

## KEY TRAITS OF AMPHIOXUS SPECIES (CEPHALOCHORDATA) AND THE GOLT<sup>1</sup>

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### Abstract

Major biological traits of amphioxus species (Cephalochordata) are presented with emphasis on the size reached by their 32 valid species in the genera *Asymmetron* (2 spp.), *Branchiostoma* (25 spp.), and *Epigonichthys* (5 spp.) and on related features, i.e., growth parameters and size at first maturity. Overall, these traits combined with features of their respiration, suggest that the cephalochordates conform to the Gill Oxygen Limitation Theory (GOLT), which relates the growth performance of water-breathing ectotherms to the surface area of their respiratory organ(s).

### Introduction

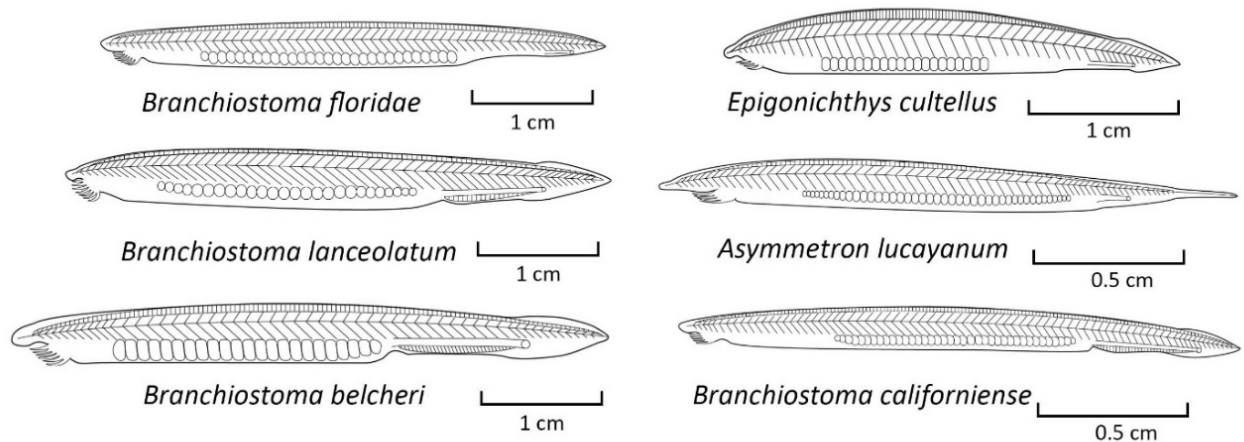
The small fish-like animals know as ‘lancelet’ or ‘amphioxius’ belong the subphylum Cephalochordata, which is either a sister group, or related to the ancestor of the vertebrate animals (see Garcia-Fernández and Benito-Gutierrez 2008). The cephalochordates consist of 3 families (the Asymmetronidae, Epigonichthyidae and Branchiostomidae), with one genus each, *Asymmetron* (2 spp.), *Branchiostoma* (24 spp.) and *Epigonichthys* (6 spp.), as detailed in Table 1 and SeaLifeBase ([www.sealifebase.org](http://www.sealifebase.org)). This contribution is to assemble some of the basic biological traits of lancelets (Figure 1), notably the maximum size each of their 34 species can reach, which is easily their most important attribute, though it is often ignored (Haldane 1926).

Finally, reported lengths at first maturity of cephalochordates were related to the corresponding, population-specific maximum length, to test whether these animals mature as predicted by the Gill-Oxygen Limitation Theory (GOLT; see Pauly 2021a, 2021b).

Also assembled here are the few length-weight relationships (LWR) and two proximate analyses, which should allow conversion of lengths into wet and dry weights. For a few species, estimates of the parameters of the von Bertalanffy growth function (VBGF; for both seasonal and non-seasonal growth) are presented that were newly computed, or corrected from publications in which the VBGF was misapplied.

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**Figure 1.** Simplified drawing of 6 species in 3 genera of lancelets. Redrawn by Elaine Chu from a variety of sources. Note uniformity of basic shape.

### Material and Method

The species names of cephalochordates in SeaLifeBase were downloaded, and for each, a reported maximal length was identified in the pertinent literature, and input into both Table 1 and into the relevant field of SeaLifeBase. Many of these lengths originated from Hubbs (1922), but some refer to the holotype or a few paratypes, and may thus may underestimate maximum lengths. The literature was scanned for published LWR of cephalochordates of the form  $W = a \cdot L^b$ , which were converted such that they referred to weight ( $W$ ) in g, and total length in cm. Note that when  $b = 3$ , growth is isometric, i.e., the body remains self-similar as it grows (Froese 2006).

