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# The Central Role of Small Vertical Substrates for the Origin of Grasping in Early Primates

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Severine Toussaint, Artémis Llamosi, Luca Morino, Dionisios Youlatos. The Central Role of Small Vertical Substrates for the Origin of Grasping in Early Primates. *Current Biology - CB*, 2020, 30 (9), pp.1600-1613.e3. 10.1016/j.cub.2020.02.012 . hal-03007069

**HAL Id: hal-03007069**

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Submitted on 16 Nov 2020

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1 **Title**

2 The central role of small vertical substrates for the origin of grasping in early primates

3

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## 26 Summary

27 The manual and pedal grasping abilities of primates, characterized by an opposable hallux, flat nails,  
28 and elongated digits, constitute a unique combination of features that likely promoted their  
29 characteristic use of arboreal habitats. These hand and foot specificities are central for understanding  
30 the origins and early evolution of primates and have long been associated with foraging in a fine-  
31 branch milieu. However, other arboreal mammals occupy similar niches and it remains unclear how  
32 substrate type may have exerted a selective pressure on the acquisition of nails and a divergent  
33 pollex/hallux in primates, or in what sequential order these traits evolved. Here, we video-recorded  
34 14,564 grasps during arboreal locomotion in 11 primate species (6 strepsirrhines and 5 platyrrhines)  
35 and 11 non-primate arboreal species (1 scandentian, 3 rodents, 3 carnivorans and 4 marsupials). We  
36 quantified our observations with 19 variables to analyze the effect of substrate orientation and  
37 diameter on hand and foot postural repertoire. We found that hand and foot postures correlate with  
38 phylogeny. Also, primates exhibited high repertoire diversity, with a strong capability for postural  
39 adjustment compared to the other studied groups. Surprisingly, nails do not confer an advantage in  
40 negotiating small substrates, unless the animal is large, but the possession of a grasping pollex and  
41 hallux is crucial for climbing small vertical substrates. We propose that the divergent hallux and pollex  
42 may have resulted from a frequent use of vertical plants in early primate ecological scenarios, while  
43 nails may not have resulted from a fundamental adaptation to arboreal locomotion.  
44

## 45 Keywords

46 Primate origins, hand, foot, grasping, pollex, hallux, nails, claws, arboreal locomotion  
47

## 48 Introduction

49 Hands and feet are crucial for understanding the origins and evolution of primates. Their unique  
50 manual and pedal prehensile capacities, associated with the possession of nails instead of claws,  
51 divergent thumb (*i.e.* pollex) and big toe (*i.e.* hallux), and elongated digits, are among the defining  
52 characters of the order [1–3] and constitute their most fundamental specializations [4–7]. These  
53 morphological features are largely considered as specializations for arboreal locomotion and an  
54 associated lifestyle, shared by their common ancestor. However, the evolutionary context of these  
55 features, their order of acquisition and the ancestral primate morphotype remain under debate.

56 There are several scenarios describing the specific details of primate ancestry and the behaviors  
57 considered most critical in their evolutionary sequence of adaptations. The primate ancestor is  
58 reconstructed as small, insectivorous, and nocturnal. In most scenarios, pedal and manual grasping  
59 functional mechanisms, along with nails, are assumed to have promoted their early differentiation by  
60 facilitating the use of “fine branches”, and thus the ability to cautiously move and forage on peripheral  
61 tree zones and shrubs [2,7–11]. However, what actually characterizes the fine branch milieu of early  
62 tropical forests remains poorly defined [6,12]. “Fine branch” is a relative concept that needs to be  
63 considered in relation to the size of the studied animals [13]. Furthermore, the terminal-branch  
64 environment is characterized by substrates of varying diameter and orientation with an overall high  
65 degree of spatial complexity, which significantly influence the locomotor behavior of an animal [14–  
66 16]. Recent studies have questioned the small branch niche environment and proposed that prehensile  
67 foot proportions and nails on the lateral digits may well have been acquired after the radiation of  
68 crown primates, *i.e.* in parallel in different euprimate lineages, and that leaping specializations and  
69 large vertical substrate use evolved prior to nails on the lateral digits [17–20]. Understanding the  
70 relationships between hand and foot postures during climbing on vertical substrates is important, as  
71 many fundamental primate morphological features have been associated with climbing [17,18,21].  
72 Vertical climbing implies particular biomechanical constraints, but is energetically comparable to  
73 horizontal walking for some small primates, although not for larger species [22]. For small mammals,

74 large vertical substrates are biomechanically difficult to negotiate, unless functional claws are engaged  
75 to provide a secure firm grip [23]. Also, prehensile grasping extremities and, to some extent, functional  
76 claws appear to accommodate effective use of narrower vertical substrates [24–27]. Despite the  
77 established variety of arboreal locomotor behaviors of living primates [28,29], it is still unclear how the  
78 different substrate types may have exerted a selective pressure toward the acquisition of nails and the  
79 divergence of the hallux/pollex.

80 Experimental studies have shown that primate forelimbs and hind limbs play distinctive roles  
81 during arboreal locomotion, the foot being more strictly related to locomotion, and the hand also  
82 involved in feeding and social interactions [30,31]. Hence, primate hands have been extensively  
83 studied in relation to primate origins [32–35]. However, hands and feet presumably constitute  
84 genetically related, homologous structures [36] and their morphological adaptations are obviously  
85 interrelated. This can undermine evolutionary analyses performed on hands or feet separately and  
86 calls for a systematic approach in which hand and foot postures are studied jointly, considering key  
87 related contexts (*i.e.* substrate and activity).

88 Living strepsirrhines (*e.g.* lemurs) are often regarded as models for the last common ancestor of  
89 primates [37,38]. But platyrrhine primates such as tamarins (*i.e.* callitrichines) are also considered as a  
90 model for an hypothetical stem lineage of primates as they possess nails secondarily modified as claws,  
91 and a relatively short hallux and manual digits [33,39]. Treeshrews (scandentians) present  
92 morphological similarities to primates stemming from their common euarchontan ancestry.  
93 Particularly, the genus *Ptilocercus* has been shown to exhibit a capacity for opposable pedal grasping  
94 [40,41]. Moreover, some arboreal marsupials share gait specializations with primates and possess an  
95 opposable hallux with a flat nail-like terminal phalanx, capable of apparently powerful hallucal  
96 grasping, albeit retaining a relatively primitive hand with claws and a non-opposable pollex (*e.g.*  
97 *Caluromys*) [24,42,43]. Other arboreal mammals, lacking primate grasping adaptations, such as  
98 squirrels [27,44], mice and dormice [25,26,45], or even carnivorans [46], are also capable of efficiently  
99 moving and foraging on terminal branches. However, shared specializations related to arboreality have  
100 not yet been fully documented and remain poorly understood [47,48].

101 All these arboreal mammals exhibit a great size range, from tiny mice to large carnivorans. A  
102 similar size range is encountered in extant arboreal primates (from the tiny mouse lemurs to the large  
103 colobines), but the earliest primates are often considered as very small (around or below 50g, [38]).  
104 Body size does play an important role on locomotor biomechanics, and therefore on selection of  
105 substrate characteristics and grasping patterns [49]. Consequently, exploring the diverse ways these  
106 phylogenetically and morphologically different models employ their hands and feet during arboreal  
107 activities should be quite informative on the interaction of factors that may affect grasping patterns.

108 Within the context of primate origins, the present study aims to better understand the adaptive  
109 value of features characterizing hands and feet through an assessment of their behavioral associations  
110 and evolutionary context. To do so we investigate the functional importance of manual and pedal  
111 morphological specializations during locomotion, by documenting their postural repertoire in relation  
112 to different substrate types. More precisely, we test whether nails and/or opposable pollex/hallux  
113 constitute a fundamental condition for the use of small or vertical substrates. To that end, we  
114 developed an integrative approach involving a large set of quantitative postural parameters to  
115 precisely quantify the interaction between substrate orientation and diameter and hand and foot  
116 postures during locomotion in strepsirrhine and platyrrhine primates, and a variety of non-primate  
117 arboreal mammals (scandentians, rodents, carnivorans and marsupials).

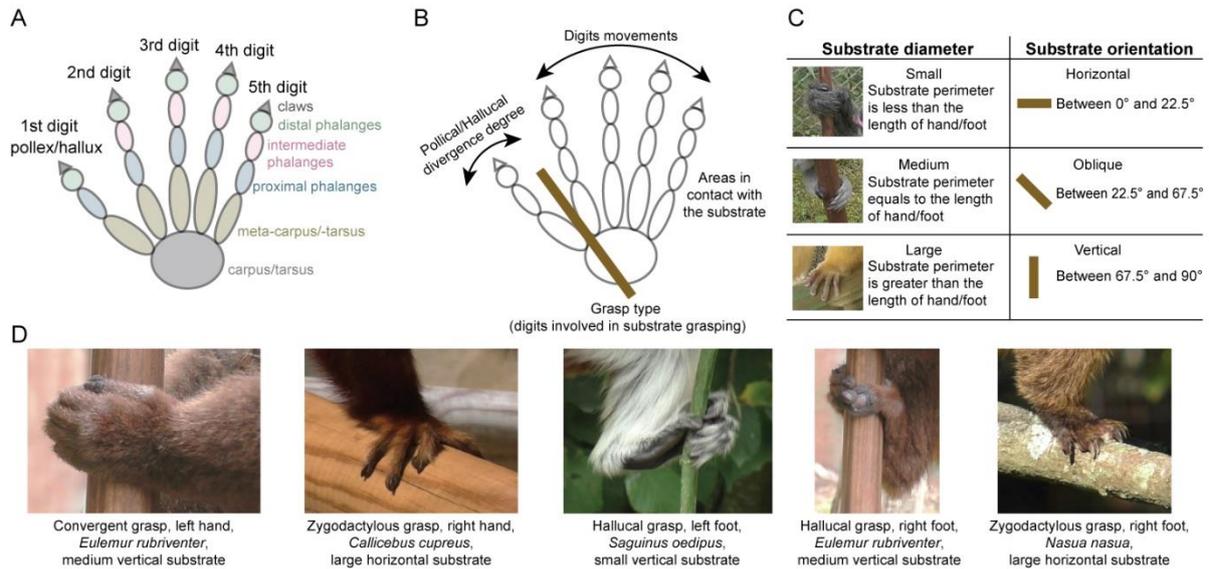
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## 119 Results

### 120 Multivariate quantification of hand and foot postures

121 We collected data for a total of 58 individuals, with 31 primates belonging to 6 strepsirrhine  
122 species and 5 platyrrhine species, and 27 non-primate individuals belonging to 3 carnivoran species, 1  
123 scandentian species, 3 rodent species and 4 marsupial species (Table 1). We recorded 9 variables to

124 detail each hand grasp and 10 variables to detail each foot grasp, grouped into 3 categories: general  
 125 postures, grasping postures, and contact areas with the substrates (Figure 1B and Table 2). We  
 126 analyzed hand and foot postures during locomotion (*e.g.* walking and climbing) in 9 defined substrate  
 127 types varying in orientation and diameter (Figure 1C). The final analyzed dataset resulted in a total of  
 128 7,282 hand grasps and 7,282 foot grasps.



