needs to be extended far to reach it.

In summary, several lines of evidence support the existence of a novel vertebrate feeding mechanism in sunbirds: 1) they do not immerse their tongues deep inside the nectar to use fluid trapping; 2) they do not wring their tongues with their bill tips, precluding expansive filling of the lingual cylinders; 3) the nectar flow in the tongues is closest to the fluid model for active suction, as it changes linearly, and does not decrease in flow rate over time as predicted with other models; 4) while feeding, sunbirds sometimes draw in bubbles of air into their tongues if they do not make complete contact with the nectar reservoir, meaning that capillarity alone is not responsible for the nectar flow; 5) sunbirds depress their tongue in their mouths simultaneously with the flow of nectar, pointing to use of the tongue as a means of generating a pressure differential leading to suction.

The mechanistically unique feeding style of sunbirds adds another interesting physical solution to the evolutionary challenge of feeding on small quantities of nectar concealed in flowers. While some insects are known to use suction through separately evolved structures, we revealed a previously unknown method to generate suction through a straw-like tongue in vertebrates without cheeks or lips. This discovery raises new mechanistic questions for other vertebrate and invertebrate groups that have solved the challenge of extracting small-volume and hard-to-reach liquid food with the many diverse materials, structures, and physics phenomena of which the biological world is composed.

Figures:

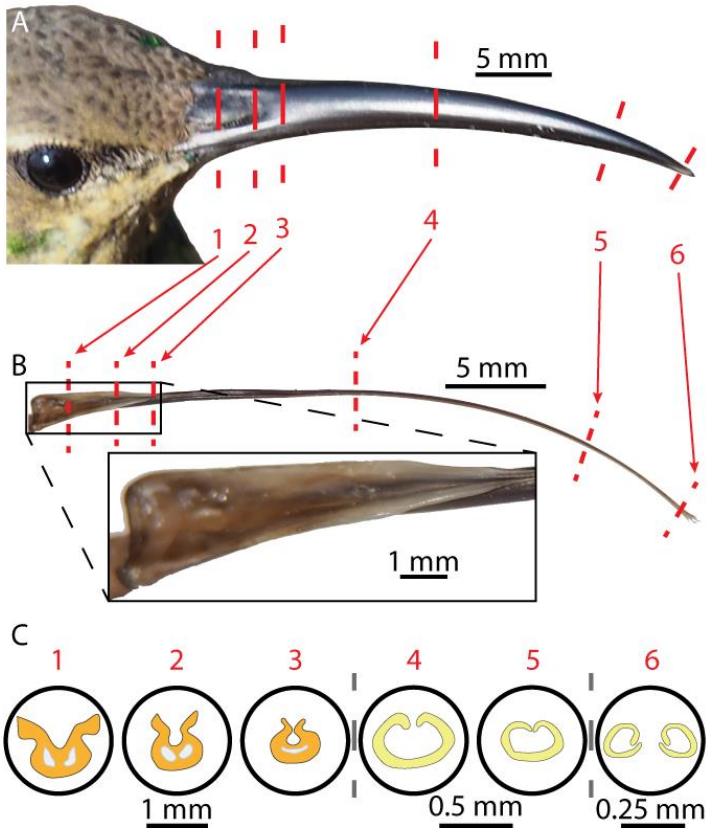

Figure 1: Sunbird bill, tongue, and cross-sections from microCT images. The sunbird tongue can convey fluid along its entire length, with the lateral edges of the tongue base capable of sealing against the inside of the upper bill. **(A)** Lateral view of a *Nectarinia famosa* from the study. Red dashed lines correspond with the locations of the microCT cross-sections. **(B)** Lateral view of the dissected tongue from the above *N. famosa* with cross-section lines marked. **(Inset)** magnified proximal portion of the tongue showing dorsal and lateral edges. **(C)** Enlarged cross-sections from different locations along the length of the sunbird bill and tongue. Cross sections (XS) 1-3 show the proximal portion of the tongue, the “U” shaped section at the back that becomes narrower further down the tongue. Orange parts are thick keratin and white are internal paraglossal bones. XS4 and XS5 show the hollow middle section formed by the inward curling edges of the tongue walls, forming an elliptical space. Yellow parts are the thin keratin. XS6 shows the bifurcated tip of the tongue, with the walls rolling inward to form tube-like structures.

