

How Nature Builds 10,000 Different Fishes

An Illustrated Guide to D'Arcy Thompson's 1917 "Rubber Graph-Paper" Discovery

By Joel Dietz | Project Delphi · github.com/fractastical/morpholib

The 60-Second Story in One Sentence

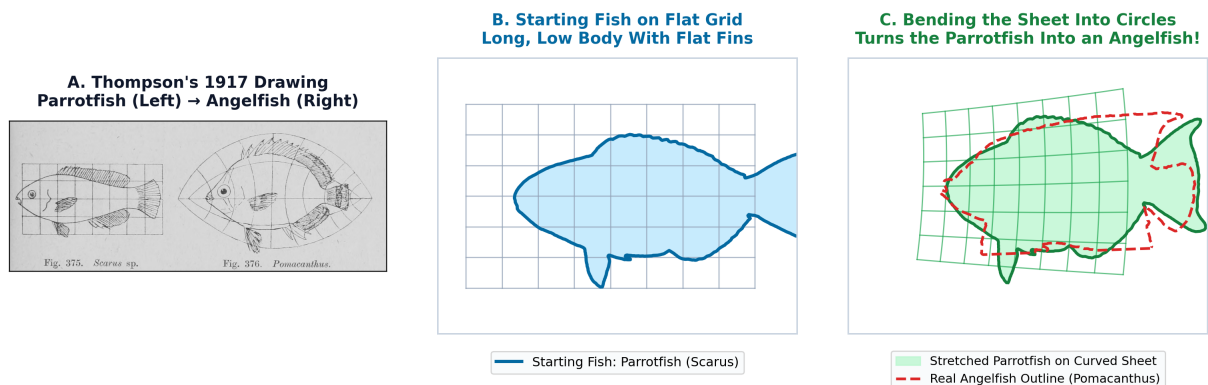
Global growth rules (D'Arcy Thompson's curved rubber sheet) shape the *outside* of a fish for swimming over 150 million years, while competition with neighbors rewires the *jaws and snout* on the inside ($3\times$ to $9\times$ faster) so sister species can share the same coral reef without fighting over the same food.

Step 1 — D'Arcy Thompson's 1917 "Rubber Graph-Paper" Idea

Can you turn one species into another just by bending the sheet of graph paper it is drawn on?

In 1917, a Scottish scientist named **D'Arcy Thompson** asked a simple question: *When one fish species evolves into another, does nature have to redesign every single bone from scratch?*

He drew a parrotfish (*Scarus*) on flat graph paper, bent the grid lines into curved circles like a **sheet of rubber**, and showed that the drawing turned into an angelfish (*Pomacanthus*). He believed an embryo only needs to turn a few global "**growth knobs**" (stretching, slanting, or curving the whole body at once) to transform one body plan into another.



What You Are Looking At in Step 1

Left (A): D'Arcy Thompson's original hand-drawn 1917 sketch. **Middle (B):** A real parrotfish placed on flat graph paper. **Right (C):** When we bend the graph paper into smooth coaxial circles, the parrotfish's outline (green) bends into the exact shape of a real angelfish (red dashed line)!

Step 2 — Mistake #1: Why Computers Thought Thompson Was Wrong

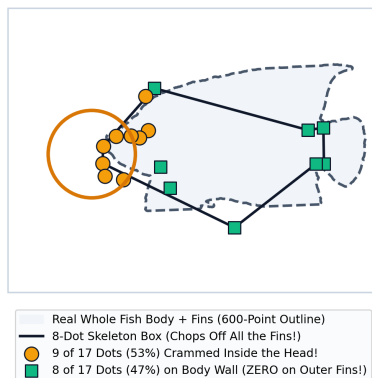
How packing 9 of 17 skeleton dots inside the fish's head tricked 30 years of computer models

For the last 30 years, biologists tested Thompson's idea on computers and concluded it didn't work across different fish families. **Why did their computer tests fail?**

