



## **Euclidean geometry explains why lengths allow precise body mass estimates in terrestrial invertebrates: the case of oribatid mites**

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2 **Euclidean geometry explains why lengths allow precise body mass estimates in**  
3 **terrestrial invertebrates: the case of oribatid mites**

4

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24 **Abstract**

25 Indirect measures of soil invertebrate body mass  $M$  based on equations relating the latter to  
26 body length ( $l$ ) are becoming increasingly used due to the required painstaking laboratory  
27 work and the technical difficulties involved in obtaining some thousands of reliable weight  
28 estimates for animals that can be very small. The implicit assumption of such equations is that  
29  $\frac{dM}{dV} = \delta$ , where  $V$  is body volume and  $\delta$  is a constant density value. Classical Euclidean  
30 scaling implies that  $V \propto l^3 \propto M$ . One may thus derive  $M$  from  $l$  when the latter can provide a  
31 good estimate of  $V$  and the assumption of a constant  $\delta$  is respected. In invertebrates, equations  
32 relating weight to length indicate that the power model always provides the best fit. However,  
33 authors only focused on the empirical estimation of slopes linking the body mass to the length  
34 measure variables, sometimes fitting exponential and linear models that are not theoretically  
35 grounded. This paper explicates how power laws derive from fundamental Euclidean scaling  
36 and describes the expected allometric exponents under the above assumptions. Based on the  
37 classical Euclidean scaling theory, an Equivalent Sphere is defined as a theoretical sphere  
38 with a volume equal to that of the organism whose body mass must be estimated. The  
39 illustrated application to a data set on soil oribatid mites helps clarify all these issues. Lastly,  
40 a general procedure for more precise estimation of  $M$  from  $V$  and  $\delta$  is suggested.

41

42 **Key words: volume; density; scaling; weight; indirect estimate; soil invertebrates**

43

43 **Introduction**

44 Weighing soil invertebrates with accurate electronic microbalances involves painstaking  
45 laboratory work to obtain a very high number of measures for animals that can be very small  
46 (i.e., microarthropods  $< 0.5 \text{ mm}^3$ ). Completing accurate estimates for relatively large  
47 terrestrial invertebrates (molluscs, coleopterans) can be very time consuming, especially for  
48 community studies requiring thousands of measures. There are high quality ecological works  
49 based on indirect measures of body mass derived from equations relating the latter to body  
50 size (e.g. Saint-Germain *et al.* 2007). Thanks to earlier research, similar equations are  
51 available for other animal groups, including microarthropods such as oribatid mites (i.e.,  
52 Berthet 1964; Lebrun 1971) and springtails (Petersen, 1975), and many insects (Rogers et al.  
53 1976). However, when using size equations for weight estimates, different parameters are  
54 required for different shape types (Berthet 1967; Lebrun 1971). Bias may also arise from  
55 sexual dimorphisms (females bigger than males) or life cycles (gravid vs non-gravid).  
56 Unfortunately, equations are usually built on empirical grounds: authors search for the model  
57 that best fits data on body mass ( $M$ ) and length ( $l$ ). In some cases models not theoretically  
58 grounded in biometrical and geometrical principles, for example linear models, were also  
59 tested and (not surprisingly) found to have a very poor fit (i.e. Brady and Noske 2006). The  
60 present paper undertakes a theoretical analysis of the implicit assumptions and logic that  
61 underlie past research on empirical  $M-l$  relationships. Furthermore, stemming from theory, a  
62 more general approach is proposed with an example of application to the soil oribatid mite  
63 data set compiled by Lebrun (1971).

64

65 **Theory**

66 In agreement with reports by specialists on many invertebrate taxa (i.e.: Petersen, 1975;  
67 Rogers et al. 1976; Berg 2000; Brady and Noske 2006), Lebrun (1971) found a very good fit  
68 when using the power model

$$69 \quad M = cL^aW^b \rightarrow \log(M) = \log c + a \log(L) + b \log(W) \text{ (eq. 1)}$$