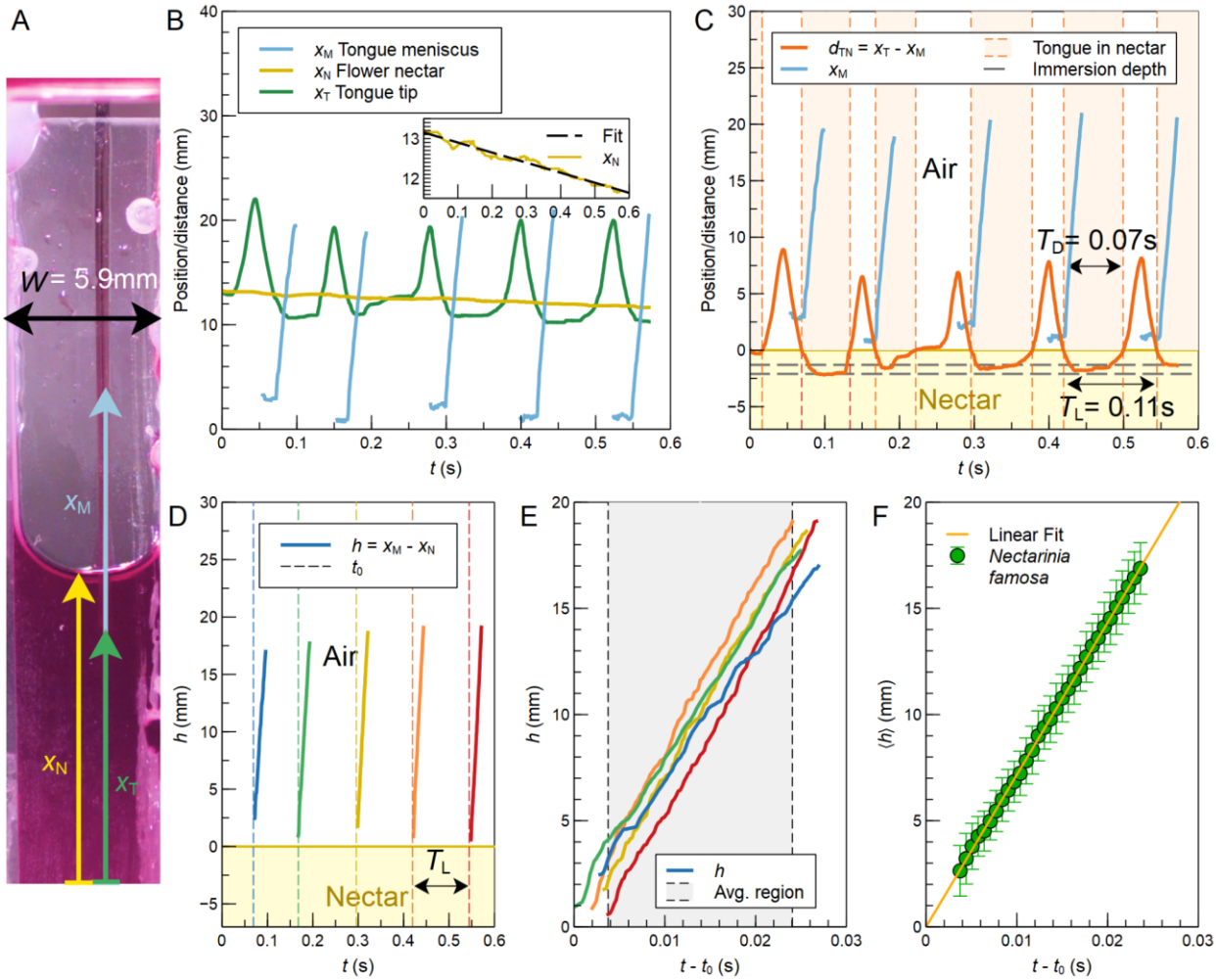

Figure 2: Kinematic measurements of a *Nectarinia famosa* tongue and red colored nectar during multiple lick cycles. (A) Video frame showing the nectar reservoir and the tongue tips immersed in the nectar (dyed magenta to improve visualization). Arrows indicate the position of the nectar meniscus of the reservoir, x_N, the meniscus inside the tongue, x_M, and the tongue tip, x_T, with respect to an arbitrary fixed point. **(B)** Position of x_N, x_T and x_M as a function of time. **Inset**: Position of x_N as a function of time together with a linear fit. **(C)** Position of the tongue tip relative to the nectar reservoir, d_{TN}, as a function of time. Tongue insertion depth varies between 1.3 and 2.1 mm. **(D)** Nectar position, h, in the tongue relative to the nectar reservoir as a function of time. t_0 corresponds to the time at which the tip of the tongue touches the nectar in the extension phase for each capture process. **(E)** Position of h as a function of $t - t_0$ for 5 licks and the time interval used to average h values. **(F)** Average and linear fit of h data in panel E.