Organic growth ( $dw/dt$ ) can be defined as resulting from two opposite processes (Pütter 1920; Bertalanffy 1938) i.e.,

$$dw/dt = Hw^d - kw \quad \dots 1.)$$

with  $Hw^d$  expressing the rate of synthesis of body tissues, and  $kw$  expressing the rate at which the proteins and other molecules making up the tissues are denatured, and thus need to be re-synthesized (Pauly 2021a, 2021b). Synthesis requires energy in the form of ATP, the synthesis of which requires oxygen ( $O_2$ ). The exponent  $d$  links the respiratory surface i.e., the  $O_2$  supply of water-breathing ectotherms (WBE) to their body weight (i.e.,  $O_2 \propto W^d$ ), and ranges between 0.5 and 0.9 in fishes and other WBE with gills (De Jager and Dekkers 1974; Pauly 2021a, 2021b). In cephalochordates, which lack gills, various external and internal body surfaces are used for respiration (Schmitz et al. 2000). Thus, to the extent that that post-metamorphosis cephalochordates maintain their basic shape as they grow (which they do, as attested by their LWR having exponents near 3, see below), their respiratory surface(s) should grow in proportion to  $2/3$  of their weight, i.e.,  $d \sim 0.67$ .

Assuming that  $d = 2/3$ , Equation (1) can be integrated into the VBGF, which, for growth in length, has the form:

$$L_t = L_\infty (1 - e^{-K(t-t_0)}) \quad \dots 2a)$$

where  $L_t$  is the mean length at age  $t$  of the WBE,  $L_\infty$  their asymptotic length, (i.e., the mean length attained by the surviving WBE after an infinitely long time),  $K$  a growth coefficient (here in year<sup>-1</sup>) and  $t_0$  is a

parameter with adjusts for the feature that the VBGF generally fails to properly describe the growth of the earliest (larval and post-larval) stages of WBE. Therefore,  $t_0$ , by expressing the age WBE would have at the size of zero if they had always grown as predicted by the VBGF, allows it to correctly represent length-at-age in larval and post-larval stages (Pauly 1998).

Growth in weight can be described by

$$W_t = W_\infty(1 - e^{-K(t-t_0)^b}) \quad \dots 2b)$$

where  $W_\infty$  is the weight corresponding to  $L_\infty$ ,  $b$  is the exponent of an LWR as defined above, and the other parameters are defined as for Equation 2a.

When the growth of WBE is seasonal (and it almost always is, even in the tropics; Pauly and Ingles 1981, Pauly 1998), the VBGF can be modified to account for seasonal growth oscillations, i.e.,

$$L_t = L_\infty \{1 - \exp[-K(t - t_0) + S(t) - S(t_0)]\} \quad \dots 3)$$

where  $S(t) = (CK/2\pi) \cdot \sin(2\pi(t - t_s))$ ,  $S(t_0) = (CK/2\pi) \cdot \sin(2\pi(t_0 - t_s))$ , and  $L_\infty$ ,  $K$  and  $t_0$  are defined as above.

Equation (3) involves two parameters more than the VBGF:  $C$  and  $t_s$ . Of these, the former is easiest to visualize, as it expresses the amplitude of the growth oscillations. When  $C = 0$ , Equation (3) reverts to Equation (2). When  $C = 0.5$ , the seasonal growth oscillations are such that growth rate increases by 50% at the peak of the 'growth season' (i.e., in 'summer'), and, briefly, declines by 50% in 'winter'. When  $C = 1$ , growth increases by 100%, doubling during 'summer', and becoming zero in the depth of 'winter'.

The other new parameter,  $t_s$  expresses the time elapsed between  $t = 0$  and the start of a sinusoid growth oscillation. However, visualization is facilitated if we define  $t_s + 0.5 = WP$  ('Winter Point'), which expresses, as a fraction of the year, the period when growth is slowest.  $WP$  is often close to 0.1 (i.e., early February) in the Northern Hemisphere and 0.6 (early August) in the Southern Hemisphere.

The growth performance of animals having the same basic shape can be compared using

$$\emptyset' = \log(K) + 2\log(L_\infty) \quad \dots 4)$$

while the growth performance of animal of different shape can be compared using the parameters of their weight growth curve growth.

Finally, we tested whether cephalochordates reach maturity and spawn at a fraction of their maximum length ( $L_{max}$ ) that is similar to that of fishes. In fish, mean length at first maturity ( $L_m$ , i.e., when 50 % of the individual have become mature) occurs when  $L_{max}^D / L_m^D \approx 1.35$ , with  $D = 3(1-d)$  (Pauly 1984, 2021a, 2021b; Meyer and Schill 2020). With few exceptions (e.g., figure 3 in Holland 2011), the cephalochordates literature reports only the minimum length at which individual mature (which we shall identify as  $L_{min}$ ), rather than the length at which 50 % mature (see, e.g., Stokes and Holland 1996). Also, in many cases, articles reporting  $L_{min}$  fail to report the corresponding  $L_{max}$  value. Nevertheless, a number of  $L_{min}$  &  $L_{max}$  data pairs could be assembled, and a mean  $L_{max}^D / L_m^D$  ratio estimated for cephalochordates. Here, it was hypothesized that this ratio would be slightly above 1.35, given that, by definition,  $L_{min} < L_m$ .

## Results

Table 1 lists the currently recognized species of cephalochordates and the maximum length (in mm) reported for each. Note that some of these values (notably that for *Branchiostoma africae*) are likely to be underestimates, as they were based on holotypes, or the largest of a few paratypes.