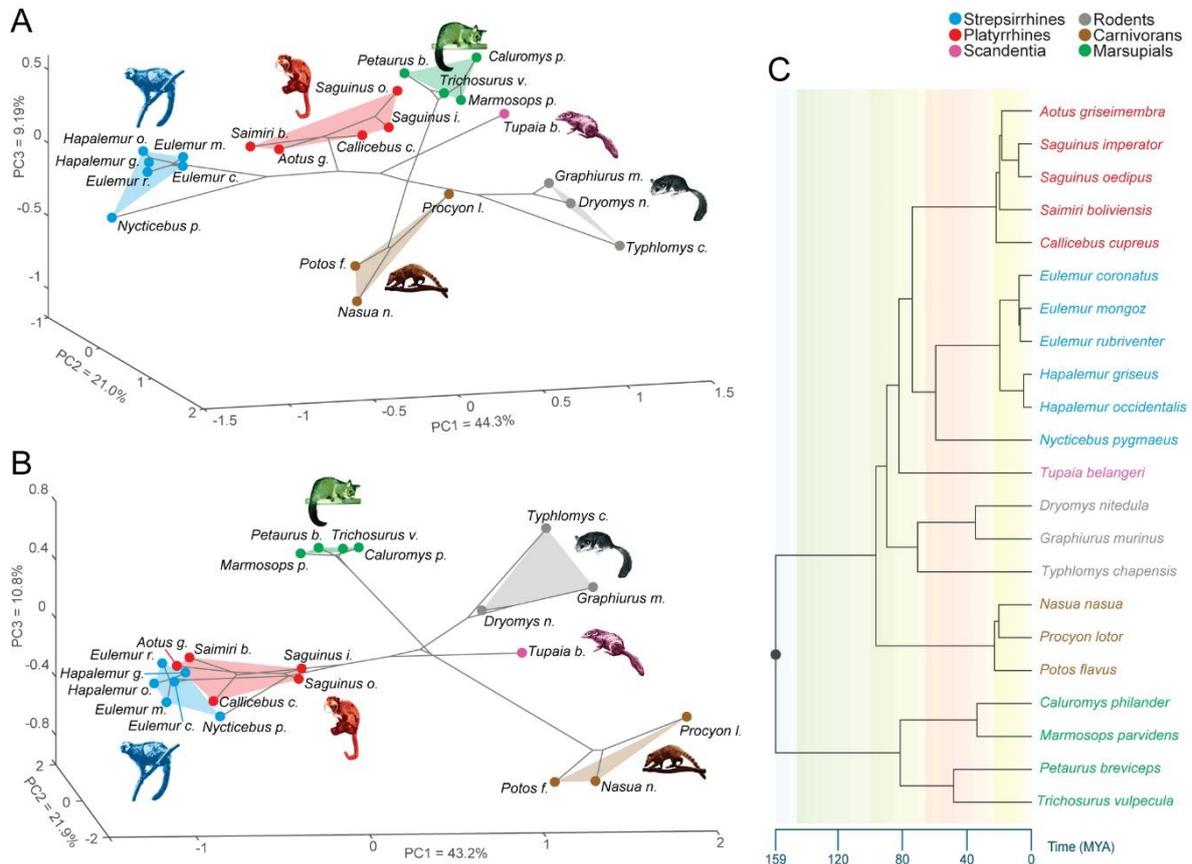
**Figure 1. Quantified postures.** A) Diagram representing hand and foot morphology (note that proportions and digit lengths vary between species). B) Outline of the types of variables used in the study to describe hand and foot postures (see Table 2 for the complete list and definitions of the 19 quantified variables). C) Categories and definitions of substrates' diameters (according to the sizes of the animals' hands and feet) and orientations. D) Examples of postures and associated grasp types in various species (see Table 1 for the list of the studied animals).

129 We found no differences between right and left hands and feet (MANOVAs, hands:  $P \geq 0.40$ ;  
 130 feet:  $P \geq 0.38$  for all individuals and variables, DataS1A) nor between males and females (MANOVAs,  $P$   
 131  $\geq 0.21$  for all species, DataS1B). Moreover, we found significant intraspecific similarity and significant  
 132 interspecific dissimilarity, allowing us to combine data at the species level (MANOVAs,  $P = 3.20 \times 10^{-9}$   
 133 for primates and  $P = 8.43 \times 10^{-5}$  for non-primates, confirmed by *post hoc* tests, DataS1C,D,E). In addition,  
 134 there was significant similarity between phylogenetically related species and significant dissimilarity  
 135 across phylogenetically divergent groups, permitting us to combine data at the phylogenetic group  
 136 level (*i.e.* the two primate groups and the four non-primate groups, MANOVA,  $P = 1.77 \times 10^{-2}$ , Figure 2,  
 137 DataS1F,G).

139  
 140 **Hand and foot postures are representative of phylogenetic relationships**

141 Our PCA analysis indicated that hand and foot postures clearly differentiate the different  
 142 mammalian groups studied, clustering all closely phylogenetically related species together (Figure 2,  
 143 Table S1). This was further confirmed by a high phylogenetic signal ( $K_{mult} = 1.34$  for hands and 1.37  
 144 for feet,  $P = 2 \times 10^{-5}$  in both cases, Table S2). Interestingly, when considering the foot, primates are more  
 145 clustered (Figure 2B), whereas for manual postures, strepsirrhines and platyrrhines are more spread  
 146 out, with *Saguinus* species being located closer to marsupials (Figure 2A). Moreover, the scandentian  
 147 *Tupaia belangeri*, the phylogenetically closest species to primates in this study, is placed closer to  
 148 rodents for foot postures, but closer to marsupials for hand postures. Carnivorans are in both cases  
 149 placed away from the other groups. Analysis of the three first PCs coefficients (Figure 2) revealed the  
 150 particular importance of the postural variables related to the grasp type, to the postures of the pollex  
 151 and hallux and to the contact areas with the substrate (Table S1), for both hands and feet.

153 Moreover, we tested for a potential cofounding factor of body mass on hand and foot postures  
 154 (see Table 1 for body mass used). Overall, we confirm the presence of a relation of body mass with  
 155 autopodial postures when considering all combined postural variables, for both hands and feet  
 156 (MANCOVAs,  $P = 0.012$ , Pillai's Trace = 0.759,  $F = 4.19$ ,  $dfs = 9;12$  for hands and  $P = 0.005$ , Pillai's Trace =  
 157 0.830,  $F = 5.36$ ,  $dfs = 10;11$  for feet). However, this effect is limited when it comes to specific postural  
 158 variables, as out of all principal components accounting for at least 95% of variance we found that no  
 159 single PC correlates significantly with body mass in our *post hoc* tests, for both hands and feet (Table  
 160 S3).



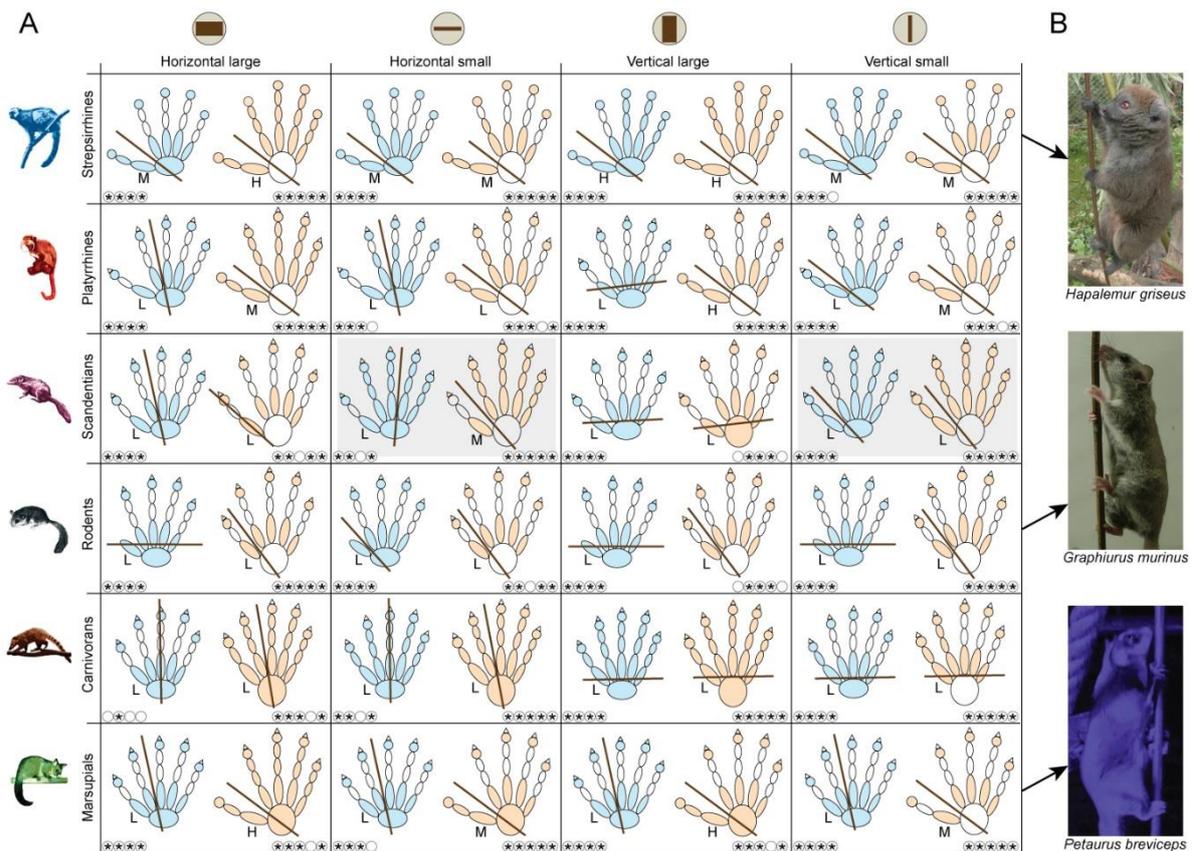
**Figure 2. Postures capture phylogenetic relationships.** A) PCA of hand posture occurrence (percentages correspond to the variance explained). B) PCA of foot postures occurrence (percentages correspond to the variance explained). See Table S1 for variables' weights in principal components. Thin lines in (A) and (B) represent the projection of the phylogeny into the principal component space, computed using the *phylomorphospace* function from *phytools* library in R [82]. C) Phylogeny used, with branches length and representation obtained from *timetree.org* [83]. Colors code species into phylogenetically related groups.

161

162 **Hand and foot postures vary according to the substrate type**

163 To obtain a summarized picture of the large dataset, we computed the most frequent postures  
 164 occurring for each variable on each substrate, combining species by phylogenetic groups (Figure 3,  
 165 using Wilcoxon tests from the frequency of all possible values, see DataS2 for associated proportions  
 166 and statistical results). We found that strepsirrhine primates most frequently displayed a pollical and  
 167 hallucal grasping mode, associated with a highly divergent pollex and hallux (Figure 3), and an  
 168 increased capacity of movements at their digital joints (DataS2) on all substrate types. This implies a  
 169 strong tendency of strepsirrhines for pollical and hallucal grasping, independently of the substrate  
 170 used. Platyrrhine primates displayed variations in their most frequently adopted postures, depending  
 171 on the substrate types. They exhibited an overall less divergent pollex and hallux (Figure 3, DataS2).  
 172 Moreover, while their foot postures appeared quite similar to those of strepsirrhines, they used

173 frequent zygodactylous hand grasps on horizontal and oblique substrates and convergent hand grasps  
174 on large vertical substrates, albeit exhibiting high amplitude of digital joint movements. The studied  
175 non-primate mammals exhibited more zygodactylous and convergent grasps as well, and lower digital  
176 joint movement ability compared to primates (Figure 3, DataS2). Tupaiids and rodents frequently used  
177 a hallucal grasp, particularly in substrates of small diameters, but with a small divergence of the hallux.  
178 Carnivorans exhibited the lowest digital mobility among the studied species, and only occasional use  
179 of the pollex and hallux. Their pollex and hallux were always convergent and placed along the same  
180 axis with the other digits so that their palmar/plantar side contacted the substrate. In contrast, during  
181 pollical/hallucal grasping, primates, and especially strepsirrhines, also applied the palmar/plantar  
182 surface of the pollex/hallux upon the substrate, but mainly due to their increased hallucal and pollical  
183 divergence and rotation movement at their metacarpal/tarsal proximal joints. *Tupaia belangeri* and  
184 rodents, although capable of grasping, did not exhibit rotation movement of their pollex/hallux, and  
185 the medial surface of these digits was in contact with the substrate. Interestingly, marsupials used foot  
186 postures that were very similar to those of strepsirrhines, with an exclusively hallucal grasping mode  
187 and a highly divergent hallux. Furthermore, their hand postures were similar to those of platyrrhines,  
188 with a less divergent pollex and a frequent use of zygodactylous grasp.



**Figure 3. Representation of the most frequent postures adopted for selected variables (grasp type, pollical and hallucal divergence degree, and areas in contact with the substrate, see Table 2 for the complete list and definitions of variables) and substrates (horizontal and vertical large and small), by phylogenetic group.**

A) Strepsirrhine primates = 6 species, Platyrrhine primates = 5 species, Scandentians = 1 species, Rodents = 3 species, Carnivorans = 3 species, Marsupials = 4 species. Blue = hands; orange = feet. Position of the brown lines represents the position of the substrate during the grasp. Degrees of pollical and hallucal divergence are coded as L= low, M= medium and H= high. Colored parts represent contact with the substrate. Circles filled with \* below each hand and foot indicate when a given posture variable is significantly most frequent (Bonferroni-Holms corrected P values from Wilcoxon signed-rank test comparing the proportion of the most frequent posture vs the second most frequent posture for a given variable) in the following order (from left to right): grasp type, degree of pollical/hallucal divergence, pollical/hallucal areas in contact, lateral digits contact areas, and tarsal area in contact with the substrate (for foot only). See DataS2 for underlying proportions, other variables and associated P values and Figures S1 to S5 for precise proportions by species for all variables. In the case of *T. belangeri* we substituted the missing values on small substrates by those on medium substrates (grey background). B) Photographs of a strepsirrhine primate, a rodent and a marsupial on small vertical substrates, illustrating their significantly most frequent hand/foot postures.

