

1 Bedload transport in rivers: size matters but so does shape!

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12

13 **ABSTRACT**

14 Bedload transport modelling in rivers, which defines the threshold for pebble movement, takes
15 into account the size and density of pebbles, but does not formally consider particle shape. The
16 lack of analyses evaluating the influences of shape and density on particle mobility presents a
17 major deficiency. To address this issue and to compare the relative roles of the density and
18 shape of particles, we performed original sediment transport experiments in an annular flume
19 using molded artificial pebbles equipped with a radio frequency identification tracking system.
20 The particles were designed with four distinct shapes and four different densities while having
21 the same volume, and their speeds and distances traveled under constant hydraulic conditions
22 were analyzed. The results show that particle shape has more influence than particle density on
23 the resting time between particle displacement and the mean traveling distance. For all densities
24 investigated, the particle shape systematically induced differences in travel distance that were
25 strongly correlated ($R^2 = 0.94$) with the Sneed and Folks shape index. Such shape influences,

26 although often mentioned, are here quantified for the first time, demonstrating why and how
27 they can be included in bedload transport models.

28

29 INTRODUCTION

30 Sediment transport is a key process in fluvial geomorphology, being important for
31 sustainable management of navigable channels, designing engineering projects, predicting
32 morphological changes and associated hydraulic risks, interpreting sedimentary archives and
33 restoring rivers ¹. It involves three phases of particle mobility: (1) entrainment ²⁻⁶; (2) motion
34 ⁷⁻⁹; and (3) deposition ^{10,11}. Sediment transport at the particle scale is a stochastic phenomenon
35 ^{7,12,8,13,14,9}, which mostly arises from the complex interactions between particle collisions and
36 highly variable friction, drag, and lift forces due to fluid turbulence. Thus, for practical
37 considerations, empirically calibrated sediment transport functions widely use Shields stress
38 number (τ^* or θ) to quantify the balance of the forces exerted on the channel bed particles, and
39 the critical Shields number (τ^*_c), which is the threshold value necessary to set particles in
40 motion, to determine the moments at which drag forces exceed stabilizing forces ($\tau^* > \tau^*_c$) and
41 particles can be entrained ¹⁵⁻²¹. Such approaches have been used to estimate particle stabilizing
42 forces from median pebble size and submerged density ¹⁶. At the river reach scale, sediment
43 transport estimates generally encapsulate a relation depending on the Shields stress, and
44 therefore also include the median grain size ^{20,22-27} of the transported sediment.

45 Published bedload transport datasets from rivers with similar flow conditions,
46 morphologies, and median grain sizes, may show different transport rates, with large variations
47 in the threshold for setting particles in motion ²⁸, variations that can be up to 10-fold ²⁹ around
48 the mean empirical Shields curve ³⁰⁻³². To explain such dispersion, many studies have focused
49 on the role of mixed grain size, hiding effects ³³⁻³⁶, macro-roughness, channel steepness, or bed
50 roughness relative to channel depth ³⁷. However, fewer studies have qualitatively related pebble

51 shape to bedload transport through the influence of pebble angularity^{38,39}, pebble imbrication
52^{34,35,40}, or bed roughness^{34,40,41} (i.e. the D/K ratio, where D is the diameter of the particles to be
53 moved and K is the bed-particle diameter). In environments with smooth-beds ($D > K$) and
54 during low to moderate flood events, coarse particles of spherical or ellipsoid shape were
55 observed⁴² to be more likely to experience entrainment and transport than flatter shapes.
56 Conversely, in rough-bed rivers ($D < K$), Demir and Walsh¹ found that displacement of flatter
57 shapes (i.e. discs and blades) seems to be promoted. Overall, selective shape entrainment and
58 travel length both decrease as flood magnitude increases and/or particle size decreases⁴³.
59 Whereas these previous studies have emphasized that robust deterministic expression of initial
60 motion should encapsulate the role of particle shape and bed roughness in particle motion
61 modelling^{38,39,44,45}, the scarcity of field and experimental data has prevented a quantitative
62 account of this role.

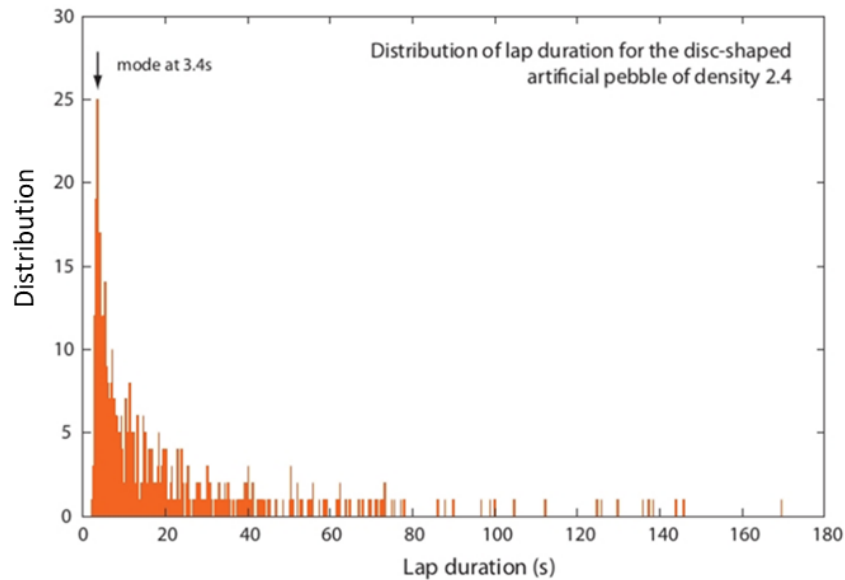
63 To partially fill this gap, we designed a parametric study based on experiments run in
64 an annular flume in which the displacements (encapsulating onset motion, travel length and rest
65 periods) of artificial pebbles of various shapes and densities were tracked for several hours.
66 Particle shape has been quantified by many different parametrizations^{46–52} expressing
67 angularity, surface roughness, or departure from sphericity. As the latter directly impacts on
68 inertial moments and pivoting angle, we investigated the influence of shape in terms of the
69 departure from sphericity, examining various ellipsoid particle shapes (from plate to blade
70 types).