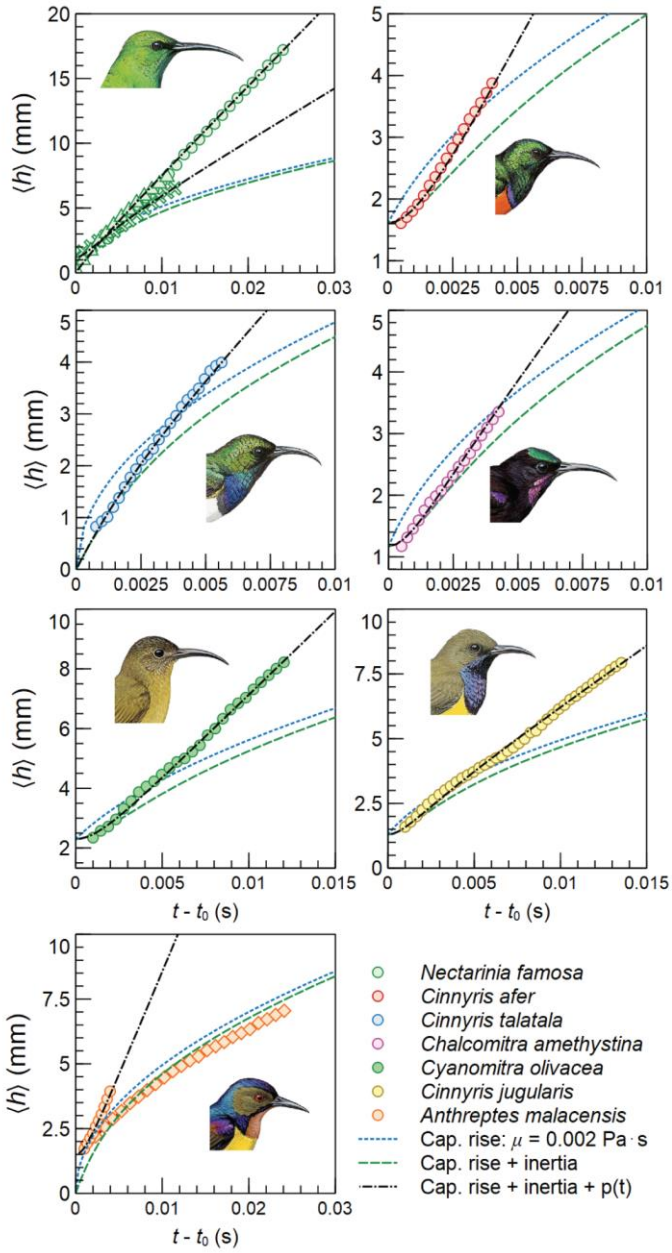

Figure 3: Intralingual suction across sunbird species. Change of ⟨h⟩, nectar position in tongue, as a function of time together with the change predicted by capillary rise only (blue dotted curve), by capillary rise and inertial effects (green dashed curve) and by capillary rise, inertial, effects, and a difference of pressure across the tongue's length varying linearly in time (black solid curve). These predictive models are adjusted based on the tongue morphology for each species. Data averaged across multiple licks from individuals from each species in the study are plotted (see Table S1). Differences in lick sequence duration (video frames) are due to different tongue lengths and bill tip to nectar reservoir distances. We only observed nectar distance motion typical of capillarity alone in one foraging bout of *Anthreptes malacensis*, and the same individual fed in the more common mode in another video where the tongue was much less extended (both plotted).