70 for relating body mass  $M$  to length measures  $L$  (total length) and  $W$  (maximum width) in  
71 oribatid mites. Interestingly, Lebrun did not seem to realise the theoretical meaning of  
72 parameters  $a$ ,  $b$  and  $c$ . Instead, he implicitly used them as typical statistical parameters of  
73 model fitting routine. We here argue that the fit of such equations is excellent because

$$74 \quad \frac{dM}{dV} = \delta \text{ (eq. 2)}$$

75 and

$$76 \quad V \propto l^3 \propto M \text{ (eq. 3)}$$

77 which implies that the constant  $c$  of (eq. 1) must also include information on density  $\delta$ . Let us  
78 assume that the body shape of oribatids is well approximated by an ellipsoid of dimensions  $L$ ,  
79  $W$  and  $H$  (Fig. 1). The letter  $H$  indicates body height, a rarely available parameter that is  
80 difficult to measure. Let us also define an equivalent sphere (EqSph) as the sphere with a  
81 volume equal to that of the above ellipsoid or of any other shape oribatids can assume. The  
82 oribatid volume is therefore

83  $V = \frac{4}{3} \pi LWH = \frac{4}{3} \pi r^3$ , where  $r$  is the radius of EqSph and  $L$ ,  $W$  and  $H$  are the three axes of  
84 the ellipsoid.

85 It follows that  $r = L^{1/3}W^{1/3}H^{1/3}$ .

86 From eq. 2 and Lebrun's model of eq. 1 it follows that

$$87 \quad V = \frac{c}{\delta} L^a W^b = \frac{4}{3} \pi r^3 \Rightarrow r^3 = \left( \frac{3c}{4\delta\pi} \right) L^a W^b \text{ eq. (4).}$$

88 From Euclidean scaling and the proportionality of eq. 3, the first perhaps evident but  
 89 important conclusion is that  $a + b = 3$  because  $V \propto l^3 \propto L^a W^b$  and  $L$  and  $W$  are lengths. This  
 90 result is empirically confirmed by the regression results of Lebrun (1971), who for example  
 91 found that in three different data sets on oribatid mites with different shapes,  $a$  and  $b$  were  
 92 respectively 1.50 and 1.50, 2.10 and 0.90, 1.60 and 1.40. This is simply a consequence of  
 93 classical Euclidean scaling by eq. 2 and 3 and indicates that  $L$  and  $W$  allow a good estimation  
 94 of the volume  $V$ . This definitely clarifies the theoretical meaning of original Lebrun's  
 95 parameters: they regulate the allometric scaling between body mass and length and are not  
 96 simple statistical parameters. The same would be true if it were possible to accurately estimate  
 97  $M$  from just  $L$ . In this case, the equation would become

$$108 \quad \delta \frac{4}{3} \pi r^3 = c L^b \Rightarrow r^3 = \frac{3c}{4\delta\pi} L^b \text{ eq. (5)}$$

99 and  $b = 3$  because  $V \propto L^3 \propto l^3$ . Accordingly, empirical results obtained for several taxa (e.g.  
 100 spiders, beetles, flies and midges) usually obey or very nearly obey this equation (Petersen,  
 101 1975; Rogers et al. 1976; Berg 2000; Brady and Noske 2006). The interpretation is that the  
 102 more  $L$  allows good estimation of  $V$ , the more it allows estimation of  $M$ . Accordingly, if  $b \neq 3$   
 103 then the one known dimension does not allow correct indirect estimation of volume.  
 104 Alternatively, the assumption of eq. 2 is wrong but, as clearly shown below, this is highly  
 105 unlikely because of the fundamental characteristics of biological tissues.

106 Eq. 5 can be written as

$$107 \quad r^3 = \frac{3c}{4\delta\pi} l^3 \Rightarrow c = \frac{4}{3} \delta\pi \left(\frac{r}{l}\right)^3 \text{ eq. (6)}$$

108 with  $l$  is any linear length that combined with the parameter  $\delta$  allows precise estimation of  $V$ .  
 109 The most interesting feature of this formulation is that when regressions relating  $M$  to  $l$  result  
 110 in a very good fit, it is possible to appropriately estimate  $V$  from  $l$ . Note that  $l$  is not  
 111 necessarily a classical standard length like total length or width. It can also be a combination