189

190 Small and vertical substrates impact the use of the nails vs. claws and of the pollex and  
 191 hallux

192 On medium substrates, all studied species frequently exhibited full contact of the lateral manual  
 193 and pedal digits, fully embracing the substrate (see DataS2, Figures S3A and S5B for precise proportions  
 194 by species). Claws of platyrrhine primates and non-primate mammals were extensively used on large  
 195 substrates, and sometimes on medium ones, but never on small ones (Figure 3, DataS2, Figures S2B,  
 196 S3A, S4C and S5B). Moreover, claw use was predominantly associated with a flexion of the digits. This  
 197 digital posture corresponds to a flexion of the joint between the proximal and the intermediate  
 198 phalanges, and results in an elevation of this joint above the plane of the metapodials. Interestingly,  
 199 this flexion of the lateral manual and pedal digits was also very frequently exhibited by all studied  
 200 species on small substrates, independently of the orientation (Figure 3, DataS2, Figures S2B, S3A, S4C

201 and S5B). This posture permits the placement of only the metapodial and distal phalangeal pads in  
202 contact with the substrate during the grasp, in both nailed and clawed species. Therefore, it seems  
203 that claws do not obstruct the ability to seize small substrates. These results suggest that nails on  
204 lateral digits are not necessary for negotiating small substrates. On the other hand, distal pads,  
205 independently of the possession of nails or claws, appear to be of particular importance to ensure an  
206 efficient grip.

207 Moreover, a greater ability of pollical and hallucal divergence was generally related to an  
208 increased adduction of the lateral digits, especially on small vertical substrates, for all species. In  
209 contrast, on horizontal substrates, lateral digits were generally more abducted and related to a less  
210 divergent pollex or hallux (Figure 3, Figures S1D, S2C, S4A,D).

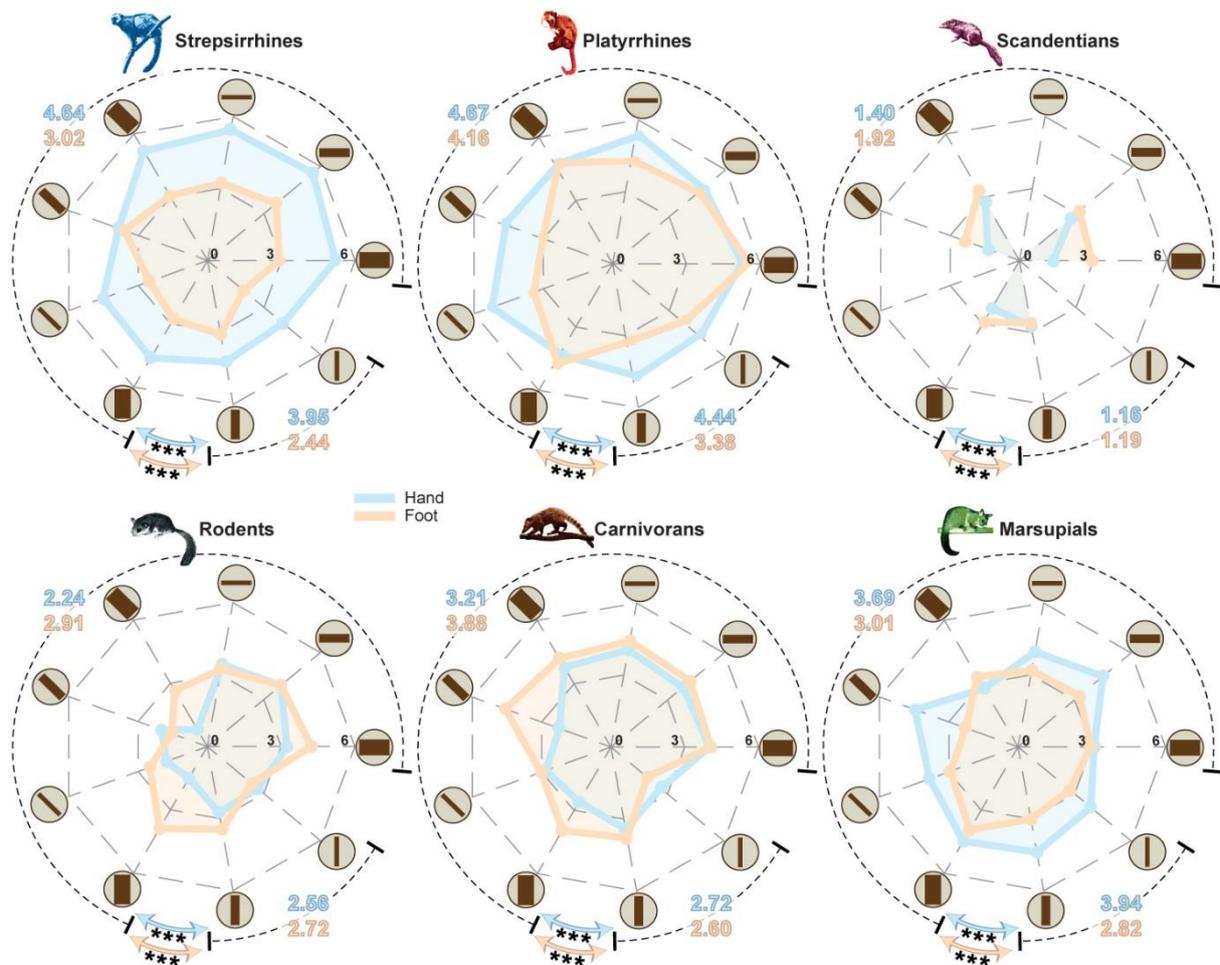
211 Finally, we found that vertical substrates of medium and small diameter appear to induce an  
212 increased use of the pollex and hallux for climbing, even in species that do not possess a  
213 morphologically divergent pollex and hallux (*i.e.* rodents, scandentians, carnivorans) (Figure 3, DataS2,  
214 Figures S1C, S3D). This implies that pollical and hallucal grasping is particularly important for climbing  
215 on medium and small vertical substrates. Interestingly, postures adopted on vertical substrates and  
216 medium substrates retain a higher phylogenetic signal compared to other orientations and diameters  
217 ( $K_{mult} = 1.41$  for vertical substrates, and  $1.51$  for medium substrates,  $P = 2 \times 10^{-5}$  in both cases, Table  
218 S2).

219

## 220 Substrate type impacts the manual and pedal positional repertoire diversity

221 In order to fully assess the manual and pedal postural repertoire diversity for each species, we  
222 computed the Shannon's entropy, a core metric in information theory which combines the size of the  
223 repertoire and how often variants are used (Figure 4). We found that primates exhibit the highest  
224 postural diversity, particularly in the hand in strepsirrhines, and in both hands and feet in platyrrhines.  
225 In fact, despite exhibiting most frequent postures, primates exhibited many postural variations of their  
226 digits, flexing and abducting the digits to adjust their grip in accordance to the substrates, and they  
227 exhibited a high mobility at their metacarpo- and metatarso-phalangeal joints (Figures S1 to S5).  
228 Shannon's entropy was also affected by variations and particularities at the specific level. For instance,  
229 strepsirrhines sometimes exhibited a manual zygodactylous grasp, or a 'grasp type 2', placing the  
230 second digit along the axis of the substrate, with frequent flexion of the digits. Grasp type 2 was  
231 particularly frequent for the slow-climber *N. pygmaeus*, which possesses a reduced second digit.  
232 Furthermore, variability in platyrrhines was mainly due to the particularities of the studied species. For  
233 instance, *S. boliviensis* used postures similar to those of strepsirrhines, with more pollical and hallucal  
234 divergence, whereas callitrichines displayed postures more similar to scandentians, rodents and  
235 marsupials, with frequent zygodactylous grasps, less digital mobility, and claw use on large substrates.  
236 Similarly to primates, marsupials displayed more diversity in their manual postures than in their pedal  
237 postures. Among marsupials, *P. breviceps* showed frequent pollical grasping, with a more divergent  
238 pollex, and increased metacarpo-phalangeal mobility. Scandentians, rodents and carnivorans  
239 exhibited overall less postural diversity, with foot postures being more diverse than hand postures,  
240 compared to primates and marsupials.

241 Finally, substrate type had a generally strong impact on postural diversity, with a decrease on  
242 medium and small, oblique and vertical substrates in almost all species, particularly in non-primate  
243 species that are less specialized for grasping (rodent feet, carnivorans, Figure 4). This is significantly  
244 pronounced when comparing medium and small vertical substrates to all others ( $P < 10^{-22}$ , Mann  
245 Whitney U test on bootstrapped entropies, Figure 4). This may suggest that vertical and slender  
246 substrates impose more constraints on postural adaptations for climbing than horizontal or larger sized  
247 substrates. Additionally, when focusing on medium and small vertical substrates, we observe that  
248 primates and marsupials display a larger average entropy for hands postures than for feet. This  
249 contrasts with other groups which have closer values between hands and feet. This supports the notion  
250 that the function of the hands and feet are more differentiated on those substrates in primates and  
251 marsupials compared to the other mammalian groups.



**Figure 4. Impact of the substrate type on the manual and pedal postural diversity, for each phylogenetic group.** Strepsirrhine primates = 6 species, Platyrrhine primates = 5 species, Scandentian = 1 species, Rodents = 3 species, Carnivorans = 3 species, Marsupials = 4 species. Radar plots show the entropy (in Shannons) of the postural repertoire, for each substrate, averaged by phylogenetic group. No data for *T. belangeri* on small substrates. The higher the entropy the more variable the postures are. Each edge of the nonagons corresponds to a substrate type (orientation and diameter). Blue= hands, orange= feet. Numbers represent the averages of entropies over vertical small and medium substrates (bottom right) and over other substrates (top left), in blue for hand and orange for feet. Arrows with \*\*\* indicates significant differences between these averages with  $P < 10^{-22}$  (Mann-Whitney-U test on bootstrapped distributions of entropy) for hands in blue and feet in orange. See also Figures S1 to S5 for precise proportions by species and variables.

252

## 253 Discussion

### 254 Extant models to represent arboreal grasping patterns of early primates

255 This study provides an indication of the diversity of manual and pedal postures among arboreal  
 256 mammals and underlines the importance of substrate characteristics in relation to grasping patterns.  
 257 We found that manual and pedal postural repertoires are good indicators for establishing  
 258 phylogenetically related behavioral profiles, at least for the studied species.

259 In arboreal locomotion, hand and foot postural specificities are strongly related to species  
 260 morphology and evolutionary history and promote the exploitation of specific arboreal niches. The  
 261 results of this study support observations that primates are behaviorally distinguishable from other  
 262 mammals regarding their foot postures, whereas differences within primates reside mainly in hand  
 263 postural variation [4,50]. The general similarity of foot postural behavior across primates likely  
 264 indicates its more primitive and conservative nature [4–7], whereas the hand appears to have a more

265 complex evolutionary and functional history [32]. Furthermore, we found that primates exhibit the  
266 broadest repertoire of hand and foot postures and greater digital mobility. The ability to execute more  
267 postural combinations with a higher amplitude of movements may provide an advantage for safe and  
268 secure locomotion upon a wide range of substrates, and for precise and efficient foraging on a wide  
269 variety of exploitable resources, promoting a higher adaptability to complex arboreal environments.

270 In addition, the bulk of our data provide quantitative behavioral evidence supporting hypotheses  
271 for the functional basis of morphological differences between strepsirrhines and platyrrhines, with  
272 strepsirrhines being specialized for powerful pollical and hallucal grasping [4,17,19] and platyrrhines  
273 exhibiting higher variability across species [32,51,52]. Although the studied strepsirrhines were  
274 phylogenetically more closely related than the studied platyrrhines, platyrrhines are generally  
275 considered as more diversified in their morphology and positional behaviors [51,53]. Our results are  
276 consistent with the hypothesis that callitrichines represent an adequate model for an ancestral stage  
277 in early primate evolution, as we found that their manual postures are somewhat comparable to those  
278 of scansorial mammals, like treeshrews, opossums and rodents [39,53–55]. Interestingly, the manual  
279 and pedal postures of the scandentian *T. belangeri* (the closest relative of primates in this study) were  
280 not convergent with primates, but rather in between rodents and marsupials. However, the genus  
281 *Tupaia* is morphologically and behaviorally different from the more primitive arboreal representative  
282 of the group *Ptilocercus*, often considered as a model of the ancestral primate morphotype [40,41]. As  
283 *Ptilocercus* was not sampled in this study, and due to its morphological similarities to primates  
284 [33,56,57], we cannot rule out the possibility that it would behave differently from *Tupaia* and closer  
285 to primates. Finally, our results add evidence on the functional convergence of the foot grasping  
286 mechanism between primates and some marsupials [58,59]. However, although *C. philander* is often  
287 seen as a functional analogue to early primates based on its gait patterns [24,42], we found that *P.*  
288 *breviceps* is more similar to primates in its grasping postures and digital mobility. We suggest that a  
289 better model should consider both gaits and associated pollical and hallucal grasping to approximate  
290 early primate evolution.