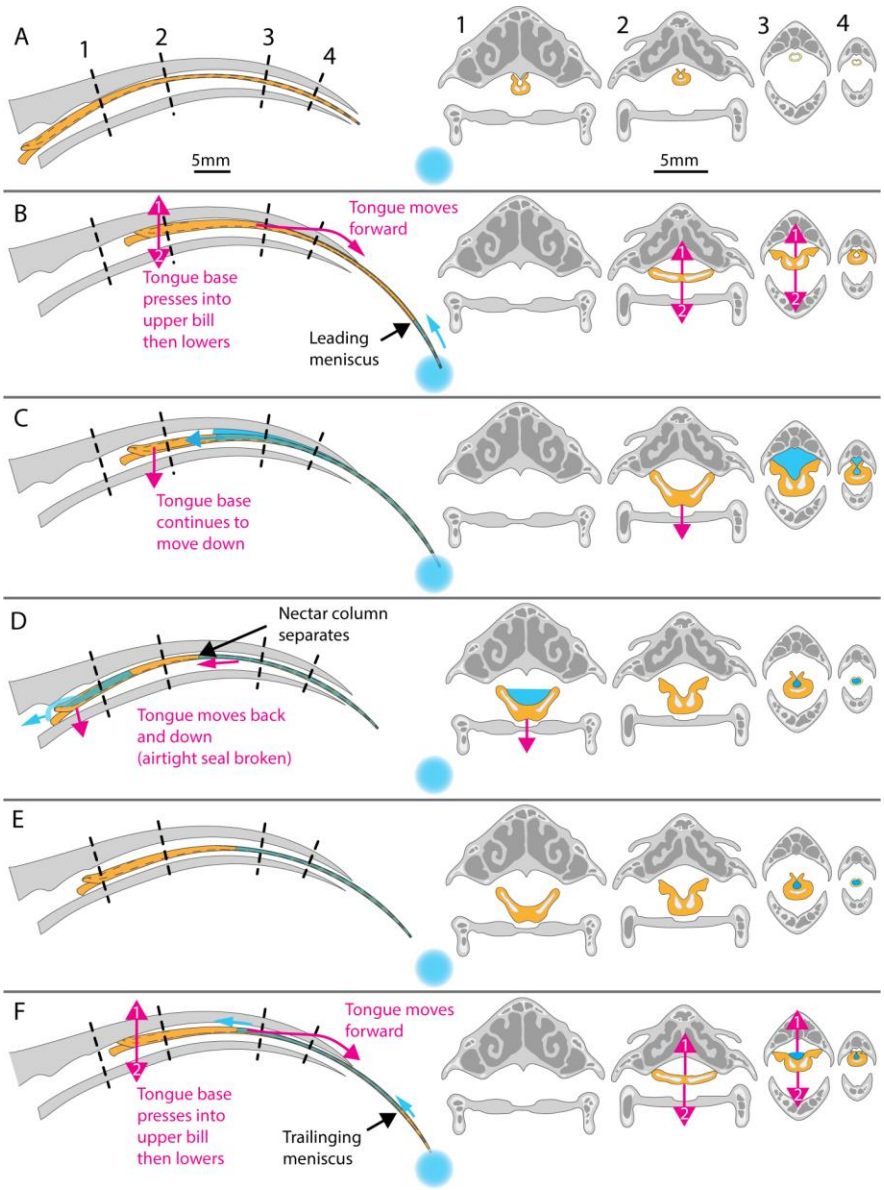

Figure 4: Biomechanical hypothesis of sunbird suction feeding. Sagittal cross sections of the bill and tongue of a sunbird while feeding **(left)**. Coronal cross sections of the bill and tongue while feeding **(right)**. These cross sections combine anatomically accurate information from µCT scans, hypothetical motions, and deformations inferred from our external high-speed video observations. (A) Initial position of the tongue at the start of the first lick. (B) Tongue extension and base pressed into the mouth's roof before depression. (C) The tongue continues to depress while tongue edges are sealed against the upper bill. (D) Partial retraction of the tongue, proximal portion lowered from the oral roof. The hermetic seal is released and nectar can move from the back of the tongue to the proximal oral cavity and throat. (E) The tongue has completed a lick cycle. Some nectar often remains in the tubular portion of the tongue from the previous lick cycle. (F) During re-extension for the second lick, the nectar left over from the previous cycle is drawn back into 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.