112 of several  $l$  that allow a good estimation of  $V$ . This is more clearly explained below. The more  
 113  $l$  is similar to  $r$ , the more  $c$  is near to  $\delta$  in the sense that

$$114 \quad \lim_{l \rightarrow r} c = \frac{4}{3} \delta \pi$$

115 If one can therefore find any  $l$  for which the volume of EqSph can be calculated assuming  $r =$   
 116  $l$ , then the regression model allows the estimation of animal density. In practice this is very  
 117 difficult. However, in theory, assuming that one can find such an  $l$ , one must then collect a  
 118 large array of weights and lengths for the best estimate of  $\delta$ : under the above assumptions, this  
 119 is achieved using the model that provides the most accurate estimate of  $M$  based on  $l$ , and this  
 120 is possible because  $l$  allows estimation of  $V$ . If one finds a very good model ( $R^2 > 0.98$ ), then  
 121 the estimated  $\delta$  can be used to also estimate the  $M$  of other animals, provided that one has an  
 122 equation for estimating  $V$  from length measures. This would eliminate the need to estimate the  
 123 parameters of eq. (4), which seem to be affected by shape variations, as stressed in earlier  
 124 works (e.g. Lebrun, 1971). Unfortunately, there is no principle or geometrical rule allowing  
 125 the *a priori* identification of an  $l = r$ . The only solution is to obtain precise estimates of  
 126 density  $\delta$  through direct laboratory measurements. Firstly, this would help verify the  
 127 reasonable assumption of eq. 2. Secondly, when a close estimate of  $\delta$  is obtained, it is possible  
 128 to fit models derived from eq. (5). If these provide an excellent fit ( $R^2 > 0.98$ ), the ratio ( $r/l$ )  
 129 can be precisely estimated from  $\delta$  and  $c$ , the latter being the regression constant. One can then  
 130 use this ratio and the experimental value of  $\delta$  to estimate any  $M$  using the EqSph volume.  
 131 Knowledge of  $r/l$  and  $\delta$  from the model estimate of  $c$  allows *a priori* calculation of any

132 organism volume by estimating the volume of the EqSph with  $r^3 = \frac{3c}{4\delta\pi} l^3$ . One can then use

133  $M = \delta V$  to estimate body mass.

134 An important feature of this theory is that, at first approximation, an almost optimal value of  $\delta$   
 135 can be derived on physical and basic biological grounds. Oribatid mites float in a NaCl-  
 136 saturated water solution, which has a specific gravity  $\approx 1.20$ : this means that the specific

137 gravity of oribatids is below this value. This characteristic buoyancy allows wet extraction of  
138 soil animals and does not come as a surprise. Indeed, the specific gravity of all biological  
139 tissues is slightly higher than that of water (1.00) because cells and tissues mainly consist of  
140 water and dissolved or suspended macromolecules and organelles. For instance, early works  
141 already indicated that the specific gravity of arthropod blood ranges from 1.012 to 1.043  
142 (Rustum Maluf, 1969). Accordingly, the specific gravity of *Chironomus* larvae ranges from  
143 1.026 to 1.045 (Edwards, 1957). In general, classical laboratory measurements of specific  
144 gravity performed across several phyla (from protozoa to higher invertebrates) result in values  
145 of 1.001 to 1.046 (Williams, 1900). Such narrow ranges are characteristic of living organisms,  
146 including vertebrates, notwithstanding the macroscopic differences between tissues like bone  
147 and blood (i.e. Morales et al., 1945; Watanabe et al. 2006). For example, recent measures on  
148 Baikal seals indicate that this species has a specific gravity of 1.027 to 1.046 (Watanabe et al.  
149 2006). Although small variations of the third decimal digit may have important biological  
150 implications because, for instance, they affect body buoyancy, for the aim of this paper and  
151 given the lack of precise experimental measurements on oribatid mites, an average value of  
152  $1.030 \pm 0.015$  is assumed. Specific gravity is a dimensionless number equal to the ratio  
153 between the density of the target object and that of water at 4 °C and 1 atm, which is  $0.999 \approx$   
154  $1 \text{ g/cm}^3$ . However, at a given environmental pressure, water density changes as function of  
155 temperature. Nevertheless, between 4°C and 30 °C water density varies from  $0.999 \text{ g/cm}^3$  to  
156  $0.996 \text{ g/cm}^3$  and thus, given the adopted approximation for specific gravity, a density  $\delta = 1.03$   
157  $\text{g/cm}^3$  can be assumed.