71

72 **RESULTS**

73 The number of revolutions made by the monitored particles ranged between 439 laps
74 for an elongated blade and 2270 laps for a sphere, making the lap duration observations were
75 taken from large sample sizes. Although the lap durations within the annular flume displayed

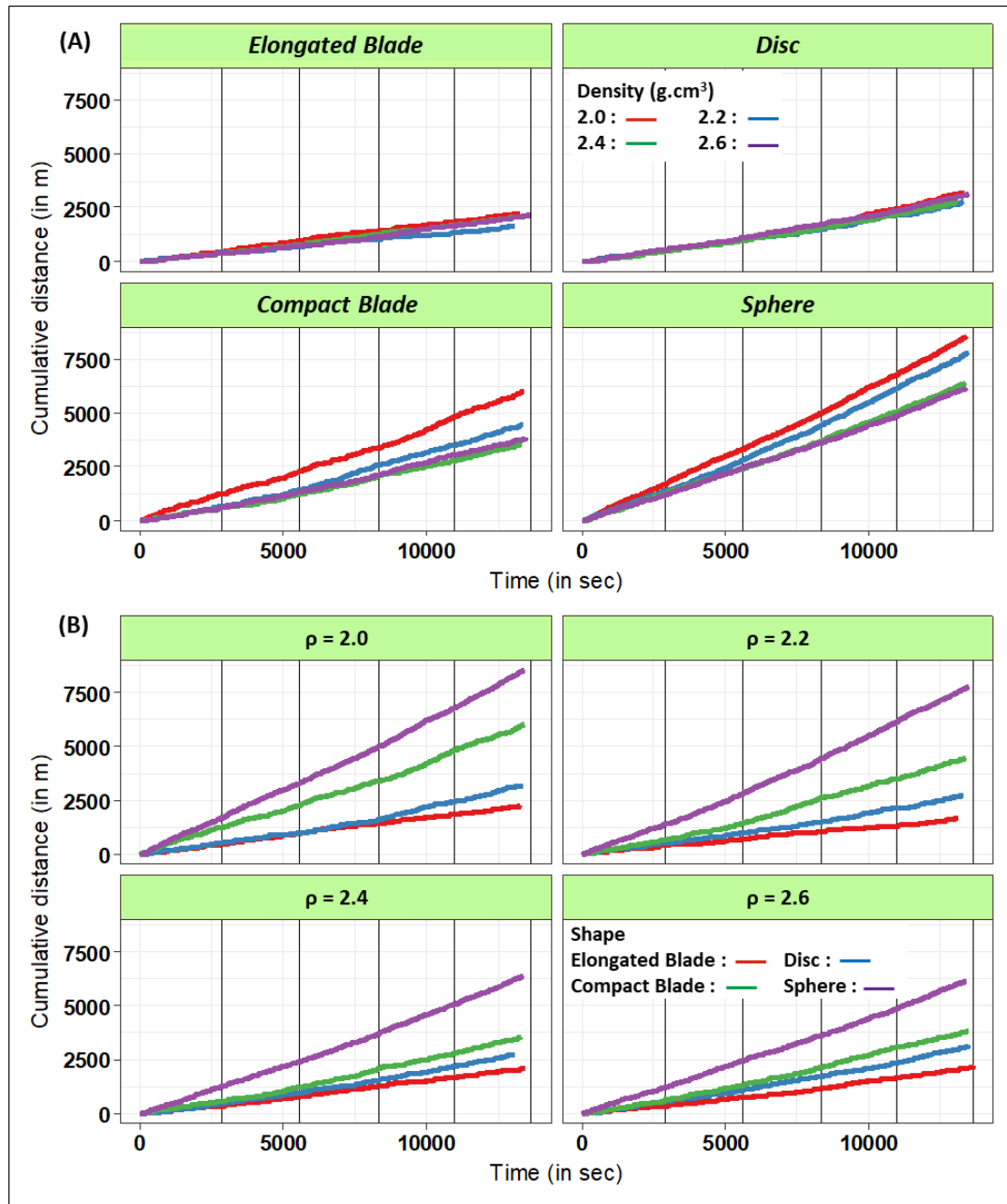
76 large variations (from 3 seconds up to a few minutes; see example in Figure 1) over the total
77 run duration, the cumulative travel distances of the particles (Figure 2) displayed a fairly
78 constant slope that permitted the average traveling velocities of the different artificial pebbles
79 to be defined.