**Table 1:** The 32 species of cephalochordate in SeaLifeBase ([www.sealifebase.org](http://www.sealifebase.org)) and WoRMS ([www.worms.org](http://www.worms.org)) and the maximum length (in mm) reported for each; the latter will be underestimates when their sources are the original descriptions, as they will be based on holotypes, or a few paratypes.

| No | Scientific name                    | Author           | Max. length <sup>a)</sup> | Source                       |
|----|------------------------------------|------------------|---------------------------|------------------------------|
| 1  | <i>Branchiostoma africae</i>       | Hubbs, 1927      | (20)                      | Webb (1955)                  |
| 2  | <i>Branchiostoma arabiae</i>       | Webb, 1957       | 41                        | Webb (1957a); Dawson (1964)  |
| 3  | <i>Branchiostoma bazarutense</i>   | Gilchrist, 1923  | 42                        | Gilchrist, 1923              |
| 4  | <i>Branchiostoma belcheri</i>      | Gray, 1847       | 65                        | Feng et al. (2008)           |
| 5  | <i>Branchiotoma bennetti</i>       | B&G 1966         | 34                        | Boschung & Gunter (1966)     |
| 6  | <i>Branchiostoma bermudae</i>      | Hubbs, 1922      | 54                        | Hubbs (1922)                 |
| 7  | <i>Branchiostoma californiense</i> | Andrews, 1893    | 84                        | Hubbs (1922)                 |
| 8  | <i>Branchiostoma capense</i>       | Gilchrist, 1902  | 69                        | Hubbs (1922)                 |
| 9  | <i>Branchiostoma caribaeum</i>     | Sundevall, 1853  | 51                        | Hubbs (1922)                 |
| 10 | <i>Branchiostoma elongatum</i>     | Sundevall, 1852  | 64                        | Webb (1957b)                 |
| 11 | <i>Branchiostoma floridae</i>      | Hubbs, 1922      | 61                        | Hubbs (1922)                 |
| 12 | <i>Branchiostoma gambiense</i>     | Webb, 1958       | 33                        | Webb (1958a)                 |
| 13 | <i>Branchiostoma indicum</i>       | (Willey, 1901)   | (27)                      | Prashad (1934)               |
| 14 | <i>Branchiostoma lanceolatum</i>   | (Pallas, 1774)   | 58                        | Hubbs (1922)                 |
| 15 | <i>Branchiostoma leonense</i>      | Webb, 1956       | (28)                      | Webb (1956a; 1956b, 1958a)   |
| 16 | <i>Branchiostoma longirostrum</i>  | Boschung, 1983   | 47                        | Boschung (1983)              |
| 17 | <i>Branchiostoma malayanum</i>     | Webb, 1956       | 45                        | Webb (1956c)                 |
| 18 | <i>Branchiostoma minucauda</i>     | Whitley, 1932    | 55                        | Richardson & McKenzie (1994) |
| 19 | <i>Branchiostoma moretonense</i>   | Kelly, 1966      | 42                        | Kelly (1966)                 |
| 20 | <i>Branchiostoma nigeriense</i>    | Webb, 1955       | (35)                      | Webb (1958b)                 |
| 21 | <i>Branchiostoma platae</i>        | Hubbs, 1922      | 56                        | Hubbs (1922)                 |
| 22 | <i>Branchiostoma senegalense</i>   | Webb, 1955       | 59                        | Gosselck and Spittler (1985) |
| 23 | <i>Branchiostoma tattersalli</i>   | Hubbs, 1922      | 75                        | Tattersall (1903)            |
| 24 | <i>Branchiostoma virginiae</i>     | Hubbs, 1922      | 53                        | Hubbs (1922)                 |
| 25 | <i>Asymmetron inferum</i>          | Nishikawa, 2004  | (15)                      | Nishikawa (2004)             |
| 26 | <i>Asymmetron lucayanum</i>        | Andrews, 1893    | (28)                      | Richardson & McKenzie (1994) |
| 27 | <i>Epigonichthys australis</i>     | (Raff, 1912)     | (25)                      | Richardson & McKenzie (1994) |
| 28 | <i>Epigonichthys bassanus</i>      | (Günther, 1884)  | 44                        | Richardson & McKenzie (1994) |
| 29 | <i>Epigonichthys cingalensis</i>   | (Kirkaldy, 1895) | 30                        | Kirkaldy (1895)              |
| 30 | <i>Epigonichthys cultellus</i>     | Peters, 1877     | 34                        | Richardson & McKenzie (1994) |
| 31 | <i>Epigonichthys hectori</i>       | (Benham, 1901)   | 63                        | Paulin (1977)                |
| 32 | <i>Epigonichthys maldivensis</i>   | (Cooper, 1903)   | 30                        | Nishikawa (1980)             |

a) Lengths in brackets may also refer to annual species (see text)

Table 2 presents LWR for 5 species of *Branchiostoma*, which allow for converting their total length to their wet weight. Also, the table provides the average water content of two species, i.e. 77% in *B. floridae* and 88% in *B. senegalense*.