158

### 159 **An example: models for oribatid body mass estimates**

160 We reanalysed data reported in Appendix (1) from the original work of Lebrun (1971).

161 They consist of 44 associated measures of body length, width and weight from 36 oribatid  
162 mites species of different shape that are encountered within this ecologically important soil



163 taxon. Linear models (obtained by least squares estimates) were used to derive  $\log M$  from  $\log$   
 164  $L$  and  $\log W$ . In particular, competing models built on the above theory were: model 1,  
 165 Lebrun's model of eq. 1; model 2, called the " $L$  model", which assumes that  $l = L$ ; model 3,  
 166 called the " $W$  model", is the same as model 2 but with  $l = W$ ; model 4, called the "Mean  
 167 model", where  $l = f(L, W) = L + W$ .

168 Competing model equations were:

169 model 1:  $\log M = \log c + a \log L + b \log W$ , with  $a + b$  expected to equal 3.

170 models 2 and 3:  $\log M = \log c + a \log l$ , with  $l = L$  or  $W$  and  $a = 3$

171 model 4:  $\log M = \log c + a \log (l = f(L, W))$  with  $a = 3$  and  $l = L + W$

172 Models 2, 3 and 4 have interesting potential applications. For instance, if model 4 had the best  
 173 fit, then one could estimate the EqSph volume  $V$  by assuming  $\delta = 1.03 \text{ g/cm}^3$  and calculating  
 174 the ratio  $r/l$  using eq. 6, without having to take into account body shape and associated  
 175 variations in  $a$  and  $b$  (Lebrun, 1971). The model 4 assumption that  $l = L + W$  is based on the  
 176 idea that oribatids usually have an ovoidal shape, the volume of which could be well  
 177 approximated by a sphere with a radius intermediate between that of half the two largest body  
 178 measures (total Length and maximum Width). According to this idea, one can simply include  
 179 this information by summing the two linear measures ( $l = L + W$ ).

180 Lastly, Lebrun (1971) stated that the model 1 parameters change if one performs separate  
 181 analyses on species after grouping them into morphological categories. For example, Lebrun  
 182 (1971) identified three main categories: Achipteriforms, which have a more or less elongate  
 183 oval shape (this includes superfamilies like Pelopoidea, Oribatelloidea and Ceratozetoidea),  
 184 Caraboidiforms, which have a squared silhouette (e.g. the genera *Carabodes* and  
 185 *Tectocephus*) and Nothroiforms, with a squared to almost triangular shape (e.g. *Camisia*  
 186 and *Nothrus*). Other morphological types may include Phthiracariform (spheroidal to ovoidal)  
 187 or Hypochthoniiform, which may be approximated by a combination of different (squared

188 trapezoid shape. Lebrun's estimate of parameters  $a$  and  $b$  varied a lot among the different  
189 categories. Here, the classification used in assessing the Lebrun hypothesis does not exactly  
190 match but strongly resembles that proposed by Lebrun (1971; see the "Shape" column in  
191 Appendix 1). The following two models were thus also considered among the competing  
192 ones:

193 model 5:  $\log M = \log c + a \log L + b \log W + \text{shape}$ , under the hypothesis that shape only  
194 effects  $c$ .

195 model 6:  $\log M = \log c + \text{shape} * a \log L + \text{shape} * b \log W + \text{shape}$  under Lebrun's interaction  
196 hypothesis that different shapes also have different  $a$  and  $b$  values.

197 The model-building strategy was based on the idea that not all possible models but only those  
198 with precise theoretical foundations must be considered during statistical analysis (Burnham  
199 and Anderson, 2002; Johnson and Omland, 2004). This approach is rather different from that  
200 adopted in past similar studies, where authors just empirically searched for the best fitting  
201 model and accordingly tested several different types of regressions, including very  
202 improbable ones that assume  $M \propto I$ . In keeping with the logic of this paper, model  
203 assessment and selection was thus based on Akaike's theoretic approach and information  
204 criterion corrected for sample size ( $AIC_c$ : Burnham and Anderson, 2002; Johnson and  
205 Omland, 2004). One of the advantages of this strategy with respect to more traditional ones  
206 (e.g. hypothesis testing based on likelihood ratios) is that the competing models analysed in  
207 the present paper are not nested. In these cases, AIC is one of the best model-assessment tools  
208 (Johnson and Omland, 2004). Models were ranked according to Akaike's criterion and the  
209 minimum  $AIC_c$  (below  $AIC_{\min}$ ) was used as the reference for calculating the AIC difference  
210 ( $\Delta_i$ ) and model weights ( $w_i$ ). Models within 2 AIC units of the  $AIC_{\min}$  were considered  
211 competitive and more plausible than the others, and their weights were considered a measure  
212 of their robustness (Burnham and Anderson 2002). Linear models were performed using R

213 (The R Foundation for Statistical Computing Version 2.3.0 (2006-04-24) ISBN 3-900051-07-  
214 0), available at <http://www.r-project.org>.