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Supplementary Materials:

Materials and Methods

Experimental Design

We used high-speed cameras to capture the nectar, tongue, and bill movement of nine individuals from seven sunbird species (Table S1) while they fed on nectar from artificial flowers (described below). Sunbird species in South Africa (n = 5, Table S1) were captured in the 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 (Permits: DAFF Section 20, 12/11/1/5/2418(HP); EKZNW, OP 3034/2022; AREC, AREC/00004060/2022; AREC, AREC/00006760/2024) . Sunbird species from Indonesia (n = 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 (Permits: BRIN, 346/SIP/IV/FR/6/2023; IACUC, 4498-05). The artificial flower (Fig. S1) consisted of a red plastic ring attached to the end of a clear rectangular tube made of 4 glass microscope slides: one on the bottom, two glued on top of the bottom one with ~5mm separating them, and the fourth glued on top of those to form a 5.9 mm width x 1.5 mm height rectangular tube. The apparatus was oriented horizontally and filled with artificial nectar (20% w/w sugar concentration, within range of local flower nectar). 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. Two high-speed cameras (Chronos 1.4, Krontech) were used, one oriented to film the clear tube from above, and a second filming the side of the bird's bill and head. The artificial nectar was dyed red with food coloring to help visualize the nectar moving inside of the sunbird tongues. The cameras used Nikkor 105 mm macro lenses (Nikon) and a film rate of 1000 to 4000 frames/second with 1280x1024 to 1280x240 pixels.

Video Analysis

We analyzed the video data using dltdv8a (citation), tracking the tongue tips, bill tips, nectar meniscus in the 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.

Morphological analysis of bills and tongues

We took measurements of dissected tongues using light microscopes to input the effective internal tongue diameter into the fluid model equation. We also used micro-computed tomography (microCT) scans of an olive sunbird, *Cyanomitra olivacea,* at ~20 micron resolution

to compare morphology and measured internal tongue and oral cavity volumes to validate our light microscope measurements. The CT scanner x-ray source voltage and current was 42 kV and 560 microAmps, respectively. We analyzed the scan using the 3D Slicer software and the SlicerMorph package (Federov et al., 2012; Rolfe et al., 2021). Transverse section images were taken along the bill and tongue at six points that showed relevant anatomical features of interest.

Supplementary text:

Sunbird and hummingbird comparisons

Sunbird and hummingbird tongues share a similar distal morphology and notably distinct proximal morphology (Fig S2). Both have tongues that are long, thin, keratinous structures with longitudinal grooves used to collect nectar reaching deep inside flowers. At the tip (Fig S2, cross-section 5), both are bifurcated tubes with fringed ends. The distal section of the hummingbird tongue has two separate grooves, while that of sunbirds has bifurcated tips that fuse to one groove near the tip. In both groups, the tongues can fill with nectar in the distal to middle sections of their tongue (Fig S2, cross-section 4), but differ notably at the proximal portion of the tongue. Hummingbird tongues become a solid keratin structure at their longitudinal midpoint 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 S2, cross-sections 1 and 2). The tongue morphology of hummingbirds aids in their feeding as they need a strong, rigid structure to keep the tongue oriented properly when it is pushed between the compressed bill tips. This allows the hummingbird tongue to store elastic energy before rapidly expanding and filling its hollow portions with nectar, in a process known as elastic-filling. Sunbird tongue morphology, by contrast, 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 may interact with the tongue and aid in nectar-feeding (Fig. S2; Rico-Guevara and Rubega, 2011). It has been hypothesized for hummingbirds that the 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 tip to wring the tongue of the nectar it held from the previous lick and to elastically load the tongue for the next expansion (Rico-Guevara and Rubega, 2011). Sunbird bills also have some protrusions on the internal surfaces (Fig. S2). However, when the bill is closed the tongue is not compressed at any point along its length.

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 use different biophysical solutions with superficially convergent adaptations of their feeding apparatus to extract energy efficiently enough from the flowers they co-evolved with. These differences likely arose from their very different evolutionary origins: sunbirds evolved from a general passerine form, while hummingbirds evolved from a clade comprised of nocturnal birds. Comparing across taxonomic classes, we now find that both a bird clade, sunbirds, and at least

one species of bat share similar nectar-feeding adaptations: both convey nectar along the length of the tongue, although by different means (Tschapka et al., 2015).