**Table 2** Length-weight relationships of 4 *Branchiostoma* species

| Species                 | Location           | a       | b     | N   | Source                                   |
|-------------------------|--------------------|---------|-------|-----|--|
| <i>B. belcheri</i>      | Hong Kong          | 0.003   | 2.853 | 30  | Chen et al. (2008)                       |
| <i>B. belcheri</i>      | Naozhou Isl. China | 0.0014  | 3.290 | 530 | Feng et al. 2008                         |
| <i>B. californiense</i> | B.C. Mexico        | 0.00522 | 3.01  | 60  | Campos-Dávila et al. (2019)              |
| <i>B. floridae</i>      | Tampa Bay, Fla.    | 0.00236 | 2.895 | 44  | Stokes (1996) <sup>a)</sup>              |
| <i>B. malayanum</i>     | Hong Kong          | 0.003   | 2.922 | 30  | Chen et al. (2008)                       |
| <i>B. senegalense</i>   | N.W. Africa        | 0.0069  | 2.71  | --  | Gosselck & Spittler (1979) <sup>b)</sup> |

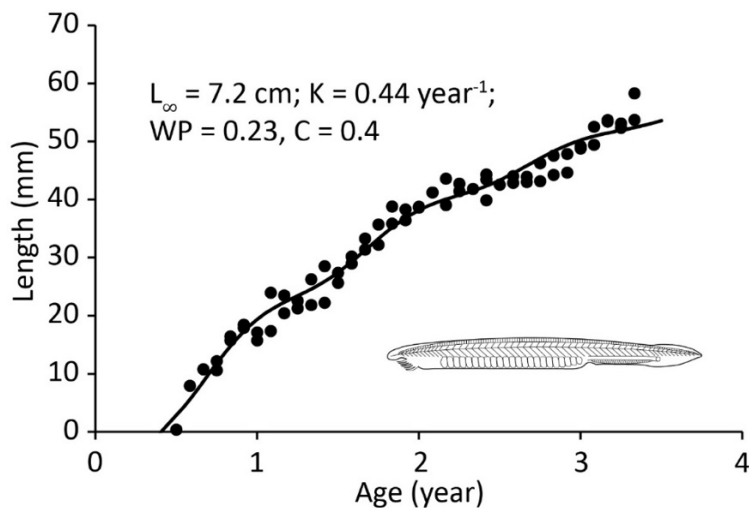
a) Mean water content = 77%; b) mean water content 88%

Table 3 provides 6 estimates of growth parameters for 4 species; 2 sets of growth parameters account for seasonal growth oscillations (see also Figure 2). All pertain to the VBGF and are either new estimates, or correct for inconsistencies in their original presentations.

**Table 3.** Growth parameters of *Branchiostoma* species ;  $L_{\infty}$  = cm;  $K$  = year<sup>-1</sup>;  $\phi' = \log(K) + 2 \cdot \log(L_{\infty})$

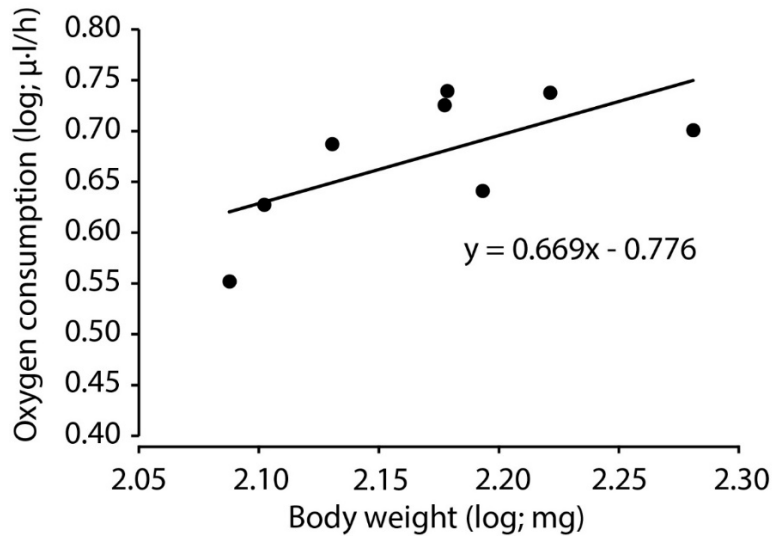
| Species               | Location           | $L_{\infty}$ | $K$  | $\phi'$ | Remark / Source                                  |
|-----------------------|--------------------|--------------|------|---------|--|
| <i>B. belcheri</i>    | Xiamen, China      | 7.2          | 0.44 | 1.36    | See Figure 3                                     |
| <i>B. elongatum</i>   | Chile              | 6.5          | 0.45 | 1.28    | Vergara et al. (2012) <sup>a)</sup>              |
| <i>B. senegalense</i> | N.W. Africa        | 6.4          | 0.47 | 1.28    | Gosselck and Spittler (1979)                     |
| <i>B. lanceolatum</i> | Helgoland, Germany | 6.3          | 0.50 | 1.30    | from Sager & Gosselck. (1985)                    |
| <i>B. belcheri</i>    | Hong Kong          | 4.5          | 0.89 | 1.26    | Recomputed from Chen et al. (2008) <sup>a)</sup> |
| <i>B. malayanum</i>   | Hong Kong          | 3.6          | 1.72 | 1.35    |  |

a) The parameters were recomputed because the authors used a variant of the VBGF, which later misled Vergara et al. (2012) into performing inappropriate comparisons.