215

## 216 **Results and concluding remarks**

217 All models resulted in an excellent fit with very high adjusted  $R^2$ , but ranking based on  
218 Akaike's criterion (Tab. 1) clearly showed that model 4 was the best model with a weight  $>$   
219 0.80 and  $\Delta AIC_c$  with respect to the second-best model  $> 3$ , indicating that all other  
220 competing models are weak to very weak with respect to the best one (Burnham and  
221 Anderson 2002). Although Lebrun's interaction hypothesis represented by model 6 apparently  
222 resulted in the best fit because it had the highest  $R^2$ , it was highly penalised by Akaike's  
223 information criterion because of the very high number of parameters, which make it non-  
224 parsimonious relative to its predictive power (Burnham and Anderson 2002). This shows that  
225 one can simply estimate the EqSph volume without taking into account shape variations: they  
226 do play a role, but in the framework of the presented theory their role seems irrelevant.

227 The estimated  $a$  parameter is always consistent with theoretical expectations (Table 2): the  
228 only significant exception is the poor fit of model 3, which indicates that  $W$  alone does not  
229 provide a reliable estimate of  $V$  and thus of  $M$ . In general, the two worst models are those that  
230 consider only one measure; it therefore seems fundamentally important to have at least two  
231 linear measures to jointly represent body size and allow a reliable estimate of body volume.  
232 For the best model the constant  $\log c = -17.17 \pm 0.46$ . For  $\delta = 1.03 \cdot 10^{-6} \mu\text{g}/\mu\text{m}^3$ ,  $(r/l) = 0.201$   
233 (the same units of Appendix 1 were used in these calculations). Therefore, future estimates of  
234 the body mass  $M$  of an oribatid can be based on the volume of the EqSph with  $r =$   
235  $0.201(L+W)$ . For example, one can take  $L = 571 \mu\text{m}$  and  $W = 249 \mu\text{m}$  from the first entry of  
236 Appendix (1). This results in an  $r = 165 \mu\text{m}$ , an oribatid volume  $V = \text{EqSph } V = 4/3\pi r^3 = 1.88$   
237  $10^7 \mu\text{m}^3$  and body mass  $M = 19.4 \mu\text{g}$ . The observed  $M = 18.1 \mu\text{g}$ . One can also estimate  $r$  for  
238 each datum and plot  $M$  as function of  $r$  or, equivalently, of its EqSph  $V$  (Fig. 2). A power law

239 with exponent  $a \approx 3$  obviously relates  $r$  to  $M$ , whereas a linear model with slope  $\approx \delta$  relates  $M$   
240 to EqSph  $V$ .

241 Part of the residual variations are likely due to the fact that  $\delta$  was assumed and not  
242 experimentally measured. It probably also varies slightly (of the order of  $10^{-3}$ ) across species,  
243 populations and individuals. Nevertheless, the collected data allow reliable estimates and are  
244 therefore promising for future application, especially if one considers the very small size of  
245 these animals. Ecological studies which aim to obtain precise population biomass and energy  
246 estimates would of course require accurate length measures of the populations inhabiting the  
247 study area, because generic measures from literature are subject to very high local variability  
248 (known since Lebrun, 1971). Furthermore, error propagation occurs when estimates are  
249 derived from functions combining estimated variables and their errors. Lastly, the formulated  
250 theory has been particularly successful in the case of oribatids and its extension to other taxa,  
251 especially to those for which weight and length data are already available, deserves further  
252 attention.

253

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256

#### 257 **References**

- 258 Berg, M., 2000. Mass-length and mass-volume relationships of larvae of *Bradysia paupera*  
259 (Diptera: Sciaridae) in laboratory cultures. Eur. J. Soil Biol. 36, 127–133.
- 260 Berthet, P., 1964. L'activité des Oribatides (Acari: Oribatei) d'une chênaie. Mem. Inst. Roy.  
261 Sci. Nat. Belg. 152, 1–152.
- 262 Brady, C.J., Noske, R.A., 2006. Generalised regressions provide good estimates of insect and  
263 spider biomass in the monsoonal tropics of Australia. Aust. J. Entomol. 45, 187–191.

