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# Weierstrassian Lévy walks are a by-product of crawling

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**Abstract** Weierstrassian Lévy walks are one of the simplest random walks which do not satisfy the central limit theorem and have come to epitomize scale-invariance even though they were initially regarded as being a mathematical abstraction. Here I show how these Lévy walks can be generated intrinsically as a by-product of crawling, a common but ancient form of locomotion. This may explain why Weierstrassian Lévy walks provide accurate representations of the movement patterns of a diverse group of molluscs – certain mussels, mud snails and limpets. I show that such movements are not specific to molluscs as they are also evident in *Drosophila* larvae. The findings add to the growing realization that there are many idiosyncratic, seemingly accidental pathways to Lévy walking. And that the occurrence of Lévy walks need not be attributed to the execution of an advantageous searching strategy.

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**Keywords:** Weierstrassian Lévy walks; crawling; molluscs; *Drosophila*; optimal searching

## 1. Introduction

25 Movement patterns resembling Lévy walks have been identified across all biological scales  
from the sub-cellular to the ecological [1,2]. The movement patterns of a diverse group of  
molluscs – certain mussels, mud snails and limpets along with those seen in swarming  
bacteria– stand apart because they resemble so-called ‘Weierstrassian’ Lévy walks rather  
than conventional Lévy walks [3-6]. Weierstrassian Lévy walks comprise a hierarchy of nested  
30 movement patterns which if extended indefinitely would correspond to a Lévy walk. They can  
be characterized by a hyper-exponential step-length distribution:

$$p(l) = \frac{q-1}{q} \sum_{j=0}^{\infty} q^{-j} b^{-j} L^{-1} \exp(-l/b^j L). \quad (1)$$

A step drawn from an exponential distribution with mean length  $Lb^j$  is  $q$  times more likely than  
is a step drawn from an exponential with the next longest mean. Therefore, a walker will  
35 typically make a cluster of  $q$  steps with mean length  $L$  before making a step of mean length  
 $bL$ , and so initiating a new cluster. About  $q$  such clusters separated by a distance of about  $bL$   
are formed before a step of mean length  $b^2L$  is made and so on. Eventually a hierarchy of  
clusters within clusters is formed. This scale-free pattern is the hallmark of a Lévy walk. Lévy  
exponent  $\mu = 1 + \ln q / \ln b$ . Weierstrassian Lévy walks are one of the simplest random walks  
40 which do not satisfy the central limit theorem and have come to epitomize scale-invariance  
[7]. Although initially regarded as a mathematical abstraction [8], Weierstrassian Lévy walks  
have subsequently been linked mathematically to dynamical chaos [9,10]. This suggests that  
the generative mechanism for Weierstrassian Lévy walks in molluscs [3-5], like that for their  
occurrence in swarming bacteria [6], is chaotic. Moreover, because Weierstrassian Lévy walks  
45 are evident in the movement patterns of a diverse group of molluscs the essential ingredients  
of the generative mechanism must be generic rather than organism specific.

Here I show that a simple, minimal mechanical model of crawling, i.e., stick-slip locomotion, is  
chaotic and so capable of producing Weierstrassian Lévy walks. The simplicity of the model  
50 allows for the identification of the minimal ingredients necessary to account for the occurrence  
of Weierstrassian Lévy walks in crawlers. It’s simplicity also allows for direct connections to  
be made between crawling and an extensive literature on chaos and Weierstrassian Lévy  
walks; a literature that stretches back decades but has yet not permeated into biology  
[9,10]. Indeed, I show analytically that the simple model of crawling is **approximately** analogous  
55 to the so-called ‘standard map’ – a prototype model of chaos. More complicated, more realistic  
models of crawlers that are not amenable to such analysis can easily be constructed, as