291

## 292 Grasping small diameter substrates: are nails fundamental?

293 Our results show a clear effect of the substrate diameter on the digital contact areas with the  
294 substrate. This entails implications on the forces applied by the digits and the biomechanical  
295 constraints at play during grasping. Tamarins and non-primate mammals used exclusively their claws  
296 on large substrates, associated with a flexion of the digits, confirming their functional efficiency on  
297 trunks and large branches. However, small substrates, independently of orientation, also induced  
298 flexed postures of both manual and pedal digits, with only the palmar/plantar surface and the distal  
299 digital pads in contact with the substrate, for all species. This indicates that flexion of the terminal and  
300 middle phalanges, accomplished by the action of the digital flexors, increases the applied force at the  
301 distal apical pads and/or claws to ensure a more stable and secure grasp, either for climbing on large  
302 substrates or grasping small substrates. Moreover, we found that distal apical pads are central in  
303 grasping small substrates, even in clawed species. Pads of primates and non-primates are very different  
304 in their morphology, with the former being flatter and larger, and the latter thicker and narrower [23].  
305 The particular morphology of primate pads and nails has long been proposed as an adaptation for  
306 negotiating small diameter substrates [7,11]. However, our results show that several clawed non-  
307 primate species are also capable of grasping and negotiating narrow substrates. In this regard, it is  
308 clear that narrow substrates require specific biomechanical adaptations of the extremities, but the  
309 possession of nails alone may not be a sufficient condition to justify a fine branch adaptation.

310 Arguably, a narrow substrate can be a very relative notion and depends on the size of the animal.  
311 Body mass imposes biomechanical constraints and correlates with digit length (*e.g.* in some prosimians  
312 [13]), and is thus expected to affect the ability to efficiently negotiate small substrates. Also, body size  
313 does affect selection of substrate size and inclination in free-ranging arboreal primates [60], and may  
314 indirectly influence grasping patterns. However, even though we found a global effect of body mass  
315 on hand and foot postures, we could not pinpoint more specific correlations between the body mass

316 and specific aspects of manual and pedal postures as represented by PCA transformed values for the  
317 studied species. This suggests that influence of body size on hand and foot postural behavior variance  
318 is either too mild to be significant or confounded by our PCA. Therefore, although it might have an  
319 impact on specific aspects of specific variables, it should not have influence on our results that are  
320 derived from PCA transformed values. In addition, it is possible that the global effect of body size that  
321 we obtain here is more directly related to the differences in morphologies across species rather than  
322 mass per se. In our study sample, the largest species were the carnivorans, which have very different  
323 autopodial morphologies from that of the other sampled species.

324 Although we did not quantify the preference or performance on different substrate categories,  
325 our quantified results suggest altogether that, as early primates were probably small or very small [38],  
326 it is thus possible that the acquisition of nails was not fundamental for small branch use, in contrast  
327 with the ability to diverge the hallux/pollex from the lateral digits. It is thus possible that primate nails  
328 became important in grasping and/or manipulating after an increase of body mass while staying  
329 confined to the fine branch milieu. A deeper investigation of preference and performance of substrate  
330 use in these models, both in captivity and in the wild, would shed more light on this hypothesis.

331

### 332 [Negotiating small vertical substrates: an evolutionary scenario for pollical and hallucal](#) 333 [grasping](#)

334 It is well established that substrate inclination influences postural behaviors in primates and  
335 other mammals [18,21,63,64,26,31,35,39,48,55,61,62]. Interestingly, we found that manual and pedal  
336 postural variability is significantly lower on small vertical substrates, particularly in those species that  
337 do not possess a morphologically divergent pollex and hallux. This result may indicate that climbing  
338 vertical substrates of relatively small diameters induces higher constraints on the hand and foot  
339 postures adopted to hold onto the substrate, and thus results in a limitation of the postural strategies  
340 adopted. This would be consistent with previous experimental studies that showed that vertical  
341 substrates are usually considered as being biomechanically constraining, demanding higher forces and  
342 stronger hallucal grasp than horizontal displacements, especially for larger species  
343 [4,5,17,21,22,63,65]. Moreover, we found that during climbing, vertical substrates of medium and  
344 small diameters induce an increased use of pollical and hallucal grasp, even in species with relatively  
345 reduced capacity of pollical/hallucal divergence. This implies that pollical and hallucal grasping may  
346 not be related exclusively to fine branch use, as suggested for early primate differentiation and  
347 strepsirrhine specialization [2,7], but may represent crucial mechanisms which permit a more effective  
348 hold during climbing on medium and small vertical substrates. Additionally, we observed that in  
349 primates, marsupials and some rodents, the metacarpo- and metatarso-phalangeal joint mobility  
350 appears to be correlated to the ability for pollical and hallucal grasping and to the adduction/abduction  
351 of the lateral digits. This mobility enables a more adjustable, flexible, and efficient grasping  
352 mechanism. The ability to abduct the lateral digits during pollical and hallucal divergence forms a  
353 functional pincer that embraces the substrates, enlarges the contact areas, and may uniformly  
354 distribute the applied forces towards a more efficient grasp.

355 Considering our findings, medium and small vertical substrates have likely exerted a particular  
356 selective pressure toward the emergence of hallucal and pollical grasping capacity, and therefore may  
357 have played a significant role in the specialization of the first primates. We propose that the acquisition  
358 of an opposable hallux and of a divergent pollex may have been favored by the frequent use of  
359 relatively small vertical substrates, such as lianas, climbing plants or even tall grass thickets.

360 Vertical narrow substrates appear to be particularly constraining to negotiate, but they are  
361 important as they may permit access to the canopy from the ground (*e.g.* lianas), rapid changes of  
362 height within the canopy, or provide access to food sources in tree peripheries. Indeed, the Paleocene  
363 and Eocene flora of north America and Europe, where the first primates are supposed to have  
364 appeared [7,9,66], was composed of angiosperm trees, but also of climbing plants and lianas [67,68].  
365 These plants must have formed a complex and discontinuous network of abundant vertical and  
366 relatively medium to small sized substrates, also bearing food sources, such as fruits and flowers [69].

367 In this context, climbing along lianas would have offered significant advantages: ensuring a connection  
368 between the ground and the canopy, promoting the ability to rapidly change between tree layers,  
369 providing platforms for scanning for food or predators, efficient escape ways from predators, and  
370 access to valuable food sources.

371 However, other kinds of substrates are also to be considered, as it is not unanimous that the  
372 ancestral euprimates would have evolved in a canopied forest [70,71]. It is noticeable that some  
373 rodents which possess functional opposable halluces (e.g. *Micromys*, *Hapalomys*) occupy bush and  
374 grass thickets where they use their grasping hallux to hold on to fine flexible stems [25,72]. Considering  
375 that many savannah and tropical marsh environments are also populated by grasses and reeds more  
376 than a meter high, it makes it apparent that "open environments" could also present a selective  
377 pressure for grasping and climbing on vertical substrates in small animals.

378 Taken together, the ability to oppose the hallux and pollex, ensuring a higher grasping efficiency,  
379 may constitutes a significant selective advantage. This scenario, based on our results, is in accord with  
380 recent studies that advocate vertical climb, cling, and eventually leap, as the ancestral condition of the  
381 first primates [17,18,21]. This contradict those which support quadrupedal walk and run as the  
382 ancestral primate adaptations [43,73]. In contrast, this scenario does not contradict the hypothesis of  
383 early primate leaping adaptations [6,17,19], as we build upon the idea that vertical substrate use was  
384 probably an ancestral condition for primates. However, we propose that the hallucal - and possibly  
385 associated pollical - grasping capacities were probably earlier to the acquisition of nails and related to  
386 the use of small vertical substrates. In this case, nails could have evolved later, to ensure a better force  
387 distribution on digital extremities during locomotion or during food grasping in larger forms. To test  
388 this, research on force distribution in nailed and clawed mammals is currently under way. Furthermore,  
389 it is still difficult to assess whether nails appeared jointly on both hands and feet, or in parallel in  
390 different primate lineages. In effect, haplorhine and strepsirrhine nails may not be homologous, based  
391 on their morphological and functional differences, and as suggested by recent fossil evidence [74–76].

392 These findings also bear on the evolution of arboreality in mammals in general. It is very likely  
393 that pedal grasping and associated hallucal use are early adaptations in mammals [77] and could have  
394 appeared several times, convergently, but functionally differently in primates and other mammals.  
395 Indeed, many arboreal mammals appear to possess a prehensile foot. Yet, they do not always possess  
396 a prehensile hand. Hand prehensility, by further retarding the stance phase of the forelimb and  
397 increasing locomotor stability, may have further contributed to the successful restriction of primates  
398 to diagonal sequence walking gait [78], whereas other arboreal prehensile-footed mammals employ  
399 both diagonal and lateral walking gait [79,80]. This raises some questions: Why did primates evolved  
400 prehensile hands? Are there any mammals which possess prehensile hands and non-prehensile feet?  
401 Finally, future experimental studies should focus on the quantification of the spatially resolved forces  
402 under the hands and feet during locomotion, through new technologies [81], to test whether pollical  
403 and hallucal grasping and nails do indeed permit to apply more force on small and vertical substrates  
404 than non-grasping clawed structures.

405

## 406 Acknowledgments

407 We greatly thank the staff of the Zoological and Botanical Parc of Mulhouse, the Zoological Park  
408 of Paris, and the Spaycific'Zoo (France) for access to their animals and for their assistance during  
409 material installation and data collection. We thank Dr. Alexandra Panyutina and Dr. Alexander  
410 Kuznetsov (Lomonossov Moscow State University and Russian Academy of Sciences) and the Moscow  
411 Zoo staff (Russian Federation) for video recordings of *Graphiurus murinus*, *Typhlomys chapensis* and  
412 *Tupaia belangeri*. We thank Dr. Nikolaos Evangelos Karantanis and the staff of the Nowe Zoo Poznan  
413 (Poland) for the videos of *Nycticebus pygmaeus*. We thank the staff of the Laboratoire d'Ecologie  
414 Generale in Brunoy for the video recording of *Caluromys philander*. We thank Dr. Anthony Herrel and  
415 Dr. Anne-Claire Fabre for providing data for *Marmosops parvidens*. We thank Dr. Emmanuelle

416 Pouydebat for her relevant remarks. We thank the FdV doctoral school, and the CR2P laboratory for  
417 funding. Finally, we thank the four anonymous reviewers who greatly helped improved this paper.  
418

## 419 Author Contributions

420 S.T. designed the study, developed the experimental procedures, analyzed the behavioral data  
421 and wrote the manuscript. S.T., L.M. and D.Y. collected the data. S.T. and A.L. conducted the statistical  
422 analysis. All authors helped with data interpretation and manuscript writing.  
423

## 424 Declaration of interests

425 The authors declare no competing interests.

426

427

428 **Tables**

429 **Table 1. List of animals studied.** Species with an\* are nocturnal. PZP= Parc Zoologique de Paris,  
 430 France. PZBM= Parc Zoologique et Botanique de Mulhouse, France. Species are presented by their  
 431 associated phylogenetically related groups (strepsirrhine primates, platyrrhine primates,  
 432 scandentians, rodents, carnivorans and marsupials). Typical mean of body mass by species are from  
 433 literature: [84,85], animaldiversity.org (ADW, University of Michigan, Museum of Zoology) and eol.org  
 434 (encyclopedia of life, National Museum of Natural History, Smithsonian Institution).  
 435