- 264 Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference. A practical  
265 information theoretic approach. Springer, New York.
- 266 Edwards, R.W., 1957. The relation of oxygen consumption to body size and to temperature in  
267 the larvae of *Chironomus rjparius* Meigen. Exp. Biol. 35, 383-395.
- 268 Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. Trends Ecol.  
269 Evol. 19, 101-108.
- 270 Lebrun, P., 1971. Écologie et biocénotique de quelques peuplements d'arthropodes  
271 édaphique. Mem. Inst. Roy. Sci. Nat. Belg. 165, 1-203.
- 272 Morales, M.F., Rathbun, E.N., Smith, R.E., Pace, N., 1945. Studies on body composition II.  
273 Theoretical considerations regarding the major body tissue components, with  
274 suggestions for application to man. J. Biol. Chem. 158, 677-684.
- 275 Petersen, H., 1975. Estimation of dry weight, fresh weight, and calorific content of various  
276 Collembolan species. Pedobiologia 15, 222-243.
- 277 Rogers, L.E., Hinds, W.T., Buschbom, R.L., 1976. A general weight vs. length relationship  
278 for insects. Ann. Entomol. Soc. Am. 69, 387-389.
- 279 Rustum Maluf, N.S., 1939. The blood of arthropods. Q. Rev. Biol. 14, 149-191.
- 280 Saint-Germain, M., Buddle, C.M., Larrivée, M., Mercado, A., Motchula, T., Reichert, E.,  
281 Sackett, T.E., Sylvain, Z., Webb, A., 2007. Should biomass be considered more  
282 frequently as a currency in terrestrial arthropod community analyses? J. Appl. Ecol.  
283 44, 330-339.
- 284 William, S.R., 1900. The specific gravity of some fresh-water animals in relation to their  
285 habits, development, and composition. Am. Nat. 34, 95-108.
- 286

286 Table 1. Competing models ranked according to the AIC criterion

Model	R <sup>2</sup>	K	Δ AIC <sub>c</sub>	Akaike's Weight
4: $\log M = \log c + a \log[L + W]$	0.979	3	0.000	0.823
1: $\log M = \log c + a \log L + b \log W$	0.978	4	3.362	0.153
5: $\log M = \log c + a \log L + b \log W + \text{shape}$	0.978	7	7.781	0.017
6: $\log M = \log c + \text{shape} * a \log L + \text{shape} * b \log W + \text{shape}$	0.983	13	9.532	0.007
2: $\log M = \log(c) + a \log L$	0.957	3	31.435	<0.001
3: $\log M = \log c + a \log W$	0.931	3	52.520	<0.001

287 \*, interaction; R<sup>2</sup>, adjusted squared R; K, number of parameters including the estimation of  
 288 residual  $\sigma^2$ ; shape, four morphological categories defined after Lebrun (1971)

289 Table 2. Observed and expected scaling exponents

	<i>Estimated a ± SE</i>	<i>Estimated b ± SE</i>	Theoretical Value
Model 4 (Mean model)	3.00 ± 0.07	NP	a = 3
Model 1 (Lebrun)	1.90 ± 0.20	1.10 ± 0.17	a + b = 3
Model 5 (Lebrun shape)	2.01 ± 0.32	1.01 ± 0.28	a + b = 3
*Model 6 (Lebrun interaction) for shape A	2.10 ± 0.85	0.93 ± 0.74	a + b = 3
Model 2 (L model)	3.09 ± 0.10	NP	a = 3
Model 3 (W model)	2.63 ± 0.11	NP	a = 3

290 \* shape parameters for C, Q and S were not significantly different with respect to A and are  
 291 therefore not reported. NP, not present.