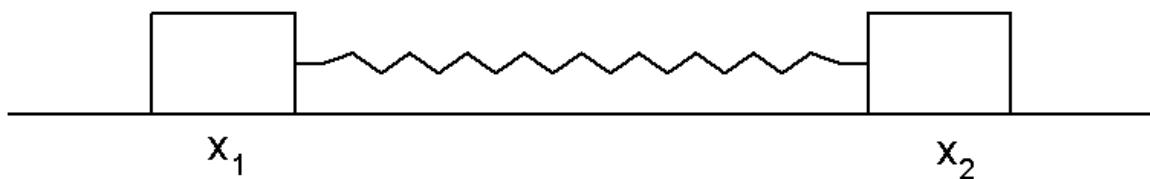
demonstrated by Loveless et al. [11] but the basic fact will remain unchanged: namely that chaos and so the propensity for producing Weierstrassian Lévy walks is ubiquitous in models of stick-slip locomotion. Finally, I show that movement patterns resembling Weierstrassian Lévy walks are also evident in *Drosophila* larvae. This shows that the generative mechanism is not specific to molluscs and may operate widely across taxa, in organisms that crawl.

The findings add to the growing realization that there are many idiosyncratic, seemingly accidental context-specific pathways to Lévy walking [1,2]. The findings are consistent with the 'free Lévy flight hypothesis' - which states that Lévy flights emerge spontaneously, naturally, and freely from innate behaviours and from banal, innocuous responses to the environment and, *if advantageous*, then there could be subsequent selection *against* losing them [1]. This runs counter to the hotly disputed 'Lévy foraging flight hypothesis' which states that natural selection should have led to adaptations for Lévy walk (also known as Lévy flights in the biological/ecological literature) foraging patterns because Lévy walks can optimize search efficiencies' [12,13].

## 2. Results

### 2.1 A minimal, heuristic model of crawling

Perhaps the simplest mechanical model of crawling and the one considered here consists of two blocks (where the local stresses are localized) that are connected by a spring (where the internal tension is stored) (Fig. 1).



**Figure 1. Schematic of the simple mechanical model of crawling**

The governing equations are

$$\begin{aligned} 85 \quad m_1 \ddot{x}_1 &= -\eta_1 \dot{x}_1 + K(x_2 - x_1 - d) \\ m_2 \ddot{x}_2 &= -\eta_2 \dot{x}_2 - K(x_2 - x_1 - d) \end{aligned} \quad (2)$$

where  $m_1$  and  $m_2$  are the masses of the blocks  $\eta_i$  is the viscous friction coefficient,  $K$  is the spring constant, and  $d$  is the equilibrium spacing of the blocks. It appears that net forces on the whole system cannot be exerted because  $m_1 \ddot{x}_1 + m_2 \ddot{x}_2 = 0$  but this is not the case if, as shown later, the crawler can occasionally redistribute its total mass between the two blocks.

90 Here pedal waves, a seemingly ubiquitous feature of crawling, that cause elongation and contraction of the body are modelled by periodically modulating the spring length,

$$d = 1 + \frac{1}{2} \sin(\omega t) \quad (3)$$

These waves can be generated either by central pattern generators, pacemaker neurons or by biomechanical feedback [11].

95 It is readily seen that in the underdamped limit (i.e., when friction can be ignored) that this mechanical model is approximately equivalent to the ‘standard map’ – a prototype model for chaos. This approximate equivalence arises when time  $t$  is replaced by  $x/\bar{v}$  where  $x = \frac{1}{2}(x_1 + x_2)$  and  $\bar{v}$  is the average velocity of the crawler. In the underdamped limit, Eqn. 2 reduces to

$$\begin{aligned} 100 \quad m_1 \ddot{x}_1 &= K(x_2 - x_1 - d) \\ m_2 \ddot{x}_2 &= -K(x_2 - x_1 - d) \end{aligned} \quad (4)$$

and consequently

$$\ddot{x}_1 - \ddot{x}_2 = (m_1^{-1} + m_2^{-1})K \left( x_2 - x_1 - 1 - \frac{1}{2} \sin(\omega t) \right) \quad (5)$$