	Family	Subfamily	Species	Housing location	Observation period	Sample size	Year of birth	Mean of body mass (g)	Reference for body mass	
Primates	Lorisidae	Lorisinae	<i>Nycticebus pygmaeus*</i>	Nowe Zoo Poznan, Poland	03-2013	4 females	unknown	362.5	Fleagle 2013	
	Strepsirrhines	Lemuridae	<i>Haplemur occidentalis</i>	Parc Zoologique de Paris (PZP), France	04-2017	1 male	2014	1017	Fleagle 2013	
			<i>Haplemur griseus</i>	Parc Zoologique et Botanique de Mulhouse (PZBM), France	09-2016	1 female	2006	709	Fleagle 2013	
			<i>Eulemur rubriventer</i>	PZBM	09-2016	2 females, 2 males	1991, 2010 & 2008, 2009	1960	Fleagle 2013	
			<i>Eulemur coronatus</i>	PZBM	09-2016	1 female, 3 males	1999 & 2005, 2015, 2015	1180	Fleagle 2013	
			<i>Eulemur mongoz</i>	PZBM	09-2016	1 female	1987	1212.5	Fleagle 2013	
					PZP	04-2017	2 males	1996, 2001		
	Pitheciidae	Callicebinae	<i>Callicebus cupreus</i>	PZP	04-2017	1 female, 1 male	2007 & 2010	1070	Fleagle 2013	
	Platyrrhines	Cebidae	Saimirinae	<i>Saimiri boliviensis boliviensis</i>	PZBM	01-2016	2 females, 2 males	2005, 2010 & 2011, 2015	871.5	Fleagle 2013
				Aotinae	<i>Aotus lemurinus griseimembra*</i>	Spaycific'Zoo, France	09-2017	1 female, 1 male	2010 & 2009	966
Callitrichinae		<i>Saguinus imperator</i>	PZBM	09-2016	2 females, 2 males	2010, 2013 & 2014, 2014	474.5	Fleagle 2013		
		<i>Saguinus oedipus</i>	Spaycific'Zoo, France	09-2017	1 female, 1 male	2016 & 2015	411	Fleagle 2013		
Scandentians	Tupaiaidae		<i>Tupaia belangeri</i>	Moscow Zoo, Russia	07-2017	3 females	unknown	160	animaldiversity.org	
Non-Primate mammals	Rodents	Gliroidae	Leithiinae	<i>Dryomys nitedula*</i>	University of Thessaloniki, Greece - wildcaught	07-2017	1 female, 1 male	unknown	26	animaldiversity.org
				Graphiurinae	<i>Graphiurus murinus*</i>	Moscow Zoo, Russia	07-2017	1 female, 1 male	unknown	28.5
		Platacanthomyidae	<i>Typhlomys chapensis*</i>	Moscow Zoo, Russia - wildcaught	07-2017	2 males	unknown	16.93	Cheng et al. 2017	
	Carnivorans	Procyonidae	<i>Procyon lotor</i>	Spaycific'Zoo, France	09-2017	1 female, 3 males	2005 & 2007, 2012, 2012	6000	animaldiversity.org	
			<i>Nasua nasua</i>	Spaycific'Zoo, France	09-2017	2 females, 2 males	unknown	3900	animaldiversity.org	
			<i>Potos flavus*</i>	Spaycific'Zoo, France	09-2017	1 female	unknown	3300	animaldiversity.org	
	Marsupials	Didelphidae	Didelphinae	<i>Marmosops parvidens*</i>	Guyane française - wildcaught	01-2017	1 female	unknown	15	eol.org
				Caluromyinae	<i>Caluromys philander</i>	Laboratoire d'écologie générale de Brunoy, France	03-1993	2 males	1990, 1991	265
		Phalangeridae	<i>Trichosurus vulpecula*</i>	Spaycific'Zoo, France	09-2017	1 female, 1 male	unknown	2850	animaldiversity.org	
		Petauridae	<i>Petaurus breviceps*</i>	Spaycific'Zoo, France	09-2017	2 females, 2 males	2010, 2014 & 2012, 2014	110	animaldiversity.org	

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**Table 2. Description and definition of the collected hand and foot variables.**

VARIABLE	DESCRIPTION	
<b>GENERAL POSTURES</b>		
Hand posture relative to the forearm	<b>Neutral:</b> midline of the hand positioned along the axis of the forearm's midline	
	<b>Abduction:</b> midline of the hand positioned laterally away from the forearm's midline	
	<b>Adduction:</b> midline of the hand positioned medially away from the forearm's midline	
Rotation of the forearm	<b>Pronation:</b> forearm rotated laterally so that the palm of the hand faced downward	
	<b>Supination:</b> forearm rotated medially so that the palm of the hand faced upward	
Foot posture relative to the leg	<b>Neutral:</b> midline of the foot positioned along the axis of the leg's midline	
	<b>Abduction:</b> midline of the foot positioned laterally away from the leg's midline	
	<b>Adduction:</b> midline of the foot positioned medially away from the leg's midline	
	<b>Reversion:</b> extreme plantarflexion and backward rotation of the foot, reorienting the plantar surface of the foot to a medial position	
Posture of the distal foot relatively to the proximal foot	<b>Neutral:</b> no distal rotational motion of the foot. Distal foot in line with the hindlimb	
	<b>Inversion:</b> rotational motion of the distal foot reorienting the plantar surface of the foot medially	
	<b>Eversion:</b> rotational motion of the distal foot, reorienting the plantar surface of the foot laterally	
Tarsal contact areas	<b>Plantigrady:</b> proximal heel in contact with the substrate during grasp	
	<b>Semiplantigrady:</b> elevation of the proximal heel resulting in loss of contact with the substrate during grasp	
<b>GRASPING POSTURES</b>		
Grasp type (digits involved in substrate grasping)	<b>Convergent grasp:</b> pollex/hallux and lateral digits grasp in unison (together)	
	<b>Pollical/hallucal grasp:</b> holding of the substrate between pollex/hallux and lateral digits	
	<b>Digit 1 grasp</b> (subtype of pollical/hallucal grasping): pollex/hallux positioned in parallel with the substrate and lateral digits angled to the substrate	
	<b>Digit 2 grasp:</b> pollical/hallucal grasping but with digit 2 positioned in parallel with the substrate and other lateral digits angled to the substrate	
	<b>Digit 2-3 grasp:</b> holding of the substrate between digits 2 and 3 (zygodactylous grasp)	
	<b>Digit 3 grasp:</b> holding of the substrate with digit 3 positioned in parallel with the substrate	
	<b>Digit 3-4 grasp:</b> holding of the substrate between digits 3 and 4	
	<b>Digit 4 grasp:</b> holding of the substrate with digit 4 positioned in parallel with the substrate	
	<b>Digit 4-5 grasp:</b> holding of the substrate between digits 4 and 5	
	Degree of pollical/hallucal divergence (angle between hallux and second digit)	<b>Low:</b> 0° to 45°
<b>Medium:</b> 45° to 90°		
<b>High:</b> 90° and more		
General movement of the lateral digits	<b>Abduction:</b> movement of the digits away from the anatomical midline of the hand/foot	
	<b>Adduction:</b> movement of the digits towards the anatomical midline of the hand/foot	
Movement of the lateral digits at the metacarpo-/metatarso-phalangeal joint	<b>Neutral:</b> lateral digits phalanges positioned in line with the metacarpals/metatarsals	
	<b>Abduction:</b> lateral digits phalanges positioned laterally away from the metacarpals'/metatarsals' midline	
Pollical/hallucal rotation (relative to the substrate)	<b>Abduction:</b> lateral digits phalanges positioned medially away from the metacarpals'/metatarsals' midline	
	<b>Lateral:</b> lateral surface of the pollex/hallux facing toward the substrate	
	<b>Palmar/plantar:</b> palmar/plantar surface of the pollex/hallux facing toward the substrate	
	<b>Medial:</b> medial surface of the pollex/hallux facing toward the substrate	
	<b>HAND/FOOT CONTACT AREAS WITH THE SUBSTRATE</b>	
	Pollex/hallux contact areas (digit 1)	<b>MC1/MT1:</b> first metacarpal/metatarsal pad
<b>PP1:</b> first proximal phalanx pad		
<b>DP1:</b> first distal pad		
<b>CL1:</b> apical part of the pollical/hallucal claw		
Lateral digits contact areas, each collected for digits 2, 3, 4 and 5	<b>MC2-3-4-5/MT2-3-4-5:</b> metacarpal/metatarsal pads	
	<b>PP2-3-4-5:</b> proximal phalanges pads	
	<b>IP2-3-4-5:</b> intermediate phalanges pads	
	<b>DP2-3-4-5:</b> distal pads	
	<b>CL2-3-4-5:</b> apical parts of the claws	

## 444 STAR Methods

## 445 Key resource table

446

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological Samples		
<i>Nycticebus pygmaeus</i>	Nowe Zoo Poznan	Dionisios Youlatos
<i>Hapalemur occidentalis</i>	Parc Zoologique de Paris	Séverine Toussaint
<i>Hapalemur griseus</i>	Parc Zoologique et Botanique de Mulhouse	Séverine Toussaint
<i>Eulemur rubriventer</i>	Parc Zoologique et Botanique de Mulhouse	Séverine Toussaint
<i>Eulemur coronatus</i>	Parc Zoologique et Botanique de Mulhouse	Séverine Toussaint
<i>Eulemur mongoz</i>	Parc Zoologique et Botanique de Mulhouse and Parc Zoologique de Paris	Séverine Toussaint
<i>Callicebus cupreus</i>	Parc Zoologique de Paris	Séverine Toussaint
<i>Saimiri boliviensis boliviensis</i>	Parc Zoologique et Botanique de Mulhouse	Séverine Toussaint
<i>Aotus lemurinus griseimembra</i>	Spaycific'Zoo	Séverine Toussaint
<i>Saguinus imperator</i>	Parc Zoologique et Botanique de Mulhouse	Séverine Toussaint
<i>Saguinus oedipus</i>	Spaycific'Zoo	Séverine Toussaint
<i>Tupaia belangeri</i>	Moscow Zoo	Dionisios Youlatos
<i>Dryomys nitedula</i>	University of Thessaloniki	Séverine Toussaint
<i>Graphiurus murinus</i>	Moscow Zoo	Dionisios Youlatos
<i>Typhlomys chapensis</i>	Moscow Zoo	Dionisios Youlatos
<i>Procyon lotor</i>	Spaycific'Zoo	Séverine Toussaint
<i>Nasua nasua</i>	Spaycific'Zoo	Séverine Toussaint
<i>Potos flavus</i>	Spaycific'Zoo	Séverine Toussaint
<i>Marmosops parvidens</i>	Guyane française	Anthony Herrel & Anne-Claire Fabre
<i>Caluromys philander</i>	Laboratoire d'écologie générale de Brunoy	Dionisios Youlatos
<i>Trichosurus vulpecula</i>	Spaycific'Zoo	Séverine Toussaint
<i>Petaurus breviceps</i>	Spaycific'Zoo	Séverine Toussaint
Software and Algorithms		
Matlab (version R2014b)	Mathworks	<a href="https://www.mathworks.com">https://www.mathworks.com</a>
R (version 3.3.3)	The R Foundation	<a href="https://www.r-project.org">https://www.r-project.org</a>
TimeTree	Kumar et al. 2017	Timetree.org
Adobe Premiere Elements 12	Adobe	<a href="https://adobe.com">https://adobe.com</a>

447

## 448 Lead contact and materials availability

449 Further information and requests for resources and reagents should be directed to and will be  
450 fulfilled by the Lead Contact, Séverine Toussaint ([severine.toussaint@cri-paris.org](mailto:severine.toussaint@cri-paris.org)). Videos of  
451 behavioral data collection are available from the Lead Contact upon reasonable request.  
452

## 453 Experimental model and subject details

454 Data were collected on both captive and wild animals (Table 1). Individuals caught in the wild  
455 were placed in specifically designed enclosures during the observation period and were subsequently  
456 released. In zoos we video-recorded the individuals directly in their enclosures. All the enclosures were  
457 large enough to allow free displacement of the animals. Non-treated wooden substrates of varied  
458 diameters and orientations were placed in each enclosure before filming to ensure an equal access to  
459 a variety of substrate types.

