

## Liza and the Flatworm

Whenever you say Liza is Judy's daughter, it is perfectly OK to restate your assertion as "Liza is the daughter of Judy." But when you say Judy is Liza's parent, you cannot restate your assertion as "Judy is the parent of Liza." Why?... Duh! Because Lisa has *two* parents. You have to say "Judy is *a* parent of Liza" instead. Were it not for uniqueness, however, the statements that Liza is Judy's daughter and that Judy is Liza's parent would be just two different ways of saying exactly the same thing: the important point is that there exists a parent-daughter relationship, and we can express it in two different ways.

Similarly for functions and their derivatives. Suppose we know a function  $G$  with the property that

$$G'(x) = g(x).$$

Then  $G$  is like Judy—in effect,  $G$  is the parent function; and  $g$  is like Liza—in effect,  $g$  is the daughter function. So there exists a parent-daughter relationship, and we can express it in two different ways: either  $g$  is  $G$ 's derivative, or  $G$  is  $g$ 's *anti-derivative*. But if we want to rewrite our assertions without apostrophes, then we have to be a little more careful: it is OK to say that  $g$  is the derivative of  $G$ , but we cannot say that  $G$  is the anti-derivative of  $g$ —rather, we must say that  $G$  is *an* anti-derivative of  $g$ , because  $g$ , like Liza, has more than one parent.

It is easy to see why. When you say that  $G'(x) = g(x)$ , you are saying that the slope of the graph of  $G$  at any point  $x$  in its domain is  $g(x)$ . But if you slide the graph upward or downward in a vertical direction by a fixed amount  $C$ ,\* then you change the function value at any point  $x$  in its domain by a constant amount  $C$ —from  $G(x)$  to  $G(x) + C$ —but you do not change its slope at all: the slope of the graph of  $G + C$  at any point  $x$  in its domain is still  $g(x)$ . In other words,

$$\frac{d}{dx} \{G(x) + C\} = g(x) + 0 = g(x)$$

for any value of  $x$ . Here's the difference between  $g$  and Liza: Liza has only two parents, whereas  $g$  has infinitely many (one for every value of  $C$ )—but in either case, "daughter of" implies uniqueness, whereas "parent of" implies an indeterminacy.

You know by now that mathematicians don't like to repeat lots of words if a symbol or two will do instead. So we clearly need a way to state " $G(x) + C$  is the generic anti-derivative of  $g$ " in symbols. For reasons that will become apparent only later, we opt to write  $\int g(x) dx = G(x) + C$ . That is

$$\int g(x) dx = G(x) + C \quad \iff \quad G(x) + C \quad \text{is the generic anti-derivative of } g.$$

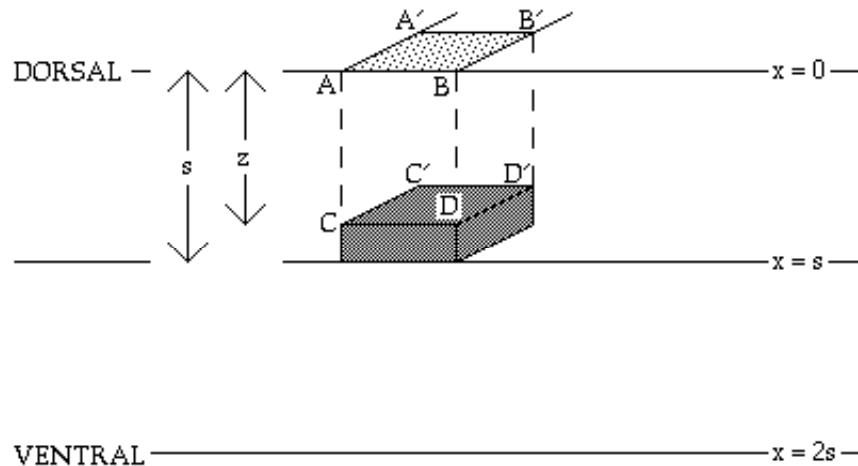
What does all this have to do with flatworms? I thought it might not be a bad idea to try to convince you that all this stuff about anti-derivatives is actually useful in answering questions about nature. So let's have a question from nature—in fact, about flatworms.†

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\*Where downward implies  $C < 0$ .

