**Supporting Information**

**Hierarchical random walks in trace fossils and the origin of optimal search behaviour**

DW Sims, AM Reynolds, NE Humphries, EJ Southall, VJ Wearmouth, B Metcalfe, RJ Twitchett

**SI Results**

**Table S1** Summary of trace fossil specimens and samples including location found, stratigraphic horizon and age. Three specimens (sample prefix UJTF) are from the collections of Geological Museum of the Jagiellonian University, Krakow, Poland, and were traced by RJT for this study. The remaining samples were found and documented in the field by the individual identified in the table and were not collected. Some samples yielded multiple specimens of the same ichnotaxon, as indicated by suffix letters in Tables S2 and S3.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Ichnotaxon** | **Sample**  | **Age** | **Horizon** | **Location** | **Notes** |
| *Helminthorhaphe flexuosa* | D1L1 | Lower-Mid Eocene | Hecho Group | N42˚36'23.0" W000˚32'41.8"  | Field: BM |
| *Helminthorhaphe**flexuosa* | D1L2 | Lower-Mid Eocene  | Hecho Group | N42˚36'24.3" W000˚32'41.0"  | Field: BM |
| *Helminthorhaphe japonica* | UJTF103 | Senonian | Sromowce Beds | Sromowce Wyżne, PL | UJTF coll. |
| *Cosmorhaphe tremens* | D2L6 | Lower-Mid Eocene | Hecho Group | N42˚43'11.6" W000˚39'44.2"  | Field: BM |
| *Cosmorhaphe* *fuchsi* | UJTF243 | Middle Eocene | Łącko Beds | Zubrzyca Górna, PL | UJTF coll. |
| *Cosmorhaphe**helminthopsoidea* | UJTF77 | Lower Eocene | Beloveža Beds | Łętownia Górna, PL | UJTF coll. |
| *Scolicia (Palaeobullia)* | MBA-1 | Lower Eocene | Higeur-Guetaria Formation | N43˚18'07.0" W002˚15'33.3" | Field: RJT |
| *Scolicia (Taphrhelminthopsis)* | MBA-3 | Lower Eocene | Higeur-Guetaria Formation | N43˚17'50.1" W002˚11'32.5" | Field: RJT |
| *Scolicia (Taphrhelminthopsis)* | MBA-4  | Lower Eocene | Higeur-Guetaria Formation | N43˚17'50.1" W002˚11'32.5" | Field: RJT |

**Table S2** Model fitting results for step-length distributions of *Helminthorhaphe* (HEL) and *Cosmorhaphe* (COS). Akaike’s Information criteria weights (*w*AIC) for model selection are shown for truncated Pareto-Lévy (power law) (TP), exponential (E), truncated exponential (TE), gamma (G), log-normal (LN), power law (P) distributions to empirical step-length data, in addition to composite Brownian walks (CB) with proportions of two, three and four exponential distributions. Strongest (least worst) support for each axis model is highlighted in bold. Note CB models were favoured in the majority of cases on one axis for individual specimens but only on both axes for three specimens.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Ichnotaxon** | **Track ID** | **TP** | **E** | **TE** | **G** | **LN** | **P** | **CB\_2** | **CB\_3** | **CB\_4** |
| *H. flexuosa* | D1L1\_X | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **0.91** | 0.00 | 0.09 |
|  | D1L1\_Y | 0.16 | 0.00 | 0.00 | 0.14 | 0.00 | 0.01 | 0.46 | 0.17 | 0.06 |
| *H. flexuosa* | D1L1a\_X | 0.26 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.10 | 0.04 | **0.60** |
|  | D1L1a\_Y | 0.47 | 0.00 | 0.43 | 0.01 | 0.00 | 0.00 | 0.06 | 0.02 | 0.01 |
| *H. flexuosa* | D1L2\_X | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **1.00** |
|  | D1L2\_Y | **0.66** | 0.00 | 0.30 | 0.02 | 0.01 | 0.00 | 0.01 | 0.00 | 0.00 |
| *H. japonica* | UJTF103\_X | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **1.00** |
|  | UJTF103\_Y | 0.39 | 0.00 | 0.42 | 0.11 | 0.07 | 0.00 | 0.01 | 0.00 | 0.00 |
| *C. tremens* | D2L6\_X | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **0.71** | 0.21 | 0.08 |
|  | D2L6\_Y | 0.07 | 0.00 | 0.00 | 0.06 | 0.00 | 0.00 | 0.00 | **0.65** | 0.22 |
| *C. fuchsi* | UJTF243\_X | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **0.66** | 0.25 | 0.09 |
|  | UJTF243\_Y | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **0.66** | 0.24 | 0.09 |
| *C. helminthopsoidea* | UJTF77\_X | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **0.66** | 0.25 | 0.09 |
|  | UJTF77\_Y | 0.02 | 0.01 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 | **0.95** | 0.00 |

**Table S3** Model selection results (*w*AIC) for *Scolicia* trails comparing truncated Pareto-Lévy (power law) (TP), exponential (E), truncated exponential (TE), gamma (G), log-normal (LN), power law (P) model distributions. The MLE fitted parameters (*x*min, *x*max, power law exponent *µ*) are for the TP distribution. Note that the truncated power law (TP) is favoured (least worst) on both axes for five *Scolicia* specimens (in bold).