**Figure 2.** Seasonally oscillating growth of *Branchiostoma belcheri* in the harbor of Xiamen, China (based on length-frequency data in Chin 1941 [figure 14] fitted with Equation 3).

The oxygen consumption of *Branchiostoma lanceolatum* was studied by Schmitz et al. (2000), and some of their results are presented in Figure 3.

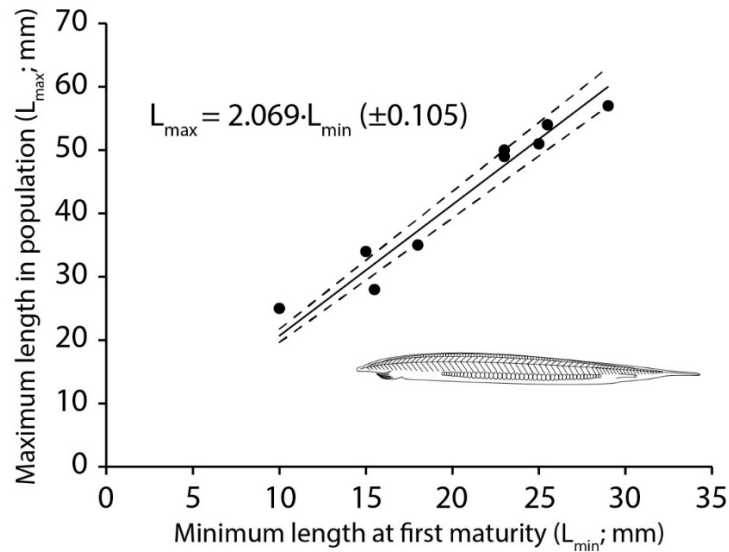


**Figure 3.** Oxygen consumption as a function of body weight in *Branchiostoma lanceolatum* at 11 °C ( $r^2 = 0.46$ ,  $p < 0.05$ ; redrawn and recomputed from Schmitz et al. 2000). Note that the slope of this relationship is about  $2/3$ .

**Table 4** presents 9  $L_{min}$  &  $L_{max}$  data pairs in 5 species and 2 genera of cephalochordates. The  $b$ -values, in the LWR of Table 2 are reasonably close to 3; thus, with  $d \sim 0.67$  (see text above and Figure 3) and  $D = 3 \cdot (1-d)$ ,  $D$  can be assumed equal to unity, and the mean  $L_{max}^D / L_{min}^D$  ratio can be estimated from the mean  $L_{max} / L_{min}$  ratio (Figure 4). This ratio was found to be 2.07, with a 95% confidence interval of  $\pm 0.105$ . As hypothesized, this is higher than the estimate of  $1.36 \pm 0.15$  for fishes.

**Table 4.** Length at first maturity ( $L_m$ ) and maximum length ( $L_{max}$ ) in lancelet (mm)

| Species                          | Location        | $L_m$ | $L_{max}$ | Source                  |
|----------------------------------|-----------------|-------|-----------|-------------------------|
| <i>Asymmetron lucayanum</i>      | Bimini, Bahamas | 10    | 25        | Holland (2011)          |
| <i>Branchiostoma belcheri</i>    | Amakusa, Japan  | 25.5  | 54        | Nagakawa (1897)         |
| <i>Branchiostoma belcheri</i>    | Xiamen, China   | 29    | 57        | Chin (1941)             |
| <i>Branchiostoma belcheri</i> ♀  | Hong Kong       | 25    | 51        | Chen et al. (2008)      |
| <i>Branchiostoma belcheri</i> ♂  | Hong Kong       | 23    | 49        | Chen et al. (2008)      |
| <i>Branchiostoma floridae</i>    | Tampa Bay, Fla. | 23    | 50        | Stokes & Holland (1996) |
| <i>Branchiostoma lanceolatum</i> | Naples, Italy   | 15.5  | 28        | Langerhans (1876)       |
| <i>Branchiostoma malayanum</i> ♀ | Hong Kong       | 18    | 35        | Chen et al. (2008)      |
| <i>Branchiostoma malayanum</i> ♂ | Hong Kong       | 15    | 34        | Chen et al. (2008)      |



**Figure 4.** Estimating the mean  $L_{max}^D$  vs.  $L_{min}^D$  ratio and its 95 % confidence interval in 5 species of lancelets, based on the data in Table 4. The insert shows *Asymmetron lucayanum*.

## Discussion

The lancelets or amphioxus, i.e., the cephalochordates, have intrigued biologists since Darwin established the descent of vertebrates – including us – from “lower” fish-like animals that may have resembled lancelets. Ernst Haeckel and other German evolutionists celebrated those animals in an almost cult-like fashion, believing them to be, the ancestors which would yield the mysteries of our existence (Hopwood 2015). Similar enthusiasm for amphioxus studies emerged a few decades later in China, which connected studies on the vertebrates' ancestry with the renewal of Chinese science (Luk 2020). Also note that China was the only country from which a targeted amphioxus fishery was reported (Light 1923; Chin 1941).