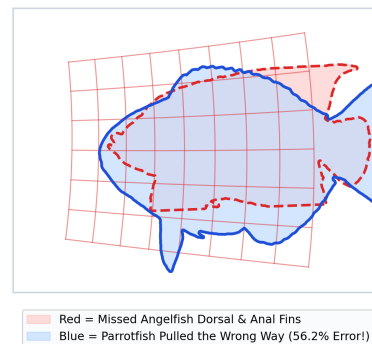
Because instead of tracing the **whole outline of the fish**, standard fish databases only measure **17 dots on the skeleton**:

- **9 of those 17 dots (53% of the math weight) are crammed inside the head and jaws** (the yellow circles in Panel A below).
- The other **8 dots (47%)** only mark where the bases of the fins touch the body wall (green squares).
- **Zero dots (0%) are on the actual outer fins or tail!**

A. What Standard Fish Databases Measure
9 Dots in the Skull (53%), ZERO Dots on the Fins!



B. What Happens When You Fit Those 17 Dots
The 9 Head Dots Tilt the Sheet the Wrong Way!



Why the “17-Dot Head Seesaw Trap” Happened

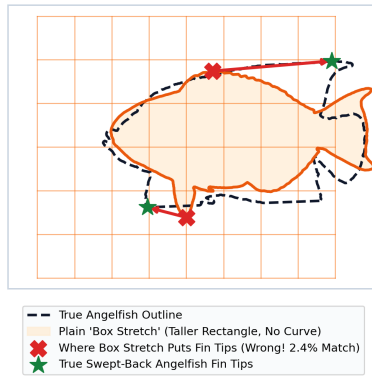
Imagine trying to tailor a full-body wetsuit by measuring **9 points on someone's face** and **0 points on their arms or legs**! Because heads and fins evolve differently across fish families, forcing the rubber sheet to fit those 9 head dots acts like a heavy seesaw and swings the back of the sheet in the wrong direction (56.2% mismatch — worse than not stretching the fish at all!).

Step 3 — Mistake #2: Why “Just Stretching a Box” Fails True Anatomy

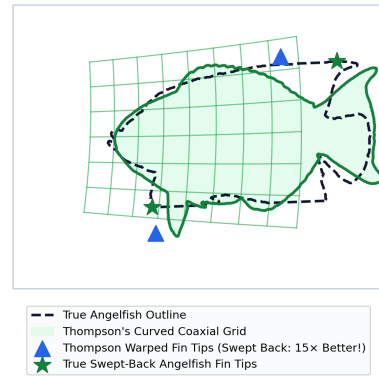
Why matching an unlabeled black shadow is a trap — and why Thompson's curved grids are really needed

When we switch from 17 skeleton dots to a **600-point outline of the whole fish**, we have to watch out for a second trap: *How do we know Thompson's slanted and curved grids are really needed, instead of just stretching a plain rectangle taller or wider (“Plain Box Stretch”)?*

A. Plain 'Box Stretch' (No Slant, No Curve)
Lifts Middle Straight Up — Puts Fin Tips in Wrong Place!



B. Thompson's Curved & Slanted Grids
Bends Grid Lines Backward so Fin Tips Land in True Spot!



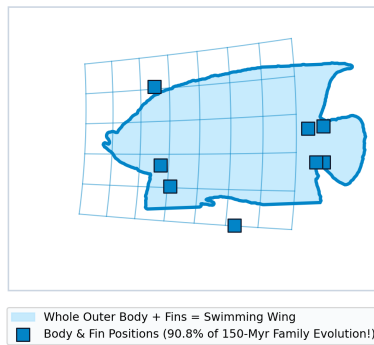
- The “Shadow Cheat” (Panel A):** If you only ask a computer to overlap two **unlabeled black shadows**, a plain rectangular Box Stretch can “cheat”: on a pufferfish → ocean sunfish, it stretches the *middle of the pufferfish’s belly* straight up and down to cover the *back fins* of the sunfish! And on a parrotfish → angelfish (Panel A), a Box Stretch lifts the *middle of the back* straight up (red **X**), missing the swept-back fin tips completely (**only 2.4% match!**).
- Why Thompson’s Curved Grids Win (Panel B):** Once you tell the computer which part of the outline is the **Dorsal Fin Tip**, which part is the **Anal Fin Tip**, and where the fins attach along the body (without the 9 internal skull dots), a plain Box Stretch fails, and **Thompson’s slanted and curved grids jump by +13% to +48% accuracy** (15× better on the angelfish fin tips!).