460 All studied individuals were adults and in good shape and did not display any stereotypical  
461 behavior before or during the experiments. Animal handling was performed in compliance with the  
462 International Primatological Society (IPS) Ethical Guidelines for the Use of Nonhuman Primates in  
463 Research and the Association for the Study of Animal Behaviour (ASAB) and the Animal Behaviour  
464 Society (ABS) ethical guidelines for the use of animals in research [86].  
465

## 466 Method details

467 We identified 3 different substrate diameters (small, medium and large, according to the size of  
468 the animals' hands and feet) and 3 different orientations (horizontal, oblique and vertical), resulting in  
469 9 substrate types tested for each individual (Figure 1B). Sequences were recorded using a portable  
470 video camera (Panasonic HC-V770 camcorder 120fps, Full HD 1080p). To ensure close ups and a  
471 complete view of the hand and foot grasps during locomotion, we also used three small action video  
472 cameras (Mobius ActionCam 60fps, HD 720p) installed in three different angles of view (frontal, lateral  
473 and ventral) and in close distance (between 20 and 50 cm) from each substrate type. After a  
474 habituation period, the individuals were recorded using an alternation of scan sampling and focal-  
475 animal sampling methods [87] in continuous recording sessions of 10 to 30 min. Animals were  
476 observed and filmed as they moved freely over substrates, and when necessary, we stimulated them  
477 by providing small pieces of food placed along the substrates. For the nocturnal species (Table 1),  
478 observations were conducted either in artificial or real nocturnal conditions, with addition of red lights  
479 spots to enable recording without disturbing the animals.  
480

481 Note on species studied: During our dataset sampling, *Nasua nasua* never used the medium and  
482 small vertical substrates, and *Procyon lotor* never used the small oblique and vertical substrates. For  
483 videos analyzed from previous experiments, there was no data for some of the sizes and inclinations  
484 of the substrates. Thereby, for *Marmosops parvidens* there was no data for oblique substrates; for  
485 *Graphiurus murinus* there was no data for oblique and small vertical substrates; for *Tupaia belangeri*  
486 there was no data for small substrates and for *Typhlomys chapensis* there was no data for oblique and  
487 medium vertical substrates.  
488

## 489 Quantification and statistical analysis

### 490 Video analysis

491 We analyzed videos using Adobe Premiere Elements 12. All video analysis was performed by the  
492 same person (S. Toussaint) in order to avoid interobserver biases. We collected a minimum of 10  
493 passing for each individual on each substrate type, with one grasp (hand and/or feet) analyzed per  
494 passing. We focused on hand and foot grasping events during locomotion only (*e.g.* horizontal and  
495 inclined walking and vertical climbing) and excluded other behaviors. On oblique and vertical  
496 substrates, we only analyzed postures during ascents. We analyzed a minimum of 10 hand grasps and

497 10 associated foot grasps for each individual on each substrate type, resulting in at least 90 hand grasps  
498 and 90 foot grasps for each individual, with the exception of some individuals for which we could not  
499 obtain data on all substrates.

500

501 Hand and foot postures analysis

502 In order to describe the overall impact of substrate orientation and diameter on hand and foot  
503 postures, we calculated the frequency of all possible values occurring for each variable on each  
504 substrate for each individual (Figures S1 to S5). Individual proportions were often averaged over all  
505 individuals of the same species. To obtain an overall picture of the large dataset, species proportions  
506 were sometimes further averaged over their phylogenetic group. We performed PCAs on these  
507 dependent raw frequencies (separating hands and feet) to obtain linearly independent transformed  
508 values which serve as low-dimensional representation of global postural data throughout this paper  
509 (see Table S1 for details on each variable's contribution to principal components). Unless stated  
510 otherwise, all statistical analysis was performed with Matlab © (version R2014b).

511

512 Data quality control analysis

513 In order to check for potential inconsistencies in the dataset, we performed multivariate analysis  
514 of variance (MANOVAs) with Bonferroni-Holms corrected *post hoc* pairwise comparisons (when  
515 applicable) to test for differences between left and right hands and feet for each individual (DataS1A);  
516 to test for differences between males and females of the same species (DataS1B); to test for  
517 intraspecific similarity (DataS1C,D) and interspecific dissimilarity (DataS1E) so as to combine data at  
518 the species level, and to test for phylogenetic similarity (DataS1F,G), so as to combine data at the  
519 phylogenetic group level. All MANOVAs were performed using *manova1* from Matlab's statistical  
520 toolbox and used PCA-transformed frequency data, keeping principal components explaining at least  
521 95% of variance.

522

523 Phylogenetic relationships analysis

524 In order to properly quantify the extent of phylogenetic information captured by postures we  
525 computed the phylogenetic signal retained in posture data (using species-level PCA-transformed data)  
526 using the K mult measure of phylogenetic signal, which is the multidimensional extension of  
527 Blomberg's K [88]. In addition to testing the global signal, we tested if hands and feet postures adopted  
528 on specific substrates would reveal phylogenetic signals of different strength, see Table S2. These were  
529 performed with R (version 3.3.3), using the *physignal* function from the *geomorph* package, with 50000  
530 iterations for each test. We only used the first three PCs and, we used the phylogeny and branch  
531 lengths provided by *timetree.org* [83] as in Figure 2C, which derives from an aggregation of molecular  
532 based data. Also, when computing the phylogenetic signal on only a subset of substrates, the PCA  
533 transformation was recomputed using only data from the substrates of interests to avoid information  
534 leaks.

535

536 Correlation with body mass analysis

537 In order to test for a potential confounding factor of the body mass on the hand and foot postures,  
538 we performed MANCOVAs using species-level PCA-transformed postural data (for hands and feet  
539 separately) as response variables and the species' log of body mass as covariate. We used typical body  
540 mass obtained from literature (Table 1). We used the *mancova* function from *jmv* package in R (version  
541 3.3.3).

542 To then quantify the extend of this relation, we used the spearman correlation to be able to  
543 capture non-linear relationship (*e.g.* logarithmic). We computed the spearman correlation between  
544 the species' typical body mass and the principal components of PCA-transformed postural data at the  
545 species level (for hands and feet separately), with Bonferroni-Holms corrected *post hoc* pairwise

546 comparisons (Table S3). Correlation and Bonferroni-Holms corrected P values were computed using  
547 the *cor.test* and *p.adjust* functions in R.

548

549 Most frequent postures analysis

550 In order to illustrate the most “typical” posture each phylogenetic group exhibits on specific  
551 substrates, we extracted the significantly most frequent postures for each variable on each substrate  
552 for these groups. To validate that this most frequent posture is indeed typical, we computed Wilcoxon  
553 signed rank tests on the two highest proportions with 500 bootstrap samples of grasps and Bonferroni-  
554 Holms *post hoc* corrections, (Figure 3 for an overview, and DataS2 for detailed results).

555

556 Positional repertoire diversity analysis

557 To investigate the positional repertoire diversity across group and whether it is influenced by  
558 the substrate type, we used the Shannon entropy which measures the quantity of information  
559 contained in a distribution (in Shannons or bits). Here, we computed entropies on the distribution of  
560 observed grasps (*i.e.* the frequency of postures represented by the joint values of all variables, to  
561 capture expected inter-dependencies between variables) for hands and feet separately. This was  
562 performed for each substrate and each species and then for each phylogenetic group. Those measures  
563 represent how “diverse” the global postural repertoire is on each substrate. The more different  
564 postures exist, the higher the entropy is. Also, the more equi-probable all possible postures are, the  
565 higher the entropy is.

566 In order to statistically compare whether small and medium vertical substrates induce a  
567 decrease in the repertoire diversity, we employed a bootstrap approach. We tested the level of  
568 entropy on vertical small and medium substrates against the other substrates. We generated 100  
569 bootstrap samples from the joint distribution of postures, with all variables included, and computed  
570 their associated entropy per substrate for each phylogenetic group and for hand and foot separately  
571 and computed the average entropy on both substrate groups. We then compared the distributions of  
572 these averaged entropies between the two substrate groups using two tailed Mann-Whitney-U tests  
573 (Figure 4).

574

575 [Data and code availability](#)

576 The data supporting the findings of this study are available within the article and its  
577 supplemental information files. Videos of behavioral data collection are available from the Lead  
578 Contact upon reasonable request.

579

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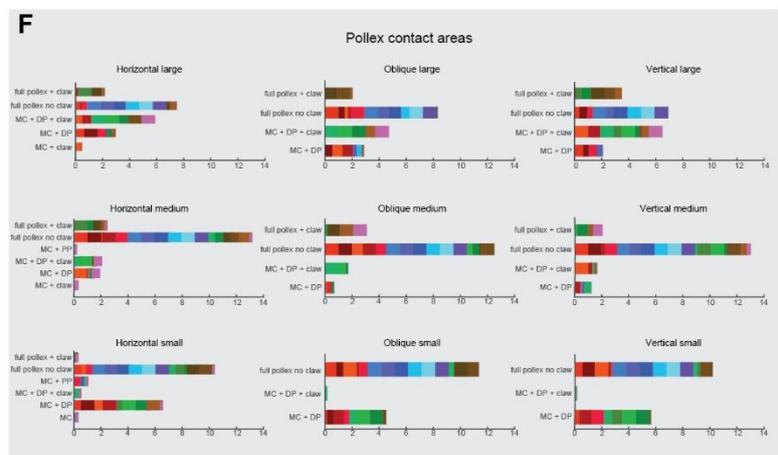
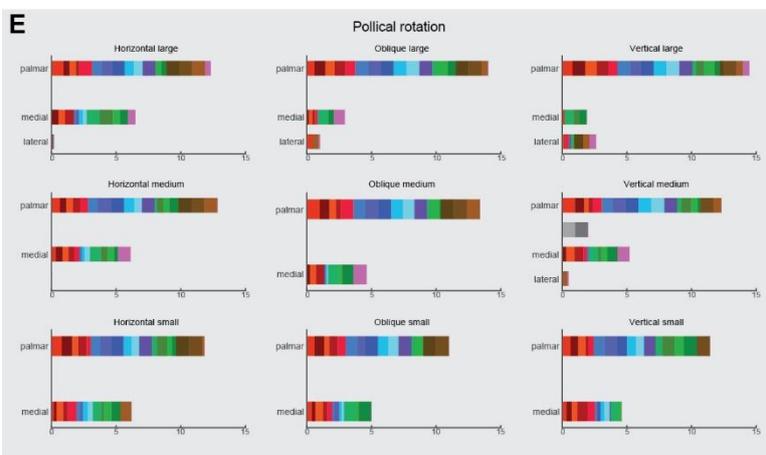
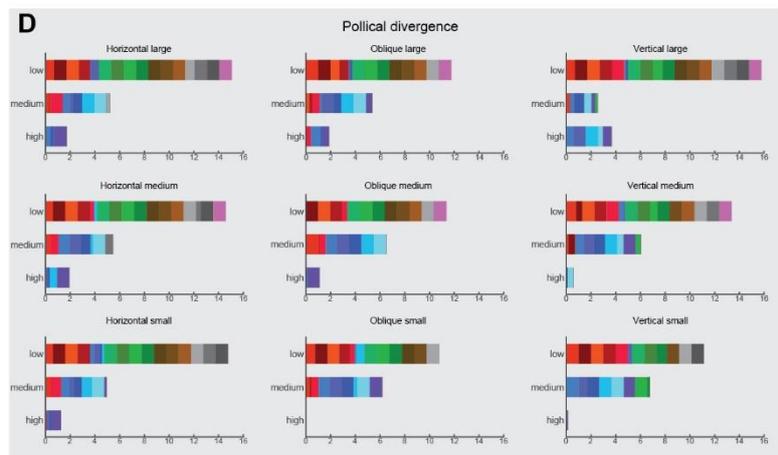
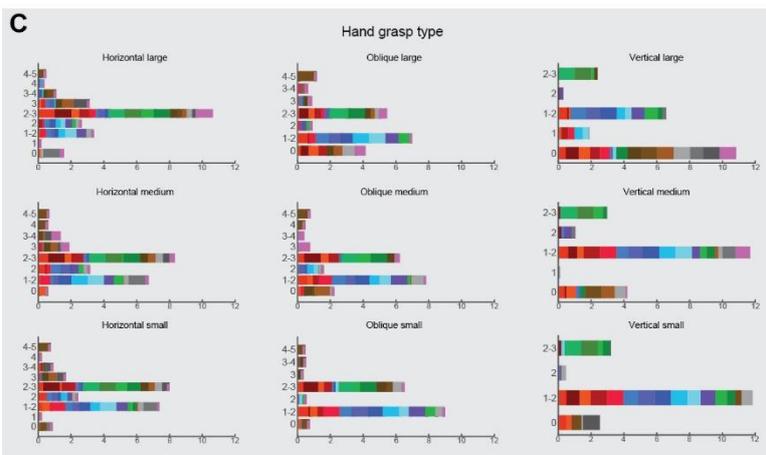
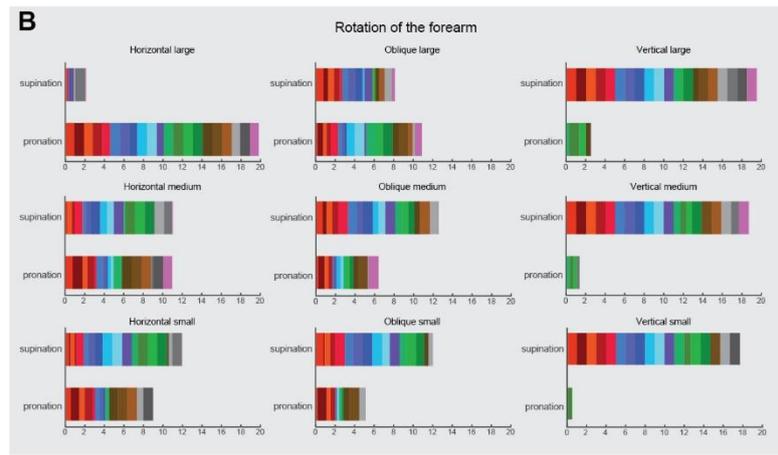
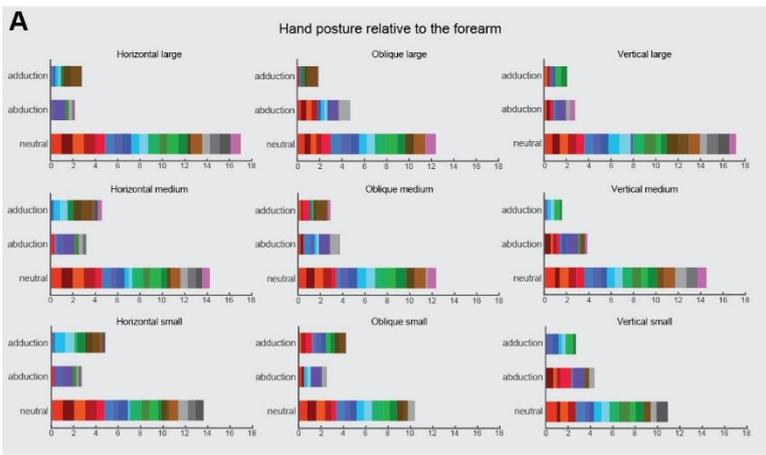
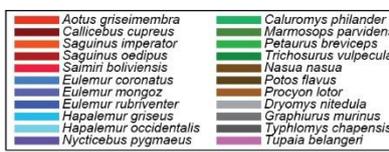
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## 802 Supplemental Information