Derivation of fluid models:

The equation of motion of a liquid flowing into a vertical tube with a circular cross-section of radius R_T is given by the Bosanquet equation [1, 2]:

$$\rho \frac{d}{dt}\left[h\frac{dh}{dt}\right] + \frac{8\mu}{R_T^2} h \frac{dh}{dt} + \rho g h = \frac{2\gamma\cos\theta}{R_M} + \Delta p, \qquad (1)$$

where ρ, μ and γ are the density, viscosity and surface tension of the liquid respectively. h and R_M are the height and radius of curvature of the air-liquid meniscus inside the tube and θ is the contact angle between the liquid and the tube. The terms on the left-hand side of this equation represents, respectively, inertial forces, viscous forces and hydrostatic pressure and are balanced on the right-hand side by the capillary forces and an applied difference of pressure Δp. In our case, because the inner part of the tongue (tube) is wet, we assume θ = 0. In addition, because the radius R_T of the tongue ($\simeq$ 0.15 mm) is much smaller than the capillary length $\ell_c = [\gamma/\rho g]^{1/2} \simeq 2.7$ mm, the radius of curvature of the meniscus is equal to the radius of the tube $R_M = R_T$.
In the absence of applied pressure, this equation admits a stationary solution, i.e. dh/dt = 0, corresponding to the maximum height reachable by the meniscus, i.e. the so-called Jurin's height: $h_\infty = 2\gamma/(\rho g R_T) \simeq 9$ cm. Since, h_∞ is significantly larger than the height reached by the meniscus in the data we analyzed, gravity can be neglected. In addition, in our case, a time-dependent applied pressure is considered which makes the role of gravity completely negligible. Therefore, Eq. (1) becomes

$$\rho \frac{d}{dt}\left[h\frac{dh}{dt}\right] + \frac{8\mu}{R_T^2} h \frac{dh}{dt} = \frac{2\gamma}{R_T} + \Delta p, \qquad (2)$$

It is usual to neglect inertia to describe a capillary rise since its effects are noticeable only at very short time. In this case, in the absence of applied pressure, Eq. (2) becomes

$$h\frac{dh}{dt} = \frac{\gamma R_T}{4\mu}. \qquad (3)$$

Using the initial condition $h(0) = h_0$, the solution reads

$$h_C^2(t) = h_0^2 + \frac{\gamma R_T}{2\mu}t, \qquad (4)$$

This square-root behavior does not describe well the data as shown in Fig. 3. Taking into account inertia without applied pressure, i.e. $\Delta p = 0$ in Eq. (2), together with $h'(0) = 0$ leads to the following solution

$$h_{\mathrm{CI}}(t)^2 = h_{\mathrm{C}}(t)^2 - \frac{\gamma\rho R_T^3}{16\mu^2}\left[1 - e^{-t/\tau}\right], \qquad (5)$$

where $\tau = \rho R_T^2/(8\mu)$ gives the typical time below which inertia dominates the viscous effects. Fig. 3 shows that adding inertia does not improve the description of the data since the curve is always below the curve without inertia as seen in Eq. (5). This indicates that the capture of nectar by sunbirds is not passive.
Finally, solving Eq. (2) with an applied pressure varying linearly in time, i.e. $\Delta p(t) = \alpha\, t$, leads to

$$h_{\mathrm{CIP}}(t)^2 = h_{\mathrm{CI}}(t)^2 + \Sigma\left[\frac{t}{\tau}\left[\frac{t}{\tau} - 2\right] + 2\left[1 - e^{-t/\tau}\right]\right], \qquad (6)$$

where $\Sigma = \alpha\rho^2 R_T^6/(8\mu)^3$. Note that, in our case, τ is quite small (about 1.5 ms) and Eq. (6) can be simplified by expanding h_{CIP} for $t >> \tau$:

$$h_{\mathrm{CIP}}(t) \simeq V\,t + C, \qquad V = R_T\left[\frac{\alpha}{8\mu}\right]^{1/2}, \qquad C = \frac{\gamma}{[2\mu\,\alpha]}\left[1 - \frac{\alpha\,\rho\,R_T^3}{16\,\gamma\,\mu}\right], \qquad (7)$$

where V is the speed at which the liquid rises in the tongue and which results from the competition between the applied pressure driving the motion and the viscosity slowing down the dynamics. The constant C is a small offset resulting from the competition between all effects

involved at small time $t \ll \tau$ (inertia, capillarity, viscosity and applied pressure) as seen by the presence of ρ, γ, μ and α in its expression.

Eqs. (4)-(6) are compared to in vivo measurements in Fig. 3 with $\gamma = 0.07$ N/m, $\mu = 0.002$ Pa s, $\rho = 1085$ kg/m³ and the values of R_T and α reported in Table S2 for each species. The difference of pressure applied by the birds during the time interval where the data have been measured is small compared to the atmospheric pressure.