80

81 **Figure 1. Example of the distribution of lap durations (shape = disc; density = 2.4 g.cm⁻³)**

82 The slight increases observed in the slopes of the cumulative distance curves over time
83 for all shapes and densities reflect the progressive augmentation of the particles' velocities
84 caused by a decrease in the mixing load due to abrasion (relative mass loss of 1.2% per
85 kilometer traveled). As this was moderate and affected all tagged particles in a similar manner,
86 we consider that it had very little impact on the first-order estimates and results of the
87 experiments.



88
89 **Figure 2. Cumulative travel distances over time according to particle shape (A) and**
90 **density (B).**

91 The four particle shapes investigated exhibited clear differences in cumulative travel
92 length, with variations in the particle densities also demonstrating effects (Figure 2). The
93 spherical particles traveled the farthest and fastest (mean velocities ranging from 0.44 to 0.60
94 m.s⁻¹), with their mean virtual velocities displaying an inverse relationship with density (Figure
95 3). The compact blade-shaped particles were the second fastest, exhibiting mean velocities
96 ranging from 0.25 to 0.44 m.s⁻¹, again displaying an inverse relationship with density, although

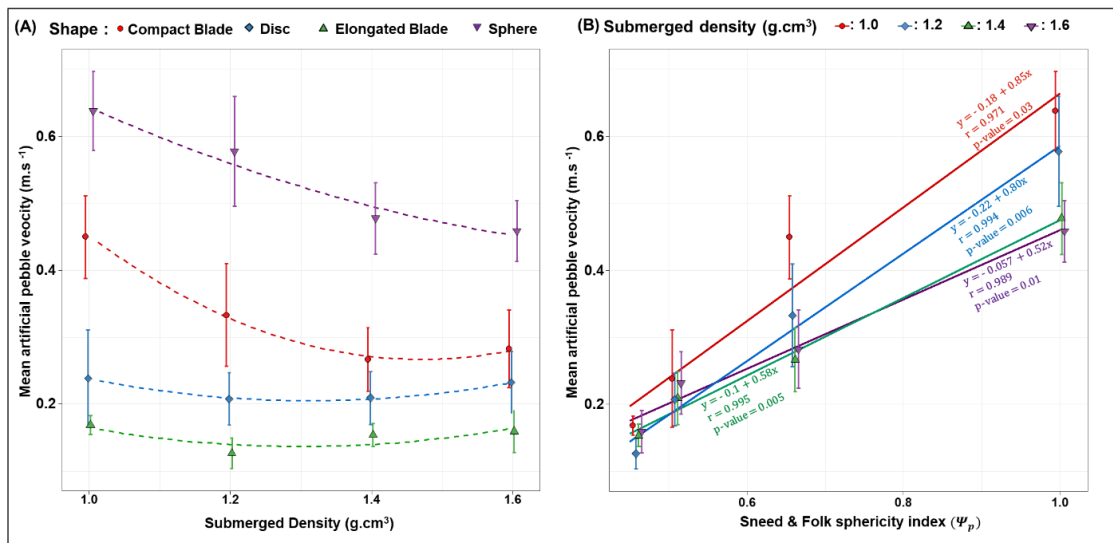
97 to a lesser extent than that of the spherical particles. In contrast, the mean virtual velocities of
 98 the disc- and elongated blade-shaped particles were minimally influenced by their densities: the
 99 mean velocities were clustered within a narrow range from 0.14 to 0.17 m.s⁻¹ and 0.19 to 0.21
 100 m.s⁻¹ respectively. Within the density classes, the distances traveled by the particles clearly
 101 showed a high variability in relation to their shapes (Figure 2B and Figure 3A). The experiments
 102 clearly indicate that the variability in velocity associated with pebble shape is substantially
 103 higher than that associated with particle density (~100% compared with ~30%).

104 To explore the influence of particle shape on mobility in a more quantitative way, we
 105 used the sphericity index, Ψ_p (1), of Sneed and Folks (1958):

$$106 \quad \Psi_p = \sqrt[3]{\frac{S^2}{LI}} \quad \text{Equation (1)}$$

107 where L , I , and S are the longest, intermediate, and shortest axes of the pebbles.

108 The sphericity index Ψ_p shows a remarkable positive relationship with the mean
 109 traveling velocity (Figure 3B). Moreover, the mean velocities increased from 0.52 to 0.85 m.s⁻¹
 110 for decreasing densities from 2.6 to 2.0 g.cm⁻³. These results suggest that it is possible to
 111 estimate differences in the mean virtual velocities and mobilities of particles according to their
 112 sphericity.