or equivalently under the approximation

$$y'' = -l_0^{-2} \left( y - \frac{1}{2} \sin(kx) \right) \quad (6)$$

105 where  $y = x_2 - x_1 - 1$ ,  $k = \frac{\omega}{\bar{v}}$ , and  $l_0^{-2} = (m_1^{-1} + m_2^{-1})K\bar{v}^{-2}$ . Eqn. 6 has the solution

$$y = \frac{1}{1 - k^2 l_0^2} \frac{1}{2} \sin(kx) \quad (7)$$

It now follows from Eqn. 7 that the acceleration of the centroid  $\ddot{x} = \frac{1}{2}(\ddot{x}_1 + \ddot{x}_2)$  is given by

$$\ddot{x} = \frac{1}{2}(m_1^{-1} - m_2^{-1})K \left( y - \frac{1}{2} \sin(kx) \right) \quad (8)$$

Net forces can be exerted if the crawler periodically shifts its weight so that momentarily **and periodically**

$m_1 \neq m_2$  (and so that the quantity  $m_1^{-1} + m_2^{-1}$  in Eqn. 5 remains nearly constant). In this case, Eqn. 8 becomes

$$\begin{aligned} u_{n+1} &= u_n + K' \sin(kx_n) \\ x_{n+1} &= x_n + u_n \end{aligned} \quad (9)$$

where the subscript,  $n$ , denotes discrete times **at which**  $m_1 \neq m_2$  and where model constants have been grouped together to form  $K'$ . Eqn. (9) is the 'standard map' which by virtue of being weakly chaotic can produce Weierstrassian Lévy walks [9,10].

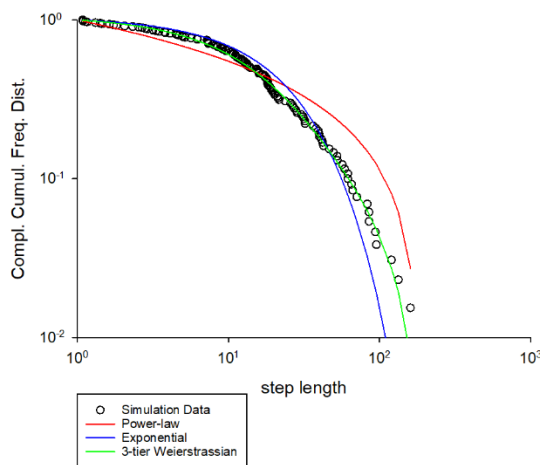
In the overdamped limit (i.e., when accelerations can be neglected), Eqn. 2 reduces to

$$\begin{aligned} \eta_1 \dot{x}_1 &= K(x_2 - x_1 - d) \\ \eta_2 \dot{x}_2 &= -K(x_2 - x_1 - d) \end{aligned} \quad (10)$$

It follows from Eqn. 10 that the centre of mass does not move when  $\eta_1 = \eta_2$  because  $(\dot{x}_1 + \dot{x}_2)/2 = 0$ . More generally, the centre of mass oscillates back and forth when the viscous friction coefficients are constant and  $\eta_1 \neq \eta_2$ . Locomotion can, however, happen if  $\eta_1 \gg \eta_2$  whenever the spring is compressed so that block 2 is pushed forwards and if  $\eta_2 \gg \eta_1$  whenever the spring is extended so that block 1 is pulled forwards. In this case unidirectional movement is punctuated by pauses wherein the centre of mass comes to rest.