With the values of the parameters mentioned above and reported in Table S2, V given in Eq. (7) varies between 0.4 and 0.8 m/s.

Supplementary Figures:

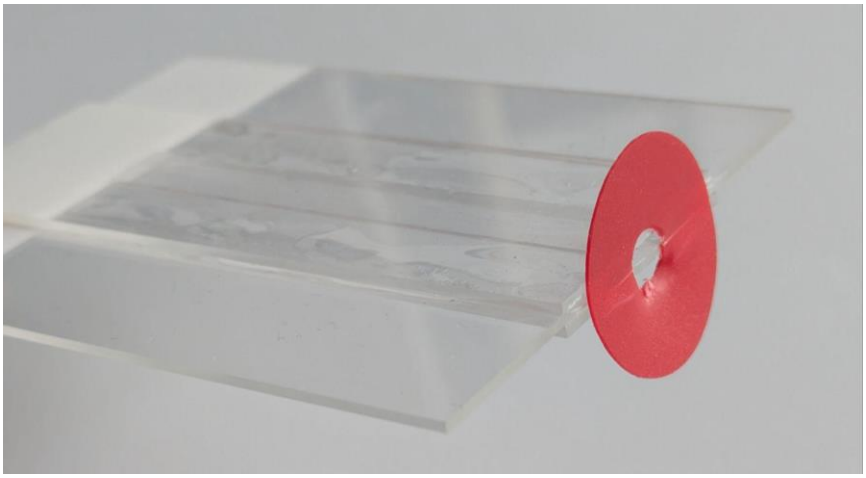

Figure S1: Image of the artificial flower. Made using 4 microscope slides glued together to make a 1mm x 6mm x 75mm hollow channel for nectar to be added. A red plastic ring is attached to the front to attract the bird.