Nowadays, genomic studies of cephalochordates appear to have established that their ancestors were not direct ancestors of vertebrates, but shared with our putative ancestors several important genes and traits, notably gill slits. However, there are no gills behind their slits – lancelets respire through their integument (Schmitz et al. 2000) and use their gill slits only for feeding.

The lack of specialized gills implies that lancelets have a lower oxygen supply than fish of similar size, which, given the GOLT, implies that they should grow more slowly than fish of similar size (Pauly 2021a, 2021b). Here, we created a profile of lancelets that differed from most extant accounts to test this inference because they are discussed primarily in the context of taxonomy (Hubbs 1922) and evolution.

This account emphasizes the (maximum) adult size, assembled for nearly all species (Table 1), and their length-weight relationship (Table 2), and growth parameters (Table 3), which allowed comparing their growth with that of fish and chaetognaths (Table 4), the latter being another gill-less group. This led to the conclusion that growth of lancelets, as predicted by the GOLT, is less rapid than that of fishes.

**Table 5.** Comparison between the growth performance of 3 species of fish and a species of cephalochordates ( $\emptyset = \log K + 2/3 \log W_{\infty}$ ).

| Species <sup>a</sup>     | $W_{\infty}$ (g) | K (year <sup>-1</sup> ) | $\emptyset$ |
|--------------------------|------------------|-------------------------|-------------|
| <i>Thunnus albacares</i> | 198,940          | 0.250                   | 2.93        |
| <i>Mugil cephalus</i>    | 13,890           | 0.110                   | 1.80        |
| <i>Cottus bubalis</i>    | 102              | 0.230                   | 0.70        |
| <i>B. senegalense</i>    | ~1               | 0.480                   | -0.32       |

a) The 3 species of fish are documented in Pauly (1981). *B. senegalense* is taken as representative of cephalochordates in general (see Table 5).

The GOLT's prediction, that length at first maturity of lancelets is reached at the same fraction of their maximum length could not be tested; researchers specialized in cephalochordates tend not to define length at first maturity as other biologists do. However, the results obtained with a substitute measure had the expected bias, given its definition. This still allows for the  $L_{\max}/L_m$  ratio of cephalochordates to be similar to that of fishes.

Overall, the asymptotic growth and other features of lancelets suggest that their biology is compatible with the predictions of the GOLT.

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## References

- Andrews, E.A. 1893. An undescribed acraniate: *Asymmetron lucayanum*. *Studies of the Biological Laboratory of John Hopkins University*, 5:213-247.
- Benham, W.B. 1901. *Heteropleuron hectori*, the New Zealand lancelet. *Quarterly Journal of Microscopical Science* (Ser. 2), 44(2): 273-280.
- Bertalanffy, L. von. 1938. A quantitative theory of organic growth (Inquiries on growth laws. II). *Human Biology*, 10: 81-213.
- Boschung, H. 1983. A new species of lancelet, *Branchiostoma longirostrum* (Order Amphioxii), from the Western North Atlantic. *Northeast Gulf Science* 6(2): 91-97.
- Boschung, H.T. and G. Gunter. 1966. A new species of lancelet, *Branchiostoma bennetti* (Order Amphioxii) from Louisiana. *Copeia*, 1966(3): 485-489.
- Campos-Dávila, L., C.J. Pérez-Estrada, R. Rodríguez-Estrella, E. Morales-Bojórquez, F.G. Brun-Murillo and E.F. Balart. 2019. Seagrass *Halodule wrightii* as a new habitat for the amphioxus *Branchiostoma californiense* (Cephalochordata, Branchiostomidae) in the southern Gulf of California, Mexico. *ZooKeys*, 873: 113-131.
- Chen, Y., P.K.S. Shin and S.G. Cheung. 2008. Growth, secondary production and gonad development of two co-existing amphioxus species (*Branchiostoma belcheri* and *B. malayanum*) in subtropical Hong Kong. *Journal of experimental Marine Biology and Ecology*, 357: 64-74.
- Chin, T.G. 1941. Studies on the Amoy amphioxus *Branchiostoma belcheri* Gray. *Philippine Journal of Science*, 75: 369-424.
- Cooper, C.F. 1903. Cephalochordata. I. Systematic and anatomical account, p. 347-360. In: J. Stanley Gardiner (ed). *The Fauna and Geography of the Maldive and Laccadive Archipelagoes, Vol. 1*. Cambridge University Press, Cambridge.
- Dawson, C.E. 1964. Records of Cephalochordata from the western Persian Gulf. *Copeia*, 1964: 229.
- De Jager, S. and W.J. Dekkers. 1974. Relations Between Gill Structure and Activity in Fish. *Netherlands Journal of Zoology*, 25, 276-308. [doi.org/10.1163/002829675X00290](https://doi.org/10.1163/002829675X00290)
- Feng, B., H.S. Lu, C.Y. Liao and J. Zhang. 2008. Growth and reproduction of amphioxus (*Branchiostoma belcheri*) in Naozhou Island area. *Chinese Journal of Ecology*, 27(8): 1327-1331.