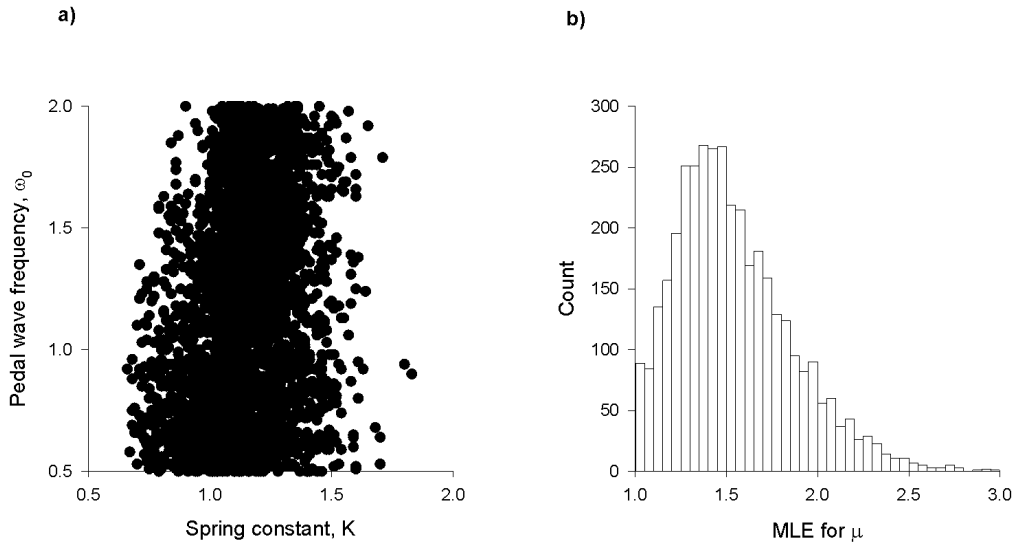
The results of numerical simulations reveal that Weierstrassian Lévy walks ensue **in the overdamped limit** when, as reported by Lai et al. [14], the frequency of the pedal waves,  $\omega$ , depends on the velocity of the centre of mass,  $v$  (Fig. 2). **This condition is not required in the underdamped limit.** Here a step length is taken to be distance travelled between consecutive pauses. Maximum Likelihood Estimation was used to fit the step length distributions, with model selection by Akaike's Information Criteria weights, where a weight of 1.0 provides **complete** support, and 0 weight no support. Step length distributions were fitted to tri-exponentials satisfying the scaling relations in Eqn. 1, power-laws and exponentials which are

indicative of 3-tier Weierstrassian Lévy walks, conventional Lévy walks and Brownian walks, a null model of the simulated movement patterns. All fitted distributions were truncated at the length of the longest step in the movement pattern. Note also that 4<sup>th</sup> and higher modes of a Weierstrassian Lévy walk are only be realized (detected) in very long trajectories because they occur relatively infrequently.



**Figure 2 The simple model of crawling, Eqn. 10, produces Weierstrassian Lévy walks.** Data are shown for  $K=2$  and  $\omega = \omega_0 + 0.001v$  with  $\omega_0 = 1$ . The Akaike weight for the 3-tier Weierstrassian Lévy walk is 1.00. The maximum likelihood estimate for the Lévy exponent of the Weierstrassian Lévy walk is 2.01; the value commonly associated with the execution of an optimal searching strategy [12].

Weierstrassian Lévy walks are predicted to arise for many choices of the model parameters that relate to an organism's mechanical properties (Fig. 3a, b).



**Figure 3a) The predicted emergence of Weierstrassian Lévy walk movement patterns does not require fine-tuning of model parameters.** Data were produced by the simple model of crawling, Eqn. 10. Combinations of model parameters ( $K$ ,  $\omega_0$ ) giving Weierstrassian Lévy walk movement patterns ( $\bullet$ ). The high tails of the predicted step-length distributed were fitted to power-laws and to exponentials using maximum likelihood estimates. If the Akaike weight for the power-law was greater than 0.95 then the movement was classified as being Weierstrassian Lévy walks. **b) Predicted distribution of the Lévy exponents,  $\mu$ .**

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## 2.2 *Drosophila* larvae

By tracking free-moving *Drosophila* larvae with (and without) blocked synaptic activity in the brain, Sims et al. [15] provided the strongest evidence yet that Lévy-like movement patterns in multicellular organisms can be generated intrinsically. Here I show that the larvae movement patterns identified by Sims et al. [15] as resembling conventional Lévy walks do, in fact, more closely resemble Weierstrassian Lévy walks that are predicted by the simple model of stick-slip locomotion, Eqn. 2.

