**The inside curve: geometry and pollination biology of curved flowers.**

**Abstract**

In pollination ecology, flower and pollinator morphology are often compared in the lateral (xz) and transverse (xy) planes. Curvature along the lateral plane (‘floral curvature’) is a widespread, convergent trait with important ecological and evolutionary implications. This review summarizes the methods used to measure floral curvature, suggests a refinement to the definition of curvature, and a translation of this definition into a field-portable methodology. The revised definition considers a curve to have a degree of curvature at every infinitesimal increment along its length. Total curvature is calculated by regressing a line (e.g. a polynomial) against landmarks placed on an image, then computing curvature at many points along the fitted line and taking their sum. The utility of this metric was tested by studying the development of nectar spur curvature in Epimedium (Berberidaceae). Using this metric, differences in the development of floral curvature were detected between Epimedium koreanum and Epimedium grandiflorum var. violaceum. Inflection points are found in wild-type Epimedium grandiflorum, but are lost in the cultivated variety ‘violaceum’, resulting in loss of total curvature. The suite of functions used to quantify floral curvature in this study are available as an open-source R package ‘curvy’. The major advantages of this definition and method are 1) precision of measurement is increased without introducing expensive field equipment or computing power, 2) precision of terminology is improved by drawing from the long-standing mathematical framework for studying line-curves, and 3) the opportunity is opened for investigating the genetic basis of curvature measured at the cellular scale.

“We are beginning to understand why some hummingbird bills are long, whereas others are short, and why some hummingbird flowers are wide, whereas others are narrow. Now, why are bills of some hummingbirds and the tubes of the flowers they visit curved?” – Temeles (1996).

**The ecological function of floral curvature**

The discovery that plant-pollinator morphology is linked to function (like pollination???) (Sprengel 1793) remains foundational to understanding the assembly of plant-pollinator communities (e.g. in insects: Harder 1985, Agosta and Janzen 2005, Newman et al 2015; in hummingbirds: Feinsinger and Colwell 1978, Stiles 1995, Maglianesi et al 2014, Sonne et al 2019). These communities are structured by a range of generalists and specialists (Jordano et al 2003), their behaviours and morphology selected by competition (López‐Segoviano et al 2017), facilitation (Bergamo et al 2018), mating behaviour (Temeles et al 2000, Krauss et al 2017), and environmental filtering (Wolowski 2017). Flower and mouth-part shapes are therefore used as partial measures of plant-pollinator specificity, synthesizing patterns in morphological diversity to the assembly and evolution of communities.

Just as corolla length and diameter are influenced by bill length (and vice versa, e.g. Temeles 1996), flower and bill curvature introduce yet another dimension of specificity: length and width constrains morphological matching in the *xy* plane, while curvature additionally constrains matching in the *xz* and *yz* plane.Curvature is therefore desirable to measure, because a flower that is “more curved” could, for example, be interpreted to be more specialized than a sister species that is “less curved”. Therefore, as pollination biologists we should have standardized protocols for measuring, quantifying, and describing curvature.

The first discussion of the importance of curvature in plant-hummingbird interactions begins with Hainsworth (1973) and is first empirically studied by Stiles (1975) - though methods for measuring curvature of bills outside of an ecological context can be found much earlier (Baldwin 1931). However, a review of the literature (Table 1) reveals that a consensus has yet to be made among pollination ecologists as to what exactly we mean by *curvature* and how to measure it, which naturally affects how we analyse, interpret, and present these data. Here, we summarize the approaches to measuring curvature within the field of plant-hummingbird pollination, identify commonalities and shortcomings, and offer a solution with the aim of standardizing how curvature is studied within the field of pollination biology.

Benefit of our method: if there is a genetic base

“Geometric morphometric methods of capturing information about curves or outlines of organismal structures may be used in conjunction with canonical variates analysis (CVA) to assign specimens to groups or populations based on their shapes.” (Sheets et al 2006, Front. Zoo.).

*Other notable methods*

Two methods stand out as having components that may lend themselves useful to the geometric morphometric toolkit. Campos et al (2015) model the curves of moth-pollinated flowers as exponents of *e*, while Cosgrove (1990) fit cubic polynomials to cucumber hypocotyls. In both cases, curvature is approximated by a function. Describing curve as polynomial functions is appealing because measures such as loci of maximum curvature, mean curvature, and total curvature (Rutter 2000) can be calculated. Parameters from curve fitting may also be useful in comparisons of things that are more or less curved. Thus, we propose that the existing methods for fitting polynomial functions to areas delimited by landmarks be adopted for studies of floral form with a focus on curvature.

Because the term *curvature* has been defined in the field of differential geometry as ‘the change in the direction of the tangent with respect to arc length’ (Jia 2018), and that this definition also has utility in an ecological context, we suggest that *curvature* be reserved for this meaning. We suggest explicit use of the terms *angle of declension* or *arc:chord ratio* in future studies that utilize these methods.

We propose that the term *curve* be used to describe the mathematical function tissue/organ

-The ‘Avena Curvature Test’ estimates curvature using a protractor. This principle was used widely in plant physiology and appears occasionally in ecological studies (eg Travers et al 2003, to measure nectar spur curvature), but doesn’t measure curvature as much as it measures the angle between some arbitrary plane (usually the ground) and the tip of the organ of interest.

-Plant physiologists talk about curvature in the context of growth in relation to gravity (graviception). In this field, curvature is discussed as the rate of change of the angle of a material element (e.g. a cell) with respect to its position (s). See: Bastien et al 2014.

-Cosgrove (1990) uses a cubic polynomial to describe curvature of cucumber hypocotyls.

-importance of the lateral view in pollination biology

Google scholar: “corolla curvature”, “flower curvature”, “hummingbirds curvature”

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| Citation | System | Method |
| Baldwin et al 1931 | Measurements of birds | Inverse radius method |
| Hamilton 1975 | Comparative Behavior of the American Avocet and the Black-Necked Stilt(Recurvirostridae) | Radius of curvature |
| Stiles 1975 | Corolla morphology of *Heliconia* and bill morphology of nine hummingbird species at La Selva, Costa Rica. | Qualitative (e.g. ‘strongly curved, moderately curved, etc.). |
| Buttrose et al 1977 | Significance of curvature of style branches in *Hibiscus trionum* for pollination | Qualitative |
| Gill and Wolf 1978 | Sunbird bill diversity and abilities to extract nectar from Kenyan *Leonotis nepetifolia* (Lamiaceae). | Curvature is “the ratio x/y, where x is the bill length measured from the anterior edge of the nostril and y is the maximum height above the longest chord of the bill.” |
| Paton and Collins 1989, Collins 2008 | Correlates (Geography, Age, Sex, Tongue structure, foraging mode) of bill morphology on nectar extraction 198 hummers (and other birds). | “Bill curvatures were defined as the maximum perpendicular height of the bottom edge of the culmen above the chord from the gape to the tip of the bill, divided by the length of this  chord”. |
| Stiles 1995 | Effects of bill morphology on insect foraging strategy by 11 species of hummingbirds at La Selva, Costa Rica. | Arc:chord ratio of exposed culmen – silhouette projected onto a screen |
| McIntyre and Browne 1996 | Phototropism in *Helianthus* and effects on cotyledon curvature | Protractor |
| Cotton 1998 | Survey and description of 16 hummingbird species occurring at  Amacayacu National Park, Colombia. | Qualitative |
| Temeles et al 2000 | Sexual dimorphism of bill shape in Purple-throated caribs (*Eulampis jugularis*), pollinatiors of *Heliconia* at Quilesse Reserve, Saint Lucia. | Not described, but presumably the same method as Temeles 2009, Temeles 2010. |
| Borgella et al 2001 | Effects of bill morphology (21 hummingbird spp.) on pollen loads (35 plant spp.) at Coto Brus, Costa Rica. | For species with decurved bills, we also used a ruler to measure a few bills along the curve to calculate a correction factor. (Not reproducible) |
| Travers et al 2003 | Nectar spurs of *Impatiens* spp. and Ruby-throated hummingbird (*Archilochus colubris*) at Franklin  County, Massachusetts. | “Angle at which the spur deviates from an arbitrary line drawn through the flower.” (Angle of deflection) |
| Temeles 2003 | Sexual dimorphism of bill shape in Purple-throated caribs (*Eulampis jugularis*), pollinatiors of *Heliconia* at Quilesse Reserve, Saint Lucia. | Not described, but presumably the same method as Temeles 2010, Temeles 2009. |
| Collins 2008 | Foraging efficiency from artificial and natural (15 spp.) flowers by 4 species of hummingbirds at Monteverde, Costa Rica | Paton and Collins 1989 |
| Stiles 2008 | Correlations of bill morphology to the elevational distributions of 150 spp. of hummingbirds in the Andes. | Arc:chord ratio of exposed culmen |
| Martén-Rodríguez et al 2009 | Testing the pollination syndrome hypothesis in Antillean Gesneriaceae. | Protractor aligned with the dorsal side of the corolla tube. (Angle of deflection) |
| Temeles et al 2009 | Effects of natural (*Heliconia*) and artificialflower morphologies on foraging performance of Purple-throated caribs (*Eulampis jugularis*) at Saint Lucia. | K=1/R ‘Inverse radius’/angle of declension method. |
| Kawabata et al 2009 | Quantitative analysis of corolla shapes and petal contours in single-flower cultivars of *Lisianthus*. | Something like geomorph?? |
| Temeles et al 2010 | Sexual dimorphism of bill shape in 21 species of Central and South American hummingbirds. | K=1/R ‘Inverse radius’/angle of declension method. |
| **Berns and Adams 2010**  (summarizes the problems with common bill morphology methods and Fig 1 visualizes the methods too!!!) | Sexual dimorphism of bill shape in Black-chinned hummingbird (*Archilochus alexandri*) and Ruby-throated hummingbird (*Archilochus colubris*). | Comparison of 3 methods: Paton and Collins 1989 (maxilla), Stiles 1975 (mandible), Temeles 2009 (inverse radius). |
| Berns and Adams 2013 | Sexual dimorphism of bill shape in 219 hummingbird spp. | Geometric morphometrics (” Thin-plate spline deformation grids revealed that in these species, females have longer, more curved bills at both the tip and main body of the bill relative to the mean, while males have straighter and shorter bills and M. minima has the largest magnitude of sexual shape dimorphism” – used GeoMorphometrics but in the end resort to just saying that the deformations of the spline ‘look different’.) |
| Maglianesi et al 2014 | Trait matching and resource use in a plant-hummingbird network, La Selva, Costa Rica. | Angle of deflection |
| Alexandre et al 2015 | QTL analysis comparing hummingbird pollinated and generalist *Rhytidophyllum* flowers(Gesneriaceae). | Angle between flower opening and flower base. |
| Campos et al 2015 | Generating 3D printed flowers to test efficacy of moth pollination | “Curvature parameter” |
| Maglianesi et al 2015a | Differential preferences of artificial and natural (65 spp.) flower populations visited by 3 species of hummingbird in Braulio Carrillo National Park, Costa Rica. | Angle of deflection |
| Maglianesi et al 2015b | Plant-pollinator specialization along an elevational gradient at Braulio Carrillo National Park, Costa Rica. 21 hummingbird spp. and 208 plant species examined. | Angle of deflection |
| Rico-Guevara and Araya-Salas 2015 | Bills as weapons in lekking *Phaethornis longirostris* at La Selva, Costa Rica. | Arc:chord ratio of exposed culmen. |
| Berger et al 2017 | Quantifying morphological modifications to floral form in gene knockdowns in *Fedia graciliflora*. | Landmark-based geometric morphometrics |
| Lagomarsino et al 2017 | Evolution of pollination syndromes in Andean Campanulaceae. | Arc:chord ratio of corolla midline and base-to-opening line. |
| Joly et al 2017 | Analysis of polliation syndromes in Antillean Gesneriaceae. | Geometric morphometrics. “PC2 represents variation in corolla curvature” (descriptive). |
| Hadley et al 2018 | Effects of forest fragmentation on hummingbird bill morphologies (19 spp.) representative of specialization. Coto Brus, Costa Rica. | Bill curvature was calculated as the angle between a horizontal line across the top of the bill and a line running the length of the bill. (Arc:chord ratio) |
| Dellinger et al 2018 | Floral trait changes correlated with the repeated shifts away from buzz‐pollination in the Melastomataceae. | Qualitative |
| Pour et al 2018 | Curvature-based pattern recognition for cultivar classification of *Anthurium* (Araceae) flowers | Calculated *k* (the rate of change in the direction of the tangent line at that point with respect to arc length) for *n* points along the flower. |
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Do Sicklebills really NEED *Centropogon*? (Jermy 1999)

MacLeod (2010) describes problems with the sliding semi-landmark method.

Tatsuta et al (2017) (entomological science) is a good review to base this review off of.

Bonhomme et al (2014) have developed an R package (Momocs 0.2) for outline analysis, but only for closed curves. However, Momocs 0.9.8.1 supports open curves.

Rohlf (1990) describes procedures for open outlines. Updated in 1993 by Marcus et al. in “Advances in Morphometrics”.

Takahashi (2006) uses polynomials to estimate pelvis curvature in humans.

Gu et al (2008) calculate mean curvature of human hip joints.

Coolidge (1952) describes the ‘unsatisfactory story of curvature’

Terral et al (2003) fit polynomials to olive seeds (olea dataset in Momocs)

Klingengburg (2010) reviews “evolution and development of shape”.

**Materials and Methods**

**Literature Search**

The literature was sourced by querying Google Scholar (Also do second, up-to-date sweep on WOS) for the terms "corolla curvature", "flower curvature", and "hummingbird curvature". We limit our analysis to hummingbird pollination because the literature for any type of plant-animal mutualism is plentiful, and though the general concepts we discuss should be portable to other pollination systems, the practical methodology will need to be customized to each broad class of pollinator (e.g. bats, moths, bees, flies, passerine birds).

**UBC Botanical Garden**

We tested the utility of this curvature metric by studying floral development in Epimedium grandiflorum C.Morren and Epimedium koreanum Nakai (Berberidaceae, Table 1 - sample sizes). Flower size was measured daily from April 3rd to May XXX, 2019 at the UBC Botanical Garden (Supp Mat 1). By correlating changes in flower size to developmental landmarks (Supp Fig 1), we were able to define 7 discrete stages of flower development (Table 2, Figure 5 - photographs of the stages). We then sampled 5 flowers from each stage of both species and photographed them at 5.0x using a Zeiss AxioCam 301.

Supp Mat 1:

In E. grandiflorum, the distance separating the outer sepals (sensu Stearn 2002) was measured using dial calipers (graduation = 0.1 mm), until the length of the inner sepals exceeded the length of the outer sepals (stage 4, Table 2 - describing the stages). From this point onwards, the inner sepal distance was measured. Because the aestivation was imbricate, we measured the sepals of the major axis (Figure demonstrating measurement technique). In E. koreanum, the inner sepals lack pigmentation and adhere closely to the petals, making them difficult to measure accurately in situ. For this reason, the outer sepals were measured until they abscised (stage 5, table 2). Flowers were sampled opportunistically and preserved in 70% ethanol.

**Microscopy**

Preserved flowers were later transferred to a glass slide and imaged using a stereo microscope (Zeiss Stemi 508) at 0.63x. Specimens that did not fit within the field of view were imaged 2x or 3x and the images joined using the Stitching Plugin (Preibisch et al 2009) in the Fiji distribution of ImageJ2 (Schindelin et al 2012, Rueden et al 2017).

**Landmarking**

1. Rotate the photographs so that the opening of the corolla tube is parallel to the y-axis.

2. Build tps file (a file listing all specimens) using tpsUtil. This tps file is used by tpsdig to add landmarks to.

3. Landmark specimens from tps file using tpsDig (steps 1 and 2 will soon be possible in MomX and could be done in geomorph). Landmarks used to measure the dorsal arc are 1) the farthest point on the apex of the spur before the spur diminishes to a tip (E. violaceum) or widens into a nectar bucket (E. koreanum), and 2) the dorsal point at which the spur widens to become an attachment point for the petal to the stem(?). 13 semi-landmarks are placed between them (15 points total).

4. Curve points are drawn in tpsDig using the “pencil tool”, from landmark 1 (see above) to landmark 2. Following the placement of points, a curve is drawn that connects them. Right-click the curve and select “Resample Curve” and then space the points evenly “by length”. Manually adjust re-sampled points onto specimen and again “resample curve”. This does not usually need to be repeated more than twice.

5.1 Set scale by going to Options->image tools and typing in desired length and units. Press ‘set scale’ and then click on both ends of the scale bar in your image. Then go back to the image options box and select ‘OK’.

5.2 Semi-landmarks need to be treated like landmarks for curve-fitting. To do this, use the ‘Append tps curve to landmarks’ function in tpsUtil. <https://www.researchgate.net/post/Which_software_should_I_use_for_placing_sliding_semilandmarks>

6. Import into R using from\_tps() function from Momit.

7. Superimpose the shape using the fgProcrustes() function in Momocs.

8. Calculate polynomials and plot curves following the “Olea” example at: https://momx.github.io/Momocs/reference/opoly.html

How do I decide what degree polynomial to use? Consult: Rohlf 1990…

X. Need to carry out multivariate stats on coefficients from polynomial equations. The eight regression parameters ‘bi’ were used as quantitative variables (Table 3). A CVA was then carried out on 1500 stones and nine variables (the eight quantitative and one qualitative expressing 50 classes corresponding to the 50 wild populations and cultivars).

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**Outline**

**Intro –** ecological significance of curvature, objective of this paper, our definition of curvature

**Materials and Methods**  - literature search and review, R pipeline, Epimedium study

**Results –** lit review, R pipeline applied to Epimedium study

**Discussion –** compare the different curvature definitions, how this R pipeline could be used to study curvature

**Introduction**

#### The ecological function of floral curvature aka why is flower shape (in general) interesting/important?

What does curvature mean to the pollination ecologist? The curvature of hummingbird bills, insect proboscises, and flowers has been used as evidence for specialization, niche partitioning, co-evolution, and a suite of other ecological and evolutionary processes. However,

For effective pollination, the phenology and morphology of the flower operates in concert with the ethological habits of the pollinator. This is exemplified by the phenomena of dichogamy, pigmentation, and constancy (Sprengel 1793). The shape and size of a flower also plays a role in effective pollination. Grant (1950) proposed that 'mutations causing the petals to grow up as a fused corolla tube around the stamens' may have been one of the primitive adaptations promoting flower constancy. Today it is generally recognized that plants with long and/or narrow corolla tubes promote visitation by hummingbirds, flies, lepitoptrans, and long-tongued hymenoptrans, and exclude those animals (e.g. beetles) unable to reach the inner hypanthium for nectar. While the co-variation of corolla length and diameter have been considered in the context of flower-hummingbird bill diversity (Temeles XXX), curvature has not received the same attention.

Our discussion focuses on those flowers with fused (Asteridds) or invaginated (Rosidds) petals that form a corolla tube or nectar spur, respectively. For brevity we refer to corolla tubes, as the implications are likely similar for spurs. The morphology of corolla tubes evolve through three spatial dimensions, length, width, and curvature. Each dimension can be thought of as a set of filters that act heirarchically, mirroring the order in which these features likely evolved. Length is the primary filter: a pollinator that cannot lick (i.e. has a tongue for extending their feeding range beyond their mouth) cannot feed from a tube with length >0. In Grant's (1950) example, this would exclude beetles while including flies and bees. Corolla diameter (width) further filters pollinators. In the case of hummingbirds, long-billed hummingbirds with an advanced reach still cannot access flower tubes adapted to small-billed hummingbirds with small diameters (Temeles XXX, Grant XXX). Curvature enables the corolla tube to occupy a third dimension, presumably filtering for the subset of pollinators able to access the inner hypanthium. In the case of hummingbirds, straight-billed species can only access the flower as much as the horizontal (x) length of the flower permits (Figure 1). The vertical length is as inaccessible as if the flower was a straight and long. For curve-billed species (e.g.) Phaethornis (Trochilidae)…

Numerous studies have measured plant-pollinator curvature in varying ecological contexts, but as pollination ecologists there is yet to be a consensus as to what is meant by *curvature*. The objective of this paper is therefore to review the methods used to estimate floral curvature (2D) and propose a standardized definition to be used in the field of pollination ecology.

**Results and Discussion**

Table 1 summarises the techniques used to measure curvature in the field of plant-hummingbird pollination. Four common approaches to measuring curvature are identified and evaluated. First, there are qualitative descriptions of curvature, which have generally been out of use since the 1970s. Second, the ‘arc:chord method’ which computes curvature as a ratio of two lines: a straight line (chord) from tip to base (of the flower or bill) and a line that traverses a path along the length of the flower/bill (arc length, Figure 1). Third, the ‘angle of deflection’ method which defines curvature as the angle between the base of the flower/bill and its tip (Figure 2). Fourth, the use of geometric morphometrics, which quantifies differences between shapes by comparing configurations of homologous points (landmarks) between samples.

The arc:chord and angle of deflection method, though perhaps the most convenient for taking *in situ* measurements, have shortcomings that have been summarised by Berns and Adams (2010). For the arc:chord method, the primary concern is that there are numerous curves with equal arc length that can connect the base and tip of a flower/bill. It is therefore possible for many different shapes to yield the same arc:chord ratio (Figure 1). For the angle of deflection method, a curve is approximated with the segment of a circle. For the many flower and bill shapes that deviate from having constant curvature, this method falls short (e.g. neotropical Campanulaceae).

Starting in 2010, landmark-based geometric morphometrics (LBGM) emerges in the pollination literature. This is a large step forward for the pollination biologist, because LBGM offers a statistical toolkit for measuring, quantifying, and comparing shape and size, as well as their covariation with variables of interest. Since its establishment by Bookstein (1997), the ongoing development of geometric morphometrics has been punctuated by reviews: Adams et al (2004), Adams et al (2013), and for a plant-focused review see Remagnino et al (2016).

For the objectives of the pollination biologist, landmark-based geometric morphometrics may often be the right solution. However, we posit that the use of LBGM has been favoured over a similar method, outline-based geometric morphometrics (OBGM), largely because of historic reasons within the morphometrics community (XXX). The common critique of OBGM is that X,Y,Z..

At present, we believe that OBGM has been refined and accepted to a point where it is of use to the pollination biology community. Indeed, these methods have emerged in the evo-devo and plant physiology literature (XXX). Outline-based methods use non-homologous landmarks to first demarcate a structure of interest. These pseudolandmarks are then used as coordinates to which a curve can be fitted. The coefficients describing this curve can then be used in multivariate analyses.

The limitation of LBGM in studying floral form is that this method is concerned with quantifying configurations of landmarks (entire shapes), not curves or segments of shapes. In LBGM, configurations of landmarks are packaged as points in shape space (Kendell XXX), and statistical analyses (e.g. PCA, XXX) are run on these points. Therefore, studies that have used this technique to analyse biological forms are able to determine if overall shapes differ between samples, taxa, etc., but are ultimately limited to making descriptive statements about how segments of shapes appear to have different curvatures (e.g. Bern and Adams 2013).

**Discussion**

### What is curvature?

Given the ecological importance of diameter and length, flowers are often studied from the axial and lateral view, respectively. In the lateral view, curves can be traced along the dorsal and ventral petals to estimate length and curvature (Fig XXX). In the case of the curve that exists on a 2-D (e.g. lateral) plane, curvature is the measure of how much a line deviates from being straight.

\*\*Figure illustrating the above paragraph

A curvature definition should be

**Random writing from “writing.txt”**

Flower constancy, the restricted visitation by a pollinator to one flower 'type' (Waser 1986) neccesitates morphological and phenological diversity. A community of plants sharing pollinators can individually benefit from reducing interspecific pollen transfer (Dobbs 1750) - floral properties that encourage constancy can be adaptive. Constancy can be mediated by phenology (XXX), floral rewards (XXX), and morphology (XXX). Considering the latter, Grant (1950) speculated that 'mutations causing the petals to grow up as a fused corolla tube around the stamens' may have been one of the primitive morphological adaptations promoting flower constancy. Today it is generally recognized that plants with long and/or narrow corolla tubes promote visitation by hummingbirds, flies, lepitoptrans, and long-tongued hymenoptrans, and exclude those animals (e.g. beetles) unable to reach the inner hypanthium for nectar. While the co-variation of corolla length and diameter have been considered in the context of flower-hummingbird bill diversity (Temeles XXX), curvature has not received the same close attention.

Our discussion focuses on those flowers with fused (Asteridds) or invaginated (Rosidds) petals that form a corolla tube or nectar spur, respectively. For brevity we continue by focusing on corolla tubes, as the implications appear to be identical for spurs. The morphology of corolla tubes evolve through three spatial dimensions, length, width, and curvature. Each dimension can be thought of as a set of filters that act heirarchically, mirroring the order in which these features likely evolved. Length is the primary filter: a pollinator that cannot lick (i.e. has a tongue for extending their feeding range beyond their mouth) cannot feed from a tube with length >0. In Grant's (1950) example, this would exclude beetles while including flies and bees. Corolla diameter further filters pollinators. In the case of hummingbirds, long-billed hummingbirds with an advanced reach still cannot access flower tubes adapted to small-billed hummingbirds with small diameters (Temeles XXX, Grant XXX). Curvature enables the corolla tube to occupy a third dimension, applying yet another filter to those pollinators able to access the inner hypanthium. In the case of hummingbirds, straight-billed species can only access the flower as much as the horizontal (x) length of the flower permits. The vertical length is as inaccessible as if the flower was a straight and long. For curve-billed species (e.g.) Phaethornis (Trochilidae).

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#### The ecological function of floral curvature aka why is flower shape (in general) interesting/important?

Many aspects of the floral phenotype have increasingly been found to be adaptive, often satisfying the age-old "why" of the diversity and function of floral forms. Nonetheless, certain components have yet to be fully understood. In order to examine this particular aspect of floral morphology, curvature, it is useful to return to first principles.

In the seed plants, pollen is necessary for fertilization (Bradley 1717), but the ideal pollen is often that which comes from another individual plant of the same species (red queen? XXX). Pollination by animals is an adaptation that can both export and import intraspecific pollen (Miller 1721) while precluding interspecific pollen transfer (Dobbs 1750). For effective pollination, the phenology and morphology of the flower operates in concert with the ethological habits of the pollinator. This is exemplified by the phenomena of dichogamy, pigmentation, and constancy (Sprengel 1793). The shape and size of a flower also plays a role in effective pollination. Grant (1950) proposed that 'mutations causing the petals to grow up as a fused corolla tube around the stamens' may have been one of the primitive adaptations promoting flower constancy. Today it is generally recognized that plants with long and/or narrow corolla tubes promote visitation by hummingbirds, flies, lepitoptrans, and long-tongued hymenoptrans, and exclude those animals (e.g. beetles) unable to reach the inner hypanthium for nectar. While the co-variation of corolla length and diameter have been considered in the context of flower-hummingbird bill diversity (Temeles XXX), curvature has not received the same attention.

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Just as corolla length and diameter are influenced by bill length [and vice versa, e.g. @temeles1996new], flower and bill curvature introduce yet another dimension of specificity: length and width constrains morphological matching in the xy plane, while curvature additionally constrains matching in the xz and yz plane. Curvature is therefore desirable to measure, because a flower that is "more curved" could, for example, be interpreted to be more specialized than a sister species that is "less curved". Therefore, as pollination biologists we should have standardized protocols for measuring, quantifying, and describing curvature.

The first discussion of the importance of curvature in plant-hummingbird interactions begins with Hainsworth [-@hainsworth1973tongue] and is first empirically studied by @stiles1975ecology - though methods for measuring curvature of bills outside of an ecological context can be found much earlier (@baldwin1931measurements). However, a review of the literature ([Table 1](#tables\_lit\_review)) reveals that a consensus has yet to be made among pollination ecologists as to what exactly we mean by \*curvature\* and how to measure it, which naturally affects how we analyse, interpret, and present these data. Here, we summarize the approaches to measuring curvature within the field of plant-hummingbird pollination, identify commonalities and shortcomings, and offer a solution with the aim of standardizing how curvature is studied within the field of pollination ecology [\*sensu\* @faegri1979the].

"On each expedition the bee does not fly from a flower of one kind to a flower of another, but flies from one violet, say, to another violet, and never meddles with another flower until it has got back to the hive." Aristotle, in History of Animals, IX, 40, trans. D'Arcy Wentworth Thompson.