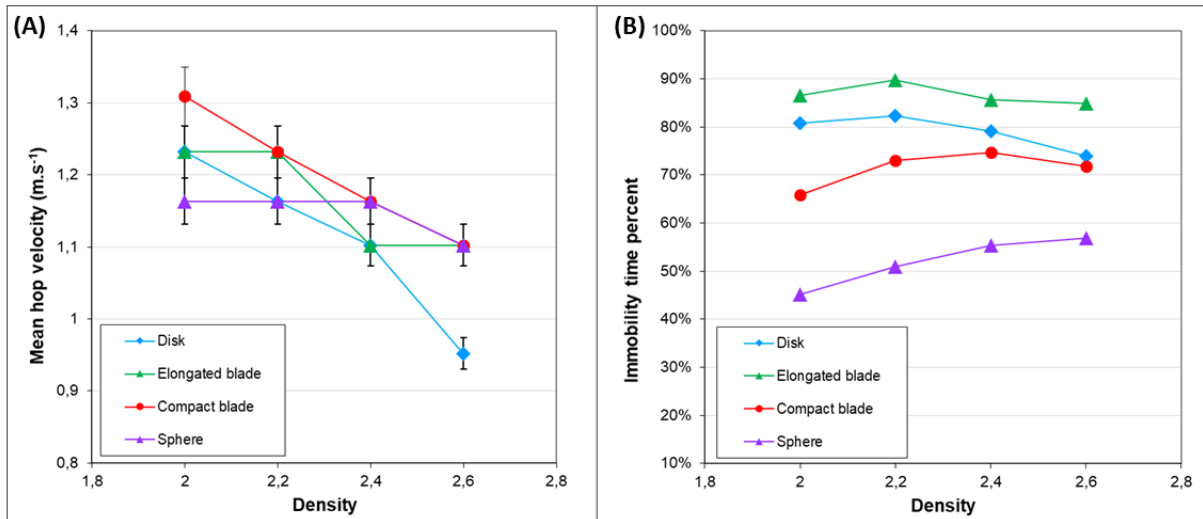


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 114 **Figure 3. Mean velocity as function of density (A) and Sneed and Folk spherical index (B).**

115 The lap-scaled average travel velocities measured integrate the duration of motion
116 phases and the resting periods in between. However, the pebble shape and density can
117 potentially impact each of these two phases differently. The lap duration distributions are
118 characterized by a first peak at around 3 s in all experiments (Figure 1), which corresponds to
119 a revolution speed of $\sim 1.2 \text{ m.s}^{-1}$. For experimental conditions similar to those used in this study,
120 high speed camera viewing⁵⁶ previously indicated a mean hop velocity of $1.2 \pm 0.2 \text{ m.s}^{-1}$ for
121 pebbles in an annular flume. This modal lap duration of ~ 3 s therefore represents a continuous
122 succession of hops over a full lap, without any resting time. These modal values decrease
123 slightly with increasing density (Figure 4A), as expected from the larger inertial effects after
124 the pebble is set in motion. More importantly, they are almost independent of the pebble shape,
125 as was also observed in a straight flume study⁶³. This implies that the impact of shape on the
126 mean traveled distance is mostly caused by its influence on the resting time between
127 movements, i.e. on the immobilization conditions and on the threshold for setting pebbles in
128 motion. To illustrate this inference, a simple calculation of the mean resting time fraction, or
129 immobility ratio (I_r), can be estimated through

130
$$I_r = \frac{T - N_l t_m}{T} \quad , \quad \text{Equation (1)}$$

131 with T being the total duration of the runs, N_l the number of achieved flume revolutions during
132 T , and t_m the modal lap duration (first mode on the distribution of Figure 1) corresponding to a
133 continuous succession of hops over a full lap.



134
 135 **Figure 4. (A) mean hop velocity and (B) time fraction of immobility of the 16 different**
 136 **artificial pebbles.**

137 Except for spherical pebbles that display a slight increase, the immobility ratio (Figure
 138 4B) is only weakly or not affected by the particle density. In contrast, the shape of a pebble
 139 deeply impacts its mobility, with the immobility ratio raging from ~50% for the spherical
 140 shapes up to $\geq 85\%$ for the elongated blades.

141
 142 **DISCUSSION**

143 The greater velocity of the spherical and compact-blade-shaped particles relative to the
 144 elongated-blade and disc-shaped particles is in good accordance with the literature^{1,39,64}, given
 145 that the flatness of the flume bottom constitutes a low roughness bed surface, despite clustering
 146 of temporary resting pebbles. As most lithologies of the pebbles present in rivers show a density
 147 close to 2.7 g.cm^{-3} , very similar to the highest value used in this study, we expect their mean
 148 velocities to be more strongly influenced by their shape than by their density. On a quantitative
 149 basis, this supports the claimed need to include a particle shape parameter in the sediment
 150 transport equation^{34,41,65}.

151 To do this, we focus on the conditions for setting a particle in motion, because pebble
 152 shape has a major influence on virtual velocity through resting periods. Following Komar and

153 Li's (1986)⁴¹ description, balancing of the moments of tractive and resisting forces for the
 154 critical stress yields:

$$155 \quad \tau_c \propto \frac{l_w \Delta \rho g S I L}{l_D A_a} \quad \text{Equation (2)}$$

156 where A_a is the apparent section exposed to the flow, and l_D and l_w the respective moment
 157 arms of the drag force and submerged weight respectively. Assuming that pebbles tend to lie
 158 with their S -axis vertically oriented, the moment arms of the drag force l_D approximately scales
 159 with the S -axis. As a pebble can orient either longitudinally or transversally, we use the
 160 intermediate variable \sqrt{LI} to account for the apparent section exposed to the flow ($A_a \propto S\sqrt{LI}$)
 161 and the moment arm of the submerged weight l_w . Therefore:

$$162 \quad \tau_c \cong k \frac{\sqrt{LI} \Delta \rho g^3 \sqrt{(SIL)^2 \tilde{D}}}{S^2 \sqrt{LI}} = k^3 \sqrt{\frac{(LI)^2}{S^4}} \Delta \rho g \tilde{D} = k \frac{1}{\Psi_p^2} \Delta \rho g \tilde{D} \quad \text{Equation (3)}$$