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Maximum Likelihood Estimation was used to fit model parameters to the empirical step-length distributions determined according to the methods described in Humphries *et al.* [16], with model selection by Akaike's Information Criteria weights. Note that in *Drosophila* larvae turns always occur during pauses [15], making definitions of step-lengths in terms of pauses and

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turns, as in Humphries et al. [16], equivalent. Following Clauset et al. [17], only individuals making at least 50 steps and with step-lengths spanning at least 1+1/2 decades are presented in detail. All fitted distributions were truncated at the length of the longest step in the movement pattern.

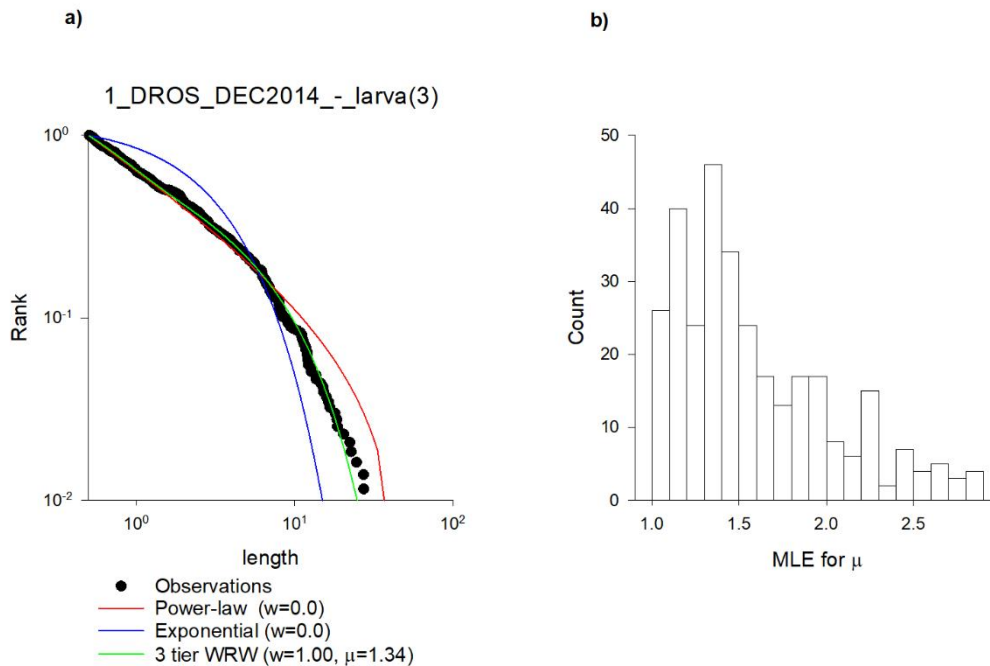
In accordance with model expectations, most of the larvae movement patterns analysed resemble truncated Weierstrassian Lévy walks (Table 1, Fig. 4a). This is not at variance at Sims et al. [15] who reported that the step-length distributions for most larvae movement patterns were best fitted by truncated power-laws rather than by 2<sup>nd</sup>, 3<sup>rd</sup> and 4<sup>th</sup>-order composite exponentials which encompass truncated Weierstrassian Lévy walks. Sims et al. [15] did not consider *truncated* composite exponents, as used here, and they did not consider the inter-dependence of parameters when calculating the Akaike weights. When viewed as truncated Weierstrassian Lévy walks the parameters in a composite random walk are not independent. From this stance, the truncated power-laws identified by Sims et al. [15] can be regarded as being simple representations of Weierstrassian Lévy walks that are compacted descriptions of the movement patterns but ones that do not facilitate identification of the underlying generative processes. The Lévy exponents vary between individuals. Their distribution (Fig. 4b) closely mirrors theoretical expectations (Fig. 3b).