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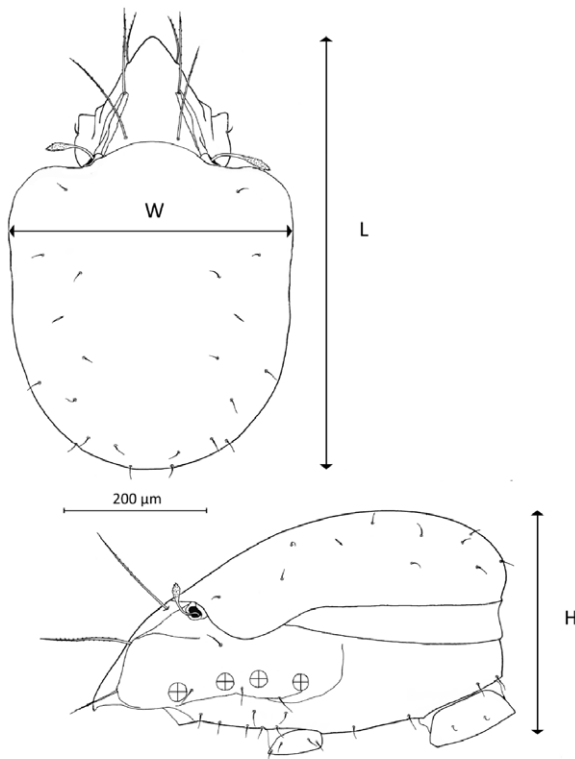
292 **Figure captions**293 Fig.1 The oribatid mite *Scheloribates laevigatus*. L = total length, W = maximum width, H = height.294 Fig. 2 Plot of observed weight versus the radius  $r$  and equivalent sphere volume EqSph, as295 estimated from model 4 (Mean model) parameters and assuming  $\delta = 1.03 \cdot 10^{-6} \mu\text{g}/\mu\text{m}^3$ 

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296 Figure 1:

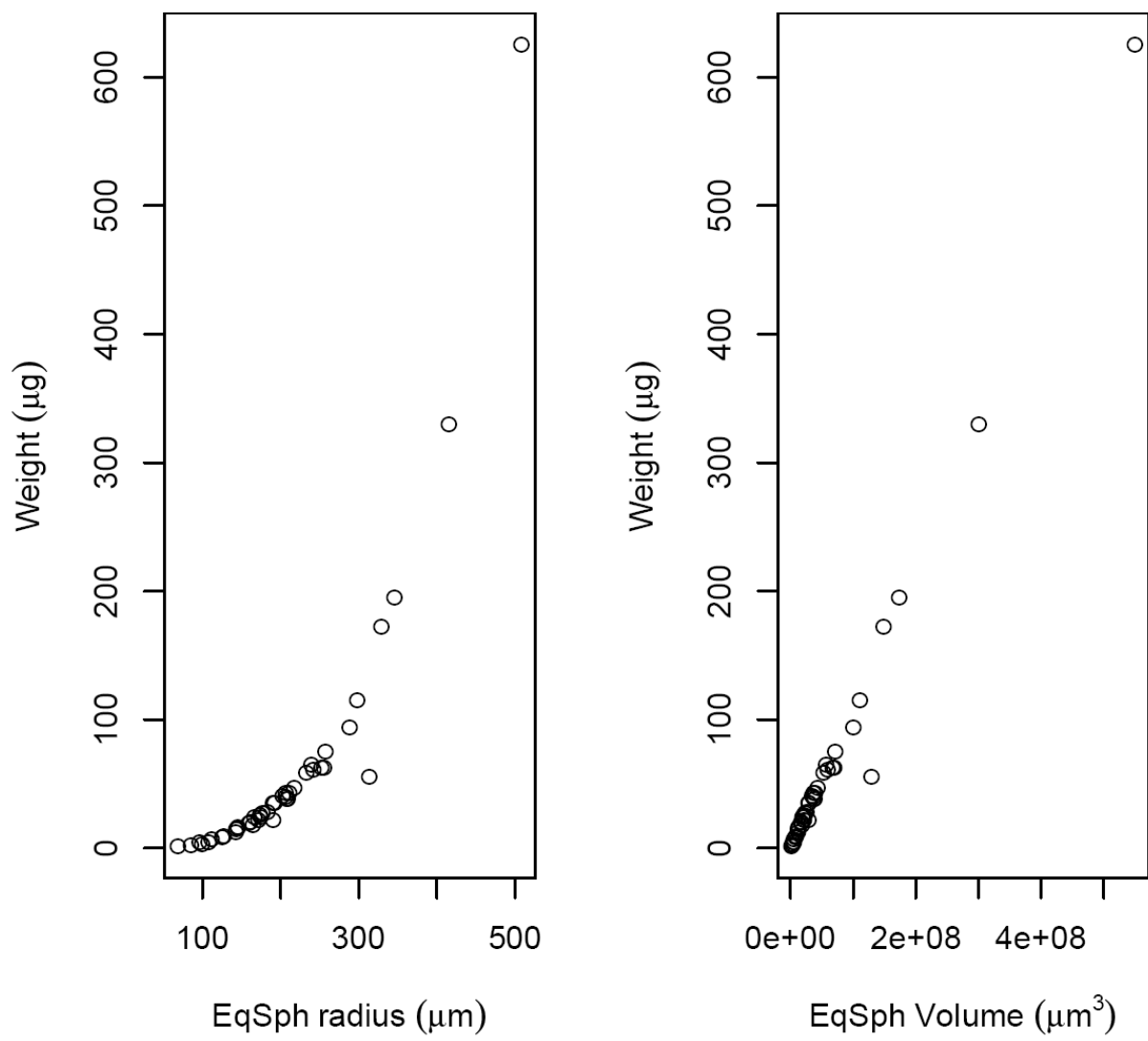


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298 Figure 2:



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300 Appendix 1. The Lebrun data set (Lebrun, 1971). The “Shape” column is after Lebrun (1971)

Species	Length ( $\mu\text{m}$ )	Width ( $\mu\text{m}$ )	Weight ( $\mu\text{g}$ )	Shape
<i>Nanhermannia nana</i>	571	249	18.1	C
<i>Hypochthonius rufulus</i>	632	316	22.1	Q
<i>Eniochthonius minutissimus</i>	358	179	4.4	Q
<i>Nothrus silvestris</i>	739	343	47.2	Q
<i>Platynothrus peltifer</i>	826	444	62.9	Q
<i>Hermannia gibba</i>	905	531	94.2	S
<i>Ceratoppia bipilis</i>	740	451	64.8	S
<i>Hermanniella granulata</i>	750	531	75.3	S
<i>Tectocepheus velatus</i>	307	173	4.2	C
<i>Xenillus tegeocranus</i>	960	600	55.8	C
<i>Cepheus cepheiformis</i>	677	483	58.8	C
<i>Carabodes femoralis</i>	646	383	42.6	C
<i>Adoristes ovatus</i>	649	401	42.8	A
<i>Oribatula tibialis</i>	435	279	14.6	S
<i>Chamobates incisus</i>	351	205	6.5	A
<i>Euzetes globulus</i>	1174	893	329.9	A
<i>Diapterobates humeralis</i>	727	476	60.9	S
<i>Achipteria coleoprata</i>	620	406	39.6	A
<i>Oribatella calcarata</i>	623	417	38.1	A
<i>Oribatella quadricornuta</i>	507	321	24	A
<i>Oppia quadricarinata</i>	220	120	1.3	S
<i>Oppia ornata</i>	275	150	2.2	S
<i>Oppia subpectinata</i>	325	170	3.2	S
<i>Damaeus auritus</i>	1030	691	195	S
<i>Damaeus onustus</i>	1511	1018	625	S
<i>Nothrus palustris</i>	1025	611	172	Q
<i>Nothrus palustris</i>	424	209	9.3	Q
<i>Nothrus palustris</i>	490	232	16.2	Q
<i>Nothrus palustris</i>	637	311	35.2	Q
<i>Nothrus palustris</i>	825	431	62.8	Q
<i>Chamobates schützi</i>	367	255	8.3	A
<i>Liebstadia similis</i>	503	289	19.4	A
<i>Scheloribates laevigatus</i>	564	348	28.1	A
<i>Parachipteria punctata</i>	572	386	34.8	A
<i>Eupelops sp</i>	474	328	19.9	A
<i>Carabodes femoralis</i>	626	382	40.7	C
<i>Odontocepheus elongatus</i>	613	243	21.4	C
<i>Nothrus silvestris</i>	503	221	15.3	Q
<i>Nothrus silvestris</i>	605	275	27.2	Q
<i>Platynothrus peltifer</i>	483	227	12.7	Q
<i>Platynothrus peltifer</i>	693	341	38.5	Q

<i>Camisia spinifer</i>	1023	459	115	Q
<i>Camisia spinifer</i>	590	276	24.1	Q
<i>Camisia exuvialis</i>	609	254	25.9	Q

301 A, achipteriform; C, caraboidiform; S, spheroidal; Q, quadrangular

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