163 where k is a function of the particles' Reynold number considered as a constant, $\tilde{D} =$
 164 $\sqrt[3]{SIL}$, the mean pebble size, and $\Psi_p = \sqrt[3]{\frac{S^2}{IL}}$, the Sneed and Folk's index. Here, $\frac{1}{\Psi_p^2}$ corresponds
 165 more or less to the term $\tan \phi$ in Komar and Li (1986): when particle flatness increases (i.e.
 166 Ψ_p decreases), the pivoting angle increases and mobility is reduced. Suppressing the unknown
 167 k , the threshold can be expressed as:

$$168 \quad \tau_c \cong \left(\frac{\Delta \rho}{\Delta \rho_{ref}} \right) \left(\frac{\Psi_{P_{ref}}}{\Psi_p} \right)^2 \tau_{c_{ref}} \quad \text{Equation (4)}$$

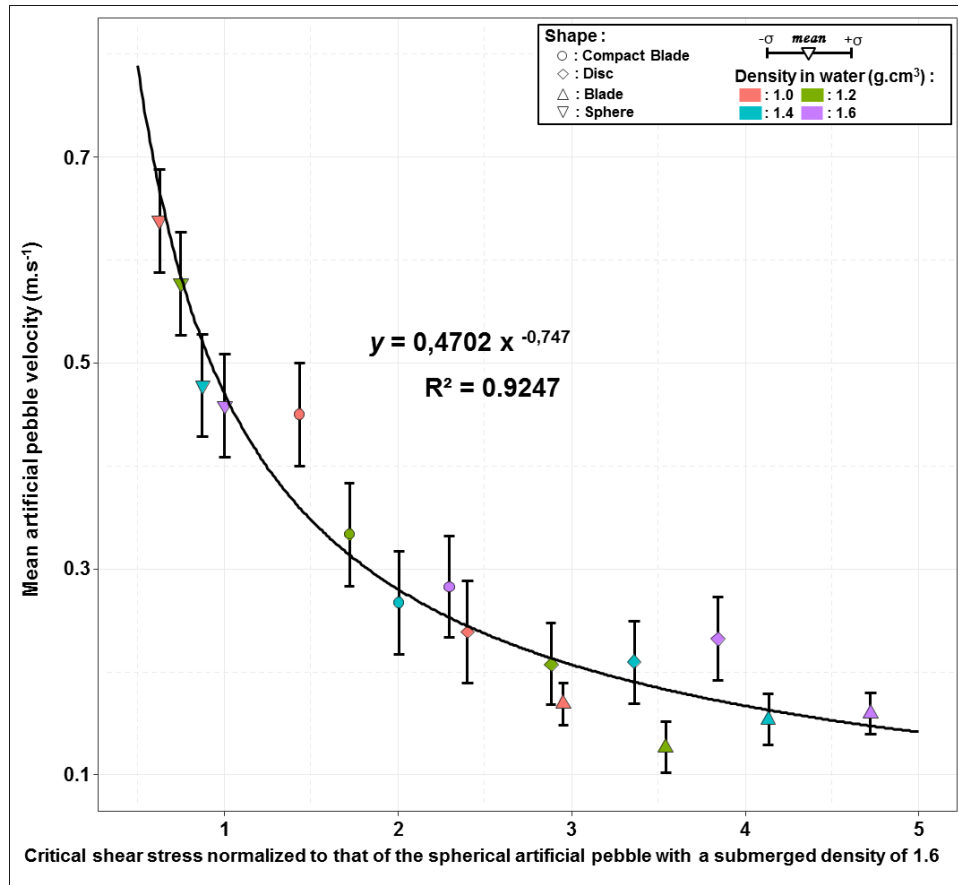
169 where $\tau_{c_{ref}}$ is the critical Shields stress of a reference pebble of similar size.

170 The non-dimensional critical threshold is expressed as:

$$171 \quad \tau_c^* \cong \frac{\tau_c}{\Delta \rho g \tilde{D}} = \frac{k}{\Psi_p^2} = \left(\frac{\Psi_{P_{ref}}}{\Psi_p} \right)^2 \tau_{c_{ref}}^* \quad \text{Equation (5)}$$

172 where $\tau_{c_{ref}}^*$ is the critical Shields stress of a reference pebble of similar size.

173 Representing the mean travel velocity of the particle as a function of the critical stress
 174 τ_c shows an inverse trend between the two variables (Figure 5): both density and departure from
 175 sphericity decrease the ratio of tractive over resistive moments and favor particle immobility.



176
 177 **Figure 5. Mean velocity of the 16 artificial pebbles vs. their critical shear stress normalized**
 178 **to that of the spherical artificial pebble with a submerged density of 1.6** ($= \frac{\tau_c}{\tau_{c_{ref}}} = \left(\frac{\Delta\rho}{1.6}\right) \left(\frac{1}{\Psi_P}\right)^2$).