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Track ID** | **Steps** | ***x*min** | ***x*max** | ***µ*** | **TP** | **E** | **TE** | **G** | **LN** | **P** |
| MBA-1\_X | 31 | 2 | 325 | 1.53 | 0.56 | 0.44 | 0.00 | 0.00 | 0.00 | 0.00 |
| MBA-1\_Y | 35 | 3 | 71 | 1.67 | **0.81** | 0.19 | 0.00 | 0.00 | 0.00 | 0.00 |
| MBA-3a\_X | 29 | 1 | 164 | 1.12 | **0.99** | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 |
| MBA-3a\_Y | 22 | 5 | 153 | 1.05 | **0.83** | 0.01 | 0.09 | 0.04 | 0.02 | 0.01 |
| MBA-3b\_X | 16 | 3 | 442 | 1.22 | **0.70** | 0.25 | 0.00 | 0.00 | 0.04 | 0.01 |
| MBA-3b\_Y | 34 | 2 | 300 | 1.43 | **0.79** | 0.21 | 0.00 | 0.00 | 0.00 | 0.00 |
| MBA-3c\_X | 20 | 4 | 102 | 1.05 | 0.25 | 0.40 | 0.22 | 0.05 | 0.09 | 0.00 |
| MBA-3c\_Y | 14 | 1 | 180 | 1.43 | 0.50 | 0.00 | 0.00 | 0.00 | 0.00 | 0.50 |
| MBA-3d\_X | 51 | 2 | 141 | 1.11 | **1.00** | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| MBA-3d\_Y | 49 | 2 | 277 | 1.30 | **0.99** | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 |
| MBA-4a\_X | 41 | 3 | 91 | 1.07 | **0.99** | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| MBA-4a\_Y | 30 | 5 | 195 | 1.10 | **0.86** | 0.00 | 0.09 | 0.04 | 0.01 | 0.00 |
| MBA-4b\_X | 32 | 2 | 90 | 0.94 | **0.98** | 0.00 | 0.01 | 0.01 | 0.00 | 0.00 |
| MBA-4b\_Y | 37 | 1 | 102 | 0.96 | **1.00** | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |

**Table S4** Model selection results (*w*AIC) for *Scolicia* tracks comparing truncated Pareto-Lévy (power law) (TP), exponential (E), truncated exponential (TE), gamma (G), log-normal (LN), power law (P) model distributions to empirical step-length data, in addition to composite Brownian walks (CB) with proportions of two, three and four exponential distributions. Note that the truncated power law (TP) is not favoured on both axes in the majority of cases, indicating marginally better fits to CB that are finely tuned to Lévy walks. For three *Scolicia* specimens (MBA-3a, 3b and 3d) there is stronger support (least worst) for one or either of the more complex CB models (CB3 or CB4) on both axes (in bold).

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Track ID** | **TP** | **E** | **TE** | **G** | **LN** | **P** | **CB\_2** | **CB\_3** | **CB\_4** |
| MBA-1\_X | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | **0.47** | 0.31 | 0.11 |
| MBA-1\_Y | **0.45** | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.31 | 0.11 | 0.04 |
| MBA-3a\_X | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **0.50** | **0.50** |
| MBA-3a\_Y | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **0.72** | 0.28 |
| MBA-3b\_X | 0.10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.11 | 0.04 | **0.73** |
| MBA-3b\_Y | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **0.97** | 0.03 |
| MBA-3c\_X | 0.01 | 0.02 | 0.01 | 0.00 | 0.00 | 0.00 | **0.63** | 0.23 | 0.08 |
| MBA-3c\_Y | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **1.00** |
| MBA-3d\_X | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.33 | **0.67** |
| MBA-3d\_Y | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.27 | **0.73** |
| MBA-4a\_X | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **0.74** | 0.26 |
| MBA-4a\_Y | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **0.62** | 0.28 | 0.10 |
| MBA-4b\_X | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | **0.66** | 0.25 | 0.09 |
| MBA-4b\_Y | **0.71** | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.19 | 0.07 | 0.03 |

**Figure S1.** Digitised tracings of all the trails of fossil *Helminthorhaphe*, *Cosmorhaphe* and *Scolicia* (irregular echinoid) used for random walk analyses in the current study. Sample codes on panels refer to those listed in Table S1.