Larva	No. of positional fixes	No. of steps	Akaike weight for WLW	$\mu$
<b>Controls</b>				
3	7277	433	1.00	1.34
4	3156	95	1.00	1.06
5	2427	117	0.98	1.11
9	2697	171	0.99	1.92
<b>Sensory deprived individuals 22 degrees</b>				
n1 7	5140	206	0.91	1.18
n1 8	5851	148	1.00	1.18
n2 0	4265	95	0.42	1.21

n2 4	8184	324	1.00	1.22
n2 9	8204	452	0.74	1.52
n3 136	2411	102	0.85	1.27
<b>Sensory deprived individuals 33 degrees</b>				
2	3563	153	0.72	1.23
3	3600	138	0.86	1.23
4	1861	88	0.98	1.80
6	3600	87	0.16	1.26
8	1894	140	1.00	2.11
22	2316	74	0.31	1.33

**Table 1. Analysis of individual movement patterns of *Drosophila* larvae in a control group (with file names 1\_DROS\_DEC2014\_-larva(\*)) and in a sensory deprived group (with file names BL-\_\_n\*\_22deg\_-\_larva(\*) and shi-\_\_n4\_33deg\_-\_larva(\*)).** In all cases the fits to Weierstrassian Lévy walks (WLW) are better than or comparable to the fits truncated Lévy walks. **Note that the Akaike weights for all the models tested sum to unity.** Data are taken from Sims et al. [15].

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**Figure 4 a) Example of a *Drosophila* larva step-length distribution closely resembling a truncated, 3-tier Weierstrassian Lévy walk.** Shown for comparison are a best fit truncated power-law and a best fit truncated exponential. **b) Distribution of the Lévy exponents,  $\mu$ , for all controls and treatments.** Data are taken from Sims et al. [15].

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### 3. Discussion

Here I argued that the occurrence of Weierstrassian Lévy walks in crawlers such as mussels, snails, limpets [3,5] and *Drosophila* larvae [herein] is not surprising given that such movement patterns are predicted by one of the simplest possible models of crawling – a model which in the underdamped limited was shown to be closely analogous to the standard map – a prototype model of chaos. I presented numerical evidence that this model is also capable of producing Weierstrassian Lévy walks in the overdamped limit (Fig. 2). Chaos and therefore the propensity to produce Weierstrassian Lévy walks is also present in more complex, more realistic models of crawling [11].

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The biomechanistic mechanism advocated here complements the purely neurological mechanisms posited by Reynolds et al. [4] and one subsequently realized concretely by Abe [18]. Abe [18] showed how the timing signals for Levy walking can arise near the critical point of a simple model for a central pattern generator (CPG) consisting of two coupled non-linear oscillators. This generic model does not explicitly consider the idiosyncrasies of crawling and

220

may not therefore account for the prevalence of Weierstrassian Lévy walking in animals that crawl [3-5] and their absence in animals that have other modes of locomotion. Nonetheless, pedal waves are a crucial ingredient component of mechanistic models of crawling and it is possible that **these** waves are generated by pace-maker neurons or by CPG that produce rhythmic outputs in the absence of rhythmic inputs. Pace-maker neurons and CPG may therefore play a central role in the production of the Lévy walks in crawlers, as advocated by Sims et al. [15]. Indeed, our modelling shows how biomechanical feedback transforms pedal waves (pace-maker neurons and CPG outputs) into Weierstrassian Lévy walks. But invoking CPG in this way may be unnecessary because pedal waves can be generated by purely biomechanical means [11]. An added complication with accessing the importance of putative neurological pathways is that the neural circuits of locomotion can be expected to adhere to the dynamical modes of the locomotion, rather than **impede** them [11] as exemplified perhaps by Hayashi et al. [19] and by Komendantov and Kononenko [20] who uncovered chaos in recordings of the electrical activity of neurons in the mollusc *Onchidium verruculatum* and in the snail, *Helix pomatia*.