179 Most bedload transport capacity formulae are functions of the excess Shields stress and
 180 follow two general forms: (1) $\Phi = K(\tau^* - \tau_c^*)^\alpha$, and (2) $W^* = (\tau/\tau_c)^\alpha$, where Φ and W^* are two
 181 distinct non-dimensional expressions of the bedload transport rate, and α and K two constant
 182 terms⁶⁶. To account for the role of pebble shape in a transport capacity relationship, one could
 183 introduce into the formula the modified expression for critical shear stress (eq. 4), or the critical
 184 Shields stress (eq. 5) that includes the Sneed and Folk Index.

185 To explore this hypothesis, we built on the fractional transport rate model developed for
 186 transport of a mixture of grain sizes (e.g. Parker et al., 1982⁶⁷). This choice was motivated by
 187 the fact that such a relation already proposes a similarity collapse for heterogeneous sediment,
 188 which is the case in our experiments with particles of variable shapes and densities mixed with
 189 a natural pebble load. We arbitrarily considered Wilcock and Crowe's (2003)⁶⁸ relation for
 190 fractional transport rate, in which the form of the similarity collapse is:

$$191 \quad W_i^* = 14 \left(1 - \frac{0.894}{\phi^{0.5}}\right)^{4.5} \quad \text{when } \phi = \frac{\tau}{\tau_{ci}} \geq 1.35 \quad \text{Equation (6)}$$

192 where τ is the bed shear stress, τ_{ci} the critical shear stress for incipient motion of a specific
 193 pebble i (more exactly it corresponds to the minimum shear stress required to achieve a small
 194 reference transport rate of $W_i^* = 0.002$ ⁶⁷), and W_i^* the dimensionless transport rate $W_i^* =$
 195 $\frac{Rgq_{bi}}{F_i\left(\frac{\tau}{\rho}\right)^{3/2}}$, with $R_i = \frac{\Delta\rho_i}{\rho}$ being the ratio of the submerged sediment (of type i) density to water
 196 density, g being gravity, q_{bi} the volumetric transport rate per unit width of the particle of type i
 197 (i.e. of similar shape, size, and density), and F_i the proportion of the pebble type being of the
 198 class i .

199 Following our simplified analysis of the force moment balance, we defined the critical
 200 (or reference) shear stress as a function (eq. 7) of the mean characteristics of the transported
 201 sediment load (i.e. mean gravel size D_m , mean shape factor Ψ_{Pm} , and mean density $\Delta\rho_m$)
 202 according to:

$$203 \quad \tau_{ci} = \left(\frac{\Delta\rho_i}{\Delta\rho_m}\right) \left(\frac{\Psi_{Pm}}{\Psi_{Pi}}\right)^2 \tau_{cm} \quad \text{Equation (7)}$$

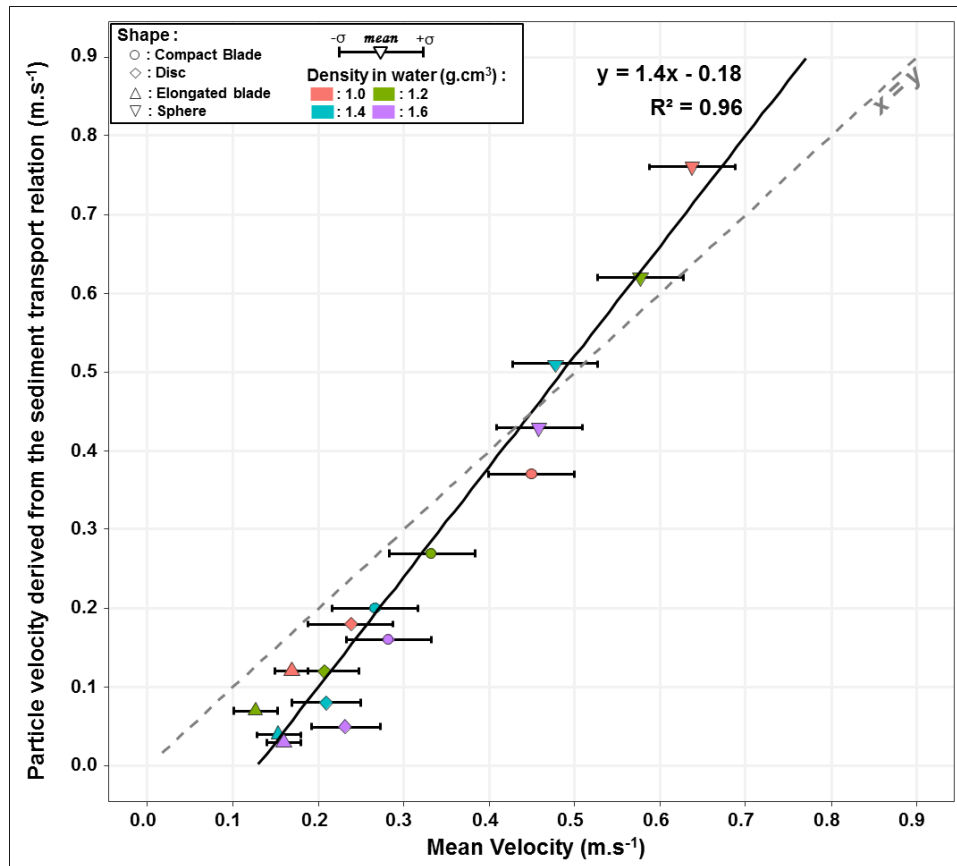
204 with τ_{cm} being the critical shear stress for the mean gravel load. Here,
 205 $\tau_{cm} = \Delta\rho_m g D_m \tau_c^* \cong 28 \text{ Pa}$ considering that $\Delta\rho = 2600 \text{ kg.m}^{-3}$, $D_m \approx 5 \text{ cm}$ for the mean
 206 gravel diameter of the 65 kg of limestone pebbles, and $\tau_c^* \cong 0.036$ ⁶⁸.