†Alexander's (1990) Section 4.3 (pp. 119-122) is the primary source for the remainder of this lecture. Note, however, some errors on p.121 of Alexander's discussion; in particular, he confuses dorsal and mid-section partial pressures in the mathematical analysis that leads to his equation (4.2).

Small animals such as platyhelminths are able to “breathe” without the help of a vascular system. They obtain all the oxygen they need by diffusion across the surface of their bodies from the surrounding respiratory medium. Why can’t large animals do this? The answer, of course, is that they are too large: they have too little surface area for oxygen to diffuse across compared to the volume of cells that must be supplied with oxygen. But how large is too large? Or to put it another way: How big can a flatworm be (and still survive without a vascular system)? That’s our question from nature.



To simplify this question let us assume at the outset that flatworms are flat (in the sense that most of their surface area is on two opposite sides), so that as much of their cell tissue is as near to the surface as possible. Then instead of asking how big a flatworm can be, we ask more specifically: How wide can a flatworm be? For the sake of definiteness, let our flatworm have thickness  $2s$  millimeters, and let  $x$  measure depth from its dorsal (upper) surface—see the figure above. Then we seek an upper bound on  $s$ .

Let  $F(x)$  be the rate per unit area ( $\text{mm}^2$ ) at which oxygen at depth  $x$  diffuses downward, perpendicular to the flatworm’s dorsal surface. That is,  $F(x)$  is the volume of oxygen transported downward per unit time (second) per unit area ( $\text{mm}^2$ ) at depth  $x$ , and so  $-F(x)$  is the rate per unit area at which oxygen at depth  $x$  diffuses upward. Now, diffusion of oxygen is simply flow of oxygen from regions of higher oxygen concentration to regions of lower oxygen concentration. The greater the imbalance between higher and lower concentration, the faster the flow. In other words, the steeper the concentration gradient, the faster the flow. By tradition, concentration of oxygen is expressed in terms of its partial pressure, which is the fraction of the total gas pressure attributable to oxygen; for example, the partial pressure of oxygen in air at atmospheric pressure is 0.21 atm (because air by volume is about 21% oxygen and 78% nitrogen, with 1% trace elements). Accordingly, let  $y$  be the partial pressure of oxygen at depth  $x$ ; and let the partial pressure at the dorsal surface be atmospheric, hence equal to 0.21 atm. The higher the value of  $\left| \frac{dy}{dx} \right|$ , the faster the flow of oxygen, i.e., the higher the value of  $|F|$ . Moreover, if  $\frac{dy}{dx} > 0$  then  $F < 0$ , because if oxygen concentration is higher at lower levels then oxygen diffuses upward; whereas if  $\frac{dy}{dx} < 0$  then  $F > 0$ , because if concentration is higher at higher levels then oxygen diffuses downward. It is consistent with these observations to assume that

downward flux of oxygen per unit area is a constant times the concentration gradient or

$$F = -q \frac{dy}{dx}$$

where  $q$  is called the diffusion coefficient. This proportional relationship between flux and concentration, satisfied remarkably well in practice, is commonly known as Fick's law.<sup>‡</sup> Alexander (1990, pp. 120-121) suggests that a suitable value for flatworm tissue is  $q = 2 \times 10^{-5} \text{ mm}^2 \text{ atm}^{-1} \text{ s}^{-1}$ .