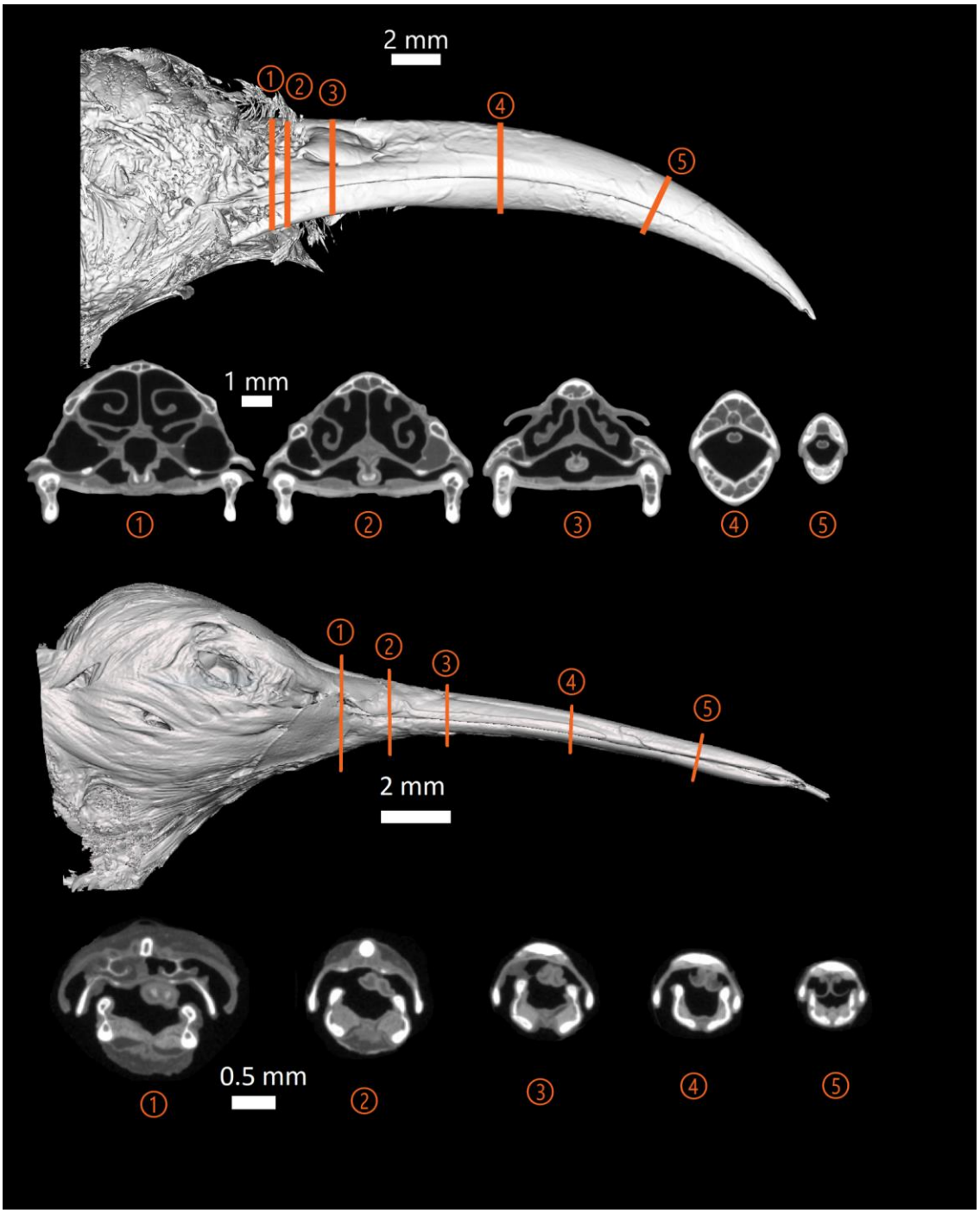

Figure S2: Cross-sections of sunbird (*Cyanomitra olivacea,* top) and hummingbird (*Calypte anna,* bottom) CT scans showing details of bill and tongue. Lateral views of a sunbird and hummingbird with multiple sectioning lines and corresponding CT cross-sections are shown from the proximal to distal regions of the bill and tongue. The shape of the sunbird tongue can be seen as a “U” shaped trough at the proximal end and an enclosed tube-like structure at the distal end. The hummingbird tongue is made of two solid rod-like structures at the proximal end that become two hollow tubular structures towards the distal end.

Supplementary tables:

Table S1: Species List

Individual	Genus	Species	Date caught (dd-mm-yy)	Location caught	Sex	Mass (grams)	Exposed culmen (mm)	Tongue insertion depth (mm)	Tongue insertion duration (s)	Licks digitized (n)
AMSB-10	*Chalcomitra*	*amethystina*	27-07-22	RWAN	M	16	28.6	2.48+-0.14	0.12+-0.01	4
GDCS-03	*Cinnyris*	*afer*	24-08-22	RWAN	M	12	26.5	5.16+-0.27	0.11+-0.01	4
OLSB-05	*Cyanomitra*	*olivacea*	19-07-24	RWAN	U	12	25.6	1.48+-0.09	0.11+-0.003	4
WBSB-01	*Cinnyris*	*talatala*	27-07-22	RWAN	M	8.5	21	0.89+-0.22	0.08+-0.01	3
MASB-01	*Nectarinia*	*famosa*	05-08-22	ZF	M	18.5	33.7	1.79+-0.14	0.08+-0.004	5
MASB-04	*Nectarinia*	*famosa*	22-08-22	ZF	M	19	31.5	0.94+-0.39	0.08+-0.007	7
MASB-09	*Nectarinia*	*famosa*	24-08-22	ZF	F	14.5	31.4	1.88+-0.23	0.07+-0.008	6
OBSB-01	*Cinnyris*	*jugularis*	19-07-23	BK	M	7.32	21.55	2.73+-0.12	0.07+-0.007	3
BTSB-01	*Anthreptes*	*malacensis*	24-07-23	GA	F	12.9	16.9	Capillary: 0.39+-0.08 Suction: 3.18+-0.26	Capillary: 0.11+-0.004 Suction: 0.08+-0.001	Capillary: 3 Suction: 4

Table S2

Species	**R_T (mm)**	**α (kPa/s)**	**Δt (ms)**	**$\Delta p/p_{atm}$**
N. famosa	0.15	329	24	0.078
N. famosa	0.15	110	12	0.013
C. afer	0.15	434	3.5	0.015
C. talatala	0.13	256	6.6	0.017
C. amethystina	0.14	240	3.8	0.009
C. olivacea	0.15	224	11	0.024
C. jugularis	0.13	199	13.5	0.027
A. malacensis	0.14	528	3	0.016

Videos:

Video S1: Video_S1.mp4

Video S2: Video_S2.mp4

Video S3: Video_S3.mp4

Video S4: Video_S4.mp4