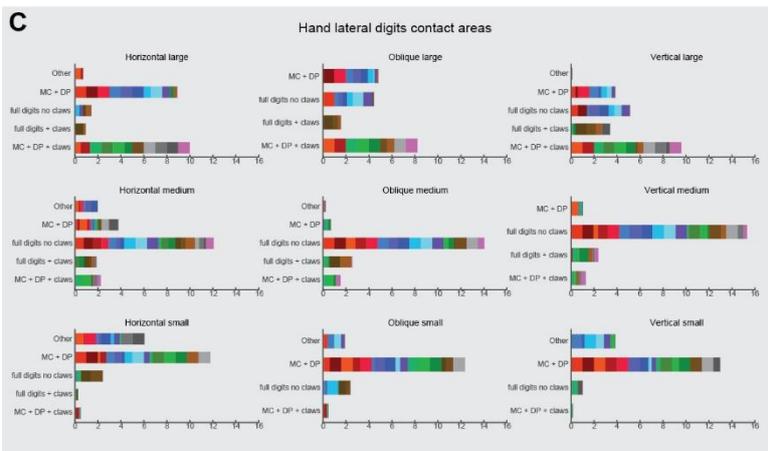
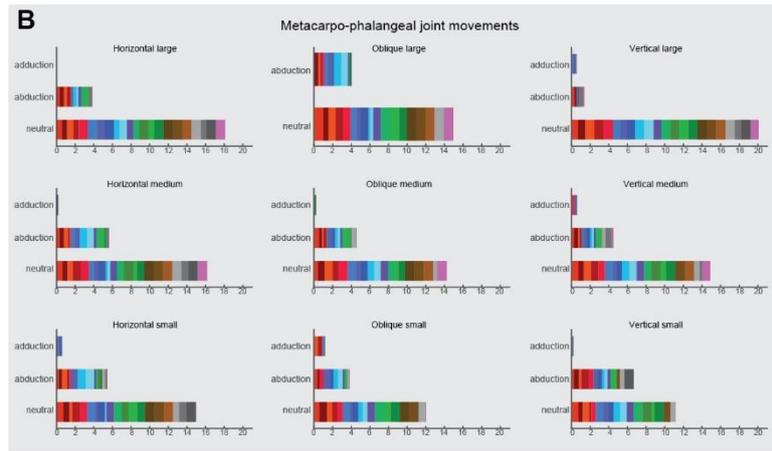
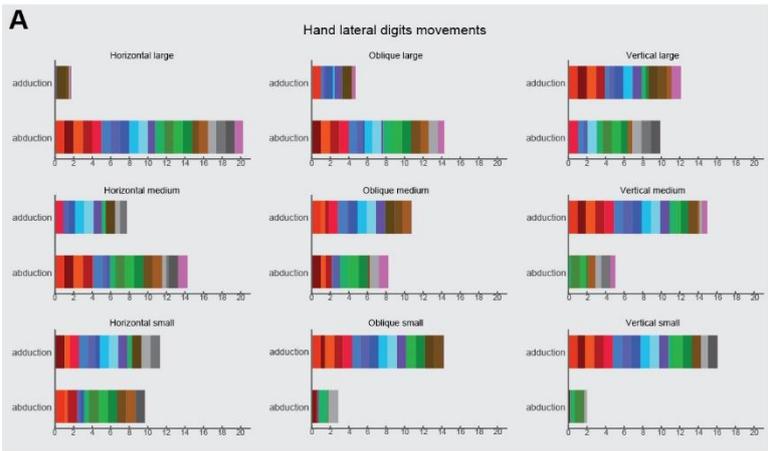
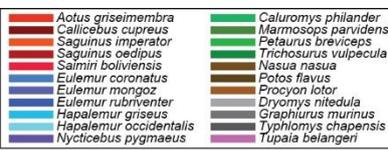
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804 **DataS1. Data quality control analysis. Related to Results section “Multivariate quantification**  
805 **of hand and foot postures”.** A) Control for differences between left and right hand and foot for each  
806 individual. P values of Wilk’s lambda test associated to MANOVAs ( $d=0$  for all) testing the effect of  
807 using the right hand/foot over the left hand/foot. Test conducted for each variable at the individual  
808 level on PCA-transformed frequency data for all substrates. For all variables, the hypothesis of a left-  
809 right bias is always rejected. These analyses were performed separately for primates and non-  
810 primates. B) Control for differences between males and females of the same species when applicable.  
811 P values of Wilk’s lambda test associated to MANOVAs ( $d=0$  for all) testing the effect of animal gender.  
812 Test conducted for each species at the individual level on PCA-transformed frequency data for hands  
813 and feet and for all substrates jointly. For all species having individuals of both genders, the hypothesis  
814 was rejected. These analyses were performed separately for primates and non-primates. C) Control  
815 for intraspecific differences for primate. Bonferroni-Holms corrected ( $\alpha = 0.05$ ) post hoc pairwise tests  
816 (Mann-Whitney-U) confirming MANOVA testing the effect of grouping primate individuals by species.  
817 Test conducted for primates at the individual level on PCA-transformed frequency data for hands and  
818 feet combined and for all substrates jointly. For all species, the hypothesis wasn’t rejected (Wilk’s  
819 lambda test  $P=3.20 \times 10^{-9}$ ,  $d=8$ ,  $\lambda=0.0510$ ,  $\chi^2=58.0378$ ,  $df=9$ ). D) Control for intraspecific  
820 differences for non-primates. Bonferroni-Holms corrected ( $\alpha = 0.05$ ) post hoc pairwise tests (Mann-  
821 Whitney-U) confirming MANOVA testing the effect of grouping non-primate individuals by species.  
822 Test conducted for primates at the individual level on PCA-transformed frequency data for hands and  
823 feet combined and for all substrates jointly. For all species, the hypothesis wasn’t rejected (Wilk’s  
824 lambda test  $P=8.43 \times 10^{-5}$ ,  $d=8$ ,  $\lambda=0.2723$ ,  $\chi^2=21.4640$ ,  $df=3$ ). E) Control for interspecific  
825 differences for all species, hands and feet combined. Ratios of min-interspecific/max-intraspecific  
826 differences derived from the MANOVAs from DataS1C and DataS1D. A ratio  $> 1$  shows intraspecific  
827 differences are minor compared to interspecific ones, which validates grouping individuals into  
828 species. F) Grouping species in phylogenetically related clusters. Bonferroni-Holms corrected ( $\alpha = 0.05$ )  
829 post hoc pairwise tests (Mann-Whitney-U) confirming MANOVA testing the effect of grouping species  
830 into phylogenetic groups. Test conducted for all groups (except tupaids which are represented by a  
831 single species) at the species level on PCA-transformed frequency data for hands and feet combined  
832 and for all substrates jointly. For all groups, the hypothesis wasn’t rejected (Wilk’s lambda test  
833  $P=1.77 \times 10^{-2}$ ,  $d=5$ ,  $\lambda=0.2138$ ,  $\chi^2=18.5117$ ,  $df=8$ ). G) Grouping species in phylogenetically  
834 related clusters. Ratios of min-intergroup/max-intragroup differences derived from the MANOVAs  
835 from DataS1F. A ratio  $> 1$  shows intragroup differences are minor compared to intergroup ones, which  
836 validates grouping species into phylogenetical groups.

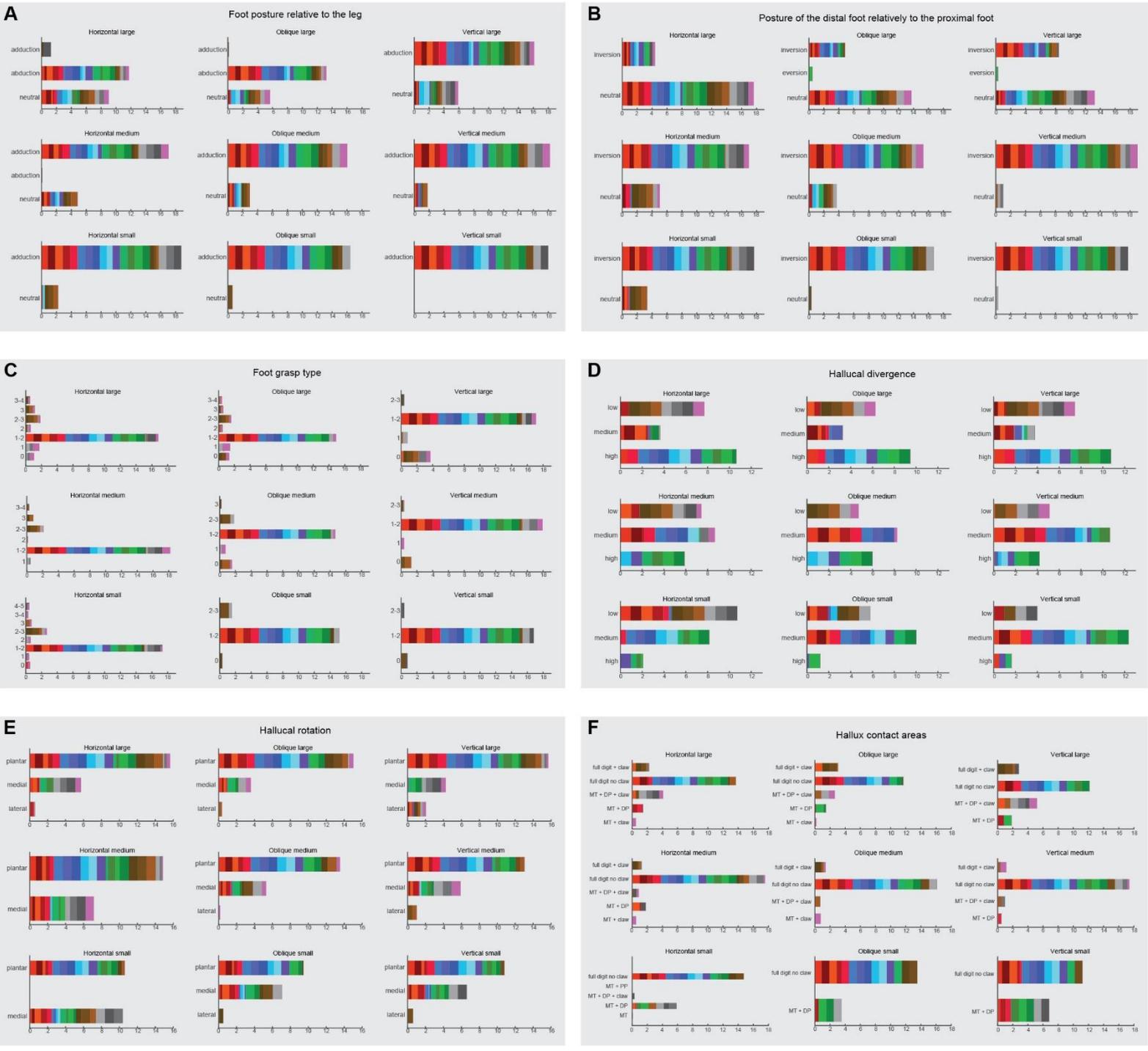
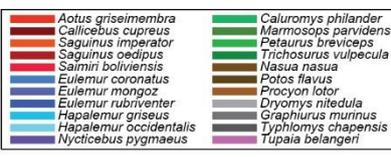
837 **DataS2. Most frequent postures for each variable and substrate, combined by groups, for A)**  
838 **hands and B) feet. Related to Figure 3.** For each most frequent posture (1<sup>st</sup> table section) are reported  
839 the associated Bonferroni-Holms corrected ( $\alpha = 0.05$ ) P values from Wilcoxon signed-rank test  
840 comparing the proportion of the most frequent posture vs the second most frequent posture. By  
841 convention, we report 0 when only one posture exists, and we report negative values for tests which  
842 failed the Bonferroni-Holms correction. In the 3<sup>rd</sup> table section are reported the associated proportions  
843 of most frequent postures. Abbreviations: MC= metacarpals, MT= metatarsals, PP= proximal  
844 phalanges, IP= intermediate phalanges, DP= distal phalanges.