207 Within the flume, provided that not all of the particles are in full motion, the conditions
 208 of alluvial rivers prevail, i.e. the sediment flux q_{si} is equated by the transport capacity q_{bi} . In our
 209 experiments, the mass sediment flux per unit width of the pebble class i can be expressed from
 210 the mean traveling velocity through: $q_{si} = \frac{F_i M}{A} V_{gi}$, with A being the surface of the flume
 211 bottom, M the mass of sediment introduced into the flume, and V_{gi} the mean displacement
 212 velocity of particles of type i . It follows that a virtual mean velocity can be derived for particle
 213 i from the above fractional transport rate equation:

$$214 \quad V_{gi} = \frac{AM\rho_{si}}{R_i g} \left(\frac{\tau}{\rho}\right)^{3/2} W_i^* \left(\frac{\tau}{\tau_{ci}}\right) \quad \text{Equation (8)}$$

215 with τ_{ci} derived from equation (7) and a mean shape factor $\Psi_{pm} = 0.7 \pm -0.08$ for the 65 kg
 216 of limestone pebbles.

217 The virtual velocities derived from the bedload transport relation show a well-defined
 218 correlation with the measured virtual velocities (Figure 6). However, the slope of the correlation
 219 line is larger than unity, and our modified version of the bedload transport tends to
 220 underestimate the observed transport for the densest elongated-blade or disk-shaped pebbles.
 221 Despite these slight discrepancies from the observations, these results suggest that the role of
 222 pebble shape on bedload transport can be predicted, and that the inclusion of pebble shape
 223 characteristics in the modelling of bedload transport offer much promise for improving bedload
 224 transport predictions.



225

226 **Figure 6. Comparison between the mean measured velocities of particles of various shapes**
 227 **and densities and the theoretical particle velocity derived from a fractional transport rate**
 228 **relation adapted from Wilcock and Crowe's (2003) relation ⁶⁸.**

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In terms of sediment dynamics, pebbles travel in the flume following an alternating pattern of resting and motion periods, as generally observed in a natural stream⁸. We therefore consider that our experiments succeeded in capturing the first order behavior of the bedload, and that the introduction of a shape factor into critical Shield stress and bedload transport models might be transposed to rivers. However, the experimental conditions are slightly distinct from those of natural rivers, in particular the use of a monodispersed sediment load and a low-roughness bottom. Additional experiments exploring distinct bottom conditions, grain size distributions, and using straight channels are probably necessary to strengthen our initial results and resolve the slight discrepancies between the model and observations. Similarly, experiments using pebbles with a unique and defined type of particle shape (for example, only

239 platy particles, as expected in sediment derived from the erosion of schist-rich lithologies),
240 instead of a single particle mixed with a large population of pebbles of distinct shapes, should
241 help to derive a more universal relationship. Nevertheless, this study represents a preliminary
242 and promising step towards addressing the role of particle shape in bedload transport.

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244 **CONCLUSION**

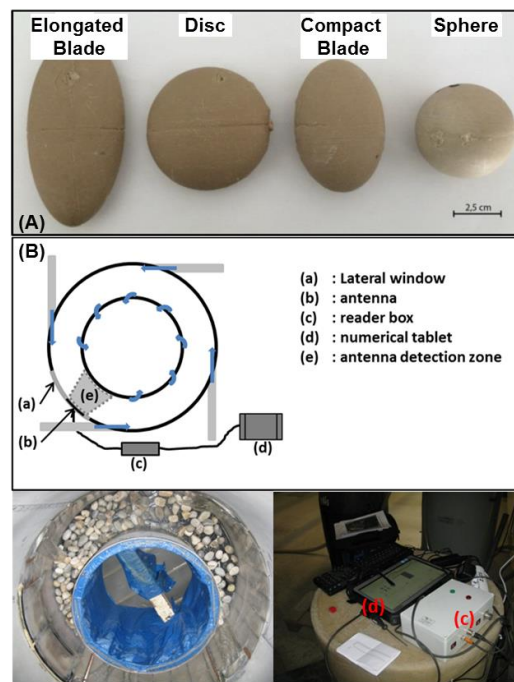
245 These experiments, based on innovative tools (artificial pebbles of controlled density
246 containing RFIDs) offer new perspectives for studying sediment transport mechanisms. The
247 comparative analysis of the shape and density of particles on their mobility highlights the
248 crucial influence of particle shape. Furthermore, it also indicates that the sphericity index (Ψ_p)
249 of Sneed and Folks (1958)⁶⁹, which correlates with mean velocity, is relevant for including
250 shape parameters in sediment transport formulae. The method developed in this study can be
251 reproduced to investigate how bed roughness (changing D/K ratio) and/or a tracer's grain-size
252 can change the balance between the effects of shape and density on particle velocity. It allows
253 investigation of whether bed roughness promotes the transport of flat-shaped particles, as
254 reported in the literature, and whether particle density can mitigate this effect. Repeating the
255 experiments with smaller particle sizes (maintaining a constant D/K ratio) would also allow
256 investigation of whether size mitigates the influence of shape and density on particle transport.