Let us assume that oxygen is supplied to the upper half of our flatworm's body by diffusion across its dorsal surface, and to its lower half by diffusion across its ventral (lower) surface. Then the cuboid shaded in the figure must receive its oxygen across its upper surface  $CC'D'D$  (and hence ultimately across speckled area  $AA'B'B$  of the dorsal surface). Let  $CC'D'D$  (and hence  $AA'B'B$ ) have area  $\epsilon \text{ mm}^2$ . Then the cuboid's volume is just  $\epsilon$  times its height, or  $\epsilon(s - x)$ . Thus if  $m$  is the rate per unit volume at which oxygen is consumed by flatworm tissue (in  $\text{mm}^3/\text{sec}$ ), then  $m\epsilon(s - x) \text{ mm}^3$  of oxygen must be supplied across  $CC'D'D$  every second. But the rate of oxygen supply across unit surface area is  $\epsilon F$ . Hence, from above (Fick's law):

$$\epsilon \left( -q \frac{dy}{dx} \right) = \epsilon m(s - x)$$

or

$$\frac{dy}{dx} = \frac{m}{q}(x - s).$$

Note that, because  $x \leq s$  inside the cuboid,  $\frac{dy}{dx} \leq 0$ .

We have shown that  $\frac{m}{q}(x - s)$  is the derivative of  $y$ . So  $y$  must be an anti-derivative of  $\frac{m}{q}(x - s)$ . But we know from the chain rule that

$$\frac{d}{dx} \left\{ \frac{m}{2q}(x - s)^2 \right\} = \frac{m}{2q} \cdot 2(x - s) \cdot 1 = \frac{m}{q}(x - s).$$

Thus we already know *one* anti-derivative of  $\frac{m}{q}(x - s)$  ... and if you've seen one, you've seen them all! So we can write

$$y = \int \frac{m}{q}(x - s) dx = \frac{m}{2q}(x - s)^2 + C$$

where at this stage  $C$  is an arbitrary constant. However, the partial pressure at the surface must be atmospheric, i.e., when  $x = 0$ ,  $y$  must be 0.21 (atm). Hence

$$0.21 = \frac{m}{2q}(0 - s)^2 + C$$

or  $C = 0.21 - \frac{m}{2q}s^2$ , implying

$$y = \frac{m}{2q}(x - s)^2 + 0.21 - \frac{m}{2q}s^2 = 0.21 + \frac{m}{2q}x(x - 2s).$$

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<sup>‡</sup>After Adolf Fick, a 19th-century professor of physiology at Wurzburg

Thus the partial pressure of oxygen at the flatworm's midsection is

$$0.21 + \frac{m}{2q}s(s - 2s) = 0.21 - \frac{ms^2}{2q}.$$

But partial pressure cannot be negative; hence  $0.21 \geq ms^2/2q$ , or  $s^2 \leq 0.42q/m$ . This means that  $4s^2 \leq 1.68q/m$ , or

$$2s \leq \sqrt{\frac{1.68q}{m}}.$$

The right-hand side of this inequality is an upper bound on the thickness of the flatworm.

According to Alexander (1990, p.119), flatworms consume oxygen at a rate in excess of  $0.1 \text{ cm}^3$  per hour per gram of body tissue. Since the density of flatworm tissue is about 1 gram per  $\text{cm}^3$  and an hour is 3600 seconds, the volume rate of consumption exceeds  $0.1 \text{ cm}^3$  of oxygen per 3600 seconds per  $\text{cm}^3$  of flatworm; or, which of course is the same thing,  $0.1 \text{ mm}^3$  of oxygen per 3600 seconds per  $\text{mm}^3$  of flatworm. Thus  $m > 0.1/3600$ , implying that  $1/m < 3600/0.1 = 3.6 \times 10^4$ . We have already seen that  $q = 2 \times 10^{-5}$ . So  $1.68q = 3.36 \times 10^{-5}$ , implying  $1.68q/m < 3.36 \times 10^{-5} \times 3.6 \times 10^4 = 1.2096$ . Hence, from above,  $2s < \sqrt{1.2096} = 1.1 \text{ mm}$ . Thus, according to our analysis, a flatworm couldn't possibly be more than 1.1 millimeters thick.

In practice, a flatworm's thickness is never more than about 0.5 mm, less than half of our upper bound. Note, however, that if our flatworm could receive oxygen only through its dorsal surface, then our analysis would predict an upper bound of 0.55 mm on thickness instead, because in that case the ventral surface in the figure would be at  $x = s$  (and the worm would have thickness  $s$ , instead of  $2s$ ).

## Reference

Alexander, R. M. 1990 *Animals*. Cambridge: Cambridge University Press.