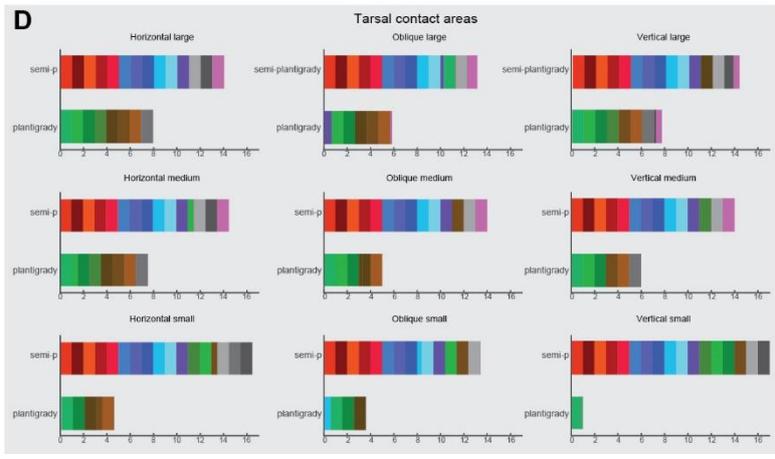
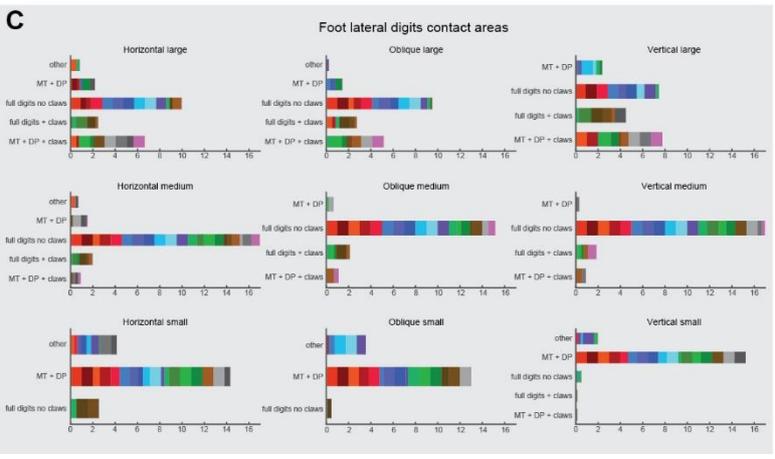
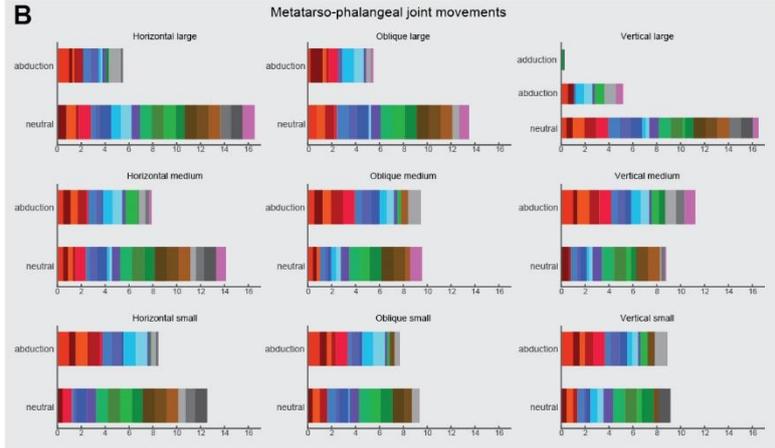
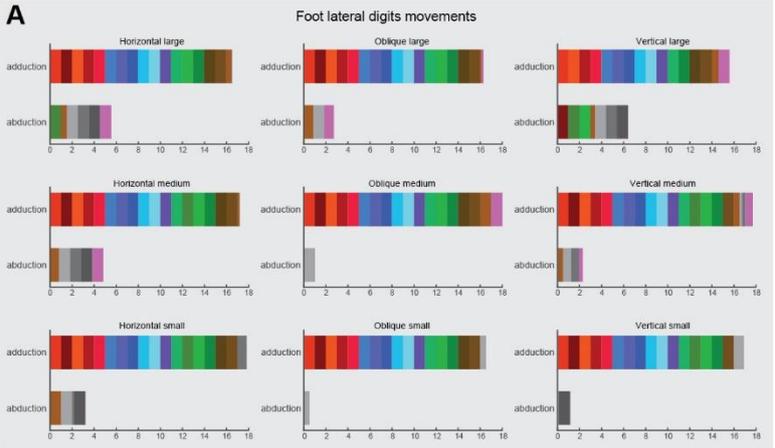
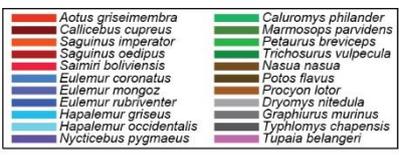
**Figure S1.** Proportions of A) the hand postures relative to the forearm, B) the rotation of the forearm, C) the hand grasp type and D) the pollical divergence, E) the pollical rotation, and F) the pollex contact areas, by species and substrates. Related to STAR Methods and Figures 3 and 4. All variable values occurring with a frequency below 1% are not included. See Table 2 for variables definitions.



**Figure S2. Proportions of A) the hand lateral digits movements, B) the metacarpo-phalangeal joint movements, and C) the hand lateral digits contact areas, by species and substrates. Related to STAR Methods and Figures 3 and 4. All variable values occurring with a frequency below 1% are not included. Table 2 for variables definitions.**



**Figure S3. Proportions of A) the foot postures relative to the leg, B) the posture of the distal foot relative to the proximal foot and C) the foot grasp type, D) the hallucal divergence, E) the hallucal rotation, and F) the hallux contact areas, by species and substrates. Related to STAR Methods and Figures 3 and 4. All variable values occurring with a frequency below 1% are not included. See Table 2 for variables definitions.**



**Figure S4. Proportions of A) the foot lateral digits movements, B) the metatarso-phalangeal joint movements, C) the foot lateral digits contact areas, and D) the tarsal contact areas, by species and substrates. Related to STAR Methods and Figures 3 and 4. All variable values occurring with a frequency below 1% are not included. See Table 2 for variables definitions.**

**HANDS**

PC	1	2	3	4
% of explained variance	44.30	21.00	9.19	4.46
<b>Variable</b>				
Grasp type	0.72	0.62	0.97	0.90
Pollex contact areas	0.80	1.01	0.80	0.53
Pollical rotation	0.56	1.01	0.76	0.32
Degree of pollical divergence	0.86	0.21	0.27	0.35
Lateral digits contact areas	0.62	0.43	0.84	1.03
Movement of the lateral digits	0.42	0.08	0.46	0.43
Hand posture relative to the forearm	0.26	0.21	0.49	0.72
Movement of the lateral digits at the metacarpo-phalangeal joints	0.21	0.22	0.40	0.26
Rotation of the forearm	0.24	0.28	0.46	0.25

**FEET**

PC	1	2	3	4
% of explained variance	43.18	21.91	10.81	5.19
<b>Variable</b>				
Degree of hallucal divergence	0.78	0.39	0.53	0.54
Hallux contact areas	0.59	0.42	0.50	0.19
Grasp type	0.57	0.26	0.58	0.06
Hallucal rotation	0.42	0.42	0.55	0.23
Lateral digits contact areas	0.53	0.35	0.59	0.55
Movement of the lateral digits	0.45	0.49	0.41	0.26
Tarsal contact areas	0.47	0.81	0.47	0.23
Foot posture relative to the leg	0.38	0.44	0.82	0.57
Movement of the lateral digits at the metatarso-phalangeal joints	0.31	0.34	0.29	0.74
Posture of the distal foot relatively to the proximal foot	0.42	0.24	0.36	0.54

**Table S1. Weights of variables in PCA at the species level. Related to STAR Methods and Figure 2.**

Total weight for each of the first 4 Principal Components for each variable. PCA are based on the frequencies of all possible values for each of the following variables, grouped at the species level. This implies that each possible value of each variable has its own coefficient in each principal component (PC). A variable's total weight is the sum of the absolute value of all coefficients associated to the variable's possible values.

	<b>P value</b>	<b>K mult</b>
<b>Hand</b>	2.00.10 <sup>-05</sup>	1,34
<b>Foot</b>	2.00.10 <sup>-05</sup>	1,37
<b>Hand and Foot</b>	2.00.10 <sup>-05</sup>	1,61
<b>Hand and Foot – Horizontal substrates</b>	2.00.10 <sup>-05</sup>	1,31
<b>Hand and Foot – Oblique substrates</b>	6.39.10 <sup>-2</sup>	0,26
<b>Hand and Foot – Vertical substrates</b>	2.00.10 <sup>-05</sup>	1,41
<b>Hand and Foot – Small substrates</b>	2.00.10 <sup>-05</sup>	0,89
<b>Hand and Foot – Medium substrates</b>	2.00.10 <sup>-05</sup>	1,51
<b>Hand and Foot – Large substrates</b>	2.00.10 <sup>-05</sup>	1,42

**Table S2. Phylogenetic relationships analysis. Related to STAR Methods.** Results of K mult phylogenetic signals and associated P values for hands and feet separately, combined, and differentiating substrates by orientation and diameter. To test if hands and feet postures adopted on specific substrates would reveal phylogenetic signals of different strength, we computed the phylogenetic signal strength for hands and feet combined, differentiating substrates by orientations (horizontal, oblique, vertical) and diameters (small, medium, large). In practice, we repeated the same PCA analysis as before, but only retaining data for each given group of substrates.

		Spearman $\rho$	P value
Hands	PC 1 (44,3 %)	-0,46	0,34
	PC 2 (21, %)	-0,32	1,00
	PC 3 (9,2 %)	-0,38	0,80
	PC 4 (4,5 %)	-0,16	1,00
	PC 5 (4, %)	-0,07	1,00
	PC 6 (3,8 %)	0,01	1,00
	PC 7 (2,6 %)	-0,21	1,00
	PC 8 (2,1 %)	0,29	1,00
	PC 9 (1,7 %)	0,05	1,00
	PC 10 (1,6 %)	-0,08	1,00
	PC 11 (1,3 %)	-0,12	1,00
Feet	PC 1 (43,2 %)	-0,15	1,00
	PC 2 (21,9 %)	-0,44	0,38
	PC 3 (10,8 %)	-0,56	0,07
	PC 4 (5,2 %)	-0,08	1,00
	PC 5 (3,8 %)	0,24	1,00
	PC 6 (3,2 %)	0,12	1,00
	PC 7 (2,8 %)	0,27	1,00
	PC 8 (2,1 %)	0,03	1,00
	PC 9 (1,5 %)	-0,17	1,00
	PC 10 (1,3 %)	-0,13	1,00

**Table S3. Univariate *post hoc* tests of impact of body mass on postures. Related to STAR Methods.** Correlation coefficients (Spearman's  $\rho$ ) with Bonferroni-Holms corrected P Values of postural data (PCA-transformed at the species level) with typical species' body mass (Table 1). Principal Components accounting for 95% of variance were retained. Percentage in parenthesis correspond to the proportion of variance explained.