- Froese, R. 2006. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology*, 22: 241–253.
- García-Fernández, J. and E. Benito-Gutiérrez. 2008. It's a long way from amphioxus: descendants of the earliest chordate". *BioEssays*, 31(6): 665–675.
- Gilchrist, J.D.F. 1923. A new species of Amphioxus from the Bazaruto Islands (*Branchiostoma bazarutense*. *Annals and Magazine of Natural History*, Series 9, 12: 62–63.
- Gosselck, F. and P. Spittler. 1979. Age structure, growth and weight of *Branchiostoma senegalense* (Acrania, Branchiostomidae) off north-west Africa. *Internationale Revue de gesamten Hydrobiologie*, 64:541–550.
- Gray, J.E. 1847. Description of a new species of Amphioxus from Borneo. *Annals and Magazine of Natural History*, 19(129): 463–464.
- Günther, A.C.L.G. 1884. Branchiostoma, p. 31–33. In: *Reports on the Zoological Collections Made in the Indo-Pacific Ocean during the Voyage of H.M.S. Alert, 1881–1882*. British Museum, London.
- Haldane, J.B.S. 1926. On being the right size. *Harper's Magazine*, 152: 424–427.
- Holland, N.D. 2011. Spawning periodicity of the lancelet, *Asymmetron lucayanum* (Cephalochordata), in Bimini, Bahamas. *Italian Journal of Zoology*, 78(4): 478–486.
- Hopwood, N. 2015. The cult of amphioxus in German Darwinism; or, Our gelatinous ancestors in Naples' blue and balmy bay. *History and Philosophy of the Life Sciences*, 36: 371–393.
- Hubbs, C.L. 1927. *Branchiostoma africanae*, p. 644–645. In: T. Monod. *Contribution à l'Etude de la Faune du Cameroun*. Société d'Éditions Géographiques, Maritimes et Coloniales, Paris.
- Hubbs, C.L. 1922. A list of all the lancelets in the world with diagnoses of five new species of *Branchiostomata*. Occasional Paper of the Museum of Zoology No. 105. University of Michigan, Ann Harbor. 16 p.
- Kelly, O.E.S., 1966. *Branchiostoma moretonensis* sp. nov. (Cephalochordata). University of Queensland Papers Department of Zoology, 2(13): 259–265.
- Kirkaldy, J.W. 1895. A revision of the Genera and Species of the Branchiostomidae. *Quarterly Journal of Microscopical Science* (Ser. 2), 37: 303–323 + plates.
- Langerhans, P. 1876. Zur Anatomie des *Amphioxus lanceolatus*. *Archiv für mikroskopische Anatomie*, 12: 290–348.
- Light, S.F. 1923. Amphioxus fisheries near the University of Amoy, China. *Science*, 58(1491): 57–60.
- Luk, C.Y.L. 2020. The First Marine Biological Station in Modern China: Amoy University and Amphioxus, p. 68–86, In: K.S. Matlin, J. Maienschein and R.A. Ankeny (eds). *Why Study Biology by the Sea?* University of Chicago Press, Chicago.
- Meyer, K. A. and D.J. Schill. 2020. The Gill-Oxygen Limitation Theory and size at maturity/maximum size relationships for salmonid populations occupying flowing waters. *Journal of Fish Biology*, 98(1): 44–49. [doi.org/10.1111/jfb.14555](https://doi.org/10.1111/jfb.14555)
- Nagakawa, H. 1897. Notes on an amphioxus obtained in Amakusa, Kyushu. *Annotationes zoologicae japonenses*, 1: 125–132.
- Nishikawa, T. 1980 Records of two lancelet species. *Asymmetron maldivense* and *A. lucayanum*, from the western North Pacific. *Publications of the Seto Marine Biological Laboratory*, 25:167–173.
- Nishikawa, T. 2004 A new deep-water lancelet (Cephalochordata) from off Cape Nomamisaki, South West Japan, with a proposal of the revised system recovering the genus *Asymmetron*. *Zoological Science*, 21:1131–1136.
- Pallas, P.S. 1774. Spicilegia zoologica, quibus novae imprimis et obscurae animalium species iconibus, descriptionibus atque commentariis illustrantur cura P.S. Pallas. Fasciculus 10, p. 1–41 + 4 plates.
- Paulin, C.D. 1977. *Epigonichthys hectori* (Benham) New Zealand lancelet (Leptocardii, Epigonichthyidae). *Records of the National Museum of New Zealand*, 1:143–147.
- Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Berichte der Deutschen wissenschaftlichen Kommission für Meeresforschung*, 28: 251–282.
- Pauly, D. 1984. A mechanism for the juvenile-to-adult transition in fishes. *ICES Journal of Marine Science*, 41(3): 280–284. [doi.org/10.1093/icesjms/41.3.280](https://doi.org/10.1093/icesjms/41.3.280)
- Pauly, D. 1998. Beyond Our Original Horizons: the Tropicalization of Beverton and Holt. *Reviews in Fish Biology and Fisheries*, 8: 307–334. [doi.org/10.1023/A:1008863215253](https://doi.org/10.1023/A:1008863215253)
- Pauly, D. 2021a. The Gill-Oxygen Limitation Theory (GOLT) and its critics. *Science Advances*, 7: eabc6050.