The case for a purely neurological mechanism would be bolstered if Weierstrassian Lévy walks were found to provide a good description of the movement patterns of an organism that walks, preferably in the absence of environmental stimuli that can result in Lévy walking as an epiphenomena [1,2]. The latter condition cannot be attained by organisms that swim or fly because these individuals are immersed in media, water and air, that can provide cues sufficient for the generation of Lévy movement patterns [21,22]. In the meantime, support for the biomechanical mechanism can be found in Rabinovich and Abarbanel [23] who were among the first to critique the role of chaos in neuronal systems. These authors focused their attention on the occurrence of chaos in synaptically isolated neurons in central pattern generators. They noted that chaotic neurons not only regulate each other's behaviours, but easily adapt to extracellular parameters such as the coupling strengths among the neurons which are determined by the concentration of neuromodulators and other factors. This led Rabinovich and Abarbanel [23] to suggest that chaos in central pattern generators is a 'waiting state' which arises when the connections among the chaotic neurons "turned off" while waiting for external signals with information to act on. When sensory inputs are applied this state transforms into one of the many organized states (e.g., synchronized oscillations) that the neurons can support, and the chaos vanishes. This implies that Weierstrassian Lévy walks will be absent in crawlers in their natural habitats if they are the result of neurological chaos rather than biomechanical chaos. This is not the case [3,5].

If the biomechanics of crawling is crucial, then this pathway to Lévy walking will also be contingent on the substrate over which the organism moves. Slugs, for example, because they crawl, have the potential to Lévy walk but such movement patterns are unlikely to be realized when moving over rough soil that disrupts locomotion.

Weierstrassian Lévy walks may have ancient origins because limbless crawling probably appeared before movement using leg-like appendages arose. However, it is likely that when a leg-like appendage first appeared on the body wall of an animal it could only function if it operated with the pre-existing mode of locomotion and its incumbent mechanical constraints. Primitive walkers may therefore have moved in a manner similar to crawling before developing legs. This may explain why the legs of organisms such as millipedes and centipedes, that are amongst some of the first animals to colonize the land (around 440 million years ago during the Siluria period), form density waves that play a role like pedal waves in limbless species [24]. Organisms such as millipedes and centipedes may therefore have accidentally retained the ability to perform Weierstrassian Lévy walks. This suggests that the ability to Lévy walk may have been lost with the evolution of legs *per se*. It is also interesting to note that Weierstrassian Lévy walk have similitude with self-avoiding random walks [25] and that self-avoiding movement patterns resembling Lévy walks have been identified in ‘trace fossils’ (ichnofossils) – the preserved impressions left by now-extinct round worms that lived in shallow marine waters during the Vendian period (544 to 565 million years ago) [26]. These trace fossils are the only direct record of the behaviour of these ancient organisms and thus provides critical indications of the early evolution of movement patterns. Crawlers along with all modern other multicellular animals are thought to have descended from these worms. And with the advent of crawling some of the hallmarks of trace fossils were preserved.

Although seemingly accidental the occurrence of Weierstrassian Lévy walk movement patterns in some crawlers could, nonetheless, be advantageous and this could result in selection pressures for maintaining them or fine-tuning them since they are plastic (Fig. 3a). There was, however, no evidence for fine-tuning in *Drosophila* larvae as the observed variety of Weierstrassian Lévy walk movement patterns closely resembled model expectations in the absence of selection pressures (Figs. 3b, 4b). Indeed, the Lévy exponents characterizing the best fit Weierstrassian Lévy walks (Fig. 4b) are clustered around 1.5 rather than around 2, the value usually and controversially associated with optimal searching [12,13] and coincidentally found to characterize the best fit conventional Lévy walks to the *Drosophila* larvae movement patterns [15].

The new findings resonate with other numerous examples of Lévy walks where putative idiosyncratic generative mechanisms appear to have been hiding in plain sight in the form of seemingly innocuous behaviours [1,2]. And they add to the growing realization that the occurrence Lévy walks need not be attributed to the execution of an advantageous searching strategy [1,2].

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