257

258 **METHODS**

259 We designed four differently-shaped particle models within the grain-size class of 45–
260 64 mm (5.5–6.0 Ψ -units), with all models having the same volume (*i.e.* 49.3 cm³) but exhibiting
261 differences in the sphericity index ⁵³ (Figure 7A ; Table 1). After creating silicon molds (RTV
262 120) for these four models, we manufactured 16 artificial pebbles using a mixture of resin and
263 corundum powder in variable proportions, creating pebbles of four different densities (2.0, 2.2,

264 2.4, and 2.6 g.cm⁻³) for each mold shape ⁵⁴. We equipped these artificial pebbles with
 265 transponders of Radio Frequency Identification, RFID, (model RI-TRP-WR2B of Texas
 266 Instrument, Dallas Texas USA, also known as PIT Tags) to monitor their displacements within
 267 an annular flume⁵⁵ (Figure 7B). A detection antenna located on the outside of the flume, along
 268 a lateral window, enabled tracking of the number of laps achieved by the RFID-equipped
 269 pebbles and the time for each revolution.



270 *Figure 7. The four particle shapes investigated (A) and the*
 271 *annular flume equipped with the RFID system (B).*
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274 **Table 1. Shape characteristics of the artificial particles tracked in the flume.**

SHAPE	<i>a</i> -axis (mm) <i>L</i>	<i>b</i> -axis (mm) <i>I</i>	<i>c</i> -axis (mm) <i>S</i>	Vol.(cm ³)	Sphericity index (Sneed and Folks, 1958)
Compact Blade	68.1	46	30	49.3	0.66
Sphere	45.5	45.5	45.5	49.3	1
Disc	65	63	23	49.3	0.51
Elongated Blade	97.2	46.1	21	49.3	0.46

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276 In an attempt to reproduce bedload transport conditions, these artificial pebbles were
277 mixed with 65 kg of limestone pebbles of a similar grain-size (i.e. class 45–64 mm) and were
278 run within an annular flume⁵⁶. A set of experiments were run following the designs of previous
279 studies^{54,56,57} for which the sediment dynamics have been characterized⁵⁶, i.e. with a low
280 roughness bottom and a monodispersed grain size distribution. During the experiments, the
281 pump discharge sustaining the fluid injection into the flume was maintained at 240 m³.h⁻¹,
282 which for the introduced sediment mass corresponds⁵⁶ to a shear stress of $\tau = 135$ Pa at the base
283 of the flume according to Euler theorem applied to the moments, a Shield stress of $\tau^* = 0.16$, a
284 mean transit velocity for pebbles of ≈ 0.4 m.s⁻¹, and a sediment flux of ~ 24 kg.m⁻¹.s⁻¹. Under
285 these conditions, high speed camera viewing⁵⁶ indicated that the pebbles were transported in
286 the annular flume in a similar manner to that observed⁸ in rivers, with alternating transport
287 phases with rolling and saltation, and resting times caused by temporary blockage and piling of
288 particles.

289 Each experimental run lasted for 45 minutes. To avoid superpositioning of radio-
290 frequency signals and missed RFID transponder detections^{54,58,59}, only the four particles of the
291 same density were simultaneously present in the flume, thereby also limiting to four the number
292 of transponders. A total of six runs were achieved for the densities of 2.6 and 2.4 g.cm⁻³, and
293 five runs for the densities of 2.0 and 2.2 g.cm⁻³. For each artificial pebble, the combined runs
294 provide a long duration of almost 4 hours and a large cumulative traveled distance, from which
295 the mean traveled velocity (or virtual velocity as defined by Haschenburger and Church⁶⁰) can
296 be computed and the distributions of the lap times estimated. Finally, we compared the virtual
297 velocities and lap distributions of the 16 artificial pebbles, to investigate the effects of the
298 different shapes and densities on bedload transport. In this study, the use of an annular flume
299 enabled the acquisition of a relatively long time series compared with typical straight flume
300 experiments⁶¹ and the sampling of a population of practically uncensored particle trajectories

301 without the limitations induced by a limited detection window or flume length⁶². This ensured
302 that the ranges of traveled distances under conditions of continuous movement were well
303 represented in the experiment. We also made sure that the duration of the experiments (45
304 minutes) was much longer than the maximum resting time recorded (~5 minutes), to avoid time
305 censorship effects on the distributions of the resting periods and lap times, and to be sure of the
306 statistical significance of the distributions.

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478 **Author contributions**

479 M.C., H.P., and J.L. contributed to the design of the experiment. M.C., J.L., and H.P. analyzed
480 experimental results; J.L., H.P., M.C., A.R., and J-R.M. wrote the manuscript.

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485 **Competing Interests**

486 The authors declare no competing interests.