- Pauly, D. 2021b. Pre-submission draft of 'The GOLT and its critics', p. 67-115. In: D. Pauly and E. Chu (eds). *Marine and Freshwater Miscellanea III*. Fisheries Centre Research Report 29(1).
- Pauly, D. and J. Ingles. 1981. Aspects of the growth and mortality of exploited coral reef fishes, p. 89–98. In: E. Gomez, C.E. Birkeland, R.W. Buddemeier, R.E. Johannes, J.A. Marsh and R.T. Tsuda (eds). *Proceedings of the 4<sup>th</sup> International Coral Reef Symposium*. Vol. I. Manila, Philippines.
- Peters, W.C.H. 1877. Über *Epigonichthys cultellus*, eine neue Gattung and Art der Leptocardii. *Monatsberichte der Königlichen Akademie der Wissenschaften zu Berlin*, 1877: 322–327.
- Prashad, B. 1934. On a collection of Indian cephalochordates, with notes on the species from the Indian waters in the Indian Museum, Calcutta. *Records of the Indian Museum*, 36: 329–334.
- Pütter, A. 1920. Studien über physiologische Ähnlichkeit VI. Wachstumsähnlichkeiten. *Pflügers Archiv*, 180: 298–340.
- Raff, J.W. 1912. A new species of *Asymmetron* from the Great Australian Bight, South Australia, p. 304–308. In: *Zoological results of the fishing experiments carried out by F.I.S. "Endeavour" 1909-10 under H.C. Dannevid, commonwealth director of fisheries, Vol 1*. Sydney, Australia.
- Richardson, B.J. and A.M. McKenzie. 1994. Taxonomy and distribution of Australian cephalochordates (Chordata: Cephalochordata). *Invertebrate Taxon*, 8(6): 1443–1459 . [doi.org/10.1071/IT9941443](https://doi.org/10.1071/IT9941443)
- Sager, G. and F. Gosselck. 1985. A contribution on the age structure of *Branchiostoma lanceolatum*. *Internationale Revue der gesamten Hydrobiologie*, 4: 613–617.
- Schmitz, A., M. Gemmel and S.F. Perry. 2000. Morphometric partitioning of respiratory function in amphioxus (*Branchiostoma lanceolatum* Pallas). *Journal of Experimental Biology*, 203: 3381–3390.
- Stokes, M.D. 1996. Larval settlement, post-settlement growth and secondary production of the Florida lancelet (= amphioxus) *Branchiostoma floridae*. *Marine Ecology Progress Series*, 130: 71–84.
- Stokes, M.D. and N.D. Holland. 1996. Reproduction of the Florida lancelet (*Branchiostoma floridae*): spawning patterns and fluctuations in gonad indexes and nutritional reserves. *Invertebrate Biology*, 115(4): 349–359.
- Sundevall, C.J. 1852. Ny art af *Amphioxus*. *Öfversigt af Kongliga Vetenskaps-akademiens Förhandlingar*, 9: 147–148.
- Sundevall, T. 1853. Ny art af *Branchiostoma*. *Öfversigt af Kongliga Vetenskaps-akademiens Förhandlingar*, 10: 11–13.
- Tattersall, W.M. 1903. Notes on the classification and geographical distribution of the Cephalochordata. *Transaction of the Liverpool Biological Society*, 17: 269-302.
- Vergara, M., M.E. Oliva and J.M. Riascos. 2012. Population dynamics of the amphioxus *Branchiostoma elongatum* from Northern Chile. *Journal of the Marine Biological Association of the United Kingdom*, 92(3): 591-599.
- Webb, J.E. 1955. On the lancelets of West Africa. *Proceedings of the Zoological Society of London*, 125(2): 421-443.
- Webb, J.E. 1956a. Cephalochordata of the coast of tropical West Africa. *Atlantide Report*, 4: 167-182.
- Webb, J.E. 1956b. On the populations of *Branchiostoma lanceolatum* and their relations with the West African lancelets. *Proceedings of the Zoological Society of London*, 127: 125-140.
- Webb, J.E. 1956c. A note on the lancelets of Singapore, with a description of a new species of *Branchiostoma*. *Proceedings of the Zoological Society of London*, 127: 119–123.
- Webb, J.E. 1957a. On the lancelets of South and East Africa. *Annals of the South African Museum*, 43: 249-270.
- Webb J.E. 1957b. Cephalochordata. *The John Murray Expeditions 1933-34 Scientific Reports*, 10(3): 121-128.
- Webb, J.E. 1958a. On a collection of lancelets from The Gambia, with a description of a new species of *Branchiostoma*. *Proceedings of the Zoological Society of London*, 131(4): 627-635.
- Webb, J.E. 1958b. The ecology of Lagos Lagoon III. The life-history of *Branchiostoma nigeriense* Webb. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 241: 335-353.
- Whitley, G.P. 1932. The lancelets and lampreys of Australia. *Australian Zoologist*, 7: 256-264.
- Wiley, A. 1901. *Dolichorhynchus indicus* n.g., n.sp. a new acraniate. *Quarterly Journal of Microscopical Science* (Ser. 2), 44:269-272