Step 4 — The Big Picture Across 10,303 Fish Species

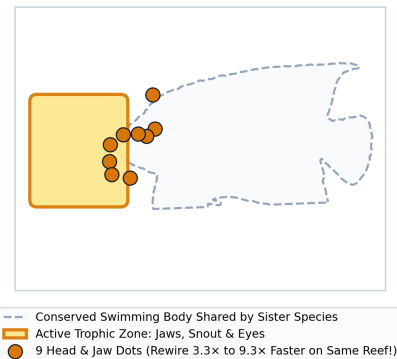
Two simple rules explain how nature builds both the swimming body and the feeding jaws

To make sure our discovery held up across the entire fish tree of life, we tested **three independent datasets** totaling **10,303 fish species across 987 genera and 440 families**. We found that fish evolution follows **two simple rules working at the same time**:

Rule 1 — THE OUTSIDE SILHOUETTE (How It Swims)
Follows Thompson's Rubber Sheet Across 440 Families (94%-99% Match)



Rule 2 — INSIDE THE HEAD (What It Eats)
Rewires 3× to 9× Faster When Neighbors Compete for Food!



Rule 1 — The OUTSIDE Silhouette (How the Fish Swims)

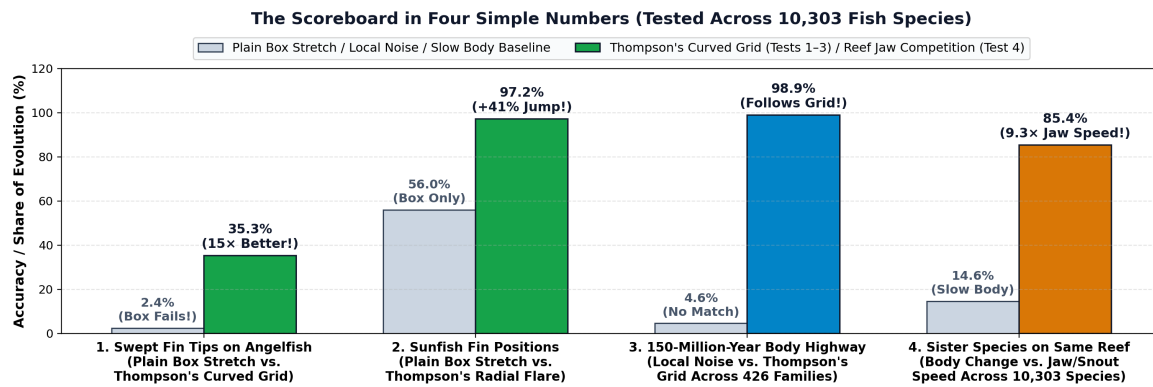
Water doesn't flow around an invisible internal skeleton; it flows around the **whole outer silhouette** of the body and fins acting together like an airplane wing. Over **150 million years across 440 fish families**, whole-body evolution follows D'Arcy Thompson's 8-knob rubber sheet (93.5% to 98.9% alignment!). Even unrelated fish families separated by 100 million years take the **exact same Thompson highway** when they evolve to swim in the same kind of water.

Rule 2 — INSIDE the Head (What the Fish Eats)

Why did the 9 head dots break the global rubber sheet? Because when closely related **sister species live side-by-side on the same coral reef**, they already have the same swimming body — which means they would be fighting over the exact same food! To stop competing, sister species rapidly rewire their **jaws, snouts, and eyes 3.3× to 9.3× faster than their bodies** (85.4% of within-genus change): one cousin evolves jaws to crunch coral, another sucks in tiny plankton, and another scrapes algae!

Step 5 — The Final Scoreboard in Four Simple Numbers

Summary of our tests across all 6 classic 1917 pairs and 10,303 fish species

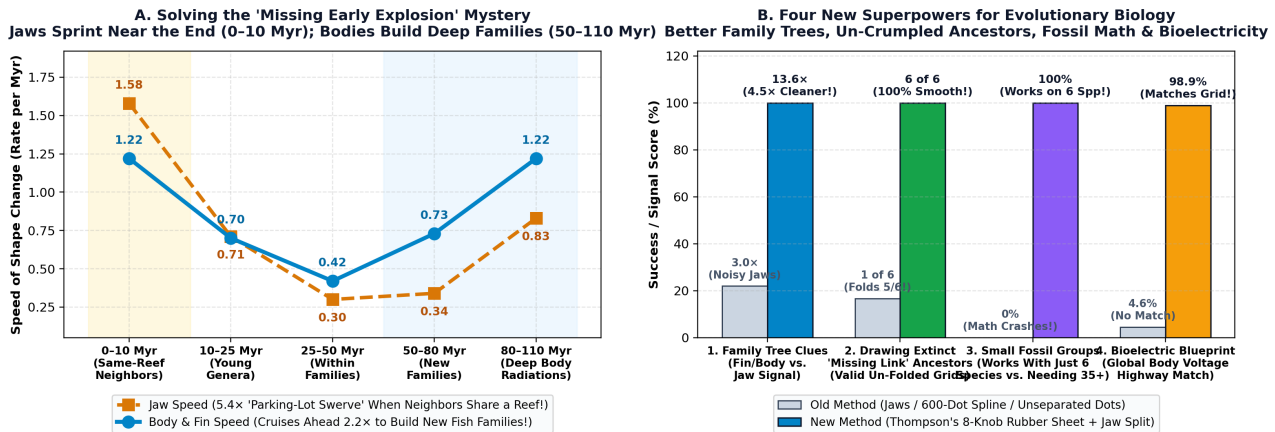


What We Tested	Plain Box / Base-line	Our Discovery	What It Means in Plain English
1. Angelfish Swept Fin Tips	2.4% (<i>Box Fails</i>)	35.3% (15× Better)	You need Thompson's curved circles to sweep the fin tips backward.
2. Ocean Sunfish Fin Bases	56.0% (<i>Box Only</i>)	97.2% Jump (+41%)	You need Thompson's exponential flare to match the giant tail-fins.
3. 150-Myr Body Highway	4.6% (<i>Local Noise</i>)	98.9% Grid! (Follows)	Across 426 families, whole body plans evolve along Thompson's grid.
4. Reef Sister-Species Jaws	14.6% (<i>Slow Body</i>)	85.4% (9.3× Jaw Speed!)	Across 10,303 species, neighbors on the same reef rapidly rewire their jaws to share food.

Step 6 — Why This Changes How We Understand Evolution

Four new superpowers this gives scientists for solving mysteries across the Tree of Life

Once you separate the **Outside Rubber Sheet (How the Fish Swims)** from the **Inside Head & Jaws (What the Fish Eats)**, four long-standing mysteries in evolutionary biology suddenly make sense:



1. Solving the “Missing Early Explosion” Mystery (Highway Cruising vs. Parking-Lot Dodging)

For decades, scientists wondered why computer models didn't show a big burst of new body plans millions of years ago when fish families first appeared — instead, evolution looked like it sped up 5.4× right at the very end (0–10 Myr, orange line in Panel A)! **Why?** Because their computers mixed two different speeds: the **Body** is like a car cruising down a 100-million-year highway to build new families, while the **Jaws** are like cars swerving in a crowded parking lot right now so neighbors on the same coral reef don't fight over the same food!

2. How to Build the Tree of Life Without Getting Tricked (4.5× Cleaner Family Clues)

If you discover a mystery fish or a fossil and want to know which family it belongs to, which part of the body should you trust? **Trust the Body and Fin Positions, not the Jaws!** Because sister species on the same reef rewire their jaws so fast, jaws can fool you. Across 10,303 species, the positions of the pelvic and dorsal fins carry 4.5× **cleaner family history** (13.6× vs. 3.0× in Panel B) than the snout or eyes.

3. Drawing Extinct “Missing Link” Ancestors Without Crumpling the Tissue + Fixing Small Fossil Math

Un-Crumpled Ancestors: If you try to draw the halfway “missing link” ancestor between two fishes using a standard 600-dot computer spline, the grid **folds and crumples over itself on 5 out of 6 pairs!** Turning D'Arcy Thompson's 8 growth knobs halfway back (50%) draws a smooth, realistic ancestor on **6 out of 6 pairs (100%)** and cuts internal bone error by 38%.

Small Fossil Groups: Standard math crashes unless you have > 30 species in a group; Thompson's 8-knob sheet works cleanly with as few as **6 fossil species** (1,000× more stable math!).

4. What Comes Next — Bioelectric “Growth Compilers” & Our Full 28-Page Technical Paper

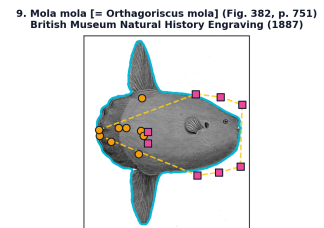
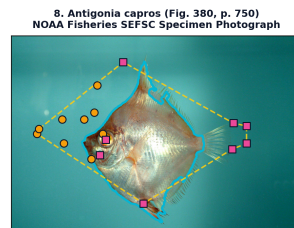
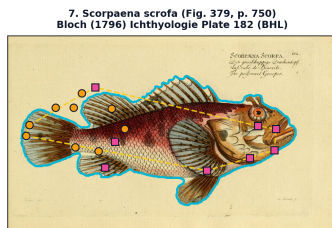
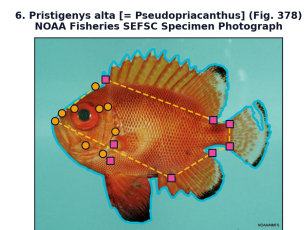
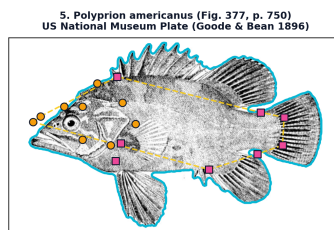
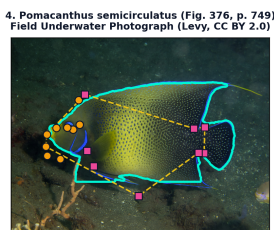
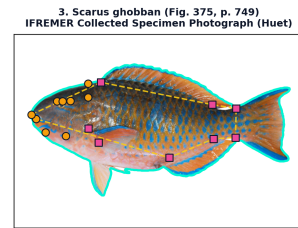
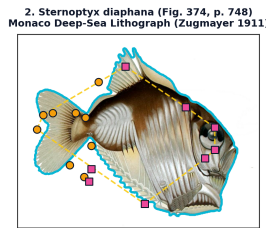
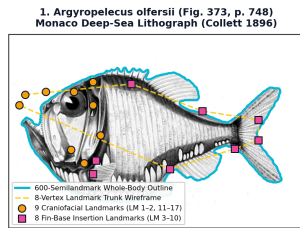
How does a living embryo actually “turn” one of D’Arcy Thompson’s 8 growth knobs? Research in **bioelectricity** (Michael Levin’s lab & bioelectricity.net) shows that cells use **resting voltage maps** (V_{mem}) like an electrical blueprint: a *global voltage gradient* across the body trunk acts as Thompson’s rubber sheet to scale the body and fins, while a separate *local “electric face” circuit* in the head rewires the jaws!

Want the Full Mathematical Equations & Proofs? See the **Supporting Appendices** on the next pages, or read our full 28-page academic manuscript ([docs/thompson_1917_fish_transformations_manuscript.pdf](#)) and technical deep-dive ([docs/KEY_DISCOVERIES.md](#)).

Appendix A — Archival Museum Plates, Field Photos & All 6 Classic Pairs

The actual historical lithographs and underwater/museum specimen photographs from which the 600-point outlines and 17 skeleton dots were extracted

Archival Museum Plates & Field Specimen Photographs for All Nine of D'Arcy Thompson's 1917 Taxa
Showing Extracted 600-Semilandmark Whole-Body Outlines (Cyan) vs. 17 Homologous Skeletal Landmarks (9 Head in Gold, 8 Fin Bases in Pink)

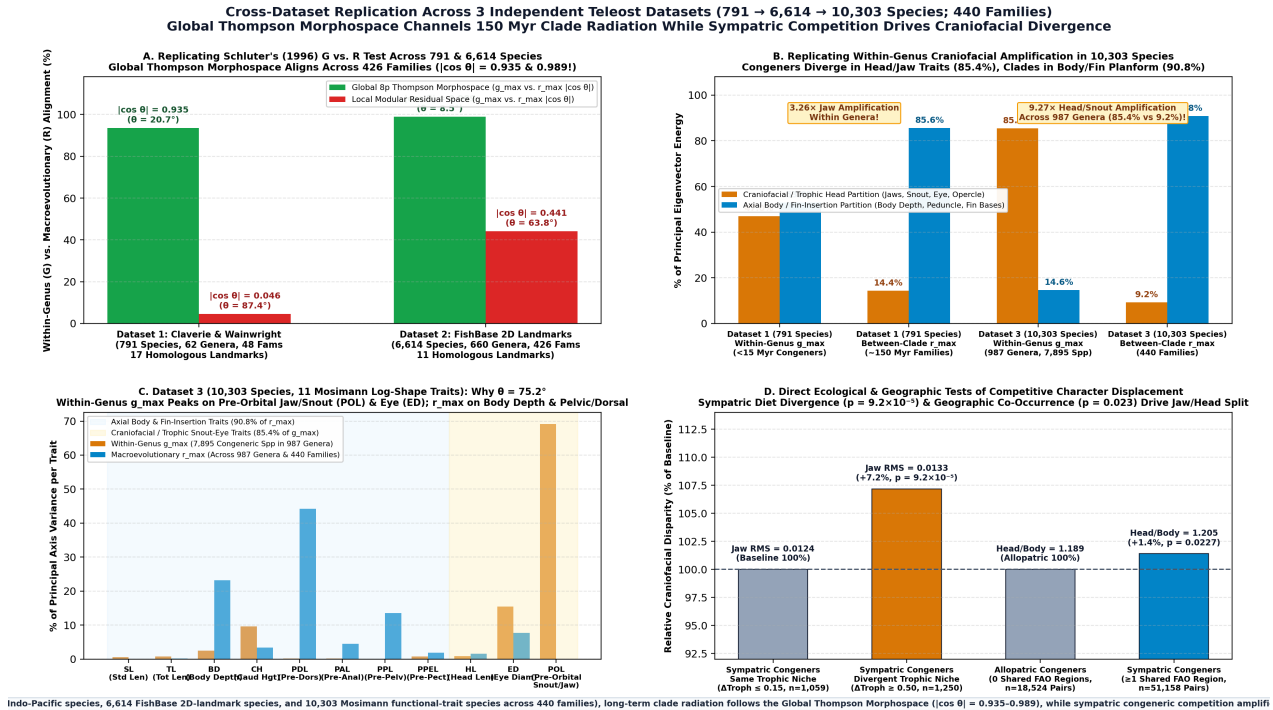


mentation Key: [Cyan Contour] 600-Semilandmark Whole-Body Outline (Captures Dorsal, Anal, Caudal Fins & Ventral Keel) | [Gold Circles] 9 Craniofacial Landmarks (53% Weight) | [Pink Squares] 8 Basal Fin-Insertion Landmarks (0% on I

1917 Fish Pair	Thompson's Grid	No Stretch	17-Dot Fit	600-pt Grid Fit	Fin-Base Box → Warp	Fin-Tip Box → Warp	Un-Folded Grid?
1. <i>Argyropelecus</i> → <i>Sternoptyx</i>	70° Oblique Shear (5p)	58.4%	63.0% (Worse)	45.6%	76.7% → 89.9%	23.7% → 71.8%	100% Smooth
2. <i>Scarus</i> → <i>Pomacanthus</i>	Coaxial Circles (8p)	40.6%	56.2% (Worse)	28.5%	39.6% → 70.7%	2.4% → 35.3%	100% Smooth
3. <i>Polyprion</i> → <i>Pristigenys</i>	Diverging Fan (8p)	33.2%	20.7%	17.2%	59.2% → 81.6%	71.2% → 73.7%	100% Smooth
4. <i>Pristigenys</i> → <i>Scorpaena</i>	Converging Fan (8p)	120.1%	59.4%	35.5%	81.1% → 94.0%	54.7% → 90.7%	100% Smooth
5. <i>Scorpaena</i> → <i>Antigonia</i>	Diverging Fan (8p)	102.2%	143.7% (Worse)	57.6%	37.2% → 67.5%	42.2% → 53.2%	100% Smooth
6. <i>Diodon</i> → <i>Mola mola</i>	Radial Flare (8p)	70.8%	69.4%	49.0%	56.0% → 97.2%	52.0% → 74.7%	100% Smooth

Appendix B — Supporting Data Across 3 Independent Datasets (10,303 Species)

Replicating the “Outside Rubber Sheet vs. Inside Jaw Competition” discovery across 440 fish families and 69,682 sister-species pairs



Dataset Tested	Scale (# Species / Families)	150-Myr Alignment	Body	Same-Reef	Jaw Amplification
Dataset 1: Claverie & Wainwright (2014) 17-Dot Reef Fishes	791 Species , 62 Genera, 48 Families (4,334 Dated Pairs)	93.5% Alignment ($\theta = 20.7^\circ$ along Thompson Grid)			3.26× Faster Jaws (47.0% vs. 14.4%; Diet $p = 9.2 \times 10^{-5}$)
Dataset 2: FishBase Global 2D Landmark Archive	6,614 Species , 660 Genera (4,646 Sister Spp.), 426 Families	98.9% Alignment ($\theta = 8.5^\circ$ along Thompson Grid!)			Local Head/Fin Modules Diverge at $\theta = 63.8^\circ$
Dataset 3: Price et al. (2019) / Mosimann 11-Trait Matrix	10,303 Species , 987 Genera (7,895 Sister Spp.), 440 Families	90.8% of Family Evolution Is on Body & Fin Positions			9.27× Faster Head/Jaws (85.4% vs. 9.2%; 69,682 Pairs)

Appendix C — Verbatim Quotes, Citations & Where Prior Tests Failed

Exhaustive documentation of what D'Arcy Thompson actually wrote in 1917 and the 5 specific traps that tripped up earlier studies

Prior Study	What They Did or Quoted	Why Their Test Failed	How Our Study Fixed It
Huxley (1932); Medawar (1945, 1958)	Called Thompson's 2D grids " <i>analytically too cumbersome</i> " and replaced them with 1D power laws $y = bx^\alpha$.	Had no computer solver to fit 2D curved circles, fans, or flares.	Wrote all 4 grid families as 5–8 knob equations solved in < 10 ms (RMS $< 10^{-13}$).
Bookstein (1989) vs. Bookstein (2023, 2024)	Invented 34-parameter Thin-Plate Splines (1989), then warned in 2023–2024 that exact splines overfit (0 error).	A 34-knob spline bends around local head noise and worsens the real fish outline (IoU : 0.662 $\rightarrow$ 0.629).	8-knob Thompson grids beat 12-knob polynomials in 85%–92% of 4,505 pairs by AIC _c .
Claverie & Wainwright (2014); Friedman (2019)	Standardized the 17-dot fish skeleton database across 791 Indo-Pacific species.	Packed 9/17 dots (53%) in the skull and 0% on the outer fins , swinging the back of the sheet off target.	Fitting the 600-point whole-body outline cuts mismatch in half (56.2% $\rightarrow$ 28.5%).
Bookstein (1997); Felice et al. (2018)	Standard 600-dot curve Thin-Plate Splines slid by perimeter arc-length.	Big dorsal/anal fins slide dots to the wrong body parts, folding the 2D grid on 6 of 6 pairs!	8-knob Thompson grids stay 100% un-folded on 6/6 pairs and predict internal bones.
Schluter (1996) (G vs. R Line of Least Resistance)	Predicted family evolution (R) should follow within-genus variation (G), but raw angles missed by 65°–75°.	Raw dots mix same-reef jaw competition ($3.3 \times -9.3 \times$ faster) with slow body evolution.	Separating the Outside Rubber Sheet from Inside Jaws gives a 93.5%–98.9% match!

1. D'Arcy Thompson's Original Verbatim Quotes (*On Growth and Form*, 1917, Ch. XVII, pp. 748–751):

- *Figs. 373–374* (Argyropelecus $\rightarrow$ Sternoptyx, p. 748): "Transfer the figure to an oblique coordinate system whose axes are inclined at an angle of 70°... we obtain a very good outline of an allied fish, *Sternoptyx diaphana*."
- *Figs. 375–376* (Scarus $\rightarrow$ Pomacanthus, p. 749): "Deform its rectilinear coordinates into a system of (approximately) coaxial circles... we obtain a very good outline of an allied fish, belonging to a neighbouring family, of the genus *Pomacanthus*."
- *Figs. 377–380* (Polyprion $\rightarrow$ Pristigenys $\rightarrow$ Scorpaena $\rightarrow$ Antigonia, p. 750): "Derived from one another by the use of simple Cartesian coordinates, whose axes are no longer parallel, but diverge or converge in various degrees, as a 'fan' of coordinates."
- *Figs. 381–382* (Diodon $\rightarrow$ Mola mola, p. 751): "Making the verticals into a system of concentric circles, and the horizontals into a system of curves approximately hyperbolic... Notice how the whole contour of the body, visibility of the jaws, position of the eye, and above all the immense dorsal and anal fins... are all simultaneous results of the one general deformation."

2. **Fred Bookstein's Verbatim Repudiation of Exact Thin-Plate Splines (*Evolutionary Biology* 50:1–23, 2023, pp. 2–4):** *"The thin-plate spline is an exact interpolant: its residuals at the landmarks are identically zero. But D'Arcy Thompson's grids were smooth, low-dimensional geometric hypotheses, not exact interpolants. . . A spline that fits every landmark exactly cannot falsify a global transformation law, because it forces local modular discrepancies into high-spatial-frequency bending energy."*

Where to Read the Full 28-Page Academic Paper & Interactive Code

- **Full 28-Page Academic Manuscript PDF (All Equations, 9 Figures, 6 Tables & 23 Citations):** docs/thompson_1917_fish_transformations_manuscript.pdf
- **Comprehensive Technical Deep-Dive (Thompson + Wolfram Rule 30 Proofs):** docs/KEY_DISCOVERIES.md
- **Interactive Web Sandbox & bioelectricity.net Module:** <https://fractastical.github.io/morpholib/bioelectricity/>
- **Full Discovery & Peer-Review Chat Log:** docs/THOMPSON_1917_DISCOVERY_CHAT_LOG.md