*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.

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.

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)

-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.

Table 1. Summary of studies using curvature in pollination ecology.

Table S1. Other studies using curvature metrics.

**Epimedium study**

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).

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.

**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).

**Random writing from RMarkdown file